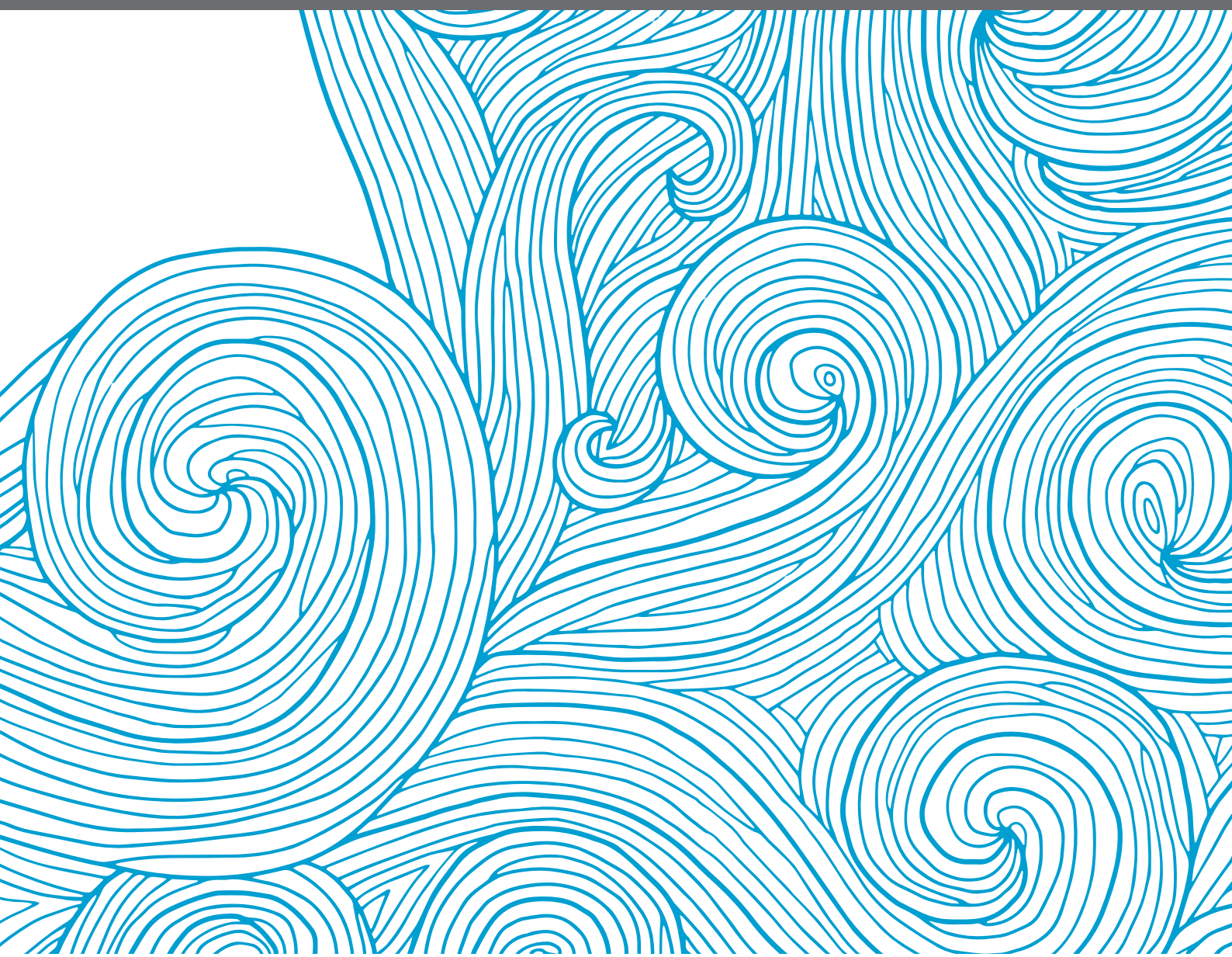
MANAGING DEEP-SEA ECOSYSTEMS AT OCEAN BASIN SCALE, VOLUME 1

EDITED BY: J. Murray Roberts and Telmo Morato
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MANAGING DEEP-SEA ECOSYSTEMS AT OCEAN BASIN SCALE, VOLUME 1

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A Multi Criteria Assessment Method for Identifying Vulnerable Marine Ecosystems in the North-East Atlantic

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In international fisheries management, scientific advice on the presence of "vulnerable marine ecosystems" (VMEs) per United Nations resolutions, has generally used qualitative assessments based on expert judgment of the occurrence of indicator taxa such as cold-water corals and sponges. Use of expert judgment alone can be criticized for inconsistency and sometimes a lack of transparency; therefore, development of robust and repeatable numeric methods to detect the presence of VMEs would be advantageous. Here, we present a multi-criteria assessment (MCA) method to evaluate how likely a given area of seafloor represents a VME. The MCA is a taxa-dependent spatial method that accounts for both the quantity and data quality available. This was applied to a database of records of VMEs built, held and compiled by the International Council for the Exploration of the Sea (ICES). A VME index was generated which ranged from 1.51 to 4.52, with 5.0 being reserved for confirmed VME habitats. An index of confidence was also computed that ranged from 0.0 to 0.75, with 1 being reserved for those confirmed VME habitats. Overall the MCA captured the important elements of the ICES VME database and provided a simplified, spatially aggregated, and weighted estimate of how likely a given area is to contain VMEs. The associated estimate of confidence gave an indication of how uncertain that assessment was for the same given area. This methodology provides a more systematic and standardized approach for assessing the likelihood of presence of VMEs in the North-East Atlantic.

Keywords: vulnerable marine ecosystems, deep-sea, multi-criteria assessment, cold-water corals, deep-sea sponges

INTRODUCTION

Recognizing the vulnerability of deep-sea biodiversity, the United Nations General Assembly (UNGA) called upon States and Regional Fisheries Management Organizations (RFMOs) to identify areas beyond national jurisdiction (ABNJ) where vulnerable marine ecosystems (VME) occur, or are likely to occur, and to prevent significant adverse impacts (UNGA, 2006). The Food

and Agricultural Organization (FAO) of the United Nations subsequently developed guidelines for the management of deep-sea fisheries in the high seas (FAO, 2009). This included criteria for defining what constitutes a VME: (1) uniqueness or rarity; (2) functional significance of the habitat; (3) fragility; (4) life history traits of component species that make recovery difficult; and (5) structural complexity. These criteria may apply to a wide variety of habitats and ecosystems of the deep-sea (e.g., hydrothermal vents, seamounts, or cold seeps). Generally, VMEs have been identified based on the occurrence of indicator taxa such as stony or gorgonian corals, or sponges. However, these taxa can occur in varying spatial densities, and the FAO guidelines do not provide threshold values for defining what constitutes "significant concentrations" of VME indicator records that would constitute an actual VME (Auster et al., 2011).

Whilst significant steps have been made to map and protect VMEs in the high-seas areas in general (e.g., Portela et al., 2010) and in the high-seas areas regulated by RFMOs (e.g., Durán-Muñoz et al., 2012a), progress has been inconsistent or incomplete (Durán-Muñoz and Sayago-Gil, 2011; Wright et al., 2014; FAO, 2016). In part, limited knowledge about their spatial distribution has impeded the application of effective protective measures in many areas (Weaver et al., 2011). Although dedicated field surveys and species distribution models of some individual VME indicator taxa are increasingly being made available (Rengstorf et al., 2013, 2014; Vierod et al., 2014; Fabri et al., 2014; Anderson et al., 2016b), there is little information on the spatial distribution of species assemblages in concentrations that might constitute a VME and therefore what is needed to trigger management actions (Ardron et al., 2014).

Vulnerable marine ecosystems are best identified using high quality underwater imagery (Remotely Operated Vehicles – ROV, towed camera, etc.), allowing accurate and quantitative description of community composition and associated fauna (e.g., Fabri et al., 2014). Because of the high cost of operations associated with such imaging technologies, observations of VMEs are only available for a tiny fraction of the area of the deep seabed. However, with rapid advances in photo- and video-survey technology, much more of the seafloor will become known in the coming years. Techniques developed to identify VMEs could therefore inform what statistical power and effect size should be used to detect VMEs in future broad-scale surveys. Currently, larger amounts of data on VME indicator taxa occurrences across large spatial scales may be available from bycatch records from fisheries surveys (e.g., Murillo et al., 2011, 2012; Portela et al., 2012), cooperative surveys (Durán-Muñoz et al., 2011, 2012b) and commercial fishing operations. The problem in using bycatch data to inform on the presence of VMEs lies in the fact that bottom fishing gear are poor sampling tools for VME indicator organisms and that bycatch data may not represent the true benthic community composition and densities (Auster et al., 2011). Although better than no data, there is a large amount of uncertainty associated with bycatch data.

In the Northwest Atlantic Fisheries Organization (NAFO) Regulatory Area, a geospatial methodology was developed to identify VMEs using data from research trawl surveys (Kenchington et al., 2014). However, this approach requires comprehensive fisheries survey programs (Murillo et al., 2011, 2012) and standardized datasets that are generally not available for most areas beyond national jurisdiction. Generally, data on VME indicator presence are derived from a wide variety of sources (commercial trawl and longline operations, ROV surveys, towed camera surveys or research surveys), which are challenging to integrate and interpret as a whole. For example, some records are bona fide VME habitat types such as those identified through recent ROV video footage of large *Lophelia* reefs while others are scientific trawl survey bycatch records and anecdotal information from commercial fishing operations. As a result, VME related data are generally qualitatively assessed using expert judgment (ICES, 2013a). Expert judgment is a common component of resource management and conservation decision-making, but comes with known limitations and inconsistencies, many of which concern how disparate information is contextualized, and a poor characterization of uncertainty (Burgman et al., 2011; Martin et al., 2012). To aid decision-making concerning the protection of VMEs, we have developed methods that are capable of integrating the wide range of existing VME data, while taking into account some of the uncertainties associated with sampling methods and reported taxonomy.

Over the past 10 years the joint ICES/NAFO Working Group on Deep-water Ecology (WGDEC) has been compiling data on the distribution and abundance of VMEs and organisms considered to be indicators of VMEs across the North Atlantic (ICES, 2011). A database of these records was built to facilitate more scientifically robust advice on the distribution of VMEs and to aid the development of possible management recommendations such as bottom fishing closures within North East Atlantic Fisheries Commission (NEAFC) waters to protect VMEs. Thus there was a need to develop a system that would formalize expert opinion and utilize as much relevant information as possible from the ICES VME database. In this paper we present a multi-criteria assessment (MCA) method that was developed to evaluate how likely an area represents a VME, through integrating as much relevant information as possible from the ICES VME database.

MATERIALS AND METHODS

The term VME is used here in the context of the FAO international guidelines (FAO, 2009) and reviewed by ICES (ICES, 2016b). The ICES VME database (ICES, 2016a) can be accessed online and is currently comprised of approximately 15,000 records (**Figure 1**).

Multi-criteria assessment is a method of aggregating data based on different criteria or attributes that contain information relevant to the decision and weighting these to provide a single metric that captures all this information. The essential feature of MCA is the development of a matrix in which the performance of the data are weighted against each criterion (e.g., the survey method) and from which an aggregate value

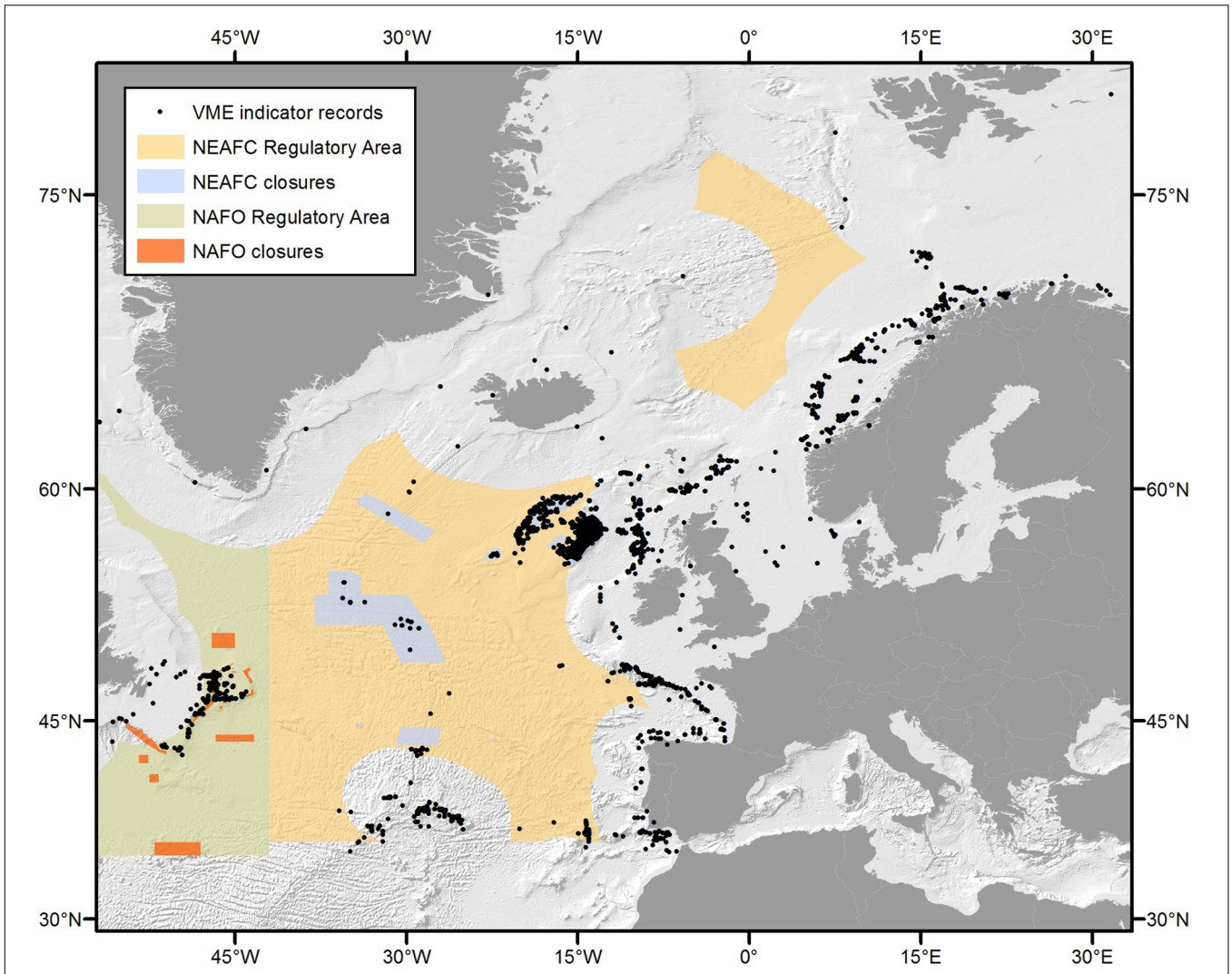


FIGURE 1 | The distribution of VME indicator records throughout the North Atlantic contained within the ICES VME database (ICES, 2016a).

is derived. The MCA was based on spatially gridded data format, i.e., multiple individual points or records contributed to the assessment of a single grid cell containing a VME. A C-square spatial grid methodology (Rees, 2003) composed of grid cell size of 0.05 degrees by 0.05 degrees was adopted, similar to that used to analyze Vessel Monitoring System (VMS) data (Hintzen et al., 2012). As described below, the MCA captures the fact that not all VME indicators within the ICES VME database have the same vulnerability to human impacts, and thus should be weighted differently. Therefore, the MCA is a taxa-dependent spatial method. Additionally, to account for data quality issues a measure of the confidence associated with each VME record was developed.

For each c-square grid cell, two values were calculated:

- A "VME index" which combines how intrinsically vulnerable to human impacts the VME indicator is deemed to be, and how abundant the VME indicator is (for example, an aggregation representing a cold-water coral reef as opposed to a record of a single individual or taxon).
- A "Confidence index" associated with the "VME index." This is a confidence (or uncertainty) estimate based upon (a) the numbers of samples available within the grid cell, (b) the provenance of the records in that cell (e.g., visual survey, fisheries data, or inferred from other methods), (c) the time span of the data (i.e., time between the first and last record), and (d) the age of the most recent survey.

"VME Index" Scoring Procedure

Because the ICES VME database includes both records of known VME habitats (ICES, 2016a) as well as VME indicators, these former bona fide records were treated separately from the latter. Bona fide records included high quality underwater imagery

from ROV surveys of anemone aggregations, cold seeps, cold-water coral reefs, coral gardens, deep-sea sponge aggregations, hydrothermal vents, and sea-pen fields. Non-VME habitat grid cells (i.e., not containing bona fide records) were evaluated by assigning a VME indicator score to each VME indicators present, based on their taxonomy and their abundance as explained below.

Assigning a VME Indicator Score to VME Indicators

Twelve VME indicator types were agreed for inclusion in the ICES VME database (ICES, 2016b), reflecting the main taxonomic groups of VME indicators occurring in the NE Atlantic (**Supplementary Table 1**). Naturally, there are some interspecific inconsistencies, for example, not all species of "Gorgonian" will be equally vulnerable. However, these categories were considered to be a reasonable compromise between a manageable list and a range of vulnerabilities that was not excessive (ICES, 2016a). The category "sponges" was found to be particularly problematic because it includes all sponges, from small encrusting species to the massive, aggregation forming species (e.g., Geodiids). The reason a generic "sponges" category was created in the past was because there is often much uncertainty in species identification and many records in the VME database are simply identified to the Phylum level of "Porifera." Nevertheless, the VME database contains sponge records identified to the lowest possible taxonomical level, which is of value for use in the MCA. When a sponge record was identified to the genus level, literature sources (e.g., Hogg et al., 2010; Murillo et al., 2012; McIntyre et al., 2016) and expert opinion was used to decide on those genera of sponges containing species that can be described as "massive" and forming aggregations. All species belonging to the following genera were classified as the type "Large Sponge" and as such would receive a different "VME" score than all other sponges: Asconema, Craniella, Chonelasma, Geodia, Pheronema, Polymastia, Stryphnus, Tetilla, Thenea, and Vazella. All other species of sponges and records for which no information of Genus were provided were ranked according to the scores in the type "Generic Sponge." Following this assessment of sponge types, thirteen VME indicator types were considered in the next phase (**Table 1**).

Vulnerable marine ecosystem indicator types included in the ICES VME database were assessed against each of the five FAO criteria for defining what constitute a VME. The FAO list of characteristics used as criteria in the identification of VMEs are (FAO, 2009):

- Uniqueness or rareness: an area or ecosystem that is unique or that contains rare species whose loss could not be compensated for by similar areas or ecosystems.
- Functional significance of the habitat: discrete areas or habitats that are necessary for the survival, function, spawning/reproduction, or recovery of fish stocks, particular life-history stages (e.g., nursery grounds or rearing areas), or of rare, threatened or endangered marine species.
- Fragility: an ecosystem that is highly susceptible to degradation by anthropogenic activities.
- Life-history of species make recovery difficult: ecosystems that are characterized by populations or assemblages of species with one or more of the following characteristics: slow growth rates, late age of maturity, low or unpredictable recruitment, or long-lived.
- Structural complexity: an ecosystem that is characterized by complex physical structures created by significant concentrations of biotic and abiotic features.

TABLE 1 | Scores for VME indicators occurring in deep-water in the ICES/NAFO area based on the degree to which each VME indicator fit each of the five FAO criteria (FAO, 2009).

	FAO criteria for defining what constitutes a VME					VME
VME indicator	**Unique.**	**Functional.**	**Fragility**	**Life history**	**Structural**	**Indicator score**
Stony coral	3	4	5	5	5	4.47
Black coral	5	2	4	5	2.5	3.91
Chemosynthetic spp. (seeps and vents)	5	5	1	4	3	3.90
Large sponge	2	5	4	4	3	3.74
Gorgonian	4	3	3	5	2.5	3.61
Xenophyophore	2	3	5	2	2	3.03
Stylasterid	4	1	4	2.5	2	2.94
Stalked crinoid	4	1	2	4	1	2.76
Generic sponge	2	3	3	3	2	2.65
Sea-pen	2	3	3	2	2	2.45
Cup coral	2	1	2	4	1	2.28
Soft coral	1	1	2	2	2	1.67
Anemone	1	1	2	2	1	1.48

Scores range from 1 (low) to 5 (high). The final VME indicator score was calculated using the quadratic mean, i.e., the square root of the mean of the squares, across the five FAO criteria being assessed. Chemosynthetic spp. (seeps and vents) refers to megabenthos species as described in ICES (2016b).

- The degree to which each VME indicator group (not the individual taxa contained) fit each of the five FAO criteria was scored from 1 (low) through 5 (high). The scoring procedure was discussed and agreed by a group of deep-sea scientists through an ICES Expert Group using existing informed expert judgment, and the following specific guidelines (**Supplementary Table 2**):
- Rarity: was scored according to presence on the IUCN red list, and if the indicator was known to be endemic, rare, threatened, or declining.
- Functionality: was scored by evaluating if the indicators were known to create nursery areas for other species, or known for having higher level ecosystem role, such as nutrient cycling and water filtration.
- Fragility: was scored according to the fragility of the indicator against physical contact, the height and complexity of its structure, and the capacity for retraction, retention or re-growth or if being naturally protected in some way.
- Life-history: was scored against the longevity, fecundity, age at maturity, growth rate, and known frequency of recruitment success.
- Structural complexity: was scored based on structural habitat created, frame-building, and presence of commensal or closely associated species.

These ratings resulted in VME indicator scores for each VME indicator type (**Table 1**) where, for example, stony corals were considered the most susceptible to degradation by anthropogenic activities and with life-history characteristics that make recovery more difficult. It should, however, be noted that these scores could change if new data were to become available and when the taxonomic resolution of the indicators present in the database is improved. As the five FAO criteria were seen as being approximately orthogonal, the final VME indicator score for each of the thirteen VME indicators was calculated using the quadratic mean, i.e., the square root of the mean of the squares.

Assigning Abundance Score to VME Indicator Records

For each record with weight data in the database, the abundance recorded was evaluated against the NEAFC (Recommendation 19 2014: Protection of VMEs in NEAFC Regulatory Areas as Amended by Recommendation 09:2015) and EU (Regulation 2016/2336) VME encounter thresholds for live corals (30 kg) or live sponges (400 kg). If the abundance was over the encounter threshold, a value of 5 was assigned. If the abundance was below the encounter threshold we used Jenks natural breaks classification method (Jenks, 1967) to identify an intermediate encounter threshold. Therefore, a value of 3 was assigned if abundance was above 1 kg (for corals) or 60 kg (for sponges) and otherwise a value of 1 was assigned. If no data for abundance were available, a score of 0 was allocated to the "abundance score" and thus had no effect on the final "VME index." As there are no agreed thresholds for VME indicators that are not "corals" or "sponges" (e.g., anemones) we used the encounter thresholds values defined for corals. Although the NEAFC thresholds are considered to be too high and not based on robust scientific data (Ardron et al., 2014), without agreed thresholds this was considered the most appropriate option, so as to be relevant for current (albeit imperfect) management practices.

Defining the Final "VME Index"

Vulnerable marine ecosystem bona fide habitats identified in the ICES VME database received the maximum "VME index" of 5. The final "VME index" for each remaining records was calculated based on the VME indicator score and the abundance score. In the current version of the MCA we gave 90% weight to the "VME indicator score" and 10% weight to the abundance score. A low weighting was assigned to the abundance score because of the limited number of records where such information is available, and because there is much uncertainty regarding encounter thresholds when little is known about how VMEs abundances and vulnerabilities have been estimated (ICES, 2012).

After assigning a VME index to each VME indicator record, the results were then aggregated to a grid cell of 0.05 degrees × 0.05 degrees. For each cell, the maximum VME index value was retained as the overall value for that cell. This was to prevent down-weighting of important records by less important records as would happen if, for example, the median or the mean value of a cell was used. It was therefore acknowledged that some cells would have high scores due to a single high scoring record even when other records in that cell may have a low score. This approach was viewed as consistent with the precautionary approach.

The final outcome was presented as VME habitat for these grid cells containing bona fide records and as three nominal categories of "VME index" scores, indicating the likelihood of encountering a VME in the assessed grid cells. Thresholds were computed using the Jenks natural breaks classification method (Jenks, 1967). The categories were: low "VME index," for total scores <2.64; medium, for total scores between 2.64 and 3.74; and high, for total scores >3.74. The breaks produced suggested that the high "VME index" scores would pick out stony corals at any abundance, and black corals, large sponges and chemosynthetic species when above the NEAFC VME threshold. The medium "VME index" scores would pick out black corals, sponges and chemosynthetic species when below the NEAFC VME threshold, and gorgonians, stylasterids, sea-pens, sponges, xenophyophores, and stalked crinoids when above the threshold.

"Confidence Index" Scoring Procedure

To account for data uncertainty such as data quality issues and the varying degree of knowledge regarding each cell (i.e., how well it has been surveyed), we developed a data confidence index similar to the ones elaborated by Wallace et al. (2011). This index served as a measure of confidence in the "VME index" scores assigned to individual grid cells and was calculated independently of the "VME index." The "Confidence index" was not calculated

TABLE 2 | Criteria used to score different components of the "Confidence index" for each grid cell.

	Confidence		
Criteria	**Low (score = 0)**	**Medium (score = 0.5)**	**High (score = 1)**
Survey method	If inferred from other survey methods or indirect methods scores, e.g., acoustic methods	Record from commercial fisheries or scientific surveys without visual information	Record originated from visual surveys
Number of surveys	<3 Surveys	3–5 Surveys	>5 Surveys
Time span or range in years	<5 Years	5–10 Years	>10 Years
Age of the last survey	>30 Years	10–30 Years	<10 Years

for bona fide VME habitats identified in the ICES VME database where a confidence index of one was allocated.

Two measures are usually incorporated in such indices (Wallace et al., 2011; Taranto et al., 2012): data quality and data deficiency. We considered using a measure of data deficiency for each grid cell but did not implement that measure as data deficiency is being partially covered in the data quality measure. Therefore, data quality here reflects the origin and nature of the collected data and was divided into three categories: low (scored as 0), medium (scored as 0.5), and high (scored as 1) data quality. The high data quality category highlights cells with information derived from scientific visual surveys, sampled by many independent surveys (>5 surveys), over a long time period (>10 years), and where the most recent record is recent (<10 years) and thus giving an idea if the VME is still present. Low quality data refers to a VME index derived from a poorly sampled grid cell (<3 surveys), where the presence of a VME had been somehow inferred, sampled for only a short period (<5 years) and a long time ago (>30 years). Consequently, four distinct criteria were used for estimating the data "Confidence index" (**Table 2**).

The resulting data "Confidence index" for each grid cell was calculated as the quadratic mean (i.e., the square root of the mean of the squares) of the scores associated with the records producing the highest "VME index," and had a minimum value of 0 (few factors scored or low data quality) and a maximum value approaching 1 (all factors scored with high data quality). As in the "VME index," the final outcome was presented by grid cell containing no uncertainty (i.e., confidence index of 1) or VME bona fide habitat, and as three nominal categories of "Confidence index" computed using the Jenks natural breaks classification method (Jenks, 1967): low confidence, for scores smaller than 0.35; medium confidence, for score between 0.35 and 0.63; and high confidence for scores greater than 0.63.

Implementation of the MCA to the ICES VME Database

The implementation of the MCA can be illustrated schematically by generating maps of the VME and Confidence indices (**Figure 2**). By combining these maps, cells with high "VME index" scores and different confidences can be highlighted. In the top panel of **Figure 2**, VME bona fide habitats with total confidence are highlighted. In the second panel of **Figure 2**, we highlighted those grid cells scoring high in the "VME index" with all confidence categories. In the third panel, grid cells scoring high in the "VME index" but excluding those cells with a low confidence index were highlighted. In the bottom panel of **Figure 2**, we highlighted only those grid cells scoring high in the VME index and high confidence. It should be noted that cells with low confidence are not unimportant, but rather the degree of uncertainty means that additional sampling is required to produce a more reliable "VME index" value. Implementation of the framework was done through the development of an R script that accessed the tables in the ICES VME database.

Prior to the application of the procedure, a detailed quality check of the ICES VME database was performed. This included: (1) standardization and correction of the information contained

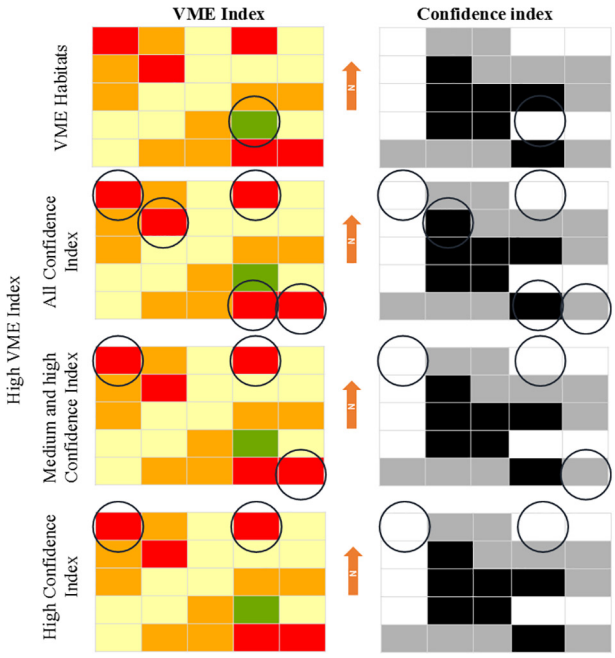


FIGURE 2 | Representation of the usefulness of the VME and Confidence indices maps. The "VME index" hypothetical map contains VME habitats in green, cells with high "VME index" scores in red, medium in orange, and low in yellow. The "Confidence index" map contained cells with high confidence score in white, medium in gray, and low confidence in black. Circles indicate those cells in the hypothetical map that meet the criteria described on the left of the panel.

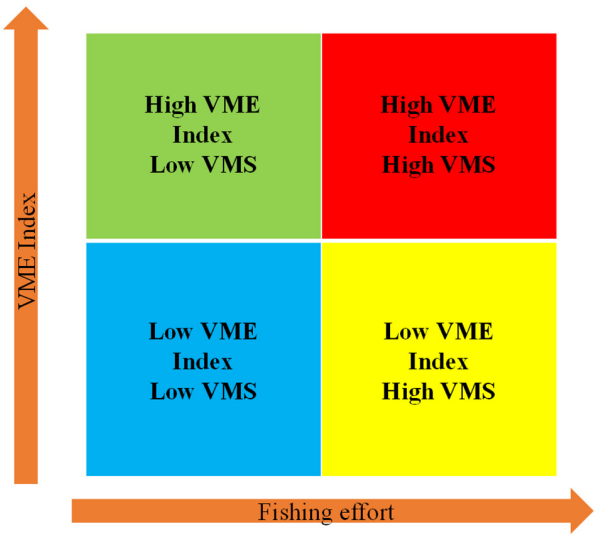


FIGURE 3 | Representation of the application of the portfolio categories concept.

in all fields; (2) filling missing mandatory fields or correcting detected errors by contacting original data providers, by thorough searches, or ultimately deleting records for which validation was not possible; (3) correction and validation of all species identifications using World Register of Marine Species database (WoRMS Editorial Board, 2017); and (4) deleting duplicated records.

VME and Fishing Effort Portfolio Categories

One of the main advantages of deriving a gridded "VME index" is that is can be directly compared to other gridded data with the same grid size, as for example fishing effort. Fishing intensity data can therefore be used to account for the anthropogenic activities occurring within each cell. We suggest an approach that combines the "VME index" and the level of fishing activity, measured through VMS data. This methodology allows the classification of individual cells into four main categories, which can help in optimizing management efforts toward spatial management: Low VME index-Low fishing; Low VME index-High fishing; High VME index-Low fishing; High VME index-High fishing. "VME index" and fishing intensity for individual cells can therefore be easily summarized and graphically compared (**Figure 3**).

The application of the VME and fishing effort portfolio categories to the ICES VME and VMS databases was tested. Here the VME index used was calculated as described above. For estimating the fishing effort for each grid cell, the cumulative number of records of trawling activity (vessel speed from 1 to 4 knots) from VMS data for the past 10 years was used (ICES, 2015). Due to the non-normal range of values, including the presence of few cells with very large records of trawling activity, the cumulative number of records was log transformed. Fishing effort was then re-scaled from 1 where no fishing activity is present to 5 where the maximum value of fishing effort was reached.

RESULTS AND DISCUSSION

The FAO guidelines provide a comprehensive list of species and habitats that form VMEs. Intuitively all types of VMEs are deemed vulnerable, however, the current scientific information on function, fragility and life-history of various types of VME indicator species suggest that some VMEs should be considered more vulnerable to anthropogenic impacts than others. For example, deep-sea stony corals aggregations create structural diverse habitats, are relatively long lived and slow growing and are very sensitive to bottom fishing impact (Clark et al., 2016 and references therein). On the other hand, sea pens, while they are much less well understood, do not appear to as slow growing or long lived (de Moura Neves et al., 2015). We sought to capture this variation in developing our methodology by developing a means of weighting the vulnerability of different types of VMEs.

Implementation of the MCA to the ICES VME Database

When applying the MCA to the ICES VME database, the VME index ranged from 1.51 to 4.52. A score of 5.0 was reserved for records of bona fide VME habitats. The observed frequency of the VME index showed a unimodal distribution with most cells being between 2 and 4 (**Figure 4**). The output appears to capture the main features of the database despite the paucity of life-history data for many of the VME indicator taxa (e.g., Ramirez-Llodra et al., 2010). The results remain to some extent dependent on the expert judgment on scoring how each VME indicator fit the FAO VME criteria. This source of variability, however, was minimal as scores were thoroughly discussed and agreed by a group of approximately 20 deep-sea experts. We recognize that knowledge gaps for some taxon are a major limitation for appropriately scoring some VME indicators (e.g., anemones or sponges). As more scientific information is gathered, this "inter-VME" weighting may be revised by WGDEC.

The VME index is also dependent on the encounter thresholds adopted by NEAFC. There is currently a recommendation to reduce these to 15 kg of live corals and 200 kg of live sponges (ICES, 2012). If new encounter thresholds are adopted, the MCA methodology should be updated accordingly.

The confidence index ranged from 0.0 to 0.75. Again a score of 1 was reserved for those records of bona fide VME habitats (**Figure 4**). Most of the cells showed a confidence index lower than 0.6 highlighting a reduced sampling effort, with records often falling into the lowest category.

Hatton-Rockall Bank

The Hatton-Rockall Bank area in the NE Atlantic provides a model case study to illustrate the application of the MCA approach. Scientific data on the presence of coral at Rockall dates back to the 1970s (Wilson, 1979) and a spate of recent surveys have revealed the occurrence of coral mounds (Wienberg et al.,

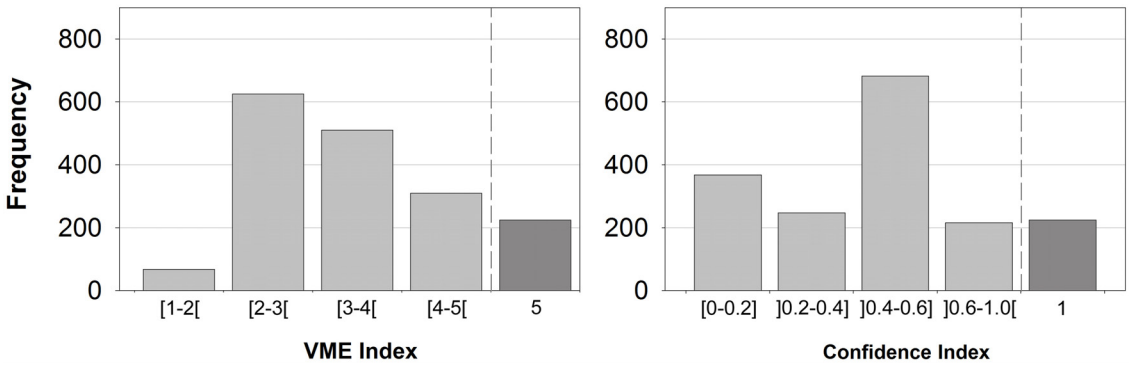


FIGURE 4 | Resulting distribution of the VME index (left) and the confidence index (right) when applied to the ICES VME database, including certain VME habitats (VME index of 5 and confidence index of 1; n = 225). Each value represents one grid cell of approximately 0.05 degrees by 0.05 degrees.

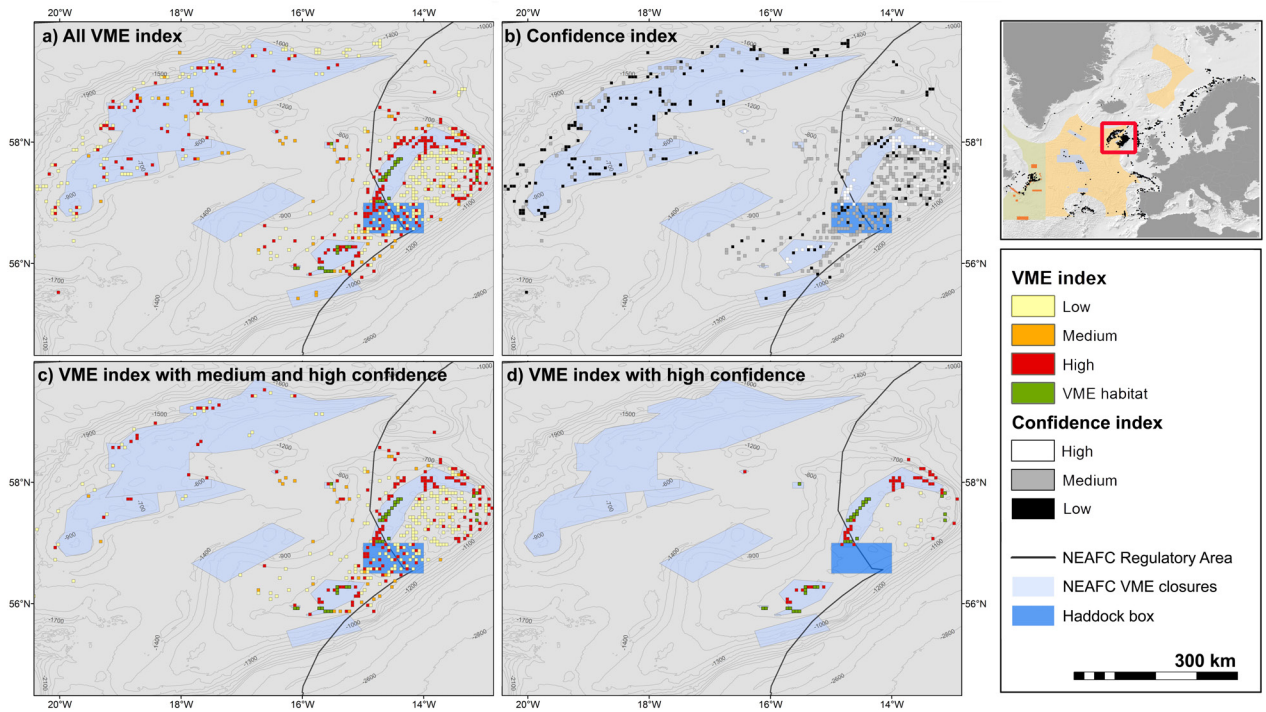


FIGURE 5 | Applying the VME index and confidence index to the VME database: Rockall and Hatton Bank. **(a)** VME index for all cells with data in the ICES VME database; **(b)** confidence index for all cells with data in the ICES VME database; **(c)** VME index for cells with medium and high confidence; and **(d)** VME index for cells with high confidence.

2008; Durán Muñoz et al., 2009), cold seep ecosystems (Neat et al., 2018), and other important geomorphological features throughout the area (Roberts et al., 2008; Sayago-Gil et al., 2010). In addition, several VME indicator species including cold-water corals and sponges have been identified in recent years through collaboration with commercial trawl and longline fisheries (Durán-Muñoz et al., 2011, Durán-Muñoz et al., 2012b). Thus the variable amount of information for this area and the range in quality of that information (e.g., fishing records vs. scientific observations), serves as a good case study to illustrate the approach.

The data outputs for the Hatton-Rockall Bank area illustrate several important aspects of the MCA (**Figure 5**). First, there were some bona fide VME habitats identified in the Rockall Bank which are clearly highlighted by the method (**Figure 5a**). Second, the areas identified by the MCA as high values of "VME index" often fell within existing NEAFC closures for example NW Rockall and SW Rockall. This suggests the method is useful for identifying areas that need protection. Third, it identified areas of medium and high value of "VME index" situated outside closed areas thereby suggesting such areas should be carefully assessed and possibly protected. Finally, in **Figure 5b**, it is apparent

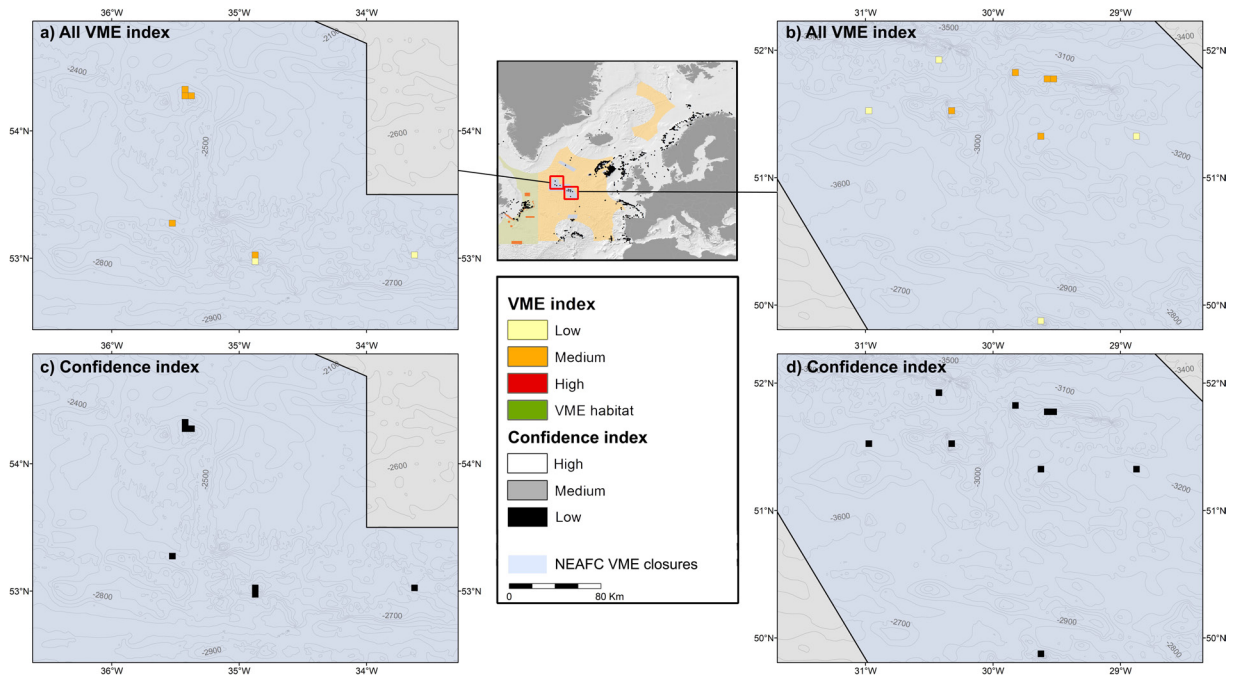


FIGURE 6 | Applying the VME index and confidence index to the VME database: Charlie-Gibbs Fracture Zone. **(a,b)** VME index for all cells with data in the ICES VME database; **(c,d)** confidence index for all cells with data in the ICES VME database.

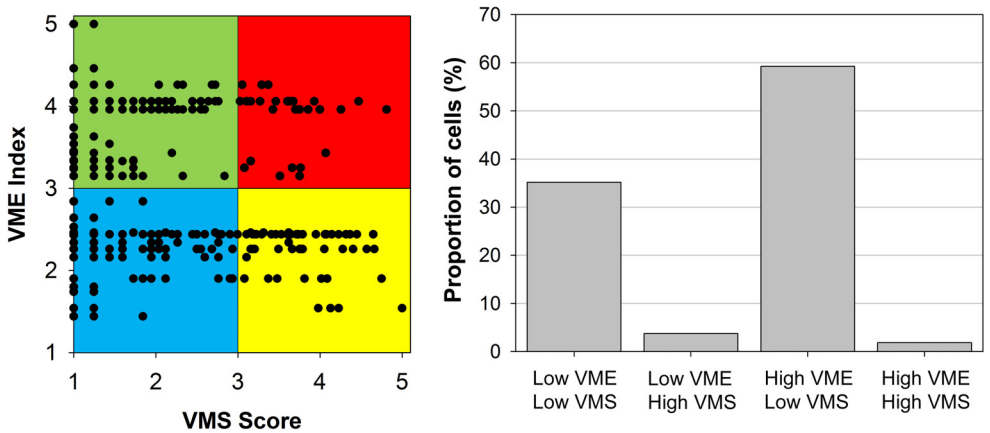


FIGURE 7 | Application of the portfolio categories concept to the ICES database. In the left panel, the different colors represent four portfolio categories: blue is low VME – low VMS, yellow is low VME – high VMS, green is high VME – low VMS, and red is high VME – high VMS. In the right panel, proportions of cells falling into those categories are shown.

that the intensive sampling on the Rockall plateau yields high confidence, whereas the less-well sampled Hatton Bank yields lower overall confidence. This can then be seen particularly clearly where only the cells with medium and high confidence are plotted (**Figures 5c,d**). This does not mean Rockall Bank is more important from a VME perspective; rather, only that we are more confident that Rockall Bank is an important VME area. There is good evidence that VMEs are present at Hatton Bank, but the confidence of these records is not as high as it is at the Rockall Bank.

Charlie-Gibbs Fracture Zone

The Charlie-Gibbs Fracture Zone (CGFZ) area in the Mid-Atlantic Ridge between Iceland and the Azores, provides a model case study to illustrate the limitations of the application of the MCA approach to data-poor areas. A portion of the CGFZ was nominated as an OSPAR MPA and adopted by NEAFC to protect the unique natural features associated with the Mid-Atlantic Ridge. Due to its remoteness, very limited information on the benthic communities is available. The main exceptions were the MAR-ECO and ECOMAR expeditions that recorded

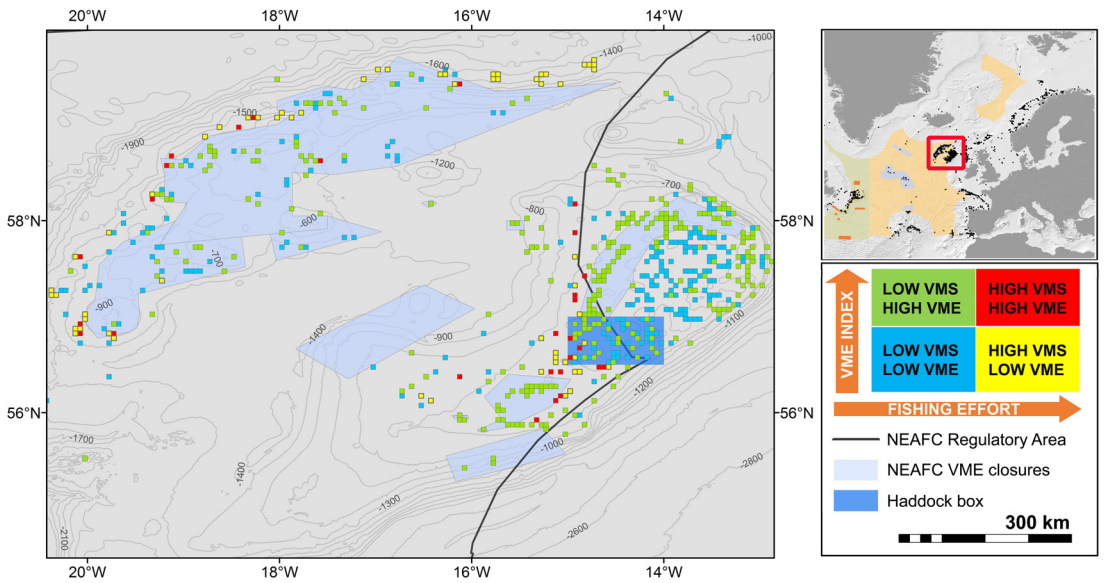


FIGURE 8 | Application of the portfolio categories concept to the Hatton-Rockall area. Blue cells are low VME – low VMS, yellow cells are low VME – high VMS, green cells are high VME – low VMS, and red cells are high VME – high VMS.

cold-water corals belonging to 34 different taxa in areas close to the CGFZ (Molodtsova et al., 2008; Mortensen et al., 2008) along with different species of hexactinellid sponges and echinoderms (Gebruk and Krylova, 2013). During the MAR-ECO expedition *Lophelia pertusa* was frequently observed but no large live reef structures have been detected (Mortensen et al., 2008). Thus the limited amount of information with limited spatial coverage for this area, serves as an illustrative data-poor case study.

The data outputs for the CGFZ area illustrate several important aspects of the ICES VME database and the MCA (**Figure 6**). Although we found literature sources describing the occurrence of stony corals in the area (e.g., Mortensen et al., 2008), those have not been transposed to the ICES VME database which highlights the need for an improved data reporting to ICES. Also, the records in the database lack important information such the survey method or the observation date preventing a proper estimation of the confidence index, highlighting the need for strictly following of the ICES VME data reporting guidelines. The application of the MCA to the CGFZ reveals some areas with medium values of "VME index" with very low confidence scores (**Figure 6**), demonstrating the limitations of the MCA applications to data-poor areas.

VME and Fishing Effort Portfolio Categories

The ICES data was assigned to all four portfolio categories (**Figure 7**). The outcomes of the framework can be visualized for comparing different areas, allowing managers to prioritize their choices or policies in terms of closing pristine VME areas, closing disturbed areas for recovery of VMEs, or both (**Figure 7**). A large portion of the cells were revealed as high VME and low VMS (59%) or low VME and low VMS (35%) (**Figure 7**). Only a small portion of the cells fell in the category high VME and high VMS (2%) (**Figure 7**). However, the high numbers of cells with low fishing effort should be considered with caution because: (1) many cells fall within national jurisdiction for where we had limited access to VMS data; (2) a large portion of the fishing vessels do not have a fishing license assigned and therefore are not considered as trawlers and were excluded from the analyses; and (3) some areas were closed to fishing in recent years but may have experienced higher impacts previously.

Mapping the outcomes of the framework can be another way to visualize areas falling in different portfolio categories. For example, in the Hatton-Rockall area (**Figure 8**), despite the shortcomings of the VMS data described above, most areas of high VME score lie inside closed areas and have low fishing effort. Only few cells with high VME index and high fishing effort are observed mostly, around the closed areas.

CONCLUSION

In general, the MCA provides a simplified, spatially aggregated and weighted estimate of the degree an area could be considered to contain VMEs under the FAO definition. The VME index clearly highlights areas where a VME is more likely to occur while the associated estimate of confidence gives an indication of how (un)certain that assessment is. The methodology is transparent and the aggregate cells can be explored in greater detail to reveal the individual data points that have contributed to the assessment. It integrates far more of the information in the ICES VME database than previous methods and as such, better captures the underlying reasoning behind much of WGDEC's past advice (e.g., ICES, 2013a). The MCA can be expected to be

updated each year as new data are submitted and thus provide an up to date, repeatable and defensible source upon which to base advice as new information is received.

The MCA approach achieved three main aims. (1) To develop a system which could provide a measure of the likelihood of a cell constituting a VME and the associated level of fishing activity. The choice of the VME scoring criteria and the definition of the most relevant fishing activities were based on the existing information but should be revisited when more information is made available; as for example on the life history of VME indicator taxa. Using quadratic means to estimate the VME indicator score was chosen to avoid several low scores adding up to a misleadingly high score; but it could still underestimate the value of abundant VME indicators that rank high in only few criteria as compared to less abundant indicators with several high scores. This problem may be overcome by increasing the weight assigned to the abundance score; however, this should only be done when more abundance data in weight are reported in the ICES VME database. (2) To design a system compatible with, and making use of all the data currently available. The major constraint faced by this analysis is the general scarcity of information, mostly related to the lack of abundance data (weight or numbers) for each VME indicator record present in the ICES VME database. Additionally, some work has to be done to develop a methodology to standardize information that has originated from very different sampling methods, as for example fisheries trawls and ROV transects. (3) To deliver an output that is simple to visualize and understand, in order to facilitate its implementation in management deliberations.

The UN General Assembly resolution that committed to protecting VMEs from destructive fishing practices also calls upon States to do so, "consistent with the precautionary approach" (UNGA, 2006, paras. 80 and 83). The inclusion of the confidence index in the MCA allows for decision-making concerning possible fisheries closures (and other management measures) to explicitly determine what level of uncertainty may still warrant precautionary actions.

Overall the MCA appears to capture most of the important elements of the ICES VME database used by WGDEC to assess VMEs. This methodology may be considered as a first step toward a systematic approach for the identification and protection of VME in the NE Atlantic. Our methodology clearly considered several of the steps proposed by Ardron et al. (2014), namely step 1 on assessing potential VME indicator taxa and habitats in a region, step 3 on considering areas already known for their ecological importance, step 4 on compiling information on the distributions of likely VME indicator species and habitats, step 6 on considering fishing impacts, and step 8 on identify ecologically important areas. However, at least one important aspect of the Ardron et al. (2014) framework is missing in the current MCA which refers to understanding the natural distribution of VMEs before significant impacts occurred. This aspect could be considered in future improvements of the MCA to encompass predicted distribution of VME as discussed in Vierod et al. (2014) and Anderson et al. (2016a).

By providing an indication of uncertainty alongside predicted occurrence, the MCA allows for management decisions to be openly discussed, logically weighed, and documented. In the future, with better recognition technology becoming available, these methods could be automated and applied to survey data as they are collected, or soon thereafter, thus avoiding delays that could leave newly identified VME areas at risk. The ability to readily incorporate new data also makes the MCA approach appropriate for adaptive management frameworks.

AUTHOR CONTRIBUTIONS

FN, TM, NG, JA, and CP designed the study. CP, NG, FN, and PDM compiled the data. CP, TM, FN, NG, and JA analyzed the data. All authors wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00460/full#supplementary-material

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METHODS
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An Efficient Multi-Objective Optimization Method for Use in the Design of Marine Protected Area Networks

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An efficient connectivity-based method for multi-objective optimization applicable to the design of marine protected area networks is described. Multi-objective network optimization highlighted previously unreported step changes in the structure of optimal subnetworks for protection associated with minimal changes in cost or benefit functions. This emphasizes the desirability of performing a full, unconstrained, multi-objective optimization for marine spatial planning. Brute force methods, examining all possible combinations of protected and unprotected sites for a network of sites, are impractical for all but the smallest networks as the number of possible networks grows as 2^m, where m is the number of sites within the network. A metaheuristic method based around Markov Chain Monte Carlo methods is described which searches for the set of Pareto optimal networks (or a good approximation thereto) given two separate objective functions, for example for network quality or effectiveness, population persistence, or cost of protection. The optimization and search methods are independent of the choice of objective functions and can be easily extended to more than two functions. The speed, accuracy and convergence of the method under a range of network configurations are tested with model networks based on an extension of random geometric graphs. Examination of two real-world marine networks, one designated for the protection of the stony coral *Lophelia pertusa*, the other a hypothetical man-made network of oil and gas installations to protect hard substrate ecosystems, demonstrates the power of the method in finding multi-objective optimal solutions for networks of up to 100 sites. Results using network average shortest path as a proxy for population resilience and gene flow within the network supports the use of a conservation strategy based around highly connected clusters of sites.

Keywords: multi-objective optimization, Pareto optimal solution, marine protected area networks, random geometric graph, connectivity, Markov Chain Monte Carlo, graph theory

1. INTRODUCTION

Connectivity of marine ecosystems is fundamental to survival, growth, spread, recovery from damage and adaptation to changing conditions, on ecological and evolutionary timescales (James et al., 2002; Cowen and Sponaugle, 2009; Burgess et al., 2014). Empirical evidence shows the benefits of connectivity information to conservation management (Planes et al., 2009; Olds et al., 2012). Knowledge of the characteristics of connectivity is rapidly expanding, with recent studies using seascape genetics approaches combining particle tracking in high resolution ocean models with state-of-the art genetic techniques (Foster et al., 2012; Teske et al., 2016; Truelove et al., 2017).

For marine conservation there is ongoing debate (see Cabral et al., 2016) over the relative merits of prioritizing site protection by network structure and connectivity (Kininmonth et al., 2011; Watson et al., 2011; Berglund et al., 2012), or by intrinsic patch characteristics such as habitat quality and extent (Carson et al., 2011; López-Duarte et al., 2012; Cabral et al., 2016). The conclusions can depend on the objectives and measures of success. Cabral et al. (2016) found the most effective way to maximize adult population was to base conservation on extent and quality of habitat, ignoring connectivity. But Kininmonth et al. (2011) used a quality measure based on metapopulation persistence to advocate prioritizing groups of highly connected reserves (hubs).

The current generation of computational tools for spatial conservation prioritization, for example Marxan (Ball et al., 2009), and Zonation (Moilanen et al., 2011; Lehtomäki and Moilanen, 2013), can incorporate information on the connectivity between spatially separate subpopulations common in marine ecosystems in their optimization methods (Schill et al., 2015; Magris et al., 2016). Other tools map static, area-based measures of importance or centrality (Carroll et al., 2012) across the landscape, these maps can be used subjectively in spatial conservation prioritization. Further, a series of papers by Jonsson, Jacobi and co-workers (Nilsson Jacobi and Jonsson, 2011; Berglund et al., 2012; Jonsson et al., 2016) used eigenvalue perturbation theory to find an optimal subset of marine protected areas (MPAs), given the total area to be protected, that maximized the growth rate of the metapopulation. All of the above methods require prior selection of the protected network size, quality or cost; and site-based network centralities are generally calculated on the full network and not updated based on the protected subnetwork configuration. By pre-selecting a target quality or cost value, these approaches greatly simplify the computational task. This convenience comes with a dramatically impoverished range of potential solutions accessible to the approach, and will inevitably miss solutions which decision-makers would find preferable, despite varying from the pre-selected target in one objective.

Once the connections are mapped (or modeled), a "graph" of nodes (sites or subpopulations) and directed edges (connections) results. Optimal spatial conservation prioritization can then make use of the rapidly expanding fields of network and complexity theory. Many network metrics are appropriate proxies for ecological processes and have been used in assessment of existing or planned marine protected area (MPA) networks, identifying the most important nodes for genetic material supply, network robustness, stepping-stones to maintain connectivity, and gaps (Treml et al., 2007; Rozenfeld et al., 2008; Andrello et al., 2015; Fox et al., 2016). With a complex network such static analysis is of limited use; inclusion or removal of a single node from the network can have implications for the function and importance of many other nodes. To produce more robust information we need methods to search the vast space of all possible subnetworks for those which give the optimal combination of desired properties.

The problem considered here is one of multi-objective optimization, where decisions need to be taken in the presence of trade-offs between two or more conflicting objectives, for example maximizing network resilience while minimizing social or economic costs. In a non-trivial multi-objective optimization problem, there is no single solution that simultaneously optimizes each objective. Instead there are a number of "Pareto optimal" solutions (Miettinen, 1999), solutions where none of the objectives can be improved without degrading some of the others. The goal is to find the set of Pareto optimal solutions, and quantify the trade-offs; a final solution would incorporate additional unmodeled information together with subjective preferences of stakeholders and expert human decision makers.

Networks of marine reserves are designed for many objectives, including socioeconomic, pragmatic and ecological—such as species and habitats of concern, connectivity and ecosystem function, natural and anthropogenic catastrophes (Leslie, 2005). Here we use a site-based economic cost together with a network metric—average shortest path—used as a proxy for network resilience (Watts and Strogatz, 1998; Manzano et al., 2015) to characterize "small world" networks and interconnectedness (Albert et al., 2000). Ecologically the average shortest path can be considered a proxy for resilience and for gene flow, with increasing gene flow potentially promoting adaptation (Tigano and Friesen, 2016). While these methods and cost functions are most naturally applicable to sessile benthic species with a pelagic phase, the multi-objective optimization and search methods presented are fully independent of the choice of objectives and cost functions.

For small networks (20–30 sites), all possible network configurations can be examined: beyond this scale, we need search methods which converge more rapidly on the optimal configurations. Here we describe a new metaheuristic search method (Voß et al., 1999; Glover and Kochenberger, 2003), based around Markov Chain Monte Carlo (MCMC) sampling methods (Gilks et al., 1995), and the expected properties of optimal solutions, to efficiently search for Pareto optimal solutions to multi-objective optimization problems. These methods are first tested on model networks, based on random geometric graphs (Penrose, 2003). These model graphs are a useful analog to marine benthic networks and allow close control of network size and connectivity (see Kininmonth et al., 2011 and Cabral et al., 2016 for the use of graph models in MPA network studies). The optimization methods are then applied to two marine network optimization problems—the first aimed at conservation of

natural populations, and the second at preserving connectivity across a network of man-made structures.

Pareto frontiers have been investigated previously in the context of marine spatial planning. Lester et al. (2013) discuss how the Pareto frontier can be used to evaluate trade-offs among ecosystem services. Meanwhile, Rassweiler et al. (2014) use "black box" genetic algorithms to identify the Pareto frontiers in optimization of fishing returns and population biomass. Here we advance this work significantly, describing in detail for the first time an efficient search method specifically designed to identify the optimal configurations of connected marine networks in marine spatial planning. The search method is tested on small networks with known solutions to confirm convergence to the correct Pareto optimal solution, it is then applied to larger model networks and real-world connected marine networks. Crucially, we examine the structure of the optimal subnetworks, compare and contrast these with previous work and demonstrate the power and value of the multi-objective optimization approach.

2. METHODS

2.1. The Sample Space

We consider selection of optimum subnetworks (or subgraphs) for protection from a network (graph) of sites (nodes) connected by directed weighted edges. In these subgraphs, each node can be either included in (protected) or excluded from (unprotected) the subgraph. Connections into and out of nodes which are not in the subgraph are removed, assuming that unprotected subpopulations are lost. Denoting the wider graph $G_T = (V_T, E_T)$ with nodes V_T and edges E_T, our sample space is then all possible subgraphs $G_S = (V_S, E_S)$ with nodes V_S and edges E_S where:

$$V_S \subseteq V_T \tag{1}$$

and

$$E_S = \{\{x, y\} \in E_T \,|\, x \in V_S \text{ and } y \in V_S\} \tag{2}$$

We use m to represent the number of nodes in G_T, and n for the number of nodes in subgraph G_S. The total possible number of subgraphs, including both the full graph and the empty graph (the size of the sample space) is 2^m.

The assumption that unprotected sites are lost represents an extreme case most applicable to highly vulnerable, slow-to-recover species like cold-water corals. More generally, protected and unprotected areas are intertwined, with spillover from protected areas contributing to productivity elsewhere and larvae produced in unprotected areas contributing to reserves (Botsford et al., 2001; Almany et al., 2009). This could be accounted for by reducing the weight of, rather than completely removing, connections into and out of unprotected areas to represent reduced larval production and recruitment.

2.2. Multi-Objective Optimization and Pareto Optimal Solutions

We can define optimization functions (also referred to as "cost functions") on the protected subnetwork, some to be maximized (e.g., connectivity, geographic range, diversity, resilience, fishing returns, or biomass) and some minimized (e.g., costs to industry). Plotting the output of such functions (**Figure 1**), we can draw a "Pareto front," connecting the Pareto optimal solutions. For example, subnetworks are Pareto optimal if all subnetworks with higher benefits cost more, or equivalently all lower cost networks have lower benefits. Multiple solutions can lead to the same point on the frontier but careful choice of objective functions can minimize this possibility. If such cases occur, other criteria would need to be used to make a final choice.

There is usually no single optimal solution. However the shape of the Pareto front gives information on solutions which may represent better, or preferred, choices. The center of convex frontal regions ("A" in **Figure 1**) represent better solutions where increased benefits require large cost increase, and cost can only be decreased with large reductions in benefit; while the center of concave regions ("B" in **Figure 1**) represent poorer solutions (Lester et al., 2013). Multi-objective approaches are always an enhancement over single-objective approaches; if automated return of a single solution is desired, then this is available by applying any desired single-objective function to those in the Pareto set; if not, a human decision maker, with input from stakeholders, can inspect the trade-off surface and make a well-informed decision (see Cabral et al., 2017 for a discussion of trade-off analysis). The Pareto front idea can be extended to optimizing more conditions, but becomes difficult to visualize; for example, with three functions the Pareto front will in general be a surface, and with $N + 1$ functions the Pareto front could be N-dimensional.

For small networks we can examine all possible subnetworks, finding the optimal solutions by "brute force." However, the number of possible subnetworks, 2^m, very quickly becomes unmanageably large. For larger networks we need an efficient search method to locate the Pareto-optimal solutions.

2.3. Search for Pareto Optimal Solutions

The broad field of *optimization* is concerned with efficiently finding good solutions to problems with non-trivial cost functions. With the exception of some special cases (such as minimal-spanning tree problems, or unconstrained linear systems), optimization algorithms do not guarantee finding true optima, but aim for the best solutions attainable in reasonable time, which in practice—when the algorithm is well-engineered for the problem at hand—tend to be either optimal or near-optimal. In the remainder of this section we will use "optimal" as shorthand for "optimal or near-optimal."

A range of optimization methods are available, categorized in terms of the structural nature of the target problem. For example, when the problem can be formulated in terms of differentiable functions of real-valued parameters, "gradient methods" from mathematical optimization can be used (Snyman, 2005); when the problem can be formulated in terms of linear functions of discrete variables, methods from operations research can be used (Hillier and Lieberman, 2015). Although approaches exist to extend the reach of techniques from operations research and mathematical optimization, further categories of optimization method have wider applicability. Prominent among the latter

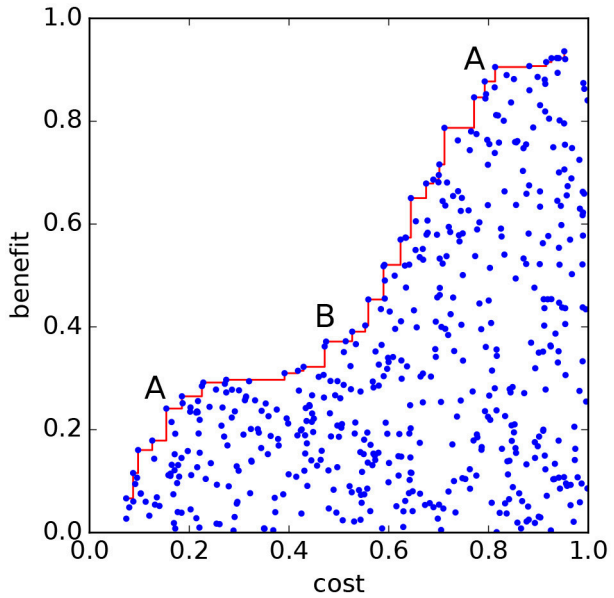


FIGURE 1 | Schematic of a Pareto front (red line), with a function to be minimized (labeled "cost") on the $x-$axis and a second function (labeled "benefit"), to be maximized, on the $y-$axis. Each blue dot represents a possible solution. The points along the Pareto front are Pareto-optimal solutions from which the benefit cannot be increased without increasing the cost; and cost cannot be reduced without reducing benefits. Convex sections of the front ("A") represent locally preferred solutions. Concave sections ("B") represent locally poorer solutions.

are "metaheuristic" approaches (Voß et al., 1999; Glover and Kochenberger, 2003), which can be used to find optimal solutions in problems of arbitrary structure. To ensure that we do not constrain the cost-functions that may be used to evaluate MPA solutions, we design our algorithm from among the latter approaches.

Metaheuristic approaches are "black box" optimizers: the design of an algorithm does not rely on properties of the function(s) to be optimized; this is key to their wide applicability. A metaheuristic search process is guided primarily by the cost function values of solutions evaluated earlier in the process. A fundamental insight that guides search in metaheuristic algorithms is that solutions that are close in terms of their design parameters will often be close in terms of their cost function values; thus, in order to seek better solutions, it will be fruitful to sample new solutions close to the best ones found so far. Metaheuristic algorithms also devote some of their search effort to mechanisms that "explore" the search space by evaluating samples that are distant from the areas currently being exploited. Among the wide variety of metaheuristic approaches that could be applied, Markov Chain Monte Carlo (MCMC) frameworks provide arguably the most principled approach toward balancing exploitation and exploration. We therefore use ideas and methods from MCMC sampling to converge toward Pareto-optimal solutions from random initial estimates.

MCMC sampling centers on the concept of a "Markov Chain," a sequence of connected "moves" through the sample space. In the current context, a "move" represents stepping from one MPA network A to another network B which is "close" to A; for example, A and B may share many sites in common. A sequence of such moves is often termed a (random) "walk." In standard MCMC sampling, a walk is performed from a random starting position, and the new solution at each step along the walk is evaluated; steps along the walk may be rejected if they fail a stochastic test based on the cost/benefit values (in which case we stay at the current position and consider an alternative step). When MCMC is used for optimization (Strens, 2003; Lecchini-Visintini et al., 2010) (rather than for characterizing complex sample distributions; Gilks et al., 1995; Gamerman and Lopes, 2006), the stochastic test boosts the probability of moves toward high-quality regions of the search space. However the standard scheme often leads to slow or poor convergence since single chains can get trapped in suboptimal areas. An alternative approach is to use a collection of parallel walks to reduce the chance of suboptimal convergence (Craiu et al., 2009). We adopt this multiple walk approach, in part because it naturally promises highly effective speedup on parallel architectures, which may be necessary for large-scale MPA scenarios. In addition we repeatedly refresh these walks by restarting at positions on the best-so-far Pareto set; repeated restarts is common in parallel-walk MCMC algorithms (Martino et al., 2014; Garthwaite et al., 2016), while the idea of repeatedly exploiting the current approximation to the Pareto set borrows from prominent and successful "many-objective" optimization methods (Corne and Knowles, 2007). Finally, in our algorithm design we simplify the individual walks by omitting the use of a stochastic test, and simply accepting all moves along the walk. As we discovered in preliminary experiments, this was more successful than using a standard MCMC approach; although individual walks have an increased chance of wandering away from promising areas, this is balanced by the repeated restarts, which emphasise exploitation of the current Pareto set. We complete our description of the algorithm by describing details of the moves and structure, along with full pseudocode.

First consider possible choices of random steps. From any subnetwork we could take a step to any one of the other $2^m - 1$ subnetworks. A useful choice of step balances exploration of the local neighborhood with the ability to traverse the whole space in reasonable time. The simplest choice of step is the switching of a single randomly selected node between in and out of the network or vice versa. This fits our conditions: while allowing exploration of "nearby" space, a walker taking such steps could reach any subnetwork from any other in at most m steps. Computationally this also has the potential advantage of rapid evaluation of network metrics with just the addition or removal of a single node. This will be our random step, the node to switch is selected using a uniformly distributed random number.

Second, to maintain pressure toward encountering solutions that will advance beyond the current Pareto set, we need to keep our random walkers in the vicinity of the better solutions found so far. In a preliminary version of the algorithm we used the recognized MCMC optimization approach in which a move was only accepted if it passed a stochastic test. However, in our

final algorithm design, every move in a walk is accepted, and the pressure toward optimal solutions instead comes from the multiple walker framework, as described next.

The algorithm operates by running repeated series of parallel but independent random walks. Initially, a simple random search is done to obtain an initial Pareto set of solutions. Then, starting from a subset of these solutions, k independent random walks are launched, each lasting for s steps, updating the current Pareto set according to the solutions evaluated along the way. This set of independent random walks is repeated, each time starting each walk from a randomly selected sample in the current Pareto set, until a termination criterion is reached. Effectively, the dynamically changing Pareto set acts to repeatedly select, prune or "multiply" search trajectories. Trajectories that did not contribute the Pareto set become "pruned," those that do contribute may be multiplied.

Result: Set of Pareto optimal subnetworks, P
randomly select an initial set of subnetworks, G;
evaluate objective functions on G;
find initial set of Pareto optimal subnetworks, P, on G;
/* discard, or 'prune', suboptimal subnetworks */
G := P;
repeat
  foreach *subnetwork in G* **do**
    /* 'split' walks */
    launch k ($k \geq 1$) MCMC walks **foreach** *walk* **do**
      take s ($s \geq 1$) steps;
      foreach *step* **do**
        add the new subnetwork to G;
        evaluate objective functions on the new subnetwork;
      end
    end
  end
  find set of Pareto optimal subnetworks, P, on G;
  /* 'prune' suboptimal subnetworks */
  G := P;
until *converged*;
/* e.g. no new Pareto optimal subnetworks found for some time */

Note that while this method must converge eventually, there is no guarantee that it converges to the correct, global, Pareto optimal solutions. Use of a larger set of initial random subnetworks, and more steps, s, in each walk reduces the chance of converging to a locally optimal solution. The efficiency of the method relies on the use of well-behaved, rather than noisy, optimization functions which vary slowly with choice of nodes in the subnetwork.

2.4. Cost Functions

To examine the use of connectivity in network optimization, we use a connectivity-based objective function—a proxy for network resilience and gene flow—and a simple site-based cost function. The merits of these objective functions and further possible choices of function are discussed in section 4.

2.4.1. Costs

For the model networks (section 2.5) and the decommissioning example (section 2.6.2) sites are considered to have equal cost so a network of k sites has a cost of k.

MPA network proposals often include industry-based estimates of financial costs to fishing, shipping, renewable energy, oil and gas, and mining industries. For the Scottish MPA network (section 2.6.1) these costs are available from the Business and Regulatory Impact Assessments (BRIAS) conducted as part of the Scottish Government MPA consultation (http://www.gov.scot/Topics/marine/marine-environment/mpanetwork) or Impact Assessments produced for consideration as a Special Area of Conservation (SAC) under the EU Habitats Directive 1992 (http://jncc.defra.gov.uk/page-4524). Here we use estimates of ongoing management costs and costs to the fishing industry from these Impact Assessments as most relevant to the protection of *Lophelia pertusa*. Upper cost estimates to fishing were used, representing the removal of all bottom-contacting fishing from protected sites. Where such estimates were not available (Hatton Bank, North West Rockall Bank and South East Rockall Bank), an estimate from a similar nearby site was used, weighted by site area. To these we add an average annual management cost, obtained from the SAC Impact Assessments, of £50,000 per year for each site. We do not claim these costs as complete or authoritative, a rigorous cost analysis would be required in a practical application. The estimated costs here cover a realistic range and serve to demonstrate the optimization method.

In the North Sea decommissioning example (section 2.6.2) minimum financial cost and maximum network connectivity may both be achieved by leaving all platforms in place. But this solution could have reputational costs to government and industry: under Decision OSPAR 98/3 Disposal of Disused Offshore Installations for parties contract to the OSPAR Convention, all topsides and substructure are to be fully removed with few exceptions for derogation. Policy change to leave installations in place could be perceived as motivated by cost-cutting rather than environmental concerns. Additionally, leaving installations in place, either wholly or partially, could restrict the opportunity for growth in the fisheries industry, so it is reasonable to consider the number of installations left in the network as a "cost" to be minimized.

2.4.2. Benefits

Average shortest path, the smallest distance to travel between any two sites in a network averaged over all pairs of sites, is one of a suite of network metrics used as indicators of network robustness (Watts and Strogatz, 1998; Manzano et al., 2015). Also used to characterize "small world" networks and interconnectedness (Albert et al., 2000), ecologically, the average shortest path gives an idea of the gene flow through a network, increased gene

flow can promote adaptation (Tigano and Friesen, 2016). Here, the average shortest path metric is calculated for each protected subnetwork G_S being considered. To avoid only selecting for the smallest fully connected networks (two nodes with a connection in both directions), we make small modifications to the standard average shortest path calculation. Firstly, we calculate the average shortest path over all the pairs of sites in the full network G_T, having first removed all connections into and out of nodes which are not in the protected subnetwork G_S. This assumption could be relaxed to instead reduce the weight of connections to and from unprotected sites (see for example Nilsson Jacobi and Jonsson, 2011). Secondly, if there is no possible path between a pair of nodes we define the shortest path to be D, longer than the distance across the full network. Finally, in the real-world examples we include self-connections in the shortest path lengths, these represent return of larvae to the source site.

We include edge weights in the average shortest path, where the edge e_{ij}, from x_i to x_j, has weight w_{ij} and corresponding length d_{ij}. The edge length is calculated directly for the model networks as described in section 2.5. For the real-world networks the larval connectivity modeling gives estimates of the relative probability of a link between any two sites, i.e., edge weights w_{ij}, where $0 \leq w_{ij} < 1$. Weights are converted to distances using

$$d_{ij} = \log \frac{1}{w_{ij}}, \tag{3}$$

this maintains the natural interpretation of the probability of a link along a chain

$$d_{13} = d_{12} + d_{23} = \log \frac{1}{w_{12} w_{23}}. \tag{4}$$

2.5. Model Networks

Various graph models have been used in studies of marine connectivity. Kininmonth et al. (2011) explores many types including minimally connected, nearest neighbor, small-world, geometric, random, and scale free graphs. Considering the physical processes underlying benthic ecological networks we use a modification of random geometric graphs (Penrose, 2003). Random geometric graphs have nodes randomly distributed in geometric space with connections between pairs of nodes separated by less than a specified distance. Benthic subpopulations can appear to be randomly distributed, although distribution is governed by water depths, substrates, local watermass properties, hydrodynamics, food and nutrient delivery, and human pressures. The fixed radius of connections in random geometric graphs models turbulent transport and random swimming of pelagic larvae in the absence of mean flows. Here we refine the definition to introduce a directional bias to the connections, analogous to the common situation of populations within a mean flow. The advantage of model graphs is we can control size and connectivity of the network for a thorough test of the search and optimization methods.

While this form of graph is chosen primarily to model the common form of sessile benthic species with a pelagic larval phase and a metapopulation/subpopulation structure, similar model graphs—which consist purely of nodes and weighted connecting edges—could easily be constructed to represent species with direct development or continuous distribution. The optimization approach described is general and applicable to any network configuration.

We construct such graphs, $G_T(V_T, E_T)$, (**Figure 2**) with nodes, V_T, and edges, E_T, in 2-d geometric, (x, y), space. Here m nodes were positioned randomly on the plane $x \in [0, 1], y \in [0, 1]$. With spreading distance r (in time t) and uniform flow u, with associated displacement s in time t (in the positive $x-$direction) each node (x_i, y_i) was connected to all nodes (x_j, y_j) according to

$$\begin{aligned} &\{(x_i, y_i), (x_j, y_j)\} \in E_T \\ &\iff \sqrt{(x_j - x_i - s)^2 + (y_j - y_i)^2} \leq r \; \forall j \neq i \end{aligned} \tag{5}$$

Each node (x_i, y_i) is connected to all other nodes (x_j, y_j) that lie within distance r of the point $(x_i + s, y_i)$. The separation length d_{ij} is the distance from the spreading center $(x_i + s, y_i)$ to node (x_j, y_j). That is

$$d_{ij} = \sqrt{(x_j - x_i - s)^2 + (y_j - y_i)^2}. \tag{6}$$

2.6. Example Real-World Networks

Two real-world cases are tested: the Scottish MPA network and a man-made network of oil and gas installations in the North Sea, with connectivity matrices derived from larval dispersal modeling (Fox et al., 2016).

2.6.1. Scottish MPA Network

In Scottish waters MPAs have been designated for the protection of cold-water coral *L. pertusa* (Roberts et al., 2006). The weighted larval connections have been modeled by Fox et al. (2016), **Figure 3**. This is a small network of 12 sites so we can easily evaluate objective functions for all possible network configurations, finding the true Pareto optimal solutions by brute force. Estimates of costs for each site, determined as described in section 2.4.1 are shown in **Table 1**.

2.6.2. North Sea Oil and Gas Installation Decommissioning Scenario

Within the North Sea, oil and gas platforms form a man-made network providing hard substrates generally unavailable in the North Sea away from the coasts. These platforms are colonized by benthic species (Roberts, 2002) including hard corals (*L. pertusa*), soft corals (*Alcyonium digitatum*), mussels (*Mytilus edulis*), barnacles (*Chirona hameri*) and anemones (*Metridium sessile*). Many installations are reaching the decommissioning stage, so work is ongoing to quantify the contribution of this man-made network to North Sea biodiversity and interconnectedness of this new man-made ecosystem (Henry et al., 2018). It is interesting therefore to examine scenarios where some of the substructure is left in place to form artificial reefs of hard substrate ecosystems.

Particle tracking experiments simulating larval connectivity among the installations were done using the Lagrangian TRANSport model (LTRANSv.2b, North et al., 2011) with a

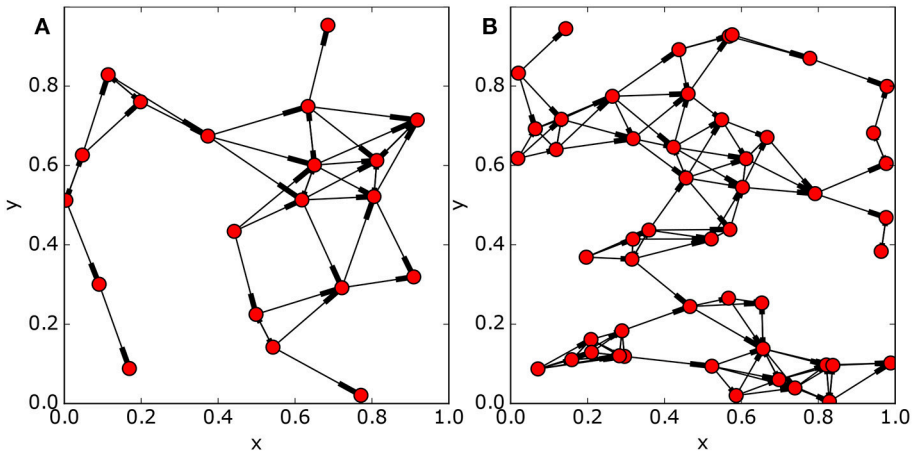


FIGURE 2 | Modified random geometric networks of 20 nodes **(A)** and 50 nodes **(B)**. Edge connections are toward the thickened end of the line. Parameters used in the construction: (a) $m = 20$, $r = 0.17$, $s = 0.085$; (b) $m = 50$, $r = 0.15$, $s = 0.085$.

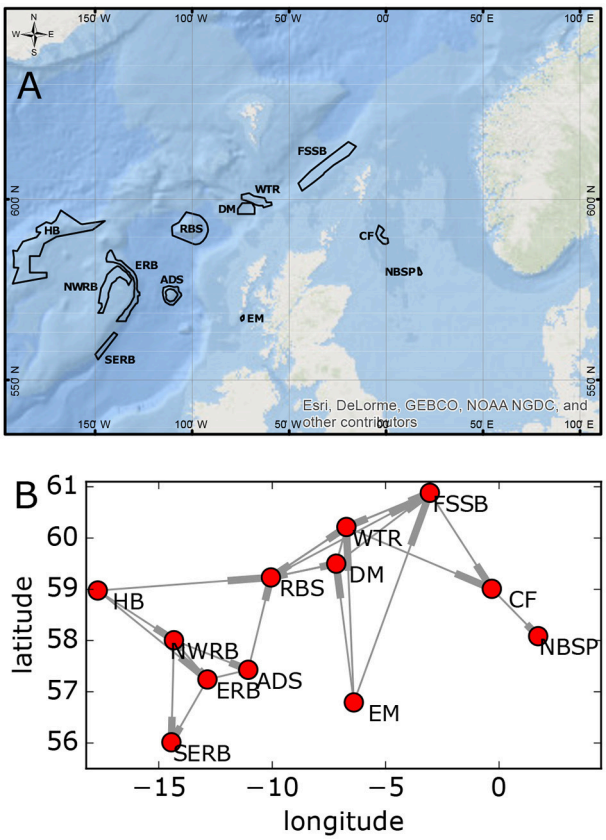


FIGURE 3 | Estimated connectivity of Scottish MPA network for *L. pertusa* from Fox et al. (2016). **(A)** Map of the network. **(B)** Diagram of the connectivity. Connection direction is toward the thickened end of the edge. Site name abbreviations are listed in **Table 1**.

high resolution configuration of the Nucleus for European Modeling of the Ocean (NEMO) for the North West European Shelf, the NEMO-AMM60 (Atlantic Margin Model ⅑ degree,

TABLE 1 | Estimated annual costs associated with Scottish MPAs (thousands of £).

MPA	Abbr.	Cost £k
Hatton Bank	HB	645
South-East Rockall Bank SAC	SERB	120
East Rockall Bank	ERB	190
North West Rockall Bank	NWRB	215
Anton Dohrn Seamount	ADS	50
Rosemary Bank Seamount	RBS	323
East Mingulay	EM	117
Darwin Mounds	DM	180
Wyville Thomson Ridge	WTR	357
Faroe-Shetland Sponge Belt	FSSB	614
Central Fladen	CF	1,167
Norwegian Boundary Sediment Plain	NBSP	50

Guihou et al., 2018). Here, 100 particles were released daily during 14 days (February 15 to 28, 2010) at the location of each installation and tracked for 40 days, near the upper limit of the pelagic larval duration for the shallow-water species observed on North Sea oil platforms. Particle trajectories were evaluated for settlement inside 1 km diameter circular polygons centerd at the subsea structures. The full network consists of over 1,000 installations, too many for the optimization method to converge in reasonable time, so we consider a gridded network of 104, 0.5 × 0.5 degree areas (**Figure 4**). Connections and connection weights in the gridded network are accumulated from the connections between all pairs of platforms in each grid cell.

All methods were implemented in python in Jupyter notebooks, an example is included as **Supporting Information**. Graph theory metrics were calculated using the networkX package and results plotted using the matplotlib package.

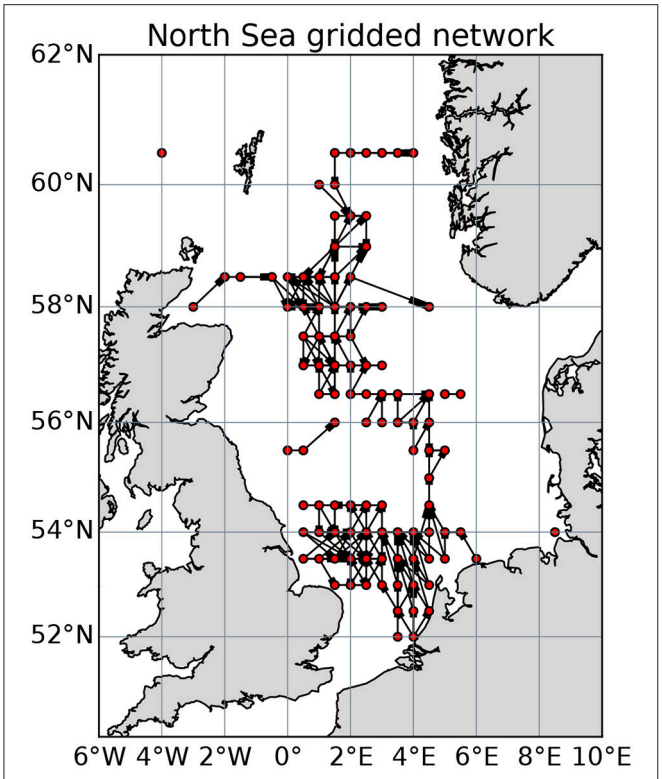


FIGURE 4 | The network of connected North Sea oil and gas installations gridded at 0.5 by 0.5 degrees. Directed connections are thickened in the direction of travel.

3. RESULTS

First we show the multivariate optimization for small networks where we can use brute force to examine all possible networks, and then we test the more efficient search method and using it to examine two larger networks.

3.1. Small Networks—Brute Force

Figure 5 shows the Pareto optimal solutions for the 20-node model network in **Figure 2**. The Pareto front (**Figure 5A**) has a uniform slope (away from the extremes) suggesting no optimal solutions are to be preferred over others (final selection would require a decision maker and stakeholder input). **Figure 5B** shows the make-up of each optimal solution, highlighting which nodes are included. Each optimal solution is built around a core of the best connected nodes, gradually expanding with the addition of nodes as costs are increased, with the poorly connected sites on the edges selected last (maps of all optimal networks are included in **Supporting Information**). **Figure 5C** shows that for each possible network size a single optimal network has been identified, except for single node solutions where none are optimal. The use of at least one optimization function that does not return identical values for any two distinct network configurations ensures the uniqueness of each optimal solution.

The Scottish MPA network uses a node-dependent cost function and also includes larval retention (or "self-loops") in the analysis (**Figure 6**). The Pareto front is less smooth than for the model networks, and the inclusions of a variable cost function produces many more points on the front. We note from **Figure 6A** that firstly, the bulk of the possible networks lie far from the optimal solutions, and secondly, changes in gradient of the Pareto front can be used to identify locally "preferred" optimal solutions, as described in section 2.3. These are the solutions that would be most valued by decision-makers. The structure of four of these preferred optimal subnetworks, are shown in **Figure 7**. The preferred optimal subnetworks are built around a central core of nodes, excluding those on the periphery. This central core of nodes begins with Anton Dohrn Seamount (ADS), East Rockall Bank (ERB), North West Rockall Bank (NWRB), and South East Rockall Bank (SERB) before expanding northeastwards to include Rosemary Bank Seamount (RBS), Darwin Mounds (DM) and Wyville Thomson Ridge. The inclusion of Norwegian Boundary Sediment Plain (NBSP) in these "preferred" solutions is interesting. Even though it is unconnected to the other protected sites it is included because it is low-cost and retains a significant proportion of the larvae it produces, thus adding to overall network resilience. The priority for protection suggested by these "preferred" results is based on a mix of cost and connectivity.

3.2. Larger Networks—Metaheuristic Search

For larger networks we use the metaheuristic search. First we tested this method to recalculate the optimal solutions for the small networks in section 3.1. In all cases the true global optimal solution was reached in much reduced time (results for the 20-node model network are in **Supporting Information**). For the 20-node model networks, the correct solution is reached while examining fewer than 0.005% of the possible solutions. The efficiency savings increase with network size.

The results of the optimal solution search for the 50-node network (**Figure 2B**) are shown in **Figure 8**. The search was ended when no new optimal solutions had been found for 100 iterations, when only 65,000 of a possible 2^{50} solutions had been examined. It is not possible to prove that this is the correct solution, but it passes some simple checks, the set of optimal solutions found is unaffected by the initial random selection.

The set of optimal solutions has features which were not observed in the smaller networks. Most notably, a step change in the structure of the network is visible in **Figure 8B** between Pareto optimal solutions with index numbers 22 and 23, with most of the protected nodes in solution number 22 being unprotected in solution 23. There is a second smaller such step change between solutions index 38 and 39. The full network has two well-connected clusters, one for nodes with $y > 0.4$ and the other for $y < 0.4$. The cluster of sites with smaller y values ("southern" sites) is better connected but smaller – so the smaller optimal networks are selected from these sites. But there is a tipping point at 23 sites, where there are no more southern sites to select. Rather than adding northern sites to the southern network, the whole optimal network switches to the northern cluster (**Figures 9A,B**).

Also observe the change in gradient of the front at 29–30 protected nodes (**Figure 8A**), here the addition of a few more

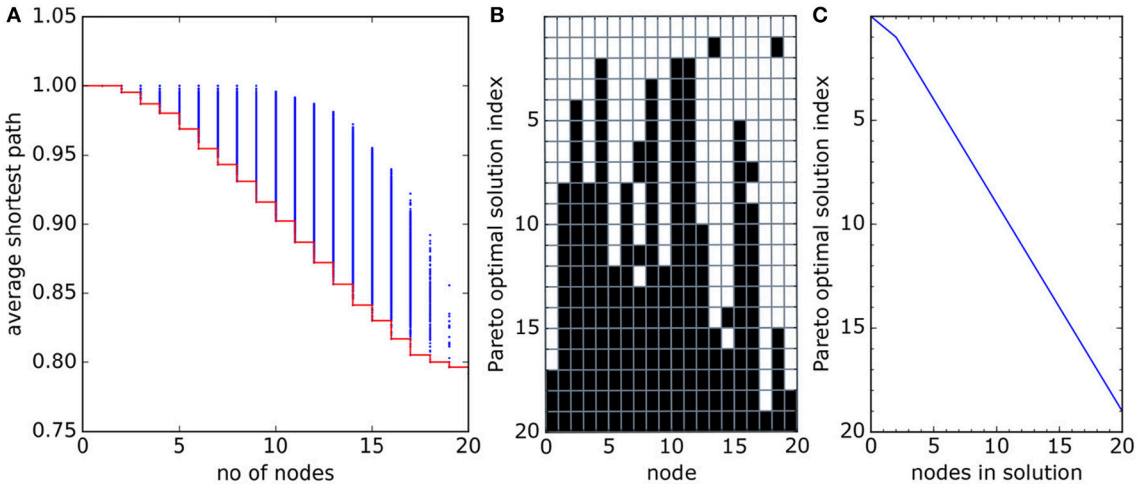


FIGURE 5 | (A) All possible cost/average shortest path function pairs ("solutions," blue dots) for the network in **Figure 2A**. The Pareto optimal solutions lie on the red line. **(B)** Node structure of the Pareto optimal solutions. Each row represents an optimal subnetwork, each column a network node. Black filled squares are nodes included in the optimal subnetwork. The "Pareto optimal solution index" (y-axis) is a numbering of the optimal subnetworks, from smallest (single node) to largest (full network), used in the text to refer to individual solutions. The network sizes are shown in **(C)**. Data for this plot were found by brute force, examining all $2^{20} = 1,048,576$ possible networks.

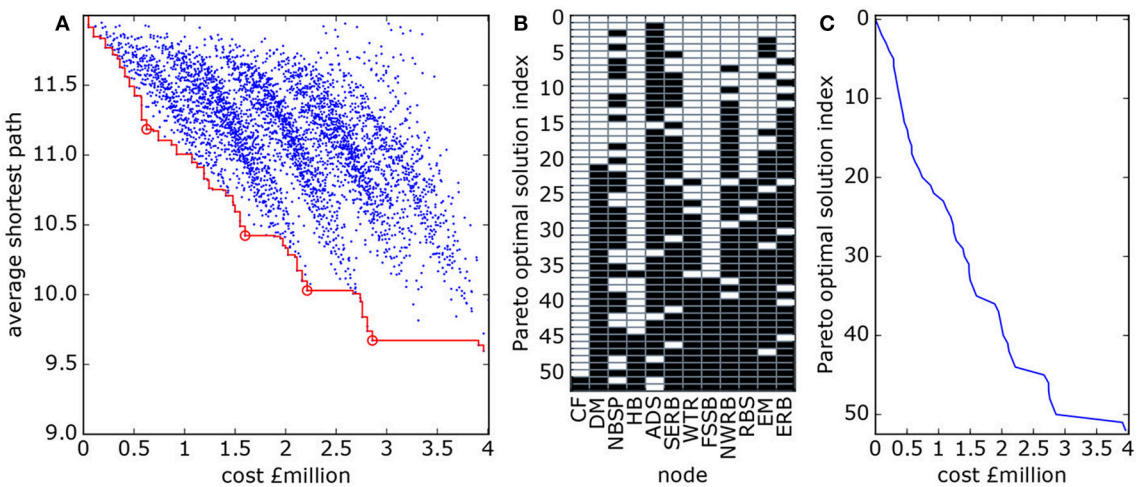


FIGURE 6 | (A) Cost and average shortest path length for all subnetworks of the Scottish MPA network shown in **Figure 3** (blue dots). The red line links the Pareto optimal points. The open circles indicate the locally "better" solutions—lower cost and shorter average shortest path—on the Pareto front. Panels **(B,C)** are the composition **(B)** and cost **(C)** of the Pareto optimal subnetworks as described for **Figure 5**. Site name abbreviations (x-axis in **B**) are listed in **Table 1**.

protected nodes causes relatively little improvement in average shortest path. This occurs as the subnetwork of northern nodes is complete and further network expansion requires inclusion of sites on both sides of the weak connection around $y = 0.4$ (**Figures 9C,D**).

Figure 10 shows results for the real-world network of oil and gas installations in the North Sea (section 2.6.2). A stable set of Pareto optimal solutions here was obtained by examining about 250,000 of the possible 2^{104} solutions.

This real-world set of Pareto optimal solutions contains many of the features described for the model network: a step change in structure (at solution number 45, **Figure 10B**) and locally preferred solutions (convex front around 40 and 75 sites, **Figure 10A**). The step change is again caused by northern and southern networks with poor connections between, the optimal subnetwork doesn't switch fully between clusters with increasing size, but switches from entirely southern sites to a combination of southern and northern sites (**Figure 11**). The preferred solutions at around 40 protected sites (**Figure 10A**) occur just before this step change. The slow-down in average shortest path improvement as more sites are protected after 75 sites occurs because the remaining unprotected sites are poorly-connected peripheral sites.

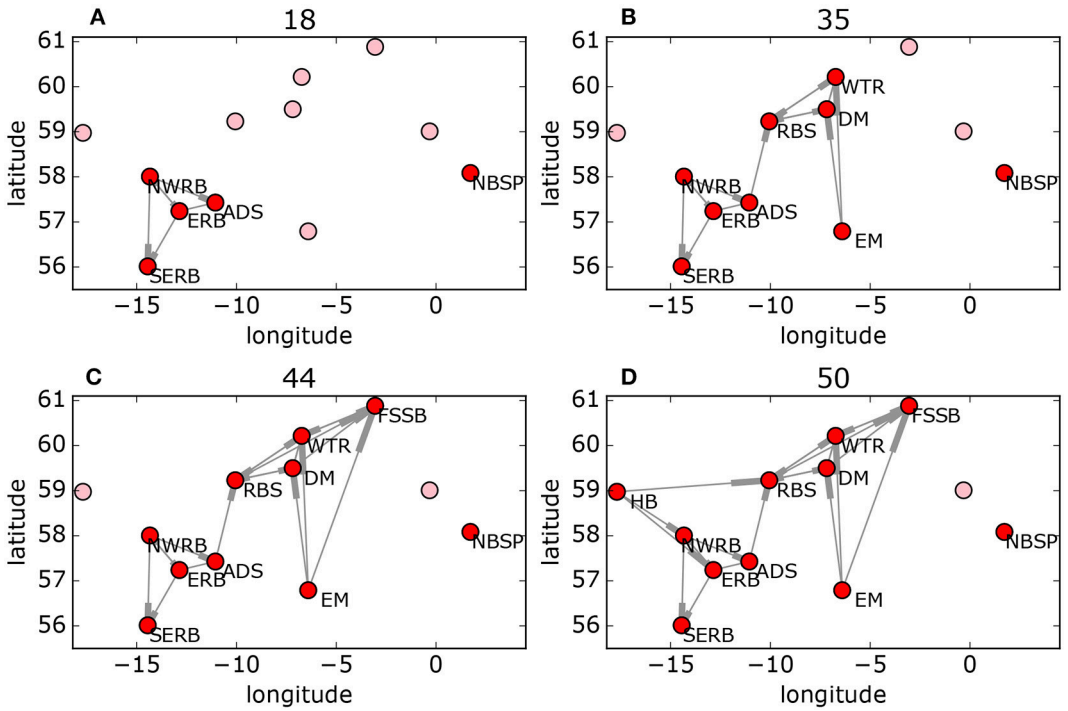


FIGURE 7 | Four of the "preferred" Pareto-optimal solutions (indicated by the circles in **Figure 6A**) for the Scottish MPA network (**Figure 3**) in order of increasing cost **(A–D)**. Red and pink circles show sites included in and excluded from the network, respectively.

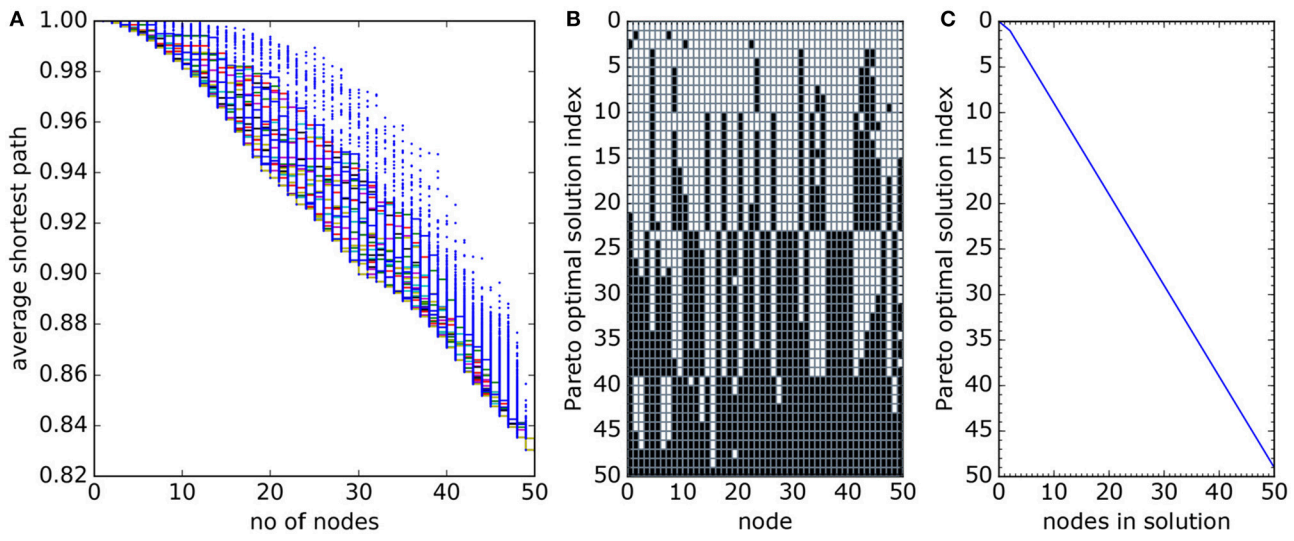


FIGURE 8 | Estimated Pareto front for the 50-node network. **(A)** Successive iterative estimates of the Pareto front (solid colored lines) with blue dots showing computed values of average shortest path for each network. **(B)** The structure of the Pareto optimal solutions and, **(C)** the number of nodes in each Pareto optimal solution. Notice the region of slightly "better" (convex front shape in **A**) solutions around 30 nodes and the sharp changes in structure of the 50-node Pareto optimal solution between solution index numbers 22 and 23, and again between 38 and 39 in panel **(B)**.

4. DISCUSSION

We have demonstrated the effectiveness and advantages of multivariate optimization of the selection of sites in networks of MPAs and man-made structures based on Pareto optimal sets. Such methods allow examination of trade-offs to inform decision-making. As the number of possible network configurations grows very rapidly with

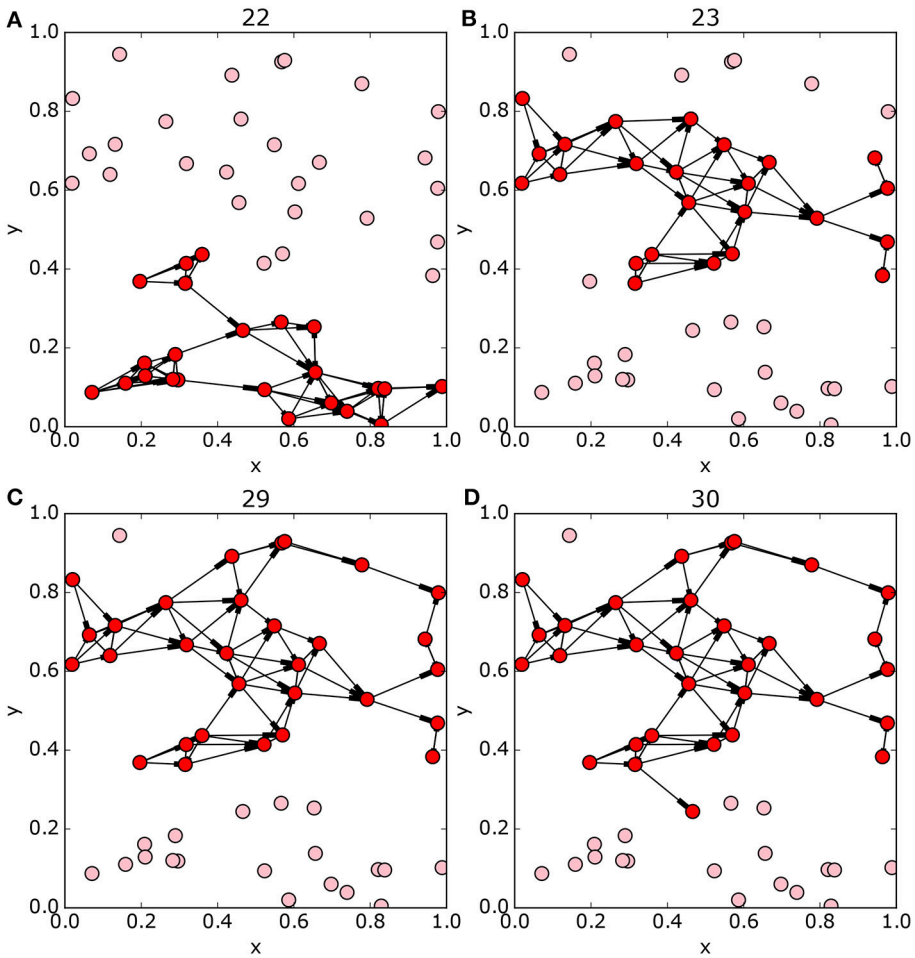


FIGURE 9 | Pareto-optimal subnetworks, bright red nodes are included in the network, light red are excluded. Panels **(A,B)** show the networks either side of the subnetwork structural discontinuity at solution 22 in **Figure 8B**. There is a step change in optimal network structure with the addition of just a single site to the optimal solution, from exclusively "southern" sites ($y < 0.4$) to exclusively on "northern" sites ($y > 0.4$). Panels **(C,D)** show the optimal subnetworks around the change in gradient in the Pareto front at 29 nodes (**Figure 8A**). Subnetworks of more than 30 nodes must include sites from both the "northern" and "southern" groups and the average shortest path improves more slowly.

network size, an efficient method of estimating the set of optimal solutions is required. We take a metaheuristic approach, suited to problems of arbitrary cost function structure, to ensure that we do not limit or constrain the potential cost-functions that may be used to evaluate MPA solutions.

The multivariate optimization locates step changes in the structure of the optimal network for small variations in cost functions. These step changes were not observed in the shape of the Pareto front, but require examination of the optimal subnetwork structure. In theory the optimal subnetwork of $n + 1$ sites may be quite different from that of n sites, the present study demonstrates that this is a common eventuality.

The methods also allow identification of "preferred" optimal solutions, particularly with larger networks and more detailed cost functions. These are solutions where increasing cost (or adding sites) produces minimal increase in benefit, and cost cannot be reduced (more sites unprotected) without a disproportionately large reduction in benefit. This identification of gradients in objective function trade-off space is a clear advantage of the multi-criteria approach.

While the optimization approach is suited to arbitrary cost function structure, the results described are based on a specific pair of objective functions: a simple site-based economic cost function and a connectivity-based function—the average shortest path. These functions were chosen for their relevance to the real-world cases considered, design of networks for protection of long-lived benthic populations where the primary threats are catastrophic anthropogenic damage.

The model and real-world examples presented are based on benthic species with sessile adult phase and at least partially pelagic larval phase. This choice was motivated by problems of conservation and management in the deep sea where this life-cycle is thought to be ubiquitous, although the method is more generally applicable. Deep-sea benthic sediment communities

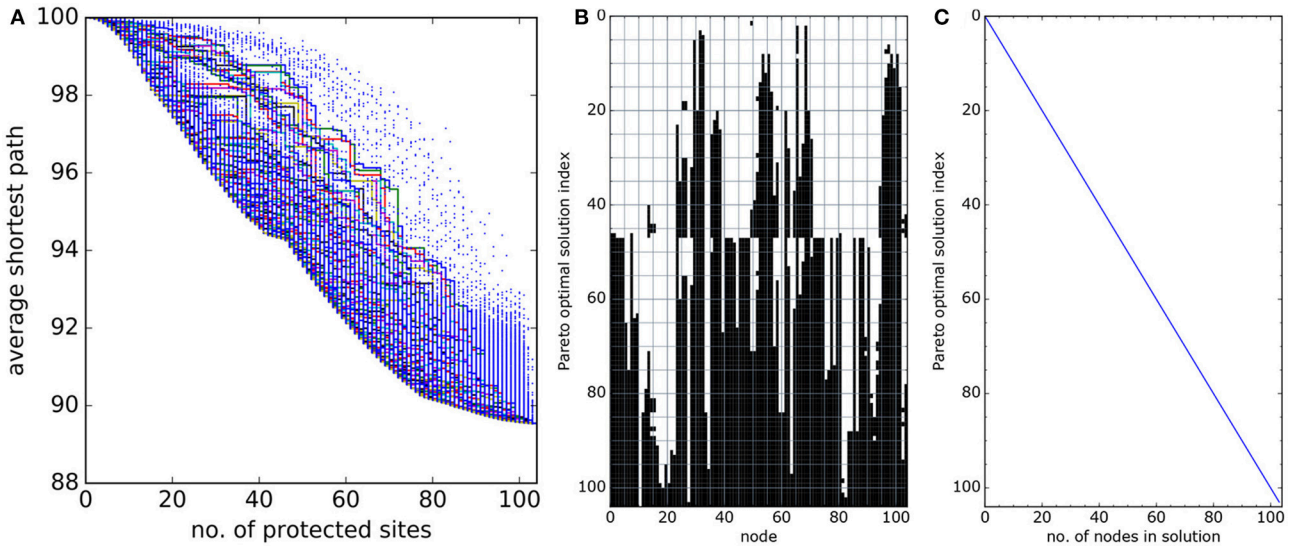


FIGURE 10 | As **Figure 8** for the network of oil and gas installations in the North Sea, **Figure 4**. **(A)** Estimates of the Pareto front. **(B)** The Pareto optimal solutions and, **(C)** the number of nodes in each Pareto optimal solution. The estimate of the Pareto optimal solutions here was found by examining 250, 000 of the possible 2^{104} subnetworks. Notice the step change in Pareto optimal subnetwork structure, visible around solution index 45 to 47 in panel **(B)**. The optimal subnetworks around this index are illustrated in **Figure 11**.

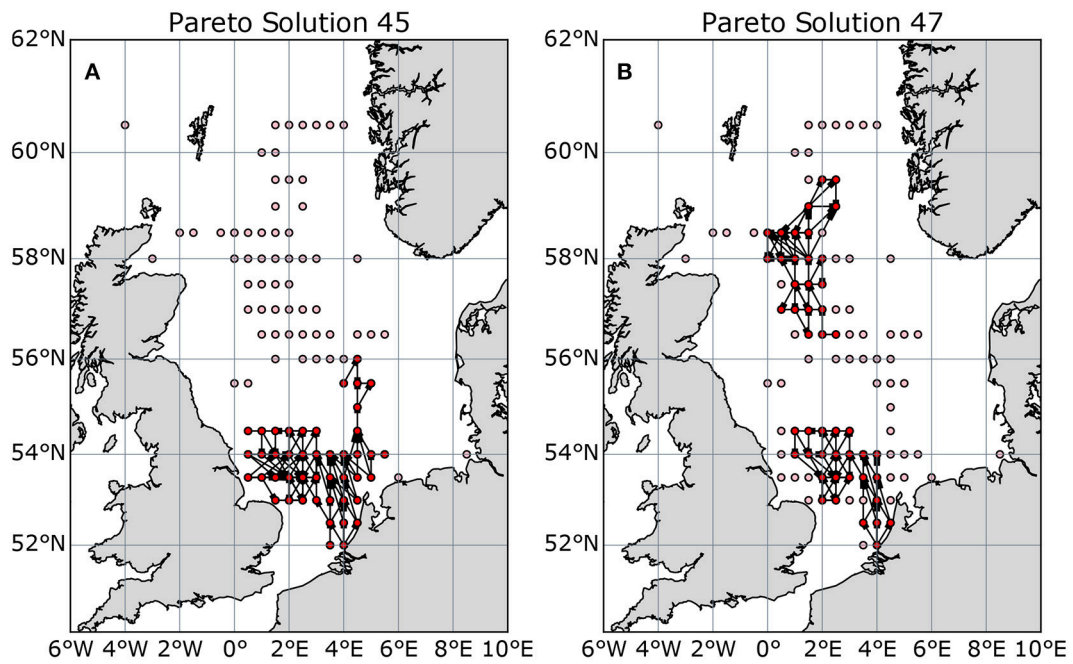


FIGURE 11 | Selected Pareto-optimal subnetworks of the North Sea gridded network, either side of the structural discontinuity at solution 45–47 (45–47 nodes protected) in **Figure 10B**. **(A)** optimal solution with 45 nodes protected; **(B)** 47 nodes protected. Bright red nodes are included in the subnetwork, light red are excluded.

are dominated by polychaetes, crustaceans, molluscs and echinoderms, with cnidarians and sponges dominant on hard substrates (Gage and Tyler, 1991). Young (2003) reviews the knowledge of embryogenesis and larval development of these groups in the deep sea. The most common larval life history pattern in all groups is thought to contain a pelagic phase of some length (Pechenik, 1999), either lecithotropic (not feeding, generally shorter duration) or planktotrophic (feeding, generally longer duration). Bradbury et al. (2008) also reviews data on marine fishes, including deep sea species, where

again the most common life history includes a pelagic larval phase.

The use of average shortest path here as a proxy for network resilience is a simplification of the ecosystem and metapopulation dynamics. However, the results closely support the conclusions of other work based on more detailed metapopulation persistence models. Kininmonth et al. (2011) found that for network persistence, protection needs to prioritize "hubs" or "clusters" with high connectivity. The optimization results of Nilsson Jacobi and Jonsson (2011) suggest a similar strategy, but they imposed an arbitrary limit on the number of sites in each "cluster" to be protected, resulting in a wider distribution of sites in their optimal solution. Hastings and Botsford (2006) show theoretically that only patterns of reproduction and connectivity which eventually lead to descendants returning to the patch from which they originate contribute to persistence. The results from the average shortest path proxy used here support this idea that such "strongly connected" clusters are given priority. The use of a weighted shortest path metric and inclusion of self-connections suggests optimal networks may contain isolated sites where large numbers of larvae are retained.

While these comparisons provide support for the use of average shortest path as a proxy for network persistence, connectivity is only part of metapopulation dynamics, and the aim of conservation planning is to ensure metapopulation persistence across a range of species (Kininmonth et al., 2011). Connectivity data must be used together with other data. Connectivity does not represent habitat quality, diversity of habitat types, and species diversity, among other factors. A focus on high connectivity doesn't necessarily ensure persistence and might decrease resilience if it leads to clumped networks on spatial scales analogous to disturbance scales (Game et al., 2008; Levin and Lubchenco, 2008; Almany et al., 2009).

We also assume throughout that connectivity is constant in time, even though on short timescales stochasticity in connectivity patterns in marine systems is common (Hogan et al., 2012; Fox et al., 2016) and on multi-decadal timescales the circulation of the North Sea could change (Holt et al., 2018). While this constant in time assumption is probably appropriate for the species considered here—benthic species with lifespans that are long compared to the dominant short-term variability of the currents but short compared to the climatic variability of the currents—it may be less valid for short-lived fish species or for connectivity in future climate scenarios.

The current work considers optimization of a network for a single species in isolation, in practice marine conservation is still often based around these individual, often vulnerable, habitat-forming, species (for example the Scottish MPA process above). In such cases, the full, unconstrained, multi-objective optimization approach would provide important information to help guide conservation planning when considered alongside other data and input from stakeholders and planning decision-makers. It must be stressed that the multiobjective optimization and search methods described are completely independent of the choice of objective functions.

Alternative objective functions could be based on meta-population or meta-community models incorporating species-species interactions and many factors determining population persistence, including stochastic effects (Hanski and Gilpin, 1991; Guichard et al., 2004). The major difficulty using these models in multiobjective optimization is the computational load incurred by the need to run the model on many subnetworks.

Additional objective functions can also easily be added to the optimization as Pareto-optimal solutions can be also calculated for more than two functions. The disadvantages are that the front becomes difficult to visualize and many more Pareto optimal points will typically exist, slowing the search. The addition of further functions could be used to extend the method to multiple species (with individual connectivity matrices), or include factors such as network spatial scale, or site-based habitat quality measures. These extensions are beyond the scope of the current work and will be the subject of further studies.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

AF, DC, JR, L-AH, and JP conceived the ideas. AF and DC designed the methodology. JP, CM, and AF produced the connectivity matrices used for the real-world cases. AF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

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frontiers in Marine Science

REVIEW
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Rockall and Hatton: Resolving a Super Wicked Marine Governance Problem in the High Seas of the Northeast Atlantic Ocean

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The Hatton-Rockall plateau in the northeast Atlantic Ocean has long been the subject of interest for fishers, prospectors, conservationists, managers, planners, and politicians. As a feature that straddles national and international waters, it is subject to a multitude of competing and confounding regulations, making the development of a holistic management plan for sustainable use fraught with difficulty. Here, the various stakeholders in the area are collated, together with the rules they have created or must abide by with respect to biodiversity assets, maritime resources, and governance frameworks. Blue Growth envisages optimal use of sea areas, including potential for additional commercial activities. Current research and stakeholder engagement efforts to achieve this integration are described, and the contribution of the EU-funded ATLAS project is analyzed. In particular, more precise, ground-truthed information has the potential to inform systematic conservation planning, providing the basis for sustainable development and improving adaptive management. By scrutinizing and exposing all the elements in this example of a spatially managed area we show how the expectations of each stakeholder can be better managed.

Keywords: Blue Growth, areas beyond national jurisdiction ABNJ, marine spatial planning MSP, ecosystem approach to fisheries management EAFM, ecologically or biologically significant area EBSA

INTRODUCTION

Beyond 200 miles from any coastline, in oceanic areas beyond national jurisdiction (ABNJ), no central authority holds the responsibility for controlling all of the activities that take place there (e.g., fishing, mineral extraction, shipping/communication, environmental protection). Instead, the regulation of each activity is entrusted to activity-specific stakeholders, whose objectives are not always compatible with each other or with long-term sustainability of the ecosystem. Resolution of any conflict between stakeholders is rarely straightforward, and no single solution is beneficial to all involved, often resulting in conflict or compromise, with unforeseen repercussions along a complex web of interacting forces. To further complicate matters, some ecosystems straddle ABNJ and the exclusive economic zone (EEZ) of a State or Union. As problems go, the governance of such straddling ecosystems and the coordinated management of activities that take place within them

(including the enforcement of restricted activities and prohibitions) represents a complex, dynamic, multifaceted and thus, inherently *wicked*[1] problem (Rittel and Webber, 1973). Consequently, there is no panacea to perfect governance of ABNJ (Ringbom and Henrikson, 2017).

As if the governance of ABNJ being a wicked problem wasn't enough of a burden—given the enormous interdependencies, uncertainties, circularities, and conflicting stakeholders implicated by any effort to improve the situation—seemingly definable examples of discrete governance practices in ABNJ can further qualify as *super wicked* problems because of even further exacerbating features that characterize them (Lazarus, 2009). Super wicked problems do not have time on their side, as current levels of resource exploitation are unsustainable; the longer it takes to address the problem, the harder it becomes to resolve it. In addition, those who are in the best position to address the problem (i.e., resource extractors and beneficiaries capable of regulation) are not only those who caused it, but also those with the least immediate incentive to act within that necessary shorter timeframe. Lastly, an absence thus far of an overarching law-making institution with a jurisdictional reach and legal authority that matches the scope of the problem only hinders any expedient regulation or resolution (Wright et al., 2019).

Here we set out to describe an ostensibly discrete example of a super wicked problem: the sustainable governance of an ecosystem that straddles ABNJ and EEZs around the Rockall and Hatton Banks in the northeast Atlantic Ocean [commonly referred to as the Hatton-Rockall plateau (Yiallourides, 2018)]. In doing so, we endeavor to capture both the complementary and the competing initiatives put forward by various stakeholders, authorities and interested parties, to illustrate the complexity of ideas and priorities held by each. By illustrating the interaction between science, policy and stakeholder imperatives, this super wicked problem is, admittedly, no closer to being solved (attesting to the impregnability of super wickedness), but at least the players and their rules, drivers, aims, and strategies can be better understood, which will hopefully allow for the better management of expectations in an effort to promote a sustainable future for all.

BACKGROUND

The Hatton-Rockall plateau (banks and associated slopes) is located midway between Greenland and Iceland to the west and Scotland and Ireland to the east. A submerged mass of continental crust, this seabed feature comprises two large elevated banks, Hatton Bank to the northwest, Rockall Bank to the southeast. They rise from the ocean floor on either side (>2,000 m deep) and are separated by a shallower basin between the two (c. 1,000 m deep). The plateau, delimited by steep-sided flanks in places, narrows as it extends north-eastwards toward the Faroe Islands (**Figure 1**), and the whole feature encompasses diverse offshore bathyal habitats with high habitat heterogeneity between 200 and 3,000 m deep.

The marine climate of the Hatton–Rockall plateau is influenced predominantly by the strength of the North Atlantic subpolar gyre (Hátún et al., 2009). Depending on its strength, the plateau is either bathed in cold subarctic waters (strong gyre) or in warmer and more saline North Atlantic waters (weak gyre). Oscillations between the two regimes have a notable effect on pelagic faunal assemblage composition and biomass on a multi-decadal time scale.

There is a history of dedicated hydrographic, fishery and oceanographic surveys of the area (reviewed by Davies et al., 2006), but with the advent of more sophisticated seabed mapping technologies (e.g., Evans et al., 2015) it has become even more evident that this is a dynamic and productive area of the ocean above a topographically complex seabed. The substrate consists of sedimentary mud and coarse sand punctuated by exposed bedrock, boulders and cobbles, all of which is host to a diverse burrowing and encrusting faunal assemblage that includes long-lived and fragile deep-sea coral gardens and sponge aggregations (Roberts et al., 2008). In places, these species aggregations can be regarded as vulnerable marine ecosystems[2] (VMEs). In addition, recent research (Berndt et al., 2012) has revealed the presence of large-scale geological features known as polygonal faults in the basin between the banks, which result from dewatering of sediments at great depth. There is also evidence that this area may support chemosynthetic species indicative of cold hydrocarbon seeps (Oliver and Drewery, 2014), as well as reduced sediments and bacterial communities (Neat et al., 2018). Given the expanse of the feature, there is likely much more to be discovered.

The Hatton–Rockall plateau has been targeted for resource exploitation, mainly fish, for at least two centuries (Blacker, 1982), although only in the latter half of the twentieth century has this gained political importance due to the feature's potential to confer oil, fishing, and continental shelf rights (Yiallourides, 2018). To date, there is no exploitation of oil and gas in the area, but bottom-fishing has impacted on the local environment (Piñeiro and Bañon, 2001; Durán Muñoz et al., 2011). A cumulative impact assessment encompassing all activities has not been conducted in the region (Gianni et al., 2016). An inventory of ecosystem goods and services around the feature to set the scene for future valuation has only recently been completed (Foley et al., 2018).

The water column overlying the feature also falls under the remit of several international activity-regulating bodies, such as the European Union (EU), the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention), the North-East Atlantic Fisheries Commission (NEAFC), the North Atlantic Salmon Conservation Organization (NASCO), the International Commission for the Conservation of Atlantic Tunas (ICCAT), the North Atlantic Marine Mammal Commission (NAMMCO), and the International Whaling Commission (IWC). Several of these

[1] In this context, the term *wicked* does not carry connotations of evil or maleficence, but instead denotes problems that are tricky, circuitous, or would appear to have a fractal dimension.

[2] VMEs constitute areas containing fragile, unique, rare, long-lived, slow-growing and/or structurally complex species, communities or habitats that may be vulnerable to impacts from fishing activities (FAO, 2009).

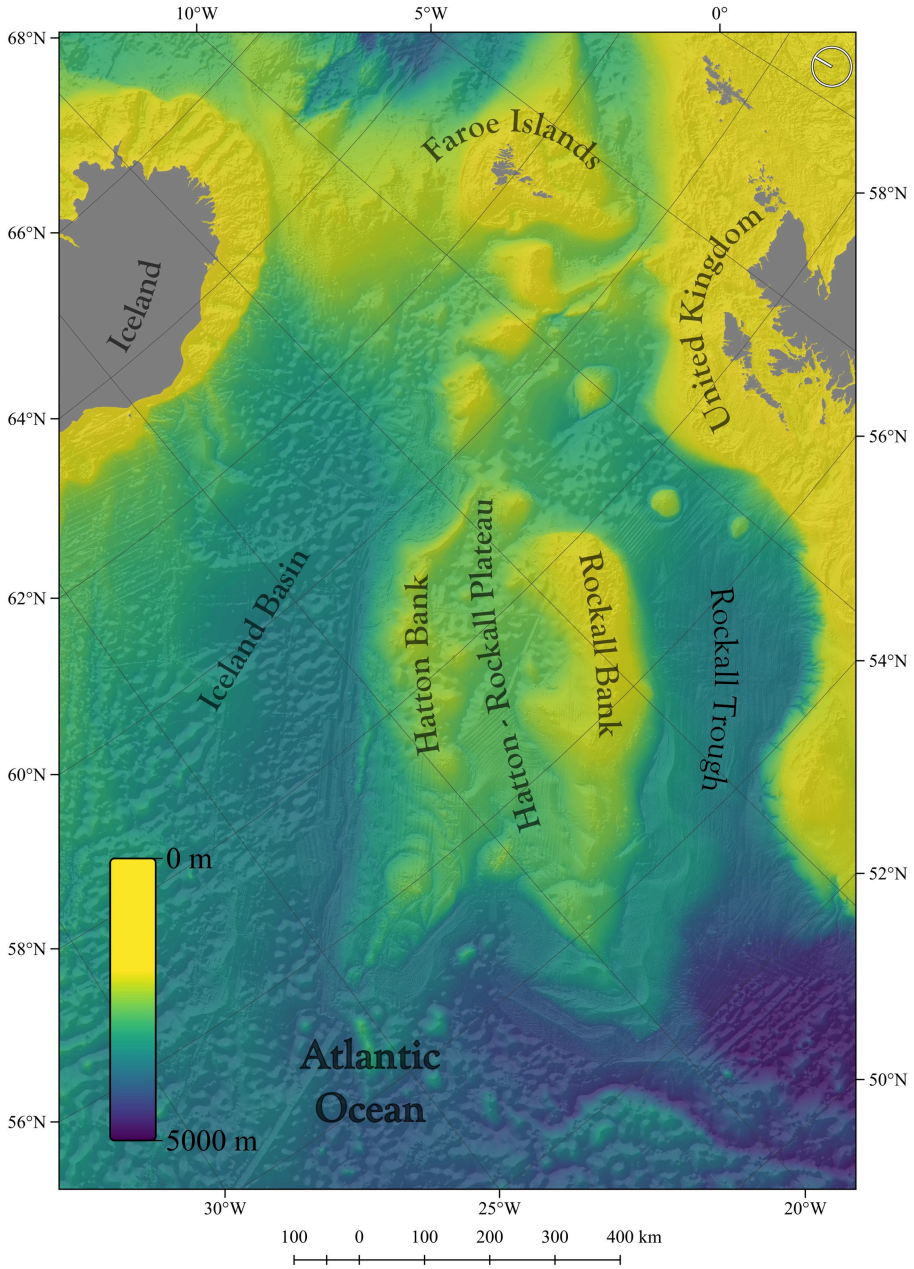


FIGURE 1 | The Hatton-Rockall plateau.

organizations, either alone or in collaboration with others, have identified species, features or areas worthy of protection from potentially harmful activities. For example, three species of deep-water sharks have been identified (*Centroscymnus coelolepis*, *Centrophorus granulosus,* and *C. squamosus*) that are threatened or declining in the region as a consequence of fishing activities (CITES, 2011). All three are also on the IUCN Red List of Threatened Species.

Established area-based environmental protection measures (or area-based management tools—ABMTs) vary in their mandate, from simple recognition of a feature's ecological significance, to the prohibition or exclusion of certain activities from a defined area or time period. For example, under the EU's Bird and Habitat Directives and the UK's equivalent 2007 Offshore Marine Conservation (Natural Habitats, etc.) Regulations, several seabed features around the Hatton-Rockall plateau have been identified and designated as offshore marine protected areas (MPAs); these include the Hatton Bank candidate Special Area of Conservation (SAC), the North West Rockall Bank SAC, and the East Rockall Bank SAC. In addition, the

Hatton Rockall Basin Nature Conservation MPA has been designated under the 2010 Marine (Scotland) Act (JNCC website[3]) (**Figure 2**). Beyond the avoidance of deterioration of feature condition, the precise conservation or management measures that apply to each MPA can vary, although they all fall under the broader aspiration of the EU's Marine Strategy Framework Directive (EC, 2008) to achieve good environmental status (GES) across European waters (ECll, 2017).

In contrast to EC-backed MPAs, NEAFC has recommended and enforced the closure of a number of defined areas to bottom trawling and fishing with static gear for the protection of VMEs—the Hatton-Rockall closures—part of which are examples of other effective conservation measures (OECMs) contributing to Scotland's portfolio of MPAs (ICES, 2013a, 2014, 2015, 2016a, 2017, 2018a). In addition, the Rockall 'haddock box' has been closed to fishing since 2001/2002 to protect pre-recruitment stocks of commercially targeted haddock. To add to the complexity, part of this closure is within national waters and under EU legislation, and the other part is in ABNJ and regulated by NEAFC. These fishery-imposed closures overlap in extent with some of the designated MPAs (**Figure 2**) and their enforcement is monitored closely with the aid of satellite vessel tracking technology (VMS and AIS), with sanctions for deliberate non-compliance. Many of the conservation measures defined by the various regulatory bodies around the Hatton-Rockall plateau, both within and beyond areas of national jurisdiction, are acknowledged and promoted by OSPAR. OSPAR also maintains a register of MPAs in the wider northeast Atlantic Ocean[4], and an expert group (ICG-MPA) gives annual consideration to candidate areas based on emerging lines of evidence.

PRESENT-DAY CONCERNS

At face value it would appear that management and governance of the sea and resources around the Hatton-Rockall plateau is relatively well-organized, integrated and comprehensive. However, to achieve adaptive management, better integration of ecological knowledge, recognition of past mistakes (e.g., destructive fishing), new prospects and evolving management frameworks, and changing stakeholder communities all require continuous and objective re-evaluation.

Biodiversity Assets

Benthic habitats and ecosystems (i.e., cold-water coral formations, rocky reefs, carbonate mounds, polygonal fault systems, sponge aggregations, steep, and gentle sedimented slopes) together with benthic and pelagic organisms (i.e., zooplankton, fish, cetaceans, turtles, and seabirds) are of ecological significance in the area. Many such organisms and ecosystems meet the criteria to feature on the IUCN Red List of Endangered Species and of Ecosystems. Species associations are thought to be particularly important; for example, cold-water coral formations reportedly support over 1,300 species (Roberts et al., 2006; Henry et al., 2013) and their propagules likely provide strong genetic links between Rockall and Hatton populations, with weaker links to those in the wider region (Fox et al., 2016).

Important areas of biodiversity deserving of protection are increasingly being recognized, as predictive data (models, proxies, and analogs) are validated by ground-truthing surveys, and together have enabled the production of large-scale habitat maps (Howell et al., 2009, 2016). The most recent surveys by Marine Scotland (600 km of transects from 150 to 1,000 m using towed video) have contributed to habitat mapping of *Lophelia pertusa* reefs, coral gardens, black corals, sea fans and whips, sponge grounds, sea pen fields, and cold seeps. These sensitive benthic invertebrate species are highly susceptible to physical damage (Hall-Spencer et al., 2002) and have lengthy recovery times. In turn, damaged habitats and ecosystems can adversely affect pelagic fish communities and fisheries (Armstrong and Falk-Petersen, 2008).

Within the Hatton–Rockall plateau cold-water coral species have been severely impacted by the deep-water trawl fishery (Hall-Spencer et al., 2002). In future, these species are also likely to be compromised further by climate change (Roberts and Cairns, 2014; Roberts et al., 2016) and ocean acidification (Perez et al., 2018). A review by Johnson et al. (2018a) considers the expected effect of changing environmental conditions under predicted climate change scenarios on taxa listed in the conservation objectives for Rockall and Hatton VMEs. It concludes that impacts will be felt within the next 20 years at a rate too fast for many species to adapt to, and resilience is already low.

Resource Pressure

Studies of fishing pressure show parts of the northeast Atlantic to be heavily impacted (Halpern et al., 2008; Benn et al., 2010), including, for example, areas of coral rubble and trawl marks on the northern Rockall Bank. The Hatton–Rockall plateau supports relatively shallow demersal fisheries targeting haddock, gurnard and monkfish (Newton et al., 2008; Neat and Campbell, 2011). Haddock has been surveyed since the 1980s, and despite volatile stock dynamics and failure to agree on an international fishery management plan, it is currently a profitable and important fishery; in 2018 it was certified as meeting the Marine Stewardship Council's standard for sustainable fisheries (MSC, 2018). Monkfish and megrim sole both contribute to a highly valuable fishery in the area, and although heavily exploited, data since 2005 suggest both are sustainable (ICES, 2016b). In the past, other important commercial species included saithe and cod, but these appear to have been over-exploited and are no longer main target species. Deep-water bottom fisheries target ling, blue ling, tusk, orange roughy, black scabbardfish, roundnose grenadier and deep-water sharks (Gordon et al., 2003; Large et al., 2013). The EU ban on trawling at depths > 800 m introduced in 2017 has ended these practices within the EU EEZ, but deep-water fisheries in ABNJ are still being undertaken on the Hatton Bank. Deep-water fisheries have impacts not only on target species, which are known to be highly susceptible to over-fishing and cannot sustain fishing intensity typical of shelf

[3]URL: http://jncc.defra.gov.uk/page-4524 (Accessed October 2018)

[4]OSPAR MPA datasheets and access to an MPA map tool can be found at http://mpa.ospar.org/home_ospar/mpa_datasheets

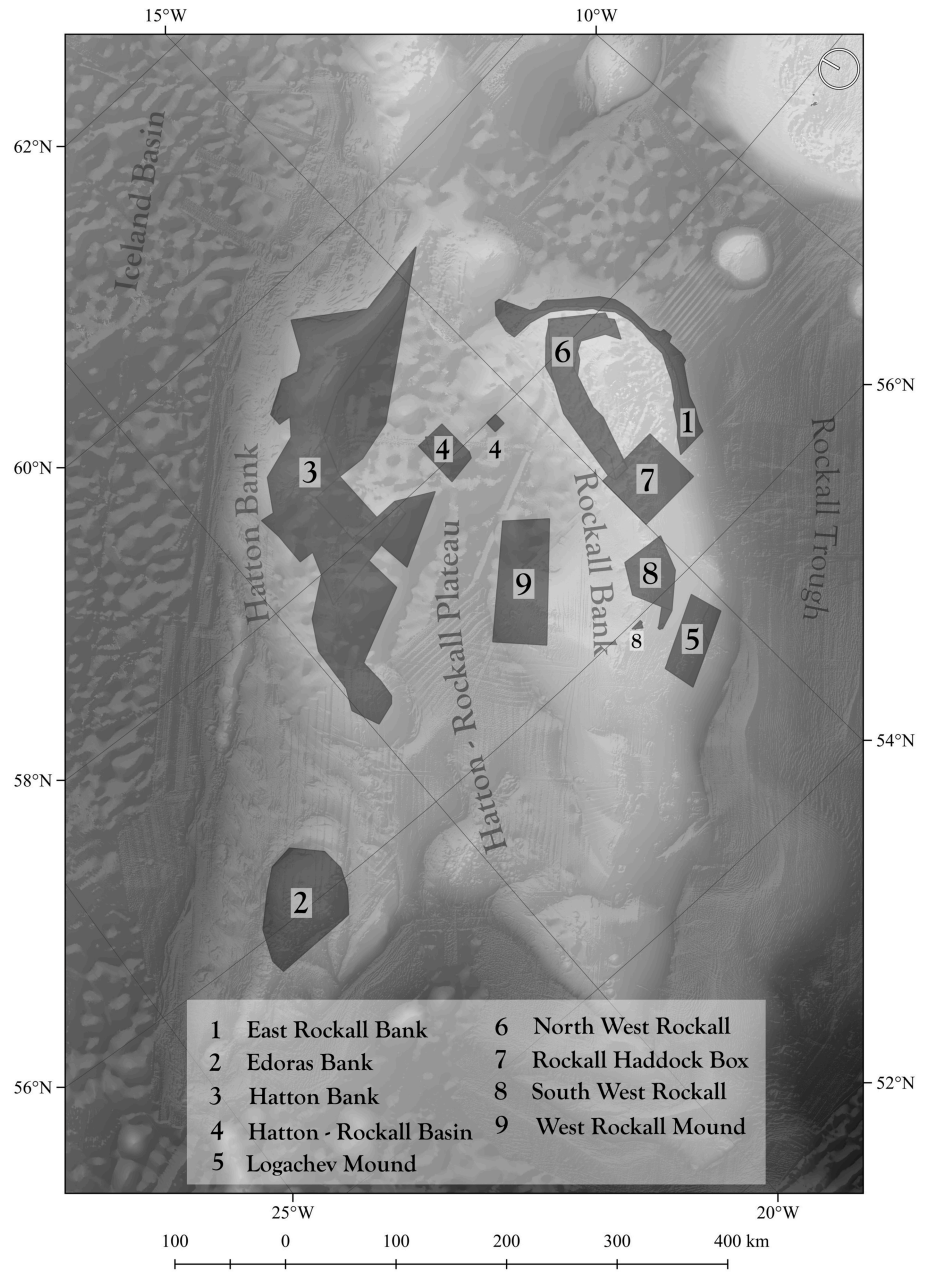


FIGURE 2 | The location of spatial management measures presently in effect at the Hatton–Rockall plateau.

seas (Bailey et al., 2009), but more generally on associated deep-sea fauna that also exhibit extreme longevity and slow growth rates, traits that make them vulnerable to repeated disturbance. International pelagic fisheries also target blue whiting in Hatton and Rockall; here, stocks have undergone periods of concern due to over-exploitation, although in recent years they have been doing well (ICES, 2018b). This is likely partly a result of reaching international agreements in 2006 for blue whiting between the EU, Norway, the Faroe Islands and Iceland, but may also be due to variation in natural environmental cycles, such as the strength of the sub-polar gyre that is known to have a strong effect on blue whiting distribution and stock dynamics (Payne et al., 2012).

Exploration drilling for oil and gas on the Hatton–Rockall plateau has been considered relatively unsuccessful, although a recent reassessment of historical drilling wells in light of an advanced understanding of the region's geology has exposed flaws in the original discouraging conclusions (Schofield et al., 2017). Newly acquired seismic data, combined with a better understanding of results from past explorations, are leading to a resurgence in interest in the area by the UK's oil and gas sector.

Adoption by the European Commission (EC) of a Blue Growth strategy in 2012 (**Box 1**) has resulted in several initiatives related to Europe's oceans, seas and coasts, all intended to facilitate the cooperation between maritime business and public authorities across borders, sectors, and stakeholders (SWD, 2017). While the focus of the strategy is on five sectors with high innovation and growth potential (see **Box 1**), no significant developments or pressure points on resources—especially around the Hatton-Rockall plateau—appear to be close to fruition yet.

Governance Framework

The Hatton-Rockall plateau exemplifies the complex legislative framework that applies to many offshore transboundary situations, incorporating ABNJ, and subject to Commission on the Limits of the Continental Shelf submissions. The need for a tiered (nested), internally consistent and mutually reinforcing planning and decision-making system has been articulated (Raakjaer et al., 2014). As noted by Freestone et al. (2014), such situations also require agreement on overarching principles by regional management bodies, an important element of prospective negotiations within the BBNJ process.[5]

In the northeast Atlantic, OSPAR and NEAFC have signed a formal memorandum of understanding (MoU; the OSPAR Agreement 2008-4) and implemented a Collective Arrangement (OSPAR agreement 2014-09) (Johnson, 2013; Hoydal et al., 2014; NEAFC and OSPAR, 2015). This represents an ongoing trust-building exercise recognizing aspects of common purpose and respecting specific legal mandates.

Despite criticisms of the global pace of implementation of conservation efforts by regional fisheries management organizations and arrangements (RFMO/As) (e.g., Wright et al., 2015), NEAFC is one of the leading RFMO proponents, having closed areas to bottom fishing where there is strong evidence for the presence of VMEs (in line with UNGA resolutions) as part of a comprehensive High Seas fishery regime. For the past decade NEAFC has requested that the International Council for the Exploration of the Sea (ICES) provides scientific advice on the presence and distribution of VMEs within its regulatory area and suggests spatial management approaches (e.g., fishery exclusion zones/boxes around vulnerable features). VME boxes (also known as closed areas or closures) have been established on Hatton Bank, NW Rockall, West Rockall Mounds, SW Rockall, an area known as the Logachev Mounds, and in the Hatton-Rockall Basin. Focus to date has been on the protection of corals and the recently discovered cold-seep ecosystem, yet much of the intensive trawling also occurs on sedimented slopes.

Stakeholders

Wright et al. (2019) highlight that given the status of ABNJ as global commons, the challenge of identifying and consulting relevant stakeholders is significant. For the Hatton–Rockall plateau there has been early recognition of the different stakeholder groups and a good dialogue between the fishing industry and government conservation agencies to assess where to apply spatial management; engagement with the fishing industry was crucial to the establishment of the first fishery closures. The ICES working group on deep-water ecology (ICES WGDEC) that provides the advice on VMEs to NEAFC is unusual in the sense that it includes members from environmental non-governmental organizations (NGOs). Therefore, the process has been stakeholder inclusive from the beginning.

SPATIAL MANAGEMENT AND PROTECTION MEASURES

Fishery Closures

The first example of spatial management at Rockall had little to do with habitat protection. In 2001, NEAFC (and in 2002, the EC in its waters) introduced a transboundary (ABNJ-EU) closed area for the protection of juvenile haddock in response to concerns over declining stock levels and the increased access to the area by international fishing fleets (prior to 1997 Rockall Bank was exclusively within the EU EEZ as part of the UK). Nevertheless, as this 'haddock box' area has remained largely closed for 17 years, it contains some important and relatively untouched benthic habitats.

In the early 2000s concerns were also growing over the impact bottom trawling was having on the cold-water coral reefs known to be in the area. With the emergence of the UNGA resolutions on VMEs (UNGA, 2006), RFMOs were called upon to protect areas where VMEs were known or likely to occur. NEAFC contracted ICES to advise on which areas were likely to contain VMEs. In 2005–6, ICES worked closely with the Scottish and Spanish fishing industries to assess where coral reefs where likely to be present. This, together with scientific survey data (from Spanish and British mapping efforts), provided the basis for several candidate areas for protection. NEAFC closed the first areas on the Rockall and Hatton Banks in 2007.

The NEAFC closures are extensive areas that capture the main distribution of coral on the plateau, although at the time ICES emphasized there was a high degree of uncertainty in the precise delineation of the boundaries. It is worth noting that not all areas proposed by ICES were acted upon by NEAFC. Where evidence for VMEs was less certain, or there were conflicting reports of intensive fishing activity, such areas (e.g., East Rockall) remained open to fishing. In the subsequent years, extensions and modifications to the closure boundaries were made as new evidence came to light on the presence of coral reefs in the area. These included a large seamount to the southwest of Hatton Bank known as Edoras Bank, and an area in the Hatton-Rockall basin where recent scientific surveys detected the presence of a cold-seep ecosystem. By 2015 all those areas where there was strong evidence for VMEs had been closed to bottom fishing (**Figure 2**). It has been a predictable process in many ways, with closed areas being accepted and implemented much more quickly in areas where fishing activity and corals are mutually exclusive of one

[5]The BBNJ process refers to the recent high-level political activities in support of the development of an international legally binding instrument under the United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine Biological diversity of Areas Beyond National Jurisdiction (http://www.un.org/depts/los/biodiversity/prepcom.htm).

BOX 1 | The Blue Growth agenda.

Blue Growth has no universally recognized definition; it embodies different meanings and approaches depending on the social contexts in which it is used (Eikeset et al., 2018). The interpretations presented here are those relevant to the stakeholders in the northeast Atlantic Ocean.

Blue Growth has its roots in the conceptualization of sustainable development, expounded over the years during four landmark international conferences: the 1972 UN Conference on sustainable development in Stockholm, the second such conference in 1992 in Rio de Janeiro, the third in Johannesburg in 2002, and lastly, the Rio+20 UN Conference in 2012. At the Rio+20 conference, the term Green Growth was coined to encompass the concept of fostering economic growth and development while ensuring that natural assets continue to provide the resources and environmental services on which our well-being relies. Translating this concept of growth into the marine realm, the multifaceted economic and social importance of the ocean and inland waters was encapsulated in the term Blue Growth. Since then, concept has been widely used and has become important in aquatic development in many nation states, regionally as well as internationally (Eikeset et al., 2018).

According to the Organization for Economic Co-operation and Development (OECD), Green/Blue Growth is the fostering economic growth and development while ensuring that natural assets continue to provide the resources and environmental services on which our well-being relies (UN, 2012). To the World Bank, the 'blue economy' comprises the range of economic sectors and related policies that together determine whether the use of oceanic resources is sustainable. This concept seeks to promote economic growth, social inclusion, and the preservation or improvement of livelihoods while at the same time ensuring environmental sustainability of the oceans and coastal areas. For the Food and Agricultural Organization, Blue Growth is a cohesive approach for environmentally compatible, integrated and socioeconomically sensitive management of aquatic resources including marine, freshwater and brackish water environments. At the global scale, Blue Growth looks to further harness the potential of oceans, seas and coasts by promoting growth, improving conservation, building sustainable fisheries, fostering cooperation between countries and acting as a catalyst for policy development.

For the European Commission (EC), Blue Growth is an initiative to harness the untapped potential of Europe's oceans, seas and coasts for jobs and growth. Blue Growth is the long-term strategy to support sustainable growth in the marine and maritime sectors as a whole (EC, 2012). It is also the maritime contribution to achieving the goals of the Europe 2020 strategy for smart, sustainable and inclusive growth. Blue Growth is possible in a number of areas which are highlighted within three components of the strategy: (1) sectors that have a high potential for sustainable jobs and growth, (2) components to provide knowledge, legal certainty and security (this includes MSP to ensure efficient and sustainable management of activities at sea), and (3) sea basin strategies to foster cooperation between countries (e.g., the Atlantic Action Plan follows the Atlantic Strategy the EC adopted in 2011). Five sectors have been identified with a high potential for Blue Growth: aquaculture, coastal and maritime tourism (blue tourism), marine biotechnology (blue biotechnology), ocean energy (blue energy), and seabed mining. Fisheries, offshore hydrocarbon production and transportation are not in the EC's Blue Growth agenda (Klinger et al., 2018).

A Technical Study of MSP for Blue Growth (EC, 2018), coordinated by the EU MSP Platform, focussed on developing visions for MSP; investigating current and future potential spatial demands for key maritime sectors and developing indicators. In many ways Blue Growth is becoming a catch-all term to express more holistic management of complex marine social-ecological systems.

another. In areas where overlap occurs between fishing activity and coral, the process has been more protracted, with greater demands for, and scrutiny of, the evidence for the existence of VMEs (e.g., Hall-Spencer et al., 2009).

Data in the VME database for the North Atlantic—set up by ICES WGDEC following FAO (2009) criteria—originally consisted of observed occurrence records for VME indicators (taxa or features). To ensure the advice on new data on VME distribution is based on the best quality data, some understanding was needed on the likelihood of the occurrence of a VME indicator representing an actual VME. Previously, this had been based on expert judgement, meaning that inconsistencies could arise. Therefore, in 2015 and 2016 the ICES WGDEC developed a multi-criteria tool known as the VME weighting algorithm, which assigns a VME index score of High, Medium or Low likelihood of an area containing VME indicators representing a VME. This scoring is based on two main criteria: vulnerability of the indicator (based on scores against the FAO (2009) criteria for identification of VMEs) and taxon abundance data. Confidence in the resulting score is then assigned based on four further criteria: survey method (e.g., trawl vs. ROV), number of surveys to the area, the time range of the surveys undertaken, and the time since the last survey. Detailed results of this application are presented in Morato et al. (2018).

In 2017, the 36th Annual Meeting of NEAFC considered aspects of area management including a review of NEAFC VME closures under NEAFC Recommendation 19:2014, as amended by Recommendation 09:2015 (**Table 1**). The meeting agreed to extend all current VME related bottom fisheries closures to 2022, and to expand the Hatton-Rockall Basin bottom-fishing closure. These decisions were based on ICES advice showing new records of VME indicator habitat (soft-bottomed deep sea sponge aggregations, including a mix of *Pheronema* spp. and *Hyalonema* spp. (stalked sponges) at a depth of c. 1,200 m) (ICES, 2017). An additional concern noted by ICES was the temporal disparity between AIS (vessel position) and VMS (vessel activity) data provided to ICES, which left unresolved will undermine the confidence that can be attributed to its advice.

Marine Protected Areas

At the same time as VMEs were being recognized, moves were afoot by States (UK and Ireland) to establish Special Areas of Conservation and MPAs on the Hatton-Rockall plateau and contribute to the Natura 2000 network (**Figure 2**). However, efforts to secure long-term *in situ* protection of biodiversity in ABNJ have been less successful. OSPAR has obligations to take necessary measures to protect and conserve the ecosystems and biological diversity of its maritime area, and to cooperate in the adoption of other relevant programmes and measures (OSPAR Convention Annex V). The latter include fisheries measures for which OSPAR has no mandate, rather OSPAR is obliged to liaise with relevant fisheries management authorities. Challenges and lessons learned have been cataloged from the OSPAR process of designating the first network of MPAs in the high seas in the period from 2000 to 2012 (O'Leary et al., 2012; Johnson et al.,

TABLE 1 | Summary of the review of NEAFC VME closures (NEAFC, 2017).

Area	Year closed	Basis for closure	New evidence on presence of VME	New evidence on absence of VME	Closure encompass VMEs	Evidence for expanding boundaries	Overlap with existing fishing areas
Hatton Bank	2007-2015	VME element (Bank feature) & VME indicators	Yes	No	Yes	No	Yes
Northwest Rockall	2007	VME habitats & VME indicators	Yes	No	Yes	Yes	Yes
Southwest Rockall (Empress of Britain Bank)	2008	VME habitats & VME indicators	Yes	No	Yes	No	Yes
Southwest Rockall	2013	VME indicators	Yes	No	Yes	No	Yes
Logachev Mounds	2007	VME habitats & VME indicators	Yes	No	Yes	No	Yes
West Rockall Mounds	2007	VME indicators	No	No	Yes	No	Yes
Hatton-Rockall Basin (cold seep)	2015	VME habitats & VME indicators	Yes	No	Yes	No	Yes
Hatton-Rockall Basin (sponge area)	2015	VME habitats & VME indicators	Yes	No	Yes	Yes	Yes

2014; Johnson, 2016). Whilst the Hatton-Rockall plateau was identified in 2007 by a University of York led scoping study as meeting the OSPAR MPA criteria, it was set aside as a candidate MPA in 2008 due to the political complexity of competing and unresolved submissions to the Commission on the Limits of the Continental Shelf (O'Leary et al., 2012).

Other Area-Based Management Tools

The outcome of a workshop convened by OSPAR and NEAFC to describe ecologically or biologically significant marine areas (EBSAs) in the Northeast Atlantic (held in Hyeres, France, 8–9 September 2011) included a proposal for an extensive area incorporating the whole of the Hatton-Rockall plateau approximating to the 3,000 m depth contour as a potential EBSA (see **Appendix** for the ranking of the proposed EBSA against the CBD EBSA criteria). A review of the workshop outcomes by ICES in March 2012 questioned the methodology and size of the EBSAs described. By further request, in 2013 ICES reviewed the EBSA proposals again and came to different conclusions to the original workshop (rankings against EBSA criteria) and proposed boundary revisions (ICES, 2013b). For Rockall and Hatton, ICES specified a more restricted area down to 1,500–1,800 m depth and excluded the abyssal plain, citing lack of evidence of biological or ecological significance at greater depth. For this area, the ICES review only modified one ranking (against the Productivity criterion, from Medium to Low on the basis that "*benthic secondary production in deep-water environments is generally considered to be low compared to other environments*"; ICES, 2013b). Subsequently, however, OSPAR and NEAFC Contracting Parties have failed to agree to submit any revised results to the CBD. Johnson et al. (2018b) provide a commentary on the global CBD EBSA process and recognize instances of evidence gaps with an underlying 'political' cause. With no EBSAs listed in the CBD EBSA Repository covering the northeast Atlantic Ocean, perhaps the whole region could be considered as a politically induced conservation gap, although CBD COP have consistently noted the ongoing process in the northeast Atlantic Ocean.

The EC's Blue Growth strategy recognizes the importance of marine spatial planning (MSP), and it works closely with EU Member States to disseminate practical information on the implementation of MSP, sharing technical briefs, facilitating workshops to foster cooperation, and supporting the exchange of best practices at sea-basin and EU level. An example of a current EC-funded project to inform and refine spatial management plans in the north Atlantic and with a specific focus on the Hatton-Rockall plateau is the ATLAS Project (**Box 2**).

Janßen et al. (2017) critically examine issues associated with integrating fisheries into MSP. They highlight challenges including techniques to analyse where fishers fish, including long-term spatial changes of commercial fish species along their successive life stages, and effects of spatial competition. Spatially explicit solutions for integration of fisheries into MSP have proved elusive and the spatial resolution of ICES statistical rectangles was deemed too coarse to reflect fisheries' requirements for spatial information. Attempts to develop a marine spatial plan for the Rockall Bank are currently underway as part of the ATLAS Project (**Box 2**; Grehan, 2018). By spatially assigning monetary value of fisheries across the area based on VMS and log-book data, the economic value of the fishing footprint can be evaluated and assessed in relation the ecological diversity and sensitivity of the area. Based on spatial overlap and mutually exclusive areas where high value fisheries persist in areas of low or average ecological diversity and sensitivity, it should be possible to develop a mutually agreeable spatial plan that meets both fisheries and conservation priorities.

FUTURE CONSIDERATIONS

ICES have provided advice on, and evaluation of, fishing abrasion pressure maps based on VMS and log-book data. This mapping of spatial and temporal intensity of fishing activities with mobile bottom-contacting gear and pelagic gear (excluding vessels <10–12 m long) appears to show decreasing intensity for Rockall and Hatton. On the basis of this information, there is no justification

BOX 2 | The EU ATLAS Project contribution.

The ATLAS Project (www.eu-atlas.org) started in 2016, with an objective to develop an integrated transatlantic assessment and deep-water ecosystem-based spatial management plan. To achieve this, ATLAS uses the output from the EU FP7 MESMA Project (2009–2013; www.mesma.org) on monitoring and evaluation of spatially managed areas to implement ecosystem-based marine management (Stelzenmüller et al., 2013). ATLAS has compiled existing information and generated new data from 12 case study areas, one of which is the Rockall Bank (see table below). All case study areas include deep-water habitats supporting a variety of VME indicator taxa across a range of jurisdictional regimes in areas where economic Blue Growth activities are either underway or are planned in the near to medium term.

ATLAS case study	Focus ecosystems	Current and BG sectors*	Jurisdiction
1. Love Observatory	CWC reefs, sponges	F, OG, T	Norway
2. W of Shetland & W Scotland slope	Sponge grounds	B, F, OG	UK (EU)
3. Rockall Bank (UK & Ireland)	***CWC reefs, coral gardens, carbonate mounds, sponge grounds, cold seeps***	***B, F, OG***	***UK & Ireland (EU) and ABNJ***
4. Mingulay Reef Complex	CWC reefs	F, T	UK (EU)
5. Porcupine Seabight	CWC reefs, coral gardens, carbonate mounds, sponge grounds	B, F, OG	Ireland (EU)
6. Bay of Biscay	CWC on slope and in canyon settings	B, F	France (EU)
7. Gulf of Cádiz/Strait of Gibraltar/Alborán Sea	CWC reefs, coral gardens, sponge grounds	B, F, OG	Spain & Portugal (EU)
8. Azores	Hydrothermal vents, seamounts, coral gardens, sponge grounds	B, F, M	Portugal (EU) and ABNJ
9. Reykjanes Ridge	Hydrothermal vents, CWC reefs, coral gardens, sponge grounds	B, F, M	Iceland and ABNJ
10. S Davis Strait/Western Greenland/Labrador Sea	CWC reefs, coral gardens, sponge grounds	B, F	Canada
11. Flemish Cap	Coral gardens, sponge grounds	B, F, OG	Canada and ABNJ
12. USA Mid-Atlantic canyons	CWC reefs on slope and in canyon settings	B, F, M, OG	USA and ABNJ

*Blue Growth (BG) sectors: **B**iotechnology, **F**isheries, **M**ining, **O**il & **G**as, **T**ourism.

The ATLAS approach offers a holistic means by which managers and policy makers can begin to grapple with High Seas ocean governance in what is now a rapidly changing ocean. For example, by using the eddy-resolving North Atlantic (30–80°N) basin-scale hydrodynamic model VIKING20 running at 1/20° resolution, ATLAS is able to conduct simulations to predict where larvae produced by VME indicator taxa would disperse under varying conditions, including during times of high and low Atlantic Meridional Overturning Circulation (AMOC) strength. By conducting parallel research using paleo-oceanographic approaches to reconstruct AMOC strength from sortable silt grain size analysis, ATLAS has recently shown that present-day AMOC strength is already exceptionally weak as compared to the last 1,500 years (Thornalley et al., 2018), a discovery mirrored using an approach comparing global sea surface temperature datasets with high-resolution climate modeling approaches (Caesar et al., 2018).

Other ATLAS outputs show substantial differences in modeled connectivity between case study areas, with Rockall Bank predicted as having a somewhat more restricted connectivity compared to other areas. Work is ongoing to ground-truth these predictions with genetic connectivity assessments from samples gathered across the Atlantic Ocean, and to infer the implications of altered AMOC strength on each case study area. These fundamental improvements in our understanding of Atlantic basin scale physical oceanography, allied with improved understanding of ecological connectivity, will be vital not only to design truly ecologically coherent offshore conservation areas but to understand their utility in the future (Roberts et al., 2016; Johnson et al., 2018a).

Spatial management at Rockall Bank is being assessed in the context of maintaining or potentially increasing fisheries productivity without compromising or significantly adversely affecting VME. The potential for hydrocarbon extraction must be considered in the context of both fisheries and the presence of VME. Thus, operational objectives are to: (i) protect areas where VME are known to occur as part of a network of MPAs, (ii) maintain current fisheries at or close to MSY taking into account wider ecosystem impacts, and (iii) assess potential impacts of potential oil and gas developments. It is hoped that analysis of the case study data (including a >15-year time series of fish communities, 600 km of transect imagery, and modeled predictions of species distributions) using marine spatial planning decision support tools will lead to evidence and advice for improved spatial management. This could be taken up in future revisions of Scotland's National Marine Plan, which extends to 200 nautical miles, and in considerations for a future deep-sea nature reserve currently under review in Scotland's Programme for Government.

for the whole of the Hatton-Rockall plateau being an MPA. The whole area fits the EBSA criteria (**Appendix**), but there are still vast areas within it that can been fished without having any major impact on biodiversity or VMEs (Weaver and Johnson, 2012). Furthermore, baseline information can change or be improved over relatively short timescales; this provides a rationale for re-examining key deep-sea areas and bringing new information to the attention of decision-makers quickly before damage is done. Area-based planning has to be responsive and adaptable, and the present situation attests to much improved dialogue and conflation of objectives between fisheries and conservation (see Friedman et al., 2018).

In addition to resolving the spatial demands of conservation and fisheries, future planning for a sustainable blue economy should evaluate synergies and/or tensions between other potential commercial interests (ABPmer, 2016). For example, securing energy supply, emission cuts related to climate change, and targets for renewable energy provision all combine to influence opportunities for investment in oil and gas and increased use of offshore renewable energy resources. The

third UK Offshore Energy Strategic Environmental Assessment (Department of Energy Climate Change, 2016) recognized a continuing and significant role for oil and gas with further seaward rounds of oil and gas licensing on the UK continental shelf. Environmental impacts, impact on existing activities, as well as co-location issues, especially with fish and shellfish farming, and future decommissioning obligations are relevant considerations if oil and gas exploitation were to go ahead within the Hatton-Rockall plateau. Here lessons can be learned from the northern North Sea where the long-term impacts of drill cuttings piles have been studied thanks to repeat industry monitoring (Kingston, 1992; Henry et al., 2017) and recent work has shown how colonies of the cold-water coral *L. pertusa* form ecological networks with potential to connect with adjacent Swedish MPAs (Henry et al., 2018).

Offshore aquaculture, also known as open ocean aquaculture, located in deeper and less sheltered waters in rigid submersible cages, is an emerging approach to mariculture still at a research stage (Troell et al., 2009). This could be relevant to the Hatton-Rockall plateau, with potential impacts on existing commercial fisheries. Upton and Buck (2010) considered that a complex and unpredictable mix of technological, biological and economic factors will determine the future profitability of open ocean aquaculture. Although government may play a role in funding research and pilot projects, large-scale production will likely depend on private investments and innovation. Others consider that a more supportive and streamlined regulatory framework is necessary to create the opportunity and the incentive for industry to invest in such endeavors (Corbin et al., 2017).

Limited evidence of bioprospecting activity around the Hatton-Rockall plateau currently exists. However, the ecosystems present suggest potential for bioresources and possible commercialization of new materials and derivatives (i.e., DNA, RNA, proteins/enzymes, metabolites), particularly from interesting strains of bacteria and sponges. Regulation of marine genetic resources is a core topic for negotiations in the BBNJ Implementing Agreement, and consideration must be given to future biotechnology demands in space that has not been compromised by other activities.

CONCLUSION

The Hatton-Rockall plateau makes an interesting case study and it now has a long enough history of scientific study, resource exploitation and governance arrangements to show what works and what does not (in terms of ABMTs). It also illustrates the complexities of how science, policy and stakeholders can interact. Here we have highlighted the interaction between the availability and quality of data (a scientific issue), the urgency of conservation (a mainly political issue) and the consequences of management (mainly a stakeholder issue). This interaction changes over time and space, so some conservation actions are readily adopted while others never see the light of day (sometimes for good reasons, sometimes not). An additional and increasingly important element for consideration is the implication of climate change, with an increased need for cold refugia and preservation of areas with resilience to predicted environmental changes.

The Hatton–Rockall plateau is an interesting and important feature for many diverse reasons, both ecological, and economic; thus, appropriate and varied management measures should be applied at the correct scale. To date there have been some real conservation success stories for the area, even if actions might not have been as precautionary as some parties may have liked. The EU ATLAS Project is seeking to develop Good Environmental Status (GES; ECll, 2017) criteria for the deep seas and relate these criteria to the area, as advocated by the European Marine Board, who have noted a lack of standards for offshore and deep water, and a harmonized methodology relating to the Marine Strategy Framework Directive (Rogers et al., 2015; EC, 2018). Current thinking is that Blue Growth scenarios will likely demand the intervention of States through the new BBNJ Implementing Agreement to impose an appropriate production-distribution system—i.e., a balance between greater competition (more micro-efficiency) and more value in the economy as a whole (more macro-efficiency) (Tirole, 2017).

Thus, State intervention in the form of a new institutional arrangement with capacity to apply an ecosystem based approach—whilst understanding the implications of changing future conditions, competing demands for ocean space, opportunities for monitoring and enforcement created by developing technologies, and better response to informed societal values—could, after all, provide a super wicked solution.

AUTHOR CONTRIBUTIONS

DEJ originated the concept of this manuscript with its emphasis on ocean governance. DEJ, CBF, and FN contributed equally to the writing of the manuscript, while DVO, DS, MJG, and JMR provided specific detail from recent research efforts.

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SUPPLEMENTARY MATERIAL

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Baseline Assessment of Marine Litter and Microplastic Ingestion by Cold-Water Coral Reef Benthos at the East Mingulay Marine Protected Area (Sea of the Hebrides, Western Scotland)

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The extent of marine litter and microplastic occurrence across ocean biomes and species remains poorly characterised, particularly in remote deep-water ecosystems. The present study in the East Mingulay Special Area of Conservation (a Marine Protected Area in the Sea of the Hebrides, western Scotland) used historic surveys and benthic samples to obtain baseline levels of anthropogenic debris and microparticle ingestion. Most debris identified in the MPA was fisheries-related. A total of 11% of benthic macrofauna from Mingulay Reef Area 1 and Banana Reef had ingested microplastics, with no statistically significant effect of feeding guild, station, or reef, on ingestion rates. However, the ingestion rate was highest at a station located in a topographic hollow along a gentle sloping area with strong variable ocean currents where fine-scale interactions between bathymetry and hydrography may have helped trap and focus microparticles. Raman spectroscopy of microparticles revealed several types of polymers being ingested, tentatively identified as polypropylene (PP), polyurethane (PU), polystyrene (PS), and polyethylene terephthalate (PET). Besides establishing a baseline assessment of marine litter and microparticles in a deep-water setting, the approach demonstrates the utility of using historic data and specimens collected for other purposes to expand the geographic and ecosystem coverage for larger more regional-scale and even basin-wide assessments such as those needed to inform Good Environmental Status in European waters, as called for by the Marine Strategy Framework Directive.

Keywords: marine litter, microplastic, marine strategy framework directive, good environmental status, cold-water corals, Raman spectroscopy

INTRODUCTION

Marine litter is entering the world's oceans at an unprecedented rate at around 4.8 to 12.7 million metric tons each year (Jambeck et al., 2015). The European Commission Decision (2017/848/EU) defined marine litter as, "…any persistent, manufactured or processed solid material discarded, disposed of or abandoned in the marine and coastal environment" (Galgani et al., 2010). These

items include artificial polymer materials such as plastics, rubber, cloths and textiles, paper, processed or worked wood, metal, glass and ceramics. Litter can pose serious threats to human health and safety, impact aesthetics and economies, cause wildlife entanglement, and ingestion, habitat destruction, act as vectors for alien species introduction and bacterial infection, bind chemical pollutants, and can cause vessel damage (Mato et al., 2001; Sheavly and Register, 2007; Rochman et al., 2015). While marine litter has been identified in almost every marine habitat, from coastal areas and continental shelves to the deep sea (Pham et al., 2014), the variability of scale makes management difficult. However, holistic and adaptive management strategies that use robust science to underpin changes in policies and management regimes can be successful at reducing litter input rates (Rochman et al., 2016), e.g., fulmar plastic ingestion has significantly decreased in the North Atlantic gyre over the last 25 years (Van Franeker and Law, 2015).

Today, plastics make up the largest percentage of accumulated marine litter because of the cheap production cost, high robustness, high disposability, low recovery, and persistence in the environment (Rocha-Santos and Duarte, 2015). In the northeast Atlantic alone, plastics make up more than 75% of the reported litter items (Galgani et al., 2013; OSPAR, 2018). Due to the pervasive nature of plastics, the costs of cleanup, and other economic damages, marine litter is now one of the fastest growing threats to world ocean health (European Commission, 2018).

A major concern is the physical mechanical degradation of marine litter, with litter items and plastic polymers being degraded into smaller fragments through exposure to ultraviolet radiation and then biodegrading more when these items become biologically available (Moore, 2008; Cole et al., 2011; Rocha-Santos and Duarte, 2015). As fragment size decreases, litter and plastics become more bioavailable to a wider range of marine organisms (Cózar et al., 2014). At the large end of the degradation size spectrum, *macro-debris* can comprise still recognizable fishing nets, large pieces of Styrofoam, or items that have been lost or discarded from cargo ships. At the smallest end of the spectrum are *nanoparticles*, which are either manufactured as such, or represent the end state of microplastic degradation, completely invisible to the naked eye. *Microparticles* comprise the middle of the size spectrum and include size fractions roughly 2–5 mm in diameter (Galgani et al., 2010; Vince and Stoett, 2018), the most commonly encountered types being microplastics and microfibres.

Primary microplastics are initially <5 mm diameter, while *secondary microplastics* are a result of photodegradation of larger items, generally 2–5 mm in diameter (Rochman et al., 2016). Primary microplastics include "nurdles" or pre-production pellets, microbeads from cosmetics and personal care, and fibres from clothes washed in washing machines (Rocha-Santos and Duarte, 2015), as well as styrene-butadiene rubbers from wearing of car tires. Pre-production nurdles are usually introduced into the environment as a result of accidents during ship transport (Ellison, 2007). Point sources for primary microplastics are also relatively easy to identify (Vince and Stoett, 2018) as these derive from personal products washed down shower and sink drains that empty into water courses. Related to these are microfibres, which arrive in the marine environment from sewage wastewater of washing facilities. The origins of secondary microplastics and fibres cannot be as easily deduced, as they are degraded by products of any source microparticles introduced into the oceans (Andrady, 2011), but these usually originate on the sea surface or close to shore where the presence of sunlight readily deteriorates them (Cole et al., 2011).

While the issue of marine litter and plastics has come into public view with greater intensity over the last decade (Jefferson et al., 2014), conclusive evidence as to the extent of the issue is still lacking. For example, until recently, the perception of the deep-sea biome was that it is free from harm (Roberts, 2003; Pahl et al., 2017). But with litter, including plastics, now being reported in some of Earth's most remote and deep ocean environments in the Southern Ocean, Arctic Ocean, the Atlantic, Pacific, and Mediterranean Sea (Van Cauwenberghe et al., 2013; Bergmann et al., 2017; Courtene-Jones et al., 2017a; Jamieson et al., 2017), it is likely that few, if any, deep or open-ocean areas are unimpacted by anthropogenic debris to some extent (Chiba et al., 2018). The topographic and hydrographic complexity of some deep marine ecosystems could act in synergy to essentially funnel and accumulate marine litter and microplastics (Jamieson et al., 2017). Not all litter and plastics remain buoyant in surface waters, with a report of microplastics being four times higher in the deep sea than in overlying waters (Woodall et al., 2014). Degradation, predation, and biofouling can remove these items from the surface and draw them down deeper into the water column and seafloor (Cózar et al., 2014). For example, microplastic abundance in Arctic deep-sea fauna was positively correlated with chlorophyll-a content of surface waters, which suggested particles were vertically transported through incorporation with ice-algal aggregates that caused plastics to sink (Bergmann et al., 2017). The ecological niches of some deep-water fauna, such as sessile invertebrates that filter-feed particles drawn from the water column, may therefore make these taxa inherently even more susceptible to litter and plastic ingestion. However, we lack even baseline assessments from which to gauge the effectiveness of changes in policies or management regimes that aim to reduce litter input rates and minimise risks to deep-water ecosystems and fauna.

Ecological impacts of microparticle ingestion on deep-water fauna have not been studied, but these could pose significant problems to individuals that may then scale up to whole ecosystem effects. Studies from shallow-water ecosystems show that ingestion may block an animal's digestive tract and cause internal injuries; it may result in diminished feeding stimuli, reduced growth rates, and lower rates of development and reproduction (Galgani et al., 2010; Wright et al., 2013). While microparticles specifically have been identified in every trophic level across many ecosystems (Rochman et al., 2015), an organism's feeding strategy can make some taxa more susceptible to ingesting microparticles than others (Cole et al., 2013). For example, microparticle ingestions could be higher in taxa that draw particles non-selectively from the water column before possibly size-selecting and finally assimilating them into their guts. Microparticle ingestion has been shown to vary across deep-sea feeding guilds, and these can vary within species

(Taylor et al., 2016; Courtene-Jones et al., 2017a). If particular taxa are disproportionately impacted, microparticle ingestion could stand to significantly alter ecosystem functioning and integrity. Some deep-water ecosystems, such as sponge grounds, seamounts, cold-water coral reefs, and gardens, are biodiversity hotspots of filter and suspension feeders, including the ecosystem engineering sponges and corals themselves (Cathalot et al., 2015). The hydraulic mechanisms by which high quality food is transported to these seafloor ecosystems could also import marine litter (Davies et al., 2009).

Unlike food supply to the deep seafloor, litter enters the marine environment from terrestrial sources and often, inputs by vessels. These reach deep-water masses and the seafloor through ocean currents and offshore winds, but also through biofilm accumulation and biofouling organisms that make litter negatively buoyant, which then sinks to the seafloor (Lobelle and Cunliffe, 2011; Cózar et al., 2014; Chapron et al., 2018). At the seafloor, regional and local bathymetry contribute significantly to the spread and topographic focusing of litter in the deep ocean (Barnes et al., 2009; Tubau et al., 2015; Jamieson et al., 2017), with high accumulation rates occurring in steeply-sided canyons and trenches. Without extreme topography, regional and local hydrodynamics can also affect rates of litter transfer and accumulation, exporting litter from onshore to offshore environments, including the deep sea (Tubau et al., 2015).

Continental shelf zones are often thought to have lower incidences of litter (Galgani et al., 2010; Pham et al., 2014) because most large items originating on the coasts are transferred, assumed to be exported by surface winds and currents to offshore environments beyond the shelf zone (Galgani et al., 2010). However, litter on Earth's continental shelves is still under-reported relative to the coasts (Woodall et al., 2014; Chapron et al., 2018). Furthermore, the density of three-dimensionally complex deep-water ecosystems, such as cold-water coral reefs, are particularly high on continental shelves around the globe (Roberts et al., 2006). These ecosystems help draw surface waters down in phenomena that may be related to local tidal downwelling (Davies et al., 2009), and fine-scale interactions with permeable living objects such as coral heads and mounds baffle sediments and locally reduce current speeds (Huvenne et al., 2009) enough to maximize particle capture rates by the underlying feeding corals and associated fauna (Roberts et al., 2009). Therefore, a straightforward prediction is that cold-water coral reefs on the continental shelf that harbour high diversity and abundances of filter and suspension feeders, and which can topographically focus matter from the surface to the seafloor, are highly likely to have marine litter and show evidence for microparticle ingestion.

The European Union (EU) developed the Marine Strategy Framework Directive (MSFD) in 2008 (Marine Strategy Framework Directive (MSFD), 2008/56/EC) as part of an adaptive management approach to protect and preserve marine resources throughout the EU. The MSFD aims to encourage Member States to ensure and promote Good Environmental Status (GES) of the marine environment by 2020. Under Article 3 of the MSFD, GES is "the environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are clean, healthy and productive". Under the MSFD, Member States are to apply criteria and indicators to assess GES across 11 Descriptors, including Descriptor 10: Marine Litter, ensuring an interdisciplinary approach to conserving and protecting the marine realm (Borja et al., 2010). The MSFD also calls for consistent and standardised monitoring methods and assessment of European seas, which may be scaled down to regional seas and sub-regional seas, i.e., the Baltic Sea, North East Atlantic Ocean, Mediterranean Sea, and Black Sea (Commission Decision, 2017/848/EU).

While the Mediterranean Sea and the North East Atlantic GES assessment regions support many cold-water coral reefs and gardens on their continental shelves, no deep-water indicators have been established for Descriptor 10. Thus, baseline assessments for these ecosystems, which cover a large number of the assessment areas and a disproportionate amount of deep-sea biodiversity (up to three times higher than non-coral areas, *sensu* Henry and Roberts, 2007), are missing from regional GES assessments. Therefore, GES assessments risk over-extrapolating the scale of monitoring to the assessment objective: Descriptor 10 (as with all other Descriptors) are only measured in certain spatial assessment units, primarily shallow water areas. These assessments are then used to allude to the status of the entire water body, including deep-water areas, and thus, the measurement truly only reflected that particular site, ecosystem, or region (Borja et al., 2010).

In the United Kingdom, the definition of GES was developed in consultation with UK government and advisors, including the Centre for Environment, Fisheries and Aquaculture Science and the Joint Nature Conservation Committee (HM Government, 2012); participation in Scotland was driven by government and non-governmental organizations, including Marine Scotland, the Scottish Coastal Forum, Crown Estate Scotland, the Marine Conservation Society, Fidra, Zero Waste Scotland, and others (Scottish Government, 2018). Currently, the only Descriptor 10 assessment for the UK is comprised of systematic beach surveys conducted by Marine Conservation Society (HM Government, 2012). Surveillance and monitoring targets of litter on the seafloor and in the water column are not yet established because baseline levels cannot be deduced (HM Government, 2015).

The purpose of the present study was to establish baseline levels of marine litter and microparticles for a deep-water setting on an area of Scotland's continental shelf that is characterised by topographical and hydrographic complexity and cold-water coral reef ecosystems densely populated by diverse feeding guilds. The study hypothesised that suspension feeders have a higher number of ingested microparticles than other feeding guilds and that specimens from hollow topographic areas have a higher number of particles compared to elevated areas. The study also provided the opportunity to demonstrate the value of using historic data and samples collected for other purposes (the "collect once, use many times principle"), from which one can obtain baseline values for marine litter and D10 in areas traditionally under-represented in GES assessments, such as deep-sea habitats (Miyake et al., 2011; Pham et al., 2014).

METHODS

Study Area: the East Mingulay Marine Protected Area

The East Mingulay Special Area of Conservation is a Marine Protected Area (MPA) located 13 km to the east of the now uninhabited island of Mingulay in the Sea of Hebrides, off western Scotland. This MPA represents the only known inshore occurrence of reefs formed by the protected species of scleractinian cold-water coral, *Lophelia pertusa* (Roberts et al., 2005). The Mingulay Reef Complex (MRC) was first mapped in 2003 (Roberts et al., 2005), and is made up of five bedrock ridges consisting of extensive *Lophelia* coverage forming reef mounds up to 5 m high, surrounded by aprons of coral rubble and shelly hash (Roberts et al., 2009). Reefs support a high biodiversity of fauna, including a biologically rich filter- and suspension feeding communities (Henry et al., 2010, 2013; Kazanidis and Witte, 2016; Kazanidis et al., 2016). Geochronology of vibrocore samples across some of these mounds demonstrate a Holocene coral occurrence, with *Lophelia* occurring periodically since at least 7,000 years ago (Douarin et al., 2013, 2014).

Potential sources of marine litter for the reef complex include litter introduced by fisheries and items originating from coastal communities that are transferred offshore. A zoned fisheries management regime is in place to protect the reefs from anthropogenic damage (Scottish Government, 2014), with all types of mobile fishing gear and some types of static gear prohibited year-round. Yet the footprint of historic fisheries operations could still be potential sources of marine litter, as would be today's *Nephrops* fisheries that continue to operate in adjacent areas. Although nearest to the uninhabited island of Mingulay, marine litter disposal from nearby inhabited islands of the Inner and Outer Hebrides could be exported from the coast to the offshore environment. Besides local fisheries and coastal communities, a third possible route for litter in the Sea of the Hebrides would originate in the open Atlantic (Lusher et al., 2014). The reef complex is supplied by ocean currents that develop as a result of the subpolar and subtropical North Atlantic gyres (Davies et al., 2009), which can collect marine litter and distribute these items globally (Law et al., 2010; Reisser et al., 2015).

Because much of the coral ecosystem's food supply is derived from diurnal tidal exchanges from the surface to the seafloor, (Davies et al., 2009), litter and microplastics from local fisheries, coastal communities, and the open Atlantic could, in theory, be rapidly downwelled from the sea surface to the reefs in under 20 min. The fine-scale and permeable morphology of the coral heads themselves can act to slow down and trap particles in the water column through sediment baffling (Huvenne et al., 2009). This mechanism not only adapts the corals to their ecosystems but could also increase ingestion of microplastics by cold-water coral reef organisms. A broad spectrum of feeding guilds is represented at the MRC; suspension feeders, filter feeders, deposit feeders, grazers, omnivores, and predators (Henry et al., 2013). The shallower, westernmost areas are located closer to the inhabited islands of Barra and Benbecula, and experience, on average, stronger currents than those in the east (Navas et al., 2014). Western sites are also characterized by higher numbers of species inhabiting the reefs (Henry et al., 2010), with higher proportions of filter and suspension feeders than in the deeper more remote eastern sites (Henry et al., 2013). Thus, not only was it expected that litter and microplastics would be found in the East Mingulay MPA, but that the frequency of occurrence would vary across the reef complex and between feeding guilds.

TABLE 1 | List of historic research cruises for which the systematic review of marine litter was conducted for the East Mingulay MPA.

Research vessel	Sampling gear	Date	Reefs surveyed
RV *Lough Foyle*	Van Veen	28 June–5 July 2003	Mingulay areas 1, 2, 3, 4, 5(N), 5(S), and Banana Reef
MY *Esperanza*	Video grab	11–20 May 2005	Mingulay area 1 and Mingulay area 5(N)
RRS *Discovery*	Video grab	26 June–4 July 2009	Mingulay area 1 and Banana Reef
RV *Calanus*	Video grab	22–24 February 2010	Mingulay area 1
RV *Calanus*	Video grab	3–6 May 2010	Mingulay area 1
RRS *Discovery*	Video grab	6 June–12 July 2011	Mingulay area 1
RRS *James Cook*	ROV	18 May–15 June 2012	Mingulay area 1 and Banana Reef

Use of Historic Surveys to Assess Marine Litter

Past underwater camera and remotely operated vehicle (ROV) surveys of the MRC were used to overcome the absence of marine litter monitoring deep on Scotland's continental shelf (the exception being offshore private sector data from post-debris field surveys). Cruise reports from several research surveys conducted between 2003 and 2012 were systematically reviewed to identify, categorize, and map marine litter occurrences (**Table 1**).

Two of these past research cruises also collected video, which was also systematically reviewed in case litter items were missed in the original cruise reports. In 2003, footage collected by a Van Veen grab equipped with video were obtained to assess biotope types (Roberts et al., 2005). For the present study, approximately 60 min of video from 56 stations were reviewed on Windows Media Player for evidence of litter (**Table 2**). In 2012, video footage collected by the Irish Marine Institute's *Holland-I* ROV was originally collected to assess fish communities on the MRC (Milligan et al., 2016) and to locate deep-sea shark nursery grounds (Henry et al., 2013). For the present study, 34 h of *Holland-I* ROV footage from 10 dive transects from the Mingulay 1 reef were reviewed in Windows Media Player to assess marine litter (see **Supplementary Material S1**).

In an effort to standardise the reporting of litter, the United Nations Environment Program/Intergovernmental Oceanographic Commission (UNEP-IOC) Guidelines on Survey and Monitoring of Marine Litter were adopted (see

TABLE 2 | Video grab stations and selected species for the assessment of microparticles at the East Mingulay MPA where *n* equals the amounts of specimens dissected.

Station	Reef	Number of specimens	Latitude (DDM)	Longitude (DDM)	Depth (m)	Species (*n*)
1485	Mingulay 1	25	56.823 N	−7.3905 W	127	*Parazoanthus anguicomus (4), Emarginula fissura (3), Serpula vermicularis (5), Hiatella arctica (5), Eunice norvegica (3), Ophiactis balli (5)*
1487	Banana	21	56.8039 N	−7.4456 W	138	*Parazoanthus anguicomus (4), Eunice norvegica (1), Ophiactis balli (3), Serpula vermicularis (3), Modiolula phaseolina (5), Hiatella arctica (5)*
1490	Banana	25	56.8015 N	−7.4533 W	165	*Parazoanthus anguicomus (5), Emarginula fissura (5), Eunice norvegica (5), Serpula vermicularis (5), Ophiura ophiura (5)*
1491	Mingulay 1	23	56.8202 N	−7.3928 W	108	*Parazoanthus anguicomus (5), Ophiura ophiura (5), Serpula vermicularis (1), Emarginula fissura (2), Hiatella arctica (5), Modiolula phaseolina (5)*
1495	Mingulay 1	18	56.8232 N	−7.3955 W	134	*Modiolula phaseolina (5), Ophiactis balli (5), Emarginula fissura (3), Eunice norvegica (5)*

Supplementary Material S2), in which items within each litter category were counted (Cheshire et al., 2009).

Use of Historic Samples for Microparticle Assessments

Harmonised protocols for microparticle assessments in benthos are needed to facilitate comparison across ecosystems (Miller et al., 2017). Therefore, the present study adapted methods developed by Courtene-Jones et al. (2017a) in the adjacent deep-sea Rockall Trough to assess microparticles in historic benthic samples collected from cold-water coral ecosystems at the MRC.

Benthic faunal samples were originally collected by video-assisted benthic grabs in 2009 during the RRS *Discovery* cruise 340b in June and July (Inall, 2009). Samples were sieved on board over a 1 mm mesh and washed with seawater, preserved in buffered 4% formalin, and then transferred to a 70% industrial methylated solution (IMS) for long-term storage. For the present study, 112 specimens already sorted and identified to species level were selected from across five stations on the MRC (**Table 2**). Station selection ensured a spatial gradient in environmental settings between Banana Reef (located closer to the nearest island) and Mingulay Reef 1 (further from the inhabited islands). All selected taxa were known to be abundant at the MRC (Henry et al., 2010, 2013; Kazanidis and Witte, 2016; Kazanidis et al., 2016), making them useful indicator taxa for the future assessment of microparticles. Taxa included suspension feeders: the zoanthid *Parazoanthus anguicomus* Norman, 1869 and the tubiculous polychaete *Serpula vermicularis* Linnaeus, 1767, filter feeders: the bivalves *Hiatella arctica* Linnaeus, 1767 and *Modiolula phaseolina* Philippi, 1844, a deposit feeder: the limpet *Emarginula fissura* Linnaeus, 1758, omnivores: the ophiuroids *Ophiactis balli* Thompson, 1840 and *Ophiura ophiura* Linnaeus, 1758, and a predator and important symbiont with *Lophelia pertusa*: the carnivorous polychaete *Eunice norvegica* Linnaeus, 1767 (**Figure 1**).

Following a protocol developed by Courtene-Jones et al. (2017b), an enzymatic 30% StableCell™ Trypsin and deionized water solution was chosen to dissociate organic material from the benthic specimens from any synthetic microparticle polymers. It is unlikely that trypsin would enzymatically degrade the robust synthetic polymers and rubbers to a significant extent under these conditions. However, due to the specimens being fixed in formalin and preserved in IMS for nine years, initial trials showed incomplete digestion even after 24 h. To aid digestion and to ensure any microparticles had been ingested and not artificially introduced during reef sampling and processing, the gut cavity of each specimen was dissected and digested instead. Guts were placed in the trypsin/deionized solution in a 50 mL covered glass jar and placed in a water bath of 38–42°C to digest for 25 min (Courtene-Jones et al., 2017a). All contents were then strained through a 0.075 mm metal gauze to separate biological material from potential non-biological materials (microparticles). The gauze was rinsed with deionised water into a glass petri dish and the contents were analysed and photographed under a Zeiss SteREO Discovery V20 stereomicroscope. Microparticles were stored in 20 ml glass vials for Raman spectroscopy analyses to identify potential microplastic candidates.

Microparticle Laboratory Quality Assurance and Quality Control (QA/QC)

Further to digesting only the animal's digestive system, additional precautionary measures were taken to ensure processing in the laboratory did not artificially introduce microparticles into the samples (Woodall et al., 2015). Clothing and laboratory coats were 100% cotton for the duration of the study. The microscope cover was used whenever the microscope was not in use, and gloves were always worn (Torre et al., 2016). The lab area was cleaned with an IMS solution three times prior to beginning any analysis. All glassware and tools were triple rinsed with deionised water (Courtene-Jones et al., 2017a). A control petri dish with damp filter paper was placed on the lab bench and analysed at the end of the study to identify any potential air contamination (Courtene-Jones et al., 2017a). Protocols to ensure a clean laboratory environment are more effective than excluding certain microparticles in analysis (Torre et al., 2016). Therefore, no particles were excluded in the analysis.

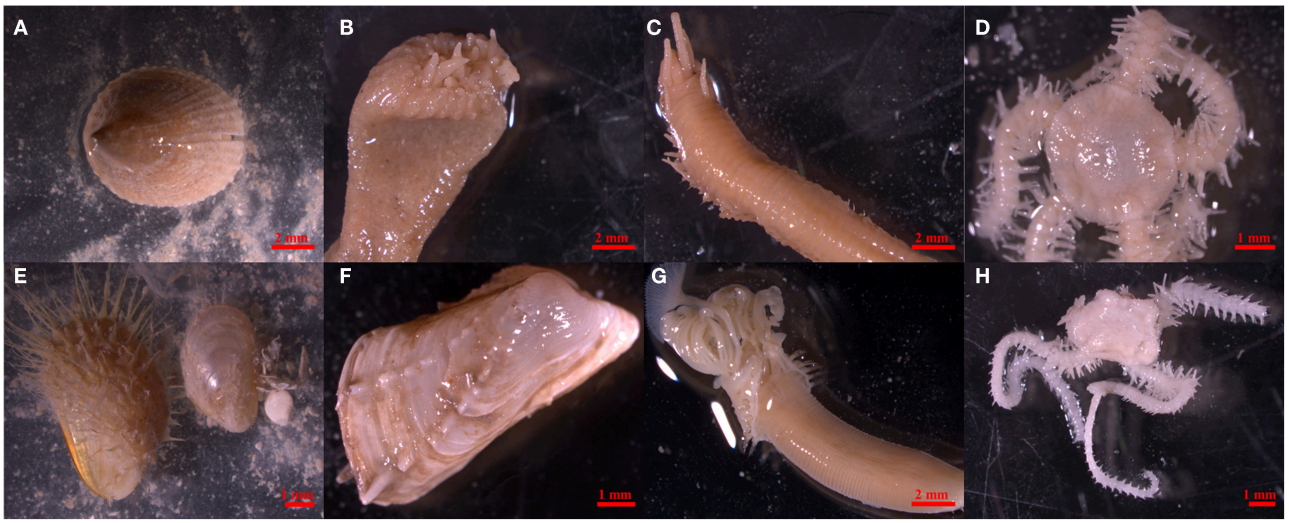


FIGURE 1 | Study organisms *Emarginula fissure* **(A)**, *Parazoanthus anguicomus* **(B)**, *Eunice norvegica* **(C)**, *Ophiactis balli* **(D)**, *Modiolula phaseolina* **(E)**, *Hiatella arctica* **(F)**, *Serpula vermicularis* **(G)**, *and Ophiura ophiura* **(H)** (From left to right, top to bottom).

Additionally, specimen vials were pre-screened prior to digestion to identify microparticles also stored in the IMS but which had not been ingested by the reef animals.

Statistical Analyses

Chi-squared analyses were used to test the null hypotheses that microparticle ingestion was equally likely across feeding guilds, reef stations, and the reefs themselves. Statistics were performed using IBM SPSS® statistics software version 24.

Raman Spectroscopy

Raman spectroscopy was used in an attempt to identify microplastics found during this study. Raman spectroscopy uses an inelastic scattering of light that vibrates off the molecular structure of an object (Araujo et al., 2018). The vibrational signatures can then be matched to known chemical structures. Raman spectroscopy was used to tentatively identify samples, referenced against existing literature and libraries. Raman data was collected on a Renishaw inVia Raman Spectrometer equipped with a Leica DM 2,500 M microscope and 785 nm diode laser (Toptica Photonics, Xtra I). The excitation beam was focussed on to the sample using a 20x/0.4 N.A objective lens (Leica, NPLAN) providing an excitation spot of a 2.5 µm diameter on the sample. Spectra were acquired between 100 and 3400 cm^{-1} in extended scan mode using a 600 lines/mm grating and collected with a cooled CCD. Due to high background fluorescence from the samples, the acquisition parameters were optimised per sample using excitation powers between 0.75 and 37.25mW and exposure times between 10 and 30s. The exposure parameters were limited by detector saturation due to the fluorescence background. Spectra were then processed using a modified multi-polynomial fitting to remove the fluorescence background and were then smoothed using a Savitzky-Golay filter (Ghosal et al., 2018).

RESULTS

Historic Litter Assessment

The systematic review of cruise reports recorded six instances of litter out of 217 benthic stations sampled by different gear (ROV dive transects and video-assisted grabbing), one of which was outside the MPA boundary but the other five were recorded from Mingulay Reef 1 and Mingulay Reef 5 North. An analysis of historic video from the 2003 survey for the present study recorded an instance of litter that had not been logged either in the main body of the cruise report or the accompanying video catalogue, but which had been reported in the cruise report's appendix. This reflects the critical need for a more rigorous and systematic approach to reviewing historic documents. It was also notable that cruise reports from surveys conducted in 2009 and 2011 recalled that lost fishing gear had directly impeded the deployment of equipment, and in 2011, caused significant damage to sampling gear.

Marine litter observed during the present study was reported in accordance with the Guidelines on Survey and Monitoring of Marine Litter (Cheshire et al., 2009), as standardised reporting is critical to promoting knowledge of litter pertaining to GES and the MSFD. The three observed litter items reported during the 2003 survey and identified during accompanying video footage analysis were best designated as "Plastic Sheet or Tarpaulin" (litter code RL16), but whether these were fisheries-related or, e.g., boating, is unclear. In the 2005 and 2009 cruise reports, observed litter was classified under UNEP-IOC's General Fishing and Boating category, which includes buoys, nets, monofilament line, and rope (litter codes RL05 and RL08 for 2005 and 2009, respectively). The 2011 survey reported litter that was best categorised as fishing-related litter, which includes sinkers, lures, hooks, traps, pots, and baskets or trays (litter code RL08). No litter was observed from ROV footage collected during the 2012 survey (**Table 3**).

TABLE 3 | Categories of marine litter observed from video footage or reported in cruise reports from the East Mingulay MPA and an adjacent area.

Vessel	Observation from cruise report or video analysis	Latitude °N (DMS)	Longitude °W (DMS)	UNEP-IOC Litter code and type
RV *Lough Foyle*	Video 22: marine litter, black plastic	56 45.32	07 27.407	RL16—Plastic sheet or tarpaulin
	Video 23: marine litter, white and blue plastic	56 45.342	70 27.406	RL16—Plastic sheet or tarpaulin
	Video 31 (out with the MPA boundary): marine litter, blue plastic waste	56 48.082	07 10.573	RL16—Plastic sheet or tarpaulin
MY *Esperanza*	Fishing net visible at 173 m, ESP05/VID/27	56 47.4010	7 25.004	RL05—Fishing net
RRS *Discovery*	Grab caught on rope, deployment abandoned.	56 49.5406	7 23.70533	RL08—Rope
RV *Calanus*	No observed or reported debris		–	–
RV *Calanus*	No observed or reported debris		–	–
RRS *Discovery*	Grab snagged on lost lobster pot and clump weight chain at 163 m. Damage to umbilical and frame.	56 49.3156	7 23.4738	RL06—Fishing related
RRS *James Cook*	No observed or reported debris		–	–

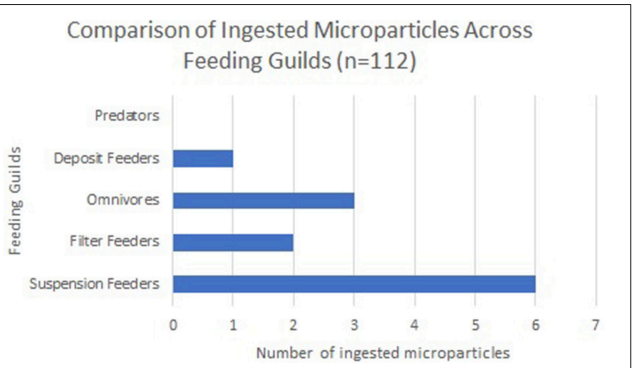


FIGURE 2 | Number of ingested microparticles across feeding guilds shows that suspension feeders most commonly ingested microparticles, followed by omnivores, and then filter feeders.

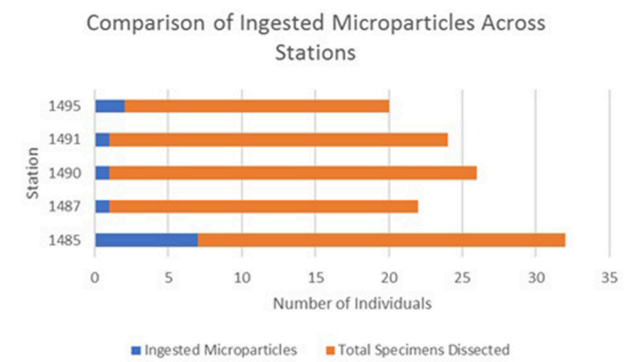


FIGURE 3 | Number of ingested microparticles across stations shows how many individual specimens were found to have ingested microparticles out of all the specimens dissected.

Microplastic Analysis

Out of the total 112 organisms sampled (**Figure 2**), 10 specimens had ingested 1 microparticle, all of which were classified as microfibres (images of all microfibres are provided in **Supplementary Material S3**) and in one case, the omnivorous ophiuroid *Ophiactis balli* had ingested both a microfibre and a microplastic particle (La Beur et al., 2019). Frequency of ingestion varied disproportionately across feeding guilds: of the 10 specimens that had ingested microparticles, five were suspension feeders, while only two filter feeders, two omnivores, and one deposit feeder had ingested microparticles. Suspension-feeding taxa (the zoanthid *Parazoanthus anguicomus* and the polychaete *Serpula vermicularis*) ingested approximately the same number of microfibres as the deposit-feeding limpet *Emarginula fissura*), with 16% and 15% of specimens having ingested microparticles, respectively. No microparticles were retrieved from the guts of the predatory worm *Eunice norvegica*.

Microparticle ingestion varied across the MPA, but all five stations showed evidence of specimens ingesting microparticles. Frequency of ingestion was highest at Station 1,485 on Mingulay Reef 1, with microfibres found in 20% of the specimens sampled here, and lowest at Station 1,490 on Banana Reef (**Figure 3**). Notably, Station 1,485 was located in a topographic seafloor depression in a gently sloping area with strong, but variable, ocean currents. In general, frequency of ingestion was three times higher on Mingulay Reef 1 (12%) than on Banana Reef (4%). Although the number of ingested microparticles clearly differed between feeding guilds, stations, and between the two reefs (**Figure 4**), none of these differences were statistically significant at $\alpha = 0.05$ ($\chi^2 = 3.85$, df = 4, critical value = 9.49 across feeding guilds; $\chi^2 = 4.63$, df = 4, critical value = 9.49 across stations; $\chi^2 = 1.98$, df = 1, critical value = 3.84 between reefs). These results are not statistically significant but may be biologically significant. More research in this area is needed.

The present study documented marine litter, including microplastics, at three of the reefs in the East Mingulay MPA, including Mingulay Reef 1, Mingulay Reef 5 North, and Banana Reef. Most records fell within the zoned managed area that now prohibits most forms of fishing, with a majority of litter (categorised mostly as associated with fisheries activity) being found at Mingulay Reef 1 (**Figure 5**).

Raman Spectroscopy Results

Raman spectroscopy yielded a unique spectrum for all samples found (**Supplementary Material S4**). Samples were baseline corrected (**Supplementary Material S5**); however, spectra could not be identified definitively, as many had significant noise, or appeared to have additional peaks to known reference samples, potentially indicative of sample degradation or biofouling. Physical degradation, biofilm, and photodegradation can all contribute to the mis-identification of polymer structures. Tentative sample identification was only possible for a few samples, and included variations of potential polystyrene, polyurethane, and poly (ethylene terephthalate).

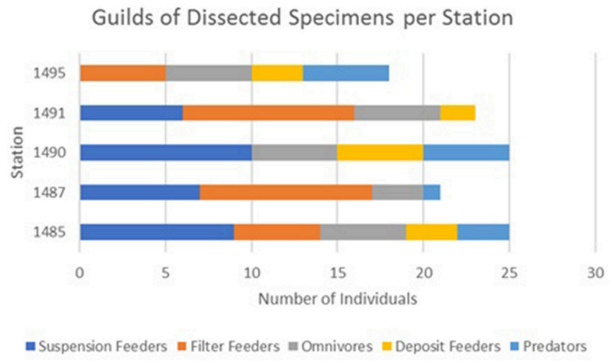


FIGURE 4 | A comparison of the individual specimen feeding guilds dissected for this experiment across reef stations.

QA/QC Laboratory Contamination Assessment

The damp Whatman filter paper was evaluated after 26 days of air contamination of the lab station. There were 37 fibres on the filter paper from the whole of the study. It is worth noting that the fibres observed on the filter were of a different size, colour, and shape than the fibres found in the specimens of the benthic analysis. When precautionary measures are taken, background contamination can be negligible (Torre et al., 2016). Therefore, it was concluded that there was no air contamination of the dissected specimens, and thus, this study did not exclude any microfibres in quantification or interpretation (Taylor et al., 2016). Additionally, in studies of marine microfibres, contamination of microscope covers has been found to be statistically insignificant, and in fact, using microscope covers drastically reduces contamination of microfibres being identified (Torre et al., 2016).

DISCUSSION

The present study on marine litter and microparticle ingestion demonstrated that archived data can be reviewed and used in new ways to obtain baseline levels of anthropogenic debris and microparticle ingestion. This "collect once, use many times" approach can help inform marine policy including regional and sub-regional GES assessments for the MSFD, without the need for costly investment in new surveys to obtain environmental baselines. This first assessment of marine litter and microparticles on the deep continental shelf to the west of Scotland showed that

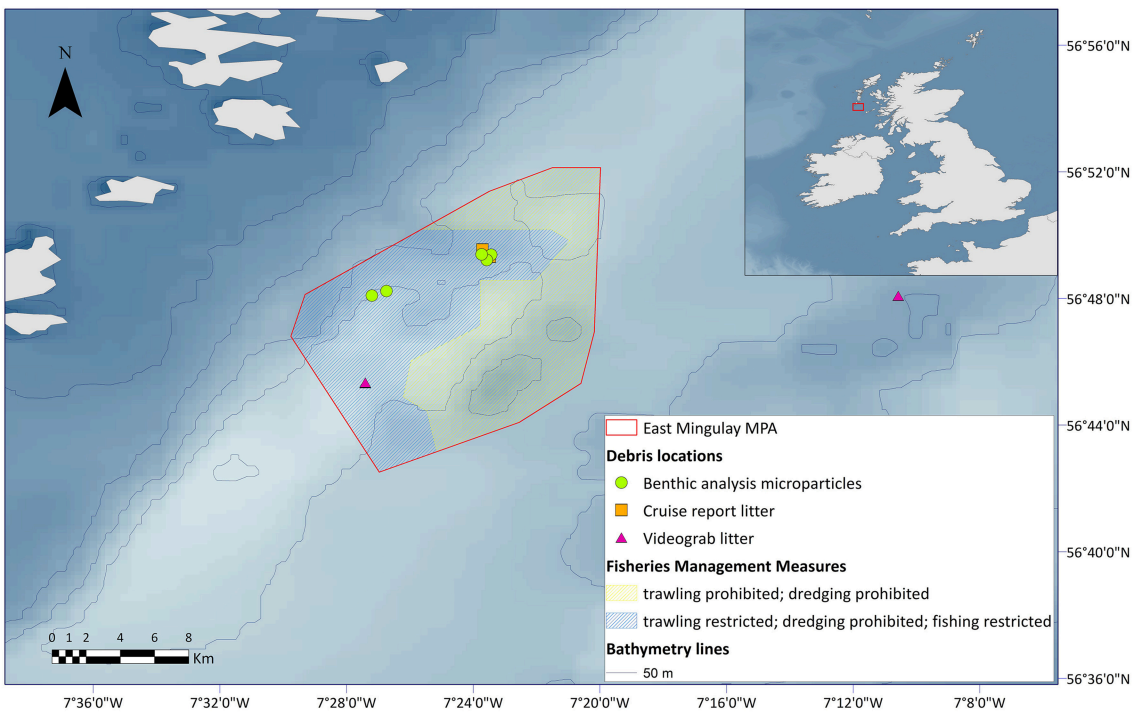


FIGURE 5 | Locations of marine litter and microparticles identified from historic cruise reports and benthic samples from the East Mingulay MPA.

most debris was lost fishing gear. The benthic fauna inhabiting the cold-water coral reef ecosystems of this area recorded the legacy of marine litter, with 11% of organisms across a range of feeding strategies having ingested microparticles of degraded anthropogenic debris. Fine-scale interactions between bathymetry and hydrography may have played a role in trapping and focusing these microparticles, with the highest ingestion rates occurring in a topographic hollow along a gentle slope in an area with strong variable ocean currents. Ingested particles were almost entirely microplastic fibres 2 to 5 mm in length, with several types of polymers tentatively identified by Raman spectroscopy, including polypropylene (PP), polyurethane (PU), polystyrene (PS), and polyethylene terephthalate (PET). Along with other related studies on marine litter and microplastics in deep Scottish waters, including the Rockall Trough (Courtene-Jones et al., 2018), the present study on a continental shelf setting provides a first baseline from which progress towards achieving GES beyond 2020 can be measured. A series of methodological recommendations are also provided to aid future studies.

Marine Debris

Trends of macrolitter across the MRC were fishing-related litter in the form of plastic sheets or tarpaulin and discarded fishing gear, commonly referred to as "ghost fishing" due to the high possibility of organisms becoming entangled or ensnared. The MRC was designated an MPA in 2010, and since that time, fishing restrictions have been in place (Scottish Government, 2014). Therefore, any fishing-related litter identified should be from before 2010 or may have been transferred in by local currents. The ROV was equipped with an Insite Mini Zeus camera with direct HDSDI fibre output, as well as two Watt Deep-sea Power & Light SeaArc2 HMI lights and two 25,000 lument Cathx Ocean APHOS LED lights; these systems may influence the amount and type of litter observed in this study. Therefore, the marine litter reported in this study may be a conservative estimate of the amount of litter at Mingulay. Without collecting the litter items, it is difficult to source its origin. Microlitter identified at the MRC was primarily comprised of fibres. This corresponds with other studies' findings, as fibres are increasingly being reported as being ingested by deep-water organisms (Courtene-Jones et al., 2018).

Ecosystem Effects on Microparticle Ingestion

The present study supports other studies globally that microfibres are frequently found in the internal cavities of deep-water and deep-sea benthic fauna beyond the coasts (Woodall et al., 2014; Taylor et al., 2016; Courtene-Jones et al., 2017a). However, in contrast to Taylor et al.'s study (2016) that found that deposit feeders were more likely to ingest microfibres than suspension feeders, ingestion rates were as frequent for suspension feeders at the MRC as they were for the deposit feeder (16% vs. 15% ingestion rates, respectively). Furthermore, none of the predatory worms (*Eunice norvegica*) at the MRC had ingested microparticles, in contrast to consumption by predatory squat lobsters reported by Taylor et al. (2016), or by the predatory sea star *Hymenaster pellucidus* and gastropod *Colus jeffreysianis* (Courtene-Jones et al., 2017a). To summarise, the present study demonstrated no statistically significant effect of feeding type on frequency of particle ingestion ($p > 0.05$). This may be due to the rapid tidal cycling currents at the MRC (Davies et al., 2009); species at Mingulay may not have a chance to ingest microparticles as frequently as species at other sites with different hydrographical conditions.

These opposing findings could point to differences between focal ecosystems, the present study being located on a deep but inshore continental shelf setting, in contrast to bathyal open-ocean seamounts (Taylor et al., 2016) or the open-ocean bathyal plains (Courtene-Jones et al., 2017a). In addition, one of the reasons that Taylor et al. found more microplastics in deposit feeders than suspension feeders may relate to the fact that hydrographic conditions in their study regions may promote the settlement of litter on the seafloor, and thus, deposit feeders may be exposed to more particles than suspension feeders. Mingulay is a very hydrographically dynamic environment in which the settlement rates of particles are likely to be lower than those in (Taylor et al., 2016), and thus, the deposit feeders in Mingulay have smaller chances to capture these items.

Inter-related to contrasting ecosystem settings could be interspecific differences in life histories and biology, wherein the ingestion rate varies more strongly between species than they do between feeding guilds (Courtene-Jones et al., 2017a). Unlike bathyal seamounts and plains, the benthic macrofaunal community at the MRC comprises mixed assemblages of both coastal and deep-sea taxa. None of the species selected for the present study are exclusive to the deep-sea, and eurybathic species such as these may have wider environmental tolerances that adapt them to dynamic coastal zones. For example, these species may be faster-growing and feed more frequently than their stenobathic deep-sea counterparts if food supply is not limited or more continuous than the often-pulsed nature of food supply in the deep sea, factors that would all essentially equalise the opportunity to ingest food across feeding guilds. Courtene-Jones et al.'s (2017a) study from the abyssal ecosystem of the Rockall Trough also recorded ingestion rates that were four times higher than those found in the present study on the continental shelf and could also implicate ecosystem effects. For example, all three species examined from the bathyal zone were mobile taxa, in contrast to only three of eight species considered in the present study, the rest being truly sessile attached to substrata. Limited mobility may therefore reduce particle encounter rate if an organism cannot move to areas when food becomes more abundant. The handful of studies that currently exist on microparticle ingestion in deep-water marine ecosystems limits more firm conclusions, except to say that interspecific differences (and not feeding guilds) may hold the key to improving the understanding of ecosystem susceptibility to plastic consumption.

Possible Transport Routes for Marine Litter in the East Mingulay MPA

Our results provide complementary data for the deep seafloor to accompany Lusher et al.'s (2014) measurement of sea surface microplastics in the Sea of the Hebrides, which were recorded to be between one to five microplastic items per cubic meter

water (relatively lower than the offshore regions, with 10 to 25 items per cubic meter). Without further analysis of surface microplastics over the MRC, it is not known whether microparticles ingested by reef organisms in the East Mingulay MPA derived entirely from downwelled surface waters, or from bottom currents. Previous studies by Duineveld et al. (2012), Kazanidis and Witte (2016), and Kazanidis et al. (2018) have shown that several species in Mingulay (including *Parazoanthus anguicomus*) depend more on surface fresh food particles, rather than on degraded bottom particles. This could be an indication about the role of downwelling of surface material vs. material transported from bottom currents.

The Raman spectroscopy analyses showed a complex mixture of anthropogenic compounds reaching the seafloor that seems to contrast with those found in the bathyal Rockall Trough further to the west of the MPA. Courtene-Jones et al. (2017a) reported that polyester dominated the water column fraction of microplastics in the deep Rockall Trough adjacent to the west of Scotland, but acrylic dominating the benthic fraction. Although definitive Raman spectroscopy results for ingested microparticles at the MRC were inconclusive, these first analyses point to a different type of microparticle assemblage being ingested by benthic fauna, including possibly polypropylene (PP), polyurethane (PU), polystyrene (PS), and polyethylene terephthalate (PET). Notably, instead of acrylics that could come from clothing fibres and washing/wastewater facilities, tentative sources of microparticles in the East Mingulay MPA could therefore derive from, e.g., marine ropes (PP), surfboards, boat hulls and decks (PU), protective packaging (PS), and food and beverage packaging (PET).

Original sources of plastics could begin to be inferred if stations closest to inhabited Outer Hebrides islands showed higher ingestion rates, but the present study demonstrated no statistically significant effect of either station, or reef. Identifying point or non-point sources of litter is important for management strategies, including source-reduction, retrieval, and mitigation (Rochman et al., 2016), and with regard to GES and the MSFD, this information would help inform management measures. In the meantime, while the present study could not identify a point source, the Raman spectroscopy results suggest that island management along the inner and outer Hebridean archipelago could take a more precautionary approach. Island communities could strive to minimise inputs from marine boating, fishing, and coastal development, e.g., by preventing the disposal of marine ropes and protective packaging, inspecting loose or chipped decks, and hulls, and offering recycling services for food packaging. Much of this litter input can be prevented by conducting regular beach clean-ups and increasing public awareness, particularly in the tourist season to prevent items from being carried offshore.

Bioindicator Candidates to Inform GES

A precautionary approach to management does not preclude the need to understand to what extent marine litter and microplastics harm deep-sea benthic organisms. Harm to these organisms, or ecosystem-scale impacts, cannot be deduced from this or other studies until long-term experiments are performed. Microparticles were most frequently observed in the zoanthid *Parazoanthus anguicomus*, which occurs in high current speed settings at the MRC (Roberts et al., 2009; Henry et al., 2010) and which may therefore be pre-adapted to processing coarse sediments and microparticles. However, microplastic ingestion could, for example, be accompanied by toxins that disrupt reproductive processes (Ryland, 2000; Cole et al., 2011).

Existing collections of MRC fauna and *P. anguicomus* in particular, could also be re-used to investigate such issues to compare zoanthid biomass, size, and reproductive traits between groups that ingested microparticles and those that did not. *Parazoanthus anguicomus* may also qualify as a good indicator species to assess abundance of microparticles for GES because the present study demonstrates it ingests microfibres and is very common across the MRC in high abundances (Henry et al., 2010).

Under the OSPAR Convention, the fulmar seabird was chosen as a sea surface interchange litter-monitoring species (OSPAR, 2018) as there are previous historical data that can be referenced as a baseline (Van Franeker and Law, 2015). For benthic fauna, no species has yet been identified as being a good indicator. Additionally, not all benthic species would make good indicators for investigating sea floor litter and it is important to understand what species are ingesting microparticles. This study demonstrates that suspension feeders and the readily abundant zoanthid *Parazoanthus anguicomus* in particular would make good sentinel species for GES assessments of D10.

Methodological Recommendations

Standardised approaches to identify and report litter during at-sea research and monitoring activities should be promoted. Standardisation will help integrate these data more easily into regional frameworks and to better inform policy, especially with regard to GES. The UNEP-IOC Guidelines on Survey and Monitoring of Marine Litter (Cheshire et al., 2009) adopted by the present study provided a simple framework by which to define litter and microparticles, for example. The UNEP does not require litter densities to be calculated, but this information, where possible, may prove valuable for assessing marine litter across larger scales.

In strong support of GES, it is recommended that, where possible, litter from the surface, water column, and seafloor be brought on deck and measured using criteria set forth by the EU Commission Decision 2010/477/EU, including: source and pathway of litter (if known); amount of litter per category in number of items (D10C1); amount of micro-litter per category in number of items and weight in grams (D10C2); amount of litter in grams and number of items per individual for each species in relation to size (as appropriate) (D10C3); and number of individuals affected per species (D10C4).

The present study demonstrates how the challenge of assessing GES in vulnerable marine ecosystems can be overcome by re-using data to obtain a baseline for GES, which then set the benchmark from which progress towards achieving GES can be established in a manner that is inclusive of such ecosystems. The re-use of historical surveys and samples in the present

study demonstrated the utility to establish baseline levels for assessments and to further understand the extent of marine litter and microparticle pollution issues. However, limitations of using data collected for other purposes must be acknowledged: future shipboard collection and preservation of specimens should include best practice for avoiding contamination of litter and microplastics, for example. Some specimens had accumulated considerable biofilms on their surfaces, which may have contributed to the indeterminate signatures overserved through Raman spectroscopy. Polyamide and polyester were found in the highest abundances over time in the Courtene-Jones et al. (2018) study of a proximate area in the North East Atlantic.

Socioeconomic growth in key industry sectors ("blue growth") including maritime and coastal tourism present challenges to achieving GES. Globally, blue growth may prioritise economic potential over environmental protection (Elliott et al., 2018). Publicly accessible media productions, such as the BBC's *Blue Planet II*, help to bridge the scientific community to wider society to coalesce abstract problems and specific solutions (Pahl et al., 2017). There was a strong audience demand for knowledge and action, to which the government responded to with the enactment of bans on single-use plastic items (Xanthos and Walker, 2017). In January 2018, the European Commission also announced a European-wide strategy to reduce plastics in the marine environment (European Commission, 2018). This plan includes strategies to restrict the unnecessary addition of microplastics in products such as personal care and hygiene, as well as to curb major sources of pollution such as vehicle tyres, textiles, and industrial plastic pellets (European Commission, 2018). These changes in social behaviours have minor significance in the global input of plastics, but these changes support a bottom-up approach to influencing the policies implemented by international frameworks, like the MSFD and Water Framework Directive (Galgani et al., 2013). In turn, this can generate momentum for large scale backs in industrial plastic consumption. Ultimately, these upper echelon policy changes have a lasting impact on the litter entering the world's oceans (Van Franeker et al., 2011).

CONCLUSION

The understanding of the extent of marine litter and the harm it causes continues to gain momentum. In Europe, Member States are obliged by the MSFD to work collectively to establish targets, criteria and indicators of the most poorly understood Descriptor, D10—Marine litter (Galgani et al., 2013). However, there are currently no coordinated national or regional monitoring programmes for marine litter in surface waters, the water column, or at the seabed within Europe, nor are there monitoring programs for microparticles (Galgani et al., 2010). The UK's position on GES and its adoption of the MSFD are unknown at the time of writing due to the "Brexit" implementation by March 2019. Yet, the present study demonstrated that the extent of marine litter and microplastics runs throughout a deep remote area on the UK continental shelf, characterised by vulnerable cold-water coral reef ecosystems, with many functional groups ingesting anthropogenic waste. With the socioeconomic push for blue growth, recommendations include adopting baseline assessments to reduce the frequency of microparticle ingestion from 11% and implementing standardized protocols for recording and analysing litter. Such recommendations can likewise be implemented with relatively little additional cost by re-using data collected for other purposes and harmonising new data collection practices across larger areas across all of the UK's different marine ecosystems.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the supplementary files.

AUTHOR CONTRIBUTIONS

LL and L-AH designed the study. JMR provided historic video and benthic samples that LL reviewed. LL and GK analysed macrobenthos for microplastics. GK provided images of the macrofauna, SH, MS, and AM ran and helped interpret the Raman spectra. All authors contributed to writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00080/full#supplementary-material

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The Fate of Cold-Water Corals in a Changing World: A Geological Perspective

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As "ecosystem engineers," framework-forming scleractinian cold-water corals (CWC) build reefs that are unique biodiversity hotspots in the deep sea. Studies using common biological techniques such as correlating the spatial occurrence of the most common CWC species with modeled environmental conditions have revealed the ecological requirements and tolerances of these species. However, limited field observations and poorly understood geographical distribution patterns of the CWC restrict the application of existing knowledge toward assessing their fate (e.g., local extinction, newly established populations) under ongoing global change. Hence, the risk to cross ecological tipping points causing the demise (or establishment) of entire CWC reefs remains unclear. A major challenge is to identify the key environmental parameters (or stressors) having the potential to control CWC vitality by providing such tipping points. This is largely hampered by the overall lack of present-day observations of such tipping point crossings. However, evidence for such events is frequently preserved in geological records revealing that entire CWC ecosystems vanished or returned at specific moments in the past. Here, a geological approach is presented that by correlating geological CWC records with paleoceanographic data describing past environmental changes allows to identify a set of key environmental drivers that directly or indirectly control CWC vitality. Thus, by combining such a geological approach with common biological techniques (see above) to describe the ecological tolerance of the most important reef-building CWC has a great potential to better assess their future spatial distribution in times of accelerating global change and to improve the sustainable management of the important deep-sea ecosystems formed by CWC.

Keywords: cold-water corals, tipping points, key environmental drivers, geological record, global change

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INTRODUCTION

Framework-forming scleractinian cold-water corals (CWC) are ecosystem engineers that form the base for biodiversity hotspots being widely distributed in water depths between 200 and 1,000 m in the Atlantic Ocean (Roberts et al., 2009). CWC reefs are considered as vulnerable marine ecosystems (Auster et al., 2011) that potentially provide very important ecosystem services. Consequently, around many CWC sites marine protected areas (MPA) have been established (e.g., off Norway and Ireland, around the Azores) to ban extraction of living and non-living resources

invoking activities that are potentially harmful to the CWC (e.g., Armstrong and van den Hove, 2008; Huvenne et al., 2016). However, MPA provide no protection against threats induced by ongoing global change (Jackson et al., 2014) such as ocean warming, acidification, deoxygenation and decreasing particulate organic matter fluxes to the seabed as these cannot be controlled locally (e.g., Sweetman et al., 2017). In addition, this range of environmental parameters might be even more critical for the proliferation or survival of CWC considering a combined effect of multiple stressors (e.g., Büscher et al., 2017). Thus, to assess the vulnerability of CWC to future global change, there is an indispensable need to comprehensively understand their sensitivity to changing environmental conditions.

The ecological requirements and tolerances of the most common framework-forming CWC species have been determined by field observations in the direct vicinity of CWC reefs (Dullo et al., 2008; Freiwald et al., 2009; Brooke et al., 2013; Flögel et al., 2014) or by correlating their spatial occurrence to gridded data bank information describing the ambient environmental setting focusing mainly on physico-chemical properties of the water masses bathing the CWC reefs (Freiwald, 2002; Davies et al., 2008; Davies and Guinotte, 2011). Subsequently, the empirically obtained ranges of individual environmental parameters have been interpreted as generally valid thresholds controlling the occurrence of CWC on a global scale (Davies and Guinotte, 2011). However, recent discoveries of hitherto unknown CWC reefs that exist today under rather "extreme" conditions [e.g., in terms of temperature (Mienis et al., 2014) or oxygen (Ramos et al., 2017)], force us to shift the upper and lower thresholds of environmental parameters beyond formerly described values. In addition, laboratory experiments conducted on several common CWC species (e.g., *Lophelia pertusa*, *Madrepora oculata*, and *Dendrophyllia*) provided additional information on their ecological requirements (e.g., in terms of temperature, carbonate system, food supply, and oxygen) (e.g., Tsounis et al., 2010; Gori et al., 2014; Movilla et al., 2014; Naumann et al., 2014; Maier et al., 2016; Büscher et al., 2017) and also indicate region-specific adaptations of CWC to particular environmental parameters (Dodds et al., 2007; Lunden et al., 2014). Furthermore, exceeding/undercutting such environmental thresholds ("tipping point") causing a local extinction of CWC so far has never been documented by field observations.

Here, we outline a geological concept and review its applicability as this geological approach has great potential to overcome such lacking observations in order to further delineate the ecological tolerances of CWC. It allows identifying CWC tipping points by taking advantage of the long-term development of CWC reefs. In the geological past, this often is marked by regional extinctions and re-occurrences of CWC concomitant with changes in climate (e.g., Kano et al., 2007; Frank et al., 2011). Correlating such events, i.e., the crossing of tipping points, to the variability of paleoenvironmental parameters allows to identify key parameters that potentially control the (regional) vitality of CWC (e.g., Dorschel et al., 2005; Wienberg et al., 2010; Raddatz et al., 2014b; Van der Land et al., 2014; Victorero et al., 2016). Thus, studying the geological record of CWC reefs enhances our understanding about the response of CWC to past climatic changes. Hence, it provides pivotal information about their likely response to those changes expected for the future. In the end, this information will allow to develop and to optimize management strategies for the sustainable protection of these important deep-sea ecosystems.

THE CONCEPT

Tipping Points Crossed in the Past

Over geological time scales of thousands to millions of years, CWC can form coral mounds (composed of CWC fragments, shells of associated fauna, and hemipelagic sediments), which occur widespread along the continental margins of the Atlantic Ocean (Wienberg and Titschack, 2017) reaching heights of up to >300 m (Mienis et al., 2006). The framework-forming CWC species mostly contributing to the formation of coral mounds are *L. pertusa*, *M. oculata*, *Solenosmilia variabilis*, *Bathelia candida*, and *Enallopsammia profunda* (e.g., Mangini et al., 2010; Frank et al., 2011; Muñoz et al., 2012; Hebbeln et al., 2014). Coral mounds are distinct from the surrounding seafloor as they constitute elevated seabed structures causing enhanced hydrodynamics that support the supply of sediment and food particles. Therefore, coral mounds induce re-settlement of CWC (that may develop into reefs) whenever the overall environmental settings turn favorable (Wienberg and Titschack, 2017).

Sediment cores obtained from coral mounds provide geological records allowing to trace CWC vitality through time (e.g., Dorschel et al., 2005; Kano et al., 2007). For most coral mound sites investigated so far, it has been found that the CWC records show alternating phases of coral vitality and absence (e.g., Eisele et al., 2008; Mienis et al., 2009; Matos et al., 2017). Precise dating by radiometric methods (e.g., uranium-series dating, radiocarbon dating) allows to define the timing of (regional) extinction or re-occurrence of CWC and to relate these "tipping point crossings" with changes in environmental conditions (e.g., Frank et al., 2011).

Interestingly, the timing of crossing CWC tipping points, resulting in either their demise or their re-settlement in a given area, often coincides with major climatic changes. For many sites in the North Atlantic (e.g., off Norway, Ireland, and the United States east coast, in the Mediterranean Sea and Gulf of Mexico), it has been found that after a long-lasting period (tens of thousands of years) of coral absence a re-settlement of CWC occurred during the transition from the last glacial period to the present interglacial along with a significant global warming (e.g., Frank et al., 2009; McCulloch et al., 2010; Taviani et al., 2011; López Correa et al., 2012; Fink et al., 2015; Matos et al., 2015, 2017). However, the exact timing has been quite variable, for instance, starting relatively early at 14,000 years before present (BP) in the Mediterranean Sea (Fink et al., 2015; Stalder et al., 2015) and relatively late at 7,000 years BP off the United States east coast (Matos et al., 2015). In contrast, off NW Morocco and Mauritania, CWC flourished during glacial conditions and went regionally extinct concurrent with the global warming of the recent interglacial

(Wienberg et al., 2010, 2018; Frank et al., 2011). This pattern of climate change-driven regional variations in coral proliferation is not just valid for the recent interglacial and last glacial (i.e., the last ∼ 70,000 years), but can also be traced further back in time comprising previous glacial and interglacial stages (Frank et al., 2011; Raddatz et al., 2014b; Van der Land et al., 2014; Matos et al., 2017; Wienberg et al., 2018). Beside major changes in CWC proliferation linked to glacial/interglacial climate variability, CWC development has regionally also been interrupted on shorter time scales, lasting for a few hundreds to thousands of years during interglacial or glacial periods (e.g., Fink et al., 2015; Raddatz et al., 2016; Wienberg et al., 2018).

Identifying Key Environmental Drivers

To identify those environmental changes that are most likely the cause for the demise or re-settlement of CWC, conventional paleoceanographic approaches can be used. At first glance, the aragonitic skeletons of the CWC appear as the prime signal carrier for paleoceanographic changes. They provide an excellent, precisely datable paleoarchive offering a range of innovative proxies to reconstruct the paleoenvironment in which they thrived (Robinson et al., 2014). However, coral-based proxy records provide no environmental information on those times the corals were absent, thus precluding any before-and-after comparisons.

Therefore, the reconstruction of the paleoenvironment controlling the vitality of CWC has to rely on sediment-based approaches. These can be applied either to the hemipelagic sediments deposited among the coral fragments on the coral mounds, so-called on-mound records, or to coral-barren sediments collected nearby ideally from the same water depth to represent the same environmental setting, so-called off-mound records (**Figure 1**; Dorschel et al., 2005). As the deposition of sediments within the coral framework can be somewhat patchy and is limited to the periods of coral growth (Thierens et al., 2013), the off-mound sites usually provide more continuous paleoenvironmental records (Dorschel et al., 2005; Rüggeberg et al., 2007; Wienberg et al., 2010; Fink et al., 2013).

To assess the paleoenvironmental conditions controlling the proliferation of CWC, various proxies can be applied to reconstruct past conditions at the seabed and within the bottom waters bathing CWC reefs. The most common proxy carrier to describe past conditions at the seabed are benthic foraminifera. The chemical composition of their calcitic shells provides information, e.g., on bottom water temperatures (using Mg/Ca ratios, Lear et al., 2002), salinities (by combining Mg/Ca-derived temperatures, Lear et al., 2002, with stable oxygen isotope data, Marchitto et al., 2014), oxygenation (using Mn/Ca ratios, Groeneveld and Filipsson, 2013), pH (using boron isotopes, Rae et al., 2011), and bottom water provenance (using εNd and stable carbon isotope data, Mackensen and Bickert, 1999; Tachikawa et al., 2017). In addition, their accumulation rate gives an indication about the food supply to the benthic realm resulting from surface ocean productivity (Herguera and Berger, 1991). Besides the information gained from benthic foraminifera, the grain-size distribution of the terrigenous portion of the sediments (originating from river and wind input) allows to reconstruct the hydrodynamic conditions at the seabed (McCave et al., 2017). These were identified as being one critical parameter for the occurrence of CWC beside productivity and the physical-chemical properties of the bottom waters (e.g., Davies et al., 2008; Hebbeln et al., 2016).

Combining these proxies in a multi-proxy approach allows for a precise description of paleoenvironmental changes (Fischer and Wefer, 1999). However, although most of these proxies provide quantitative results describing former conditions, due to rather large error bars the results usually should be seen as semi-quantitative or sometimes only as qualitative estimates. Nevertheless, these records provide reliable archives of environmental change through time and linking these records with a pattern of coral presence and absence allows to pinpoint the most dramatic paleoenvironmental changes co-occurring with the on-set/off-set of CWC reefs. With such a multi-proxy approach, key environmental drivers pushing the corals across their tipping points can be identified as it is exemplarily demonstrated in the case studies presented below.

CASE STUDIES

To highlight the applicability of the concept outlined above, here we present brief overviews of three case studies. These and other studies (e.g., Wienberg et al., 2010, 2018; López Correa et al., 2012; Fink et al., 2013; Stalder et al., 2015; Raddatz et al., 2016; Matos et al., 2017) already give some clear indications about key environmental drivers, which, can, however, be regionally very different. Nevertheless, a comprehensive approach with a similar set of proxies addressing the most likely critical environmental parameters for various CWC settings is still missing.

The Irish Margin in the NE Atlantic

The Irish margin is characterized by the widespread occurrence of thriving CWC, which today colonize the top of coral mounds. Coral mounds are arranged in large mound provinces with many of these located within the Porcupine Seabight (White and Dorschel, 2010). There, CWC began to settle ∼2.6. million years ago (Kano et al., 2007; Huvenne et al., 2009), supported by high primary productivity (Raddatz et al., 2014b) and by vigorous hydrodynamics (Thierens et al., 2010) that also play an important role for the food supply to the sessile, suspension-feeding corals (Hebbeln et al., 2016). After a major hiatus in the Irish coral mound records spanning the period from 1.7 to 1 million years ago (Kano et al., 2007), the intensification of the climatic cycles through the Late Quaternary limited CWC proliferation to warm interglacial conditions (at least during the last 300,000 years) with the most recent phase of CWC presence (re-)starting at the onset of the Holocene at 11,500 years BP (Dorschel et al., 2005; Frank et al., 2011).

During the early Holocene, the food supply to the seabed off Ireland increased, triggered by enhanced surface ocean productivity after the polar front has moved to the north of the region (Rüggeberg et al., 2007). At the same time, the bottom water dynamics also strengthened significantly due to the return of the Mediterranean Outflow Water to those water

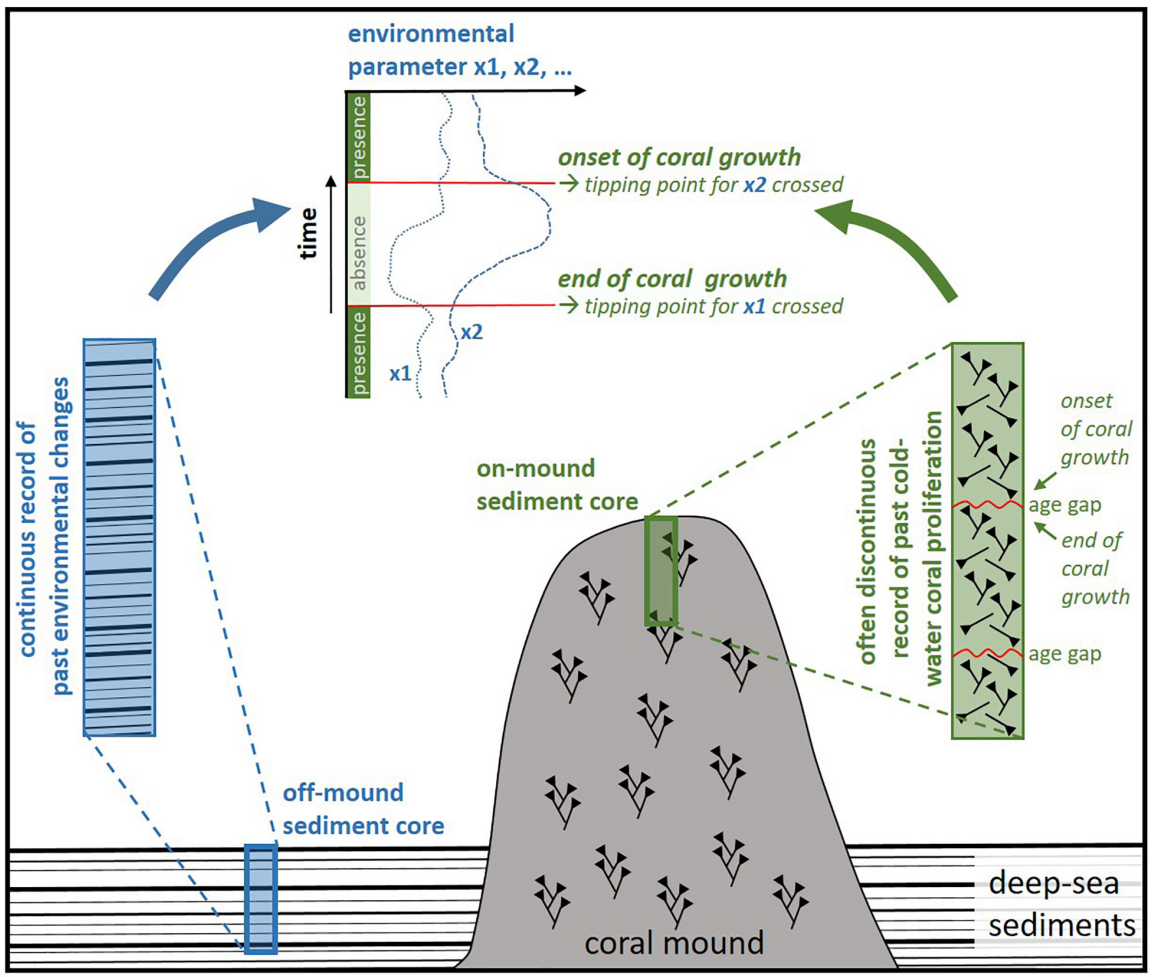


FIGURE 1 | Schematic presentation of the "geological approach" to assess the sensitivity of cold-water corals to environmental change and to identify the key ecological drivers being able to push CWC across tipping points causing the demise/return of entire populations. By combining cold-water coral records retrieved from coral mounds with continuous paleoenvironmental records, such key drivers can be identified.

depths (600–800 m) inhabited by the CWC (Dorschel et al., 2005; Rüggeberg et al., 2007). From a record obtained slightly further south, the intermediate water conditions for the last glacial period are described as well-oxygenated and marked by relatively warm temperatures (Mojtahid et al., 2017). Thus, the major environmental changes associated with the return of the CWC to the Irish margin are an increase in surface water productivity as well as a re-organization of the regional water column structure affecting the bottom water hydrodynamics. Combined, both changes clearly increased the food supply to the corals, which probably triggered the re-establishment of CWC reefs on the Irish margin at around 11,500 years BP (Frank et al., 2011).

The Cape Lookout Site in the NW Atlantic

Off the United States east coast, CWC reefs exist off Cape Lookout where they are occasionally reached by meanders of the Gulf Stream exposing them to highly variable environmental conditions especially in terms of bottom-water temperature and dynamics (Mienis et al., 2014). Sediment cores revealed that this vivid CWC site was re-established at ∼7,000 years BP, i.e., well after full interglacial conditions have been reached globally. Also at this site, bottom-water temperatures and surface ocean productivity reached interglacial levels already at ∼12,000 years BP, however, without enabling the CWC to return. The major environmental change affecting this site at ∼7,000 years BP was a dramatic increase of the hydrodynamic energy at the seabed (Matos et al., 2015). This change, most likely caused by the impingement of the Gulf Stream on the upper continental slope, is assumed to have triggered the re-establishment of the CWC by creating a setting that could provide sufficient food probably by delivering food particles at a higher rate (Matos et al., 2015).

The Santa Maria di Leuca Site in the Central Mediterranean Sea

Off Santa Maria di Leuca on the Apulian margin in the Ionian Sea, CWC reefs occur under relatively high temperatures

and salinities (Taviani et al., 2005; Freiwald et al., 2009). At this site, CWC reef development started at around 13,000 years BP (McCulloch et al., 2010; Fink et al., 2012). Most interesting here is an interruption of CWC proliferation between 11,000 and 6,000 years BP (Fink et al., 2012) that coincided with the Sapropel S1 event during which the entire eastern Mediterranean Sea below 1,800 m turned anoxic (De Lange et al., 2008). Decreasing oxygen contents also affected the CWC site at intermediate depths (∼600 m) causing a drastic reduction of the dissolved oxygen concentrations from relatively high "Holocene" values of ∼4 mL L^{-1} (Freiwald et al., 2009; Fink et al., 2012) to concentrations of <2 mL L^{-1} prevailing during the Sapropel S1 event (Fink et al., 2012). In contrast, cooler water temperatures and lower salinities combined with enhanced eutrophication during the Sapropel S1 event probably would have improved the conditions for the CWC. Thus, their temporal demise most likely has to be attributed to the poor oxygenation of the bottom waters at that time acting as a stressor to the CWC (Fink et al., 2012).

Summarizing Available Case Study Results

Analyzing the long-term development of CWC in the past reveals that CWC are apparently quite tolerant to environmental change as crossings of tipping points are mostly limited to major environmental overturns, although also short-term extinction events have been described on a regional scale (Fink et al., 2012, 2015; López Correa et al., 2012; Raddatz et al., 2016). While major environmental overturns associated with transitions from glacial to interglacial conditions and *vice versa* might cause the demise of CWC at one site, they might support coral re-settlement at another site (e.g., Frank et al., 2011) highlighting the complex response of CWC to environmental changes. Still, open questions regarding the sensitivity of CWC to environmental change relate to (i) the rate of their adaptation capability in relation to the rate of environmental change and (ii) their strategies to cope with the effects of multiple stressors.

With respect to ongoing/future global warming, increasing temperature is often mentioned as a serious threat for CWC in the future (e.g., Lunden et al., 2014; Sweetman et al., 2017). However, the still few available studies indicate that CWC react very sensitive to changes in the food supply, either driven by changing surface ocean productivity (e.g., Rüggeberg et al., 2007; Wienberg et al., 2010) or by changing hydrodynamics (e.g., Dorschel et al., 2005; Fink et al., 2013; Matos et al., 2015, 2017), and in bottom-water oxygenation (Fink et al., 2012). Nevertheless, in a recent study, the combined impact of high temperatures and low oxygenation in limiting CWC proliferation has been identified (Wienberg et al., 2018), highlighting the importance of considering the effects of multiple stressors when investigating the sensitivity of CWC to environmental change.

Although proxies are available (e.g., Raddatz et al., 2014a; McCulloch et al., 2017), the effects of ocean acidification are difficult to cover by this geological approach, as the younger geological history provides no equivalent to pH variability expected until the end of this century. However, although ocean acidification has been identified as another major future threat for CWC (Guinotte et al., 2006), the discovery of their capacity to cope with more acidic conditions by pH upregulation in the coral calcifying fluid (Anagnostou et al., 2012) makes it presently difficult to assess the sensitivity of CWC to increasing pH in the future.

OUTLOOK

Combining observational data and multivariate statistical analyses has provided a wealth of information on ranges of individual environmental parameters tolerated by CWC (e.g., Davies et al., 2008; Davies and Guinotte, 2011). In addition, laboratory experiments provided some insight into maximum and/or minimum tolerated levels of some environmental parameters (e.g., Tsounis et al., 2010; Gori et al., 2014; Movilla et al., 2014; Naumann et al., 2014; Maier et al., 2016; Büscher et al., 2017), however, with partly contrasting results from different studies and areas (e.g., Dodds et al., 2007; Lunden et al., 2014) probably hinting to regional adaptations.

However, to what extent any reported environmental ranges define tipping points that upon crossing might cause the local/regional extinction of a population remains largely unanswered, in particular because during the observational/instrumental period no crossing of such an environmental tipping point for CWC has been documented. By adding a geological perspective to this problem, the approach outlined here offers significant additional information on environmental changes that indeed ultimately resulted in the crossing of a tipping point for the CWC. Understanding the response of CWC to past environmental changes allows to identify key drivers able to push a population beyond such a tipping point – in terms of demise and of re-establishment. Interestingly, the available data indicate food supply as the most prominent key driver, which appears to be controlled by a complex interplay of surface-ocean productivity and bottom-water hydrodynamics. However, this observation might point to a hidden impact of multiple stressors that often are energetically challenging for the metabolism of marine species, which potentially can be compensated by the availability of large quantities of high quality organic matter (Diaz and Rosenberg, 1995).

Consequently, in order to estimate the likely response of individual CWC species to those environmental changes expected until the end of this century (and beyond), future geological as well as biological studies investigating their respective sensitivity need to consider the role of multiple stressors and possibly compensating factors. Of similar importance will be a better understanding of regionally varying tolerances of CWC, a topic that has just begun to emerge.

In the future, a close cooperation of biologists and geologists (and oceanographers) to define the sensitivity of CWC to environmental change bears a great potential to assess the fate of CWC in the course of ongoing global change. Knowledge gained from such a cooperation will provide pivotal information to optimize strategies for the management of the unique deep-sea ecosystems formed by CWC.

AUTHOR CONTRIBUTIONS

DH and RP-R developed the concept for this overview. JT and CW compiled information for the case studies. DH wrote the manuscript. All authors contributed substantially to the discussion of the approach outlined here.

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Relating Depth and Diversity of Bivalvia and Gastropoda in Two Contrasting Sub-Arctic Marine Regions

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The need to understand species distribution- and biodiversity patterns in high-latitude marine regions is immediate as these marine environments are undergoing rapid environmental changes, including ocean warming and ocean acidification. By the year 2100, the seas north of the Greenland-Iceland-Faroe (GIF) topographic ridge are predicted to become largely corrosive to aragonite, a form of calcium carbonate commonly formed by calcifying molluscs. We examine depth-diversity relationships in bivalves and gastropods north and south of the GIF ridge, between 200 and 2000 m depth. We also identify bivalve and gastropod species that could be monitored to identify early signs of changes in benthic communities north of the GIF ridge, due to ocean acidification. Patterns of α-diversity were estimated through rarefaction, as $E(S_{20})$. Regional and depth related β-diversity was analyzed and the additive contribution of species replacement (turnover) and species loss/gain (nestedness) to β-diversity calculated. Despite sharing a significant number of species, diversity patterns differed between the study regions. The diversity patterns also differed between bivalves and gastropods. North of the GIF ridge, the relationship between α-diversity and depth was unimodal with a predominant decrease in bivalve and gastropod α-diversity between 300 and 2000 m depth. Species assemblages in the deep bathyal zone were partly nested subsets of the assemblages in the shallow bathyal zone. South of the GIF ridge, patterns in α-diversity were more ambiguous. Alpha diversity decreased between 300 and 2000 m depth in bivalves, with no clear trend observed in gastropods. This finding contradicts the recognized increase in α-diversity in the bathyal zone in the North Atlantic basin, perhaps due to the oceanographic conditions directly south of the GIF ridge. In contrast to that observed north of the GIF ridge, nestedness did not contribute significantly to β-diversity south of the GIF ridge. This comparative study sheds new light on deep-sea diversity patterns of molluscs in the high-latitude North Atlantic and provides baseline data on species occurrences. This information can inform future assessment of the impact of environmental changes in these regions and management efforts.

Keywords: diversity, alpha diversity, beta diversity, nestedness, bivalvia, gastropoda, Arctic, Iceland

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INTRODUCTION

The benthic realm harbors a remarkable proportion of the ocean's biodiversity (Snelgrove, 1999). Marine invertebrates that reside on (epifaunal) or in (infaunal) benthic sediments make up a large proportion of this diversity and provide key ecosystem services, for example through provision of structural habitat and through bioturbation (Snelgrove, 1999; Queirós et al., 2013). The vast majority (91%) of marine benthic habitat lies below 200 m depth where darkness prevails and autotrophic activity is negligible (Kennish, 2000). Accessing the deep ocean is a very costly and logistically challenging endeavor, explaining why ecosystems in the deep sea remain insufficiently studied compared with shallow water or terrestrial systems (May and Godfrey, 1994; Higgs and Attrill, 2015). It is more urgent than ever to document and understand biodiversity patterns and ecological processes in deep-sea benthic ecosystems, as these systems, typified by environmental stability (Seibel and Walsh, 2003; Hofmann et al., 2011), limited food availability (Lutz et al., 2007) and low temperatures which limit rate processes (Childress, 1995), may be particularly sensitive to natural and human-induced environmental changes that are occurring at unprecedented rates (Crain et al., 2008; Gehlen et al., 2014; Rogers, 2015).

Since the early work of Hessler and Sanders (1967), much has been learned about general patterns of benthic species biodiversity in the deep ocean and how it changes along bathymetric gradients (Rex and Etter, 2010). Alpha (α) diversity describes local diversity, for example within a single sample or site. Regional and depth related changes in α-diversity were the focus of the majority of early studies so that spatial trends are now considered reasonably well understood for several parts of the North Atlantic (Rex and Etter, 2010). In general, the α-diversity of benthic macrofauna in the North Atlantic exhibit a unimodal diversity pattern: increasing toward the lower bathyal or upper abyssal depths and decreasing toward the deeper abyss (Rex, 1973; Andrew and Scott, 2000). Patterns of benthic diversity north of the Greenland-Iceland-Faroe (GIF) ridge, in the Nordic Seas and Arctic Ocean, are notably different from those generally described for the North Atlantic. In high-latitude regions the relationship between α-diversity and depth is unimodal as generally observed south of the GIF ridge but α-diversity peaks at a much shallower depth (higher bathyal or shallower) with remarkably low diversity at lower bathyal and abyssal depths (Svavarsson, 1997; Bett, 2001). However, the diversity on the shelfs is not considered particularly low (Piepenburg et al., 2011).

Beta (β) diversity describes changes in community composition within a region or along a gradient (Whittaker, 1960, 1972). Increased sampling effort and data availability has facilitated research on β-diversity in the ocean, with results interpreted almost exclusively as spatial replacement of species along depth or horizontal gradients (McClain and Rex, 2015). However, β-diversity can also be affected by species loss (or gain) resulting in smaller communities forming ordered subsets of the species composition of larger communities, a pattern also referred to as "nestedness" (Ulrich and Gotelli, 2007; Almeida-Neto et al., 2008). The specific ecological significance of either species replacement or nestedness has driven multiple efforts intended to mathematically quantify the contribution of these components to β-diversity (McClain and Rex, 2015). In recent years, studies of deep-sea diversity have used a method presented by Baselga (2010, 2012) to partition β-diversity into two additive components: nestedness resultant dissimilarity and dissimilarity resulting from species turnover. This partitioning has allowed for new insight into deep-sea diversity patterns (Wagstaff et al., 2014; Stuart et al., 2017). For example, Brault et al. (2013b) concluded that abyssal neogastropoda assemblies are likely supported through source-sink dynamics, partly based on a significant increase in nestedness with depth along with a decrease in α-diversity. Although not a commonly used method in research of deep-sea diversity, due to the lack of comparable sampling strategies, a regional comparison approach for α- and β-diversity patterns can also help identify the processes that drive deep-sea diversity patterns (e.g., Brault et al., 2013a).

The Mollusca is a species rich and diverse phylum whose species are among the more conspicuous and biodiverse invertebrate macrofauna in the marine environment (Alongi, 1990; Linse et al., 2006). Within the Mollusca phylum, gastropods and bivalves are the most species rich classes (Horton et al., 2019). Species belonging to both groups can play crucial roles as keystone species (Paine, 1969) or as ecosystem engineers, as a result of their feeding mechanisms or calcification traits (e.g., Hall-Spencer and Moore, 2000; Gutiérrez et al., 2003). Calcifying molluscs are considered particularly susceptible to ocean acidification and the concurrent decrease in the saturation state for calcium carbonate (Ω) (Gazeau et al., 2013; Gattuso et al., 2015). As a result of increased pressure, Ω decreases with depth (Millero, 2007), but disentangling the relative ecological importance of Ω and other environmental parameters that relate to depth, such as food availability and sediment characteristics, is challenging. Collecting information on species occurrences and biodiversity of calcifying molluscs is an important first step toward understanding the implication of changes in Ω, temperature and other large scale environmental changes in deep benthic habitats (Urban et al., 2016). The need for baseline data is especially urgent in the Nordic Seas, due to the naturally low Ω of seawater and the fact that Ω is decreasing at an alarming rate in both surface and deep waters (Olafsson et al., 2009; Skogen et al., 2014).

The GIF ridge acts as a topographic barrier that separates two ocean basins: the Nordic Sea basin to the north and the North Atlantic basin to the south. While the maximum sill depth of the Greenland-Iceland ridge and the Iceland-Faroe Island ridge is 620 and 480 m respectively, the seafloor reaches depths exceeding 3000 m south and north of the GIF ridge (Jakobsson, 2002). The biogeographic boundaries at the GIF ridge coincide with a transition between colder and warmer water masses, with Iceland coinciding with the Arctic Front (Hansen and Meincke, 1979). Thus, the island is considered to occupy a key position in the North Atlantic in terms of biogeographical species ranges (Briggs, 1970; Dahlgren et al., 2000; Jöst et al., 2018). Comparisons of biodiversity has previously been conducted between benthic habitats directly north and south of the GIF ridge for hyper-benthic amphipods

(Weisshappel and Svavarsson, 1998; Weisshappel, 2000), benthic isopods (Svavarsson et al., 1993; Svavarsson, 1997; Brix et al., 2018; Schnurr et al., 2018), ostracods (Jöst et al., 2018), and foraminifera (Gudmundsson, 1998). However, a comparison of mollusc species diversity patterns between the regions has not been conducted to date.

The main objective of this study was to increase understanding of biodiversity patterns in the high-latitude North Atlantic by investigating α- and β-diversity patterns in molluscs along the bathymetric gradient north and south of the GIF ridge. A secondary objective of this study was to identify bivalve and gastropod species which could be used as indicator species to monitor ecological integrity north of the GIF ridge (Carignan and Villard, 2002). Future monitoring efforts should preferably include a variety of taxa but as bivalves and gastropods are known to be sensitive to Ω, they could provide early warning of natural responses in areas undergoing rapid ocean acidification, such as is observed north of the GIF ridge (Gattuso et al., 2015). To achieve these goals, we use data on bivalves and gastropods collected during the sampling program BIOICE (Benthic Invertebrates of Icelandic waters).

MATERIALS AND METHODS

Study Regions

The study regions encompass the Icelandic shelf and slope within the Iceland Sea to the north of the GIF ridge and the Icelandic shelf and slope to the south of the GIF ridge (**Figure 1**). These regions share topographic similarities as they both include the Icelandic shelf and slope and parts of the Mid-Atlantic Ridge but the broad separation by the GIF ridge results in regional hydrographic differences (Stefánsson, 1962). The Iceland Sea is a part of the Nordic Seas along with the Norwegian Sea and Greenland Sea (Jakobsson, 2002). The hydrographic properties of the Iceland Sea are generally described as Arctic Intermediate Water overlying Arctic Deep Water (Stefánsson, 1962; Swift et al., 1980). These waters are characterized by sub-zero temperatures throughout the water column in winter and a shallow (∼200 m) mixed layer in the summer, in which temperatures exceed 0°C (Olafsson, 2003; Olafsson et al., 2009). The oceanographic environment south of the ridge reflects a dynamic interaction between water masses with different physical properties, with temperatures ranging from 2 to >10°C (Hansen and Østerhus, 2000; Malmberg and Valdimarsson, 2003). Ocean warming and ocean acidification have been observed at the surface in both the Iceland and the Irminger Sea (southwest of Iceland) with warming and acidification observed down to at least 1800 m in the Iceland Sea over the last two decades (Olafsson et al., 2009, 2010).

Biological Data

Benthic samples were collected between 20 and 3020 m depth during the years 1991–2004 of the BIOICE program (Gudmundsson, 1998). Four types of towed sampling gears were used in the program, depending on bottom type, but this study only includes data collected using a modified RP sled (Rothlisberg and Pearcy, 1977; Brattegard and Fosså, 1991) and a Sneli sled (Sneli, 1998) since these gears were most frequently deployed and sampled similar species assemblages (**Supplementary Material 1**). Species records and their taxonomic classification were manually examined and edited where necessary to correspond to entries in the database "World Register of Marine Species" and synonyms standardized to a single name. Information on the sample data considered for the study, a list of all species recorded, number of samples they were recorded in and their observed depth range in each study region is provided (**Supplementary Material 2**).

Analytical Approach

Sample data collected using a modified RP sled and Sneli sled were pooled for analysis of biodiversity as the sampled species assemblages were similar between the gear types. The total number of samples collected within the study regions was 366 and 383, north and south of the GIF ridge, respectively. Samples collected using a RP sled and Sneli sled contributed near equally to the total number of samples in both regions.

The number of unobserved species, in addition to the observed species richness, was estimated based on the singletons and doubletons in species matrices (Chao, 1987) along with a standard error (Chiu et al., 2014). Estimations were carried out for each region and separately for four 500 m depth ranges, between surface and 2000 m depth, below which sample data were considered insufficient for estimating species richness.

Alpha diversity was estimated using the Sanders-Hurlbert expected number of species (Sanders, 1968; Hurlbert, 1971) in a sample normalized to 20 individuals [$E(S_{20})$], excluding from the analysis samples where fewer than 20 individuals of either gastropods or bivalves were collected. Accordingly, the number of samples available for the analysis was reduced to a total of 252 and 250 for bivalves north and south of the GIF ridge respectively, and a total of 146 and 197 samples for gastropods in the same regions respectively. To investigate how $E(S_{20})$ varied with depth in each region, samples were averaged into 100 m bins and a linear least squares regression used to identify trends in $E(S_{20})$ as a function of depth within the bathyal zone, or between 300 to 2000 m.

To explore the relationship of depth and region with species assemblages of bivalves and gastropods, a 2-dimensional NMDS analysis on presences-absence (binary) species matrices was conducted, excluding species occurring in less than 5% of samples in each region. The NMDS analysis was based on Sørensen (Bray-Curtis) sample dissimilarity (Sørensen, 1948). The contribution of depth and region to MDS1 (primary NMDS axis) and MDS2 (secondary NMDS axis) were analyzed using a least squares linear regression and a Student *t*-test respectively.

Optimal methods for analysis of β-diversity along environmental gradients require data collected using standardized sampling methods but like the majority of research on deep-sea diversity patterns of macro- and/or meiofauna (Rex and Etter, 2010), this study relies on methods that are not standardized. The sampling sleds within the BIOICE were typically towed for 20 min but the average tow time was 19 ± 6 min (**Supplementary Material 2**) and the bottom substrate towed was unknown. We recognize the issues associated with the lack

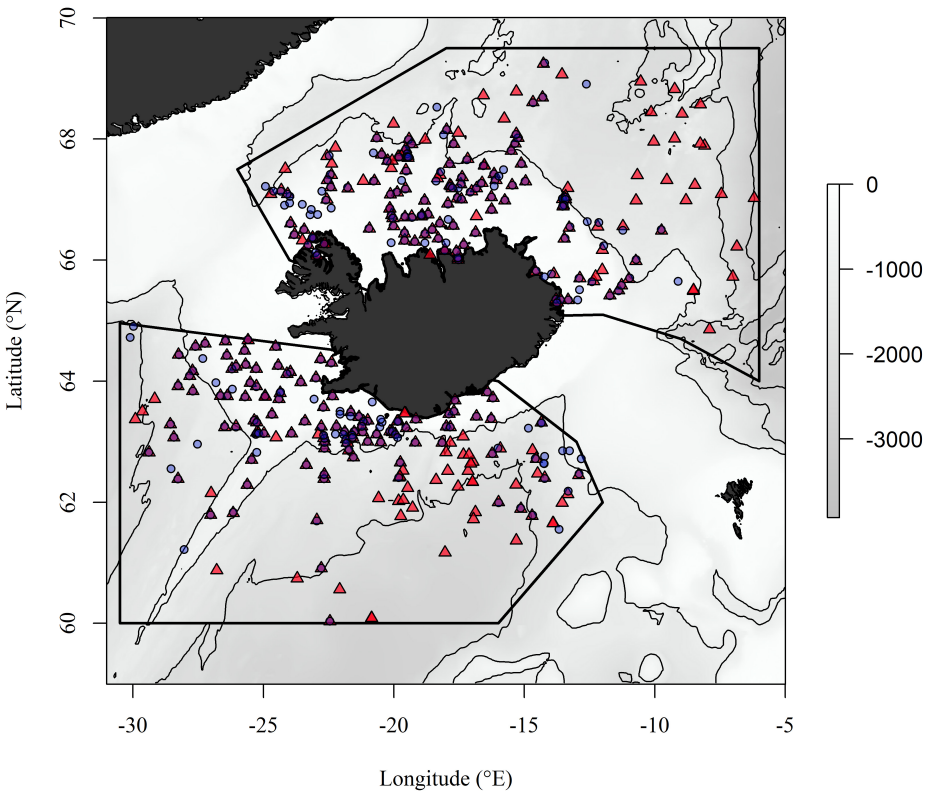


FIGURE 1 | The study regions north and south of the Greenland-Iceland-Faroe ridge and geographic location of BIOICE samples included in the study. Red triangles and blue circles are localities of benthic samples collected through towing a modified RP sled and Sneli sled, respectively. Contour lines are placed at 1000 m depth intervals.

of standardized sampling and issues resulting from the non-random and unsystematic spatial distribution of sample localities in the BIOICE program, especially the limited sampling effort at depths below 1500 m. To address these issues, sample data were aggregated into 100 m depth bins with bins containing fewer than 100 and 50 individual bivalves and gastropods respectively being discarded from the β-diversity analysis. Data were converted to presence-absence (binary) species matrices. The analysis was restricted to an upper depth limit of 300 m to exclude the shallow water communities on the Iceland shelf in the analysis of β-diversity. As a result, the analysis was applied to the depth range of 300 to 1600 m, with 14 depth bins for bivalves but 13 depth bins for gastropods, due to the exclusion of the 1200 m depth bin. To investigate β-diversity dynamics, including the contribution of nestedness to β-diversity, we use two independent methods.

Baselga (2010, 2012) described how β-diversity could be mathematically separated into two components: (A) β-diversity resulting from species replacement between sites which is commonly referred to as species turnover, and (B) the part of dissimilarity that can be attributed to the effect of species loss (or gain) or species nestedness. The calculations of β-diversity and the relative contribution of turnover and nestedness are based on Sørensen (Bray-Curtis) dissimilarity (Sørensen, 1948). Multiple site dissimilarity measures (indicated by capital letters) were generated and gave a single score for β-diversity ($\beta_{SØR}$) and the relative contribution of species turnover (β_{SIM}) and nestedness (β_{SNE}) to dissimilarity in each region. A comparison between multiple site dissimilarity scores can only be made between regions with equal sample sizes (Baselga, 2012). However, a repeated sampling of the dissimilarity scores for a subset of the original data frame yields average metrics with standard errors that can be compared between regions with different sample sizes (Baselga, 2012). Although the depth bins were standardized between regions, we report multiple site dissimilarity scores based on 100 sampling repetitions to increase the comparability of the results. Through pairwise comparisons of samples (indicated by lower case letters) we also assessed if β-diversity metrics, referred to as $\beta_{sør}$, β_{sim}, and β_{sne}, varied depending on sample depth separations. The relationship between pairwise dissimilarity scores and sample depth separation was explored through least squares linear regression but recognizing that pairwise comparisons inflate the degrees of freedom, a regression was only seen as significant where the resulting *p*-value for the slope was equal to, or below 0.001.

The direction of nestedness along the bathymetric gradient was explored using the software BINMATNEST (Rodríguez-Gironés and Santamaría, 2006, 2010). The "temperature" of the species presence-absence matrix, which is defined as the sum

of "surprises" in an arranged matrix (ranging from 0 to 100°), was determined reflecting a fully nested matrix to nested pattern respectively. The analysis also ranks the depth bins on the basis of nestedness which can be used to inform of the direction of nestedness along an environmental gradient (Stuart et al., 2017). To test if significant nestedness occurred in the species matrices and to rank depth bins on the basis of nestedness, a computation of 1000 null matrices was performed and the species matrices tested for randomness using the recommended choice of null model in BINMATNEST (model 3) (Rodríguez-Gironés and Santamaría, 2006).

Selecting Indicator Species

Bivalve and gastropod species were identified, that could be considered suitable to be monitored to identify early changes in benthic communities due to environmental changes north of the GIF ridge, with special focus on ocean acidification and the decrease in **Ω**. With the purpose of excluding rare or ubiquitous species, species were listed based on their sampling frequency and abundance in sled samples in the BIOICE dataset, which included 366 samples north of the GIF ridge. In the BIOICE program, species were counted in samples up to at least 100 individuals, so although the dataset does not include complete abundance measurements for highly abundant species, it is possible to identify bivalve and gastropod species as abundant, or not, based on a pre-defined criterion. Species were listed if they met the following criteria: (A) Detected in 40 or more samples; (B) At least 25% of samples included five or more individuals; (C) Detected in 25% or more samples collected within its observed depth range; (D) not observed beyond 1500 m depth in the BIOICE dataset.

With the exception of the BINMATNEST software, all data analysis was performed using R (R-Core-Team, 2018), and the *vegan* (Oksanen et al., 2015) and *betapart* packages for R (Baselga and Orme, 2012).

RESULTS

Species Richness

Bivalves were generally more abundant in samples than gastropods, but gastropods were roughly twice as species rich as bivalves in both study regions. The total observed bivalve species richness was 85 north of the GIF ridge and 114 in south of the GIF ridge, with 71 species shared between both regions. Based on the analysis of undetected species richness, the estimated bivalve species richness (±standard error) was 95 ± 8 and 137 ± 15 north and south of the GIF ridge respectively. A bivalve species richness of 7 ± 1 was estimated for the depth range 1501–2000 m north of the GIF ridge compared to a total of 34 ± 6 south of the GIF ridge (**Figure 2**). The observed gastropod species richness was 173 and 189 north and south of the GIF ridge respectively, with 133 species shared between regions. Estimated total gastropod species richness (±standard error) was 201 ± 12 and 266 ± 33 north and south of the GIF ridge. Gastropod species richness estimated within the depth range 1501–2000 m was 19 ± 11 and 73 ± 9 north and south of the GIF ridge, respectively (**Figure 2**).

Alpha Diversity

Analysis of $E(S_{20})$ for bivalves and gastropods north of the GIF ridge indicates a unimodal relationship with depth, reaching a maximum of ∼5 species between 100 and 600 m (**Figure 3**). A linear regression model of $E(S_{20})$ fitted within the 300 to 2000 m depth range north of the GIF ridge presents a steep decrease in both bivalve and gastropod α-diversity along the bathymetric gradient with high R^2 values found for bivalves (R^2 = 0.92) and gastropods (R^2 = 0.77) respectively (**Table 1**). South of the GIF ridge a similar unimodal relationship between α-diversity and depth was observed in bivalves with a modest decrease from 300 to 2000 m depth. In contrast with the north, R^2 values were much lower for bivalves in the south (R^2 = 0.22) while no

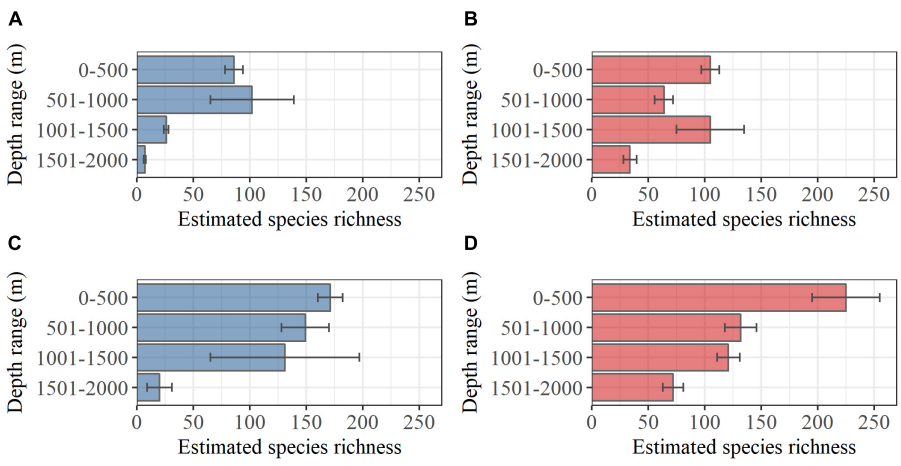


FIGURE 2 | Estimated species richness within 500 m depth intervals based on (Chao, 1987). Error bars represent standard errors of the estimates based on Chiu et al. (2014) for **(A)** bivalves north of the GIF ridge and **(B)** bivalves south of the GIF ridge, **(C)** gastropods north of the GIF ridge and **(D)** gastropods south of the GIF ridge.

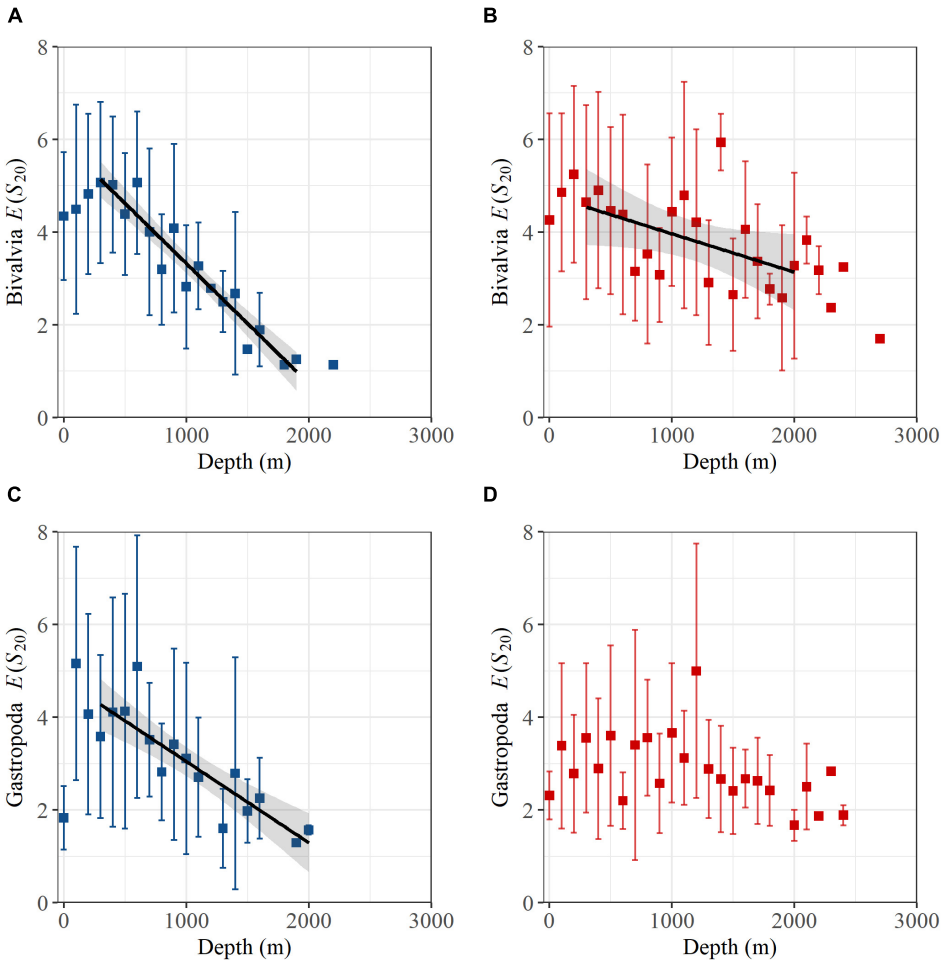


FIGURE 3 | Hurlbert-Sanders expected number of species in a sample of 20 individuals, $E(S_{20})$, for **(A)** bivalves north of the GIF ridge, **(B)** bivalves south of the GIF ridge, **(C)** gastropods north of the GIF ridge, and **(D)** gastropods south of the GIF ridge. Rarefied samples were averaged into 100 m depth bins with error bars representing standard deviations. Where only one sample was available for rarefaction there is no error bar shown. Black lines and shaded region are fitted linear regression models and standard error respectively.

clear trend was detected in gastropod $E(S_{20})$ south of the GIF ridge (**Figure 3**).

Species Assemblages

Depth influenced community composition more strongly than region in both bivalves and gastropod, but the relationships between these factors and species composition was stronger for bivalves compared to gastropods (**Figure 4**). The MDS1 score for bivalve communities was strongly correlated with the logarithm of depth (Pearson's product-moment correlation: $r = 0.84$, $t = 33$, $df = 469$, $p < 0.001$) and the MDS2 scores differed between the study regions (t-test: $t = -26$, $df = 458$, $p < 0.001$). The MDS1 score for gastropod communities was also significantly correlated with the logarithm of depth although not as strongly as in bivalves (Pearson's product-moment correlation: $r = 0.50$, $t = -12$, $df = 406$, $p < 0.001$) and the MDS2 also differed by region (t-test: $t = 11$, $df = 405$, $p < 0.001$).

TABLE 1 | Results from least square linear regression models of $E(S_{20})$ as a function of depth between 300 and 2000 m.

Class	Region	*a*	*b*	Std. Error	*t*-value	R^2	*p*-value[1]
Bivalvia	North	5.92	−0.00259	0.00020	−12.84	0.92	***
	South	4.79	−0.00083	0.00039	−2.18	0.22	*
Gastropoda	North	4.80	−0.00175	0.00028	−6.34	0.76	***
	South				ns		ns

Coefficients are based on the equation y = a + b d, where a is the intercept and b is the slope which was statistically evaluated, and "d" is depth in meters. [1] ****p < 0.001; **p < 0.01; *p < 0.05; ns = p > 0.001.*

Beta Diversity

Analysis of the β-diversity dynamics in bivalve and gastropod species assemblages between 300–1600 m suggests that although the overall β-diversity is comparable between the study regions, there are differences in the relative contribution of nestedness and turnover to β-diversity.

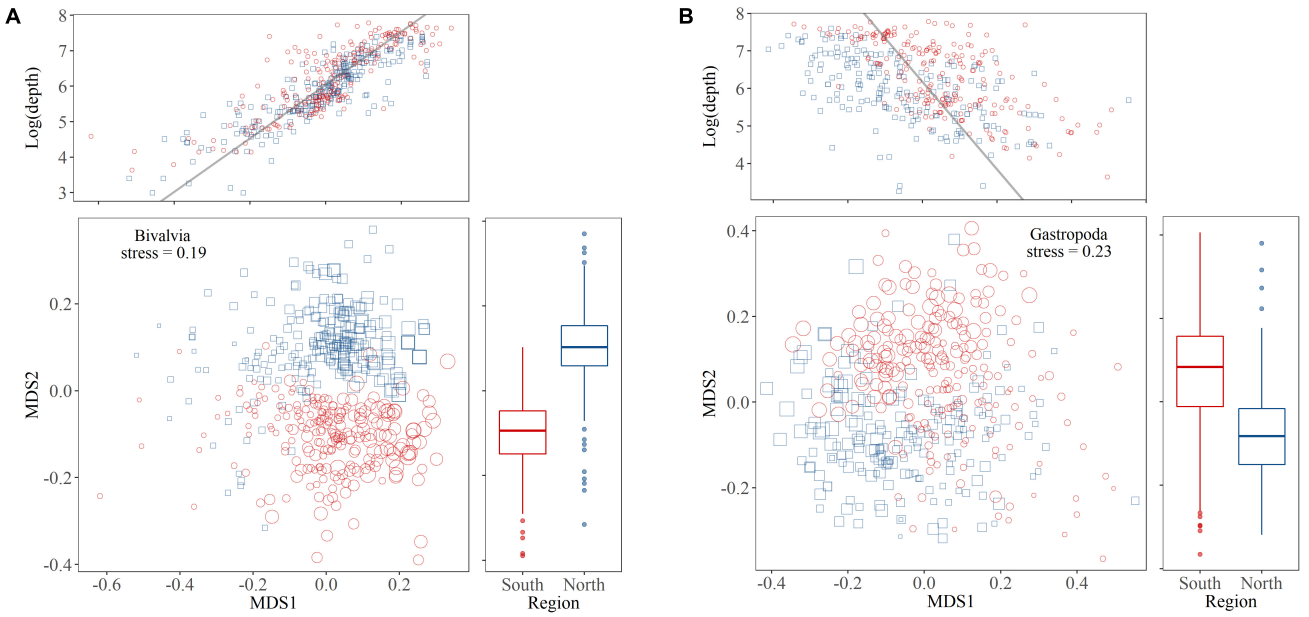


FIGURE 4 | Two-dimensional non-metric multidimensional scaling (NMDS) plots for **(A)** bivalve and **(B)** gastropod assemblages. For each class a central plot shows the results of the analysis with sample data representing the Iceland Sea basin north of the GIF ridge (blue squares) and the region south of the GIF ridge (red circles). The point size relates to the logarithm of sample depth. On top is a correlation of the MDS1 scores and the logarithm of depth which was significant in bivalves and gastropods and to the right a boxplot shows the significant regional difference for MDS2 scores in both groups.

In bivalves, β-diversity was higher north of the GIF ridge compared to that south of the GIF ridge (*t*-test on pairwise scores for $\beta_{sør}$: $t = 40.5$, $df = 189$, $p < 0.001$; **Figure 5**). Multiple site metrics (±standard deviation) for the region north of the GIF ridge indicate a similar contribution of nestedness (β_{SNE}) and turnover (β_{SIM}) to the overall β-diversity ($\beta_{SØR}$) in the region with $\beta_{SØR} = 0.76 \pm 0.02$, $\beta_{SIM} = 0.39 \pm 0.02$ and $\beta_{SNE} = 0.37 \pm 0.03$. Nestedness contributed to a lesser degree to the regional dissimilarity south of the GIF ridge where $\beta_{SØR} = 0.74 \pm 0.01$, $\beta_{SIM} = 0.58 \pm 0.03$, and $\beta_{SNE} = 0.17 \pm 0.03$. Pairwise scores suggest that species community differences increase with increasing depth separation in both regions, i.e., $\beta_{sør}$ was positively related to depth separation (**Table 2**). The increase in $\beta_{sør}$ reflect higher β_{sne} scores with increasing depth separation north of the GIF ridge, whereas species turnover contributes to a greater extent to the change in species communities south of the GIF ridge (**Figure 5**).

In gastropods, β-diversity was higher north of the GIF ridge compared to that south of the GIF ridge (*t*-test on pairwise scores for $\beta_{sør}$: $t = 47.8$, $df = 163$, $p < 0.001$; **Figure 5**). Multiple site metrics (±standard deviation) for the region north of the GIF ridge, $\beta_{SØR} = 0.81 \pm 0.01$, $\beta_{SIM} = 0.60 \pm 0.02$, and $\beta_{SNE} = 0.21 \pm 0.02$, suggest a lesser contribution of nestedness to β-diversity in gastropods compared to bivalves. Multiple site metrics for β-diversity of gastropods south of the GIF ridge were $\beta_{SØR} = 0.75 \pm 0.01$, $\beta_{SIM} = 0.64 \pm 0.02$, and $\beta_{SNE} = 0.11 \pm 0.02$. Results of pairwise comparisons for gastropods indicate an increase in β-diversity ($\beta_{sør}$) with increasing depth separation in both regions (**Table 2**). An increase in β_{sne} with increasing depth separation was observed north of the GIF ridge in gastropods, similar to the trend observed in bivalves (**Figure 5**). Regression models for gastropods did not detect a trend in β_{sim} with increasing depth separation for either region.

The BINMATNEST test rejected the null hypothesis of no nestedness in bivalve and gastropod species matrices in both regions. A correlation of the rank order of nestedness for each depth bin also indicated a significant linear increase in nestedness with increasing depth (**Figure 6**). The relationship was relatively strong north of the GIF ridge but relatively weak south of the GIF ridge in both bivalves and gastropods.

Identifying Indicator Species

Ten bivalve and five gastropod species met the criteria for monitoring ecological integrity of the benthic ecosystem north of the GIF ridge (**Table 3**).

DISCUSSION

Species richness on the Icelandic shelf north and south of the GIF ridge was similar. This finding is in agreement with the findings of Piepenburg et al. (2011) who showed that the benthic species richness on the shelfs (above ∼200 m) within the Arctic Seas is not particularly low compared to species richness at lower latitudes, as had been previously suggested based on limited sample data.

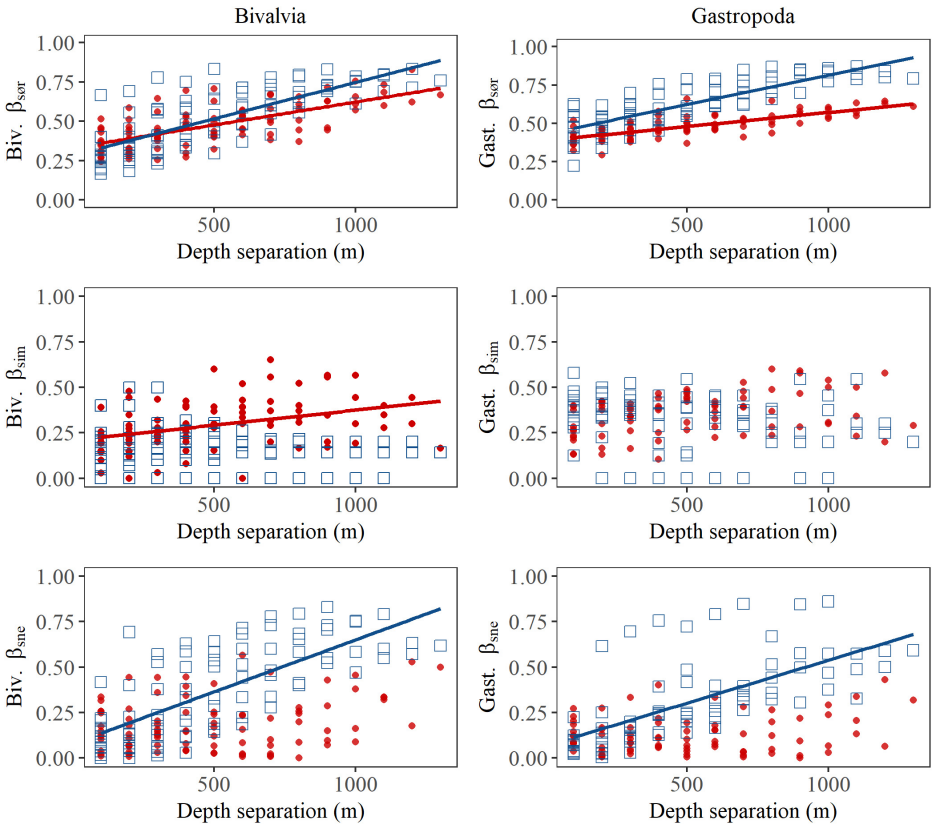


FIGURE 5 | Pairwise dissimilarity of bivalve (left) and gastropod (right) assemblages as a function of depth separation among depth bins in the Iceland Sea north of the GIF ridge (blue square) and south of the GIF ridge (red points). Pairwise overall β-diversity, or $\beta_{sør}$ is partitioned into β_{sim} or dissimilarity resulting from species replacement and β_{sne} or dissimilarity resulting from nestedness or species loss (or gain). Regression lines indicate where least square linear regression resulted in a $p < 0.001$ for the slope.

Alpha Diversity

We observed a pronounced decrease in α-diversity with increasing depth between 300 and 2000 m depth in both bivalves and gastropods north of the GIF ridge. Notably, species richness estimates indicate an order of a magnitude decrease from the 501–1000 m depth range to the 1501–2000 m depth range in bivalves. These findings are in agreement with a decrease in α-diversity with increasing depth previously described in other benthic taxa in the Nordic Seas, including isopods (Svavarsson, 1997), amphipods (Stephensen, 1940; Weisshappel and Svavarsson, 1998), polychaetes (Narayanaswamy et al., 2005; Oug et al., 2017), foraminifera (Mackensen et al., 1985; Gudmundsson, 2002), and the overall macrofauna (Bett, 2001). In fact, studies on benthic diversity in the deep Nordic Sea basin have consistently described low species richness compared to deep zones in other seas and ocean basins, including the North Atlantic south of the GIF ridge (Bouchet and Warén, 1979; Dahl, 1979; Rex et al., 2000). The cause of the low diversity in the deep Nordic Sea basin is likely linked to low temperatures and limited energy availability as discussed further in the following chapter on beta diversity. The α-diversity trends presented here are also similar to that described for the Arctic Ocean as a whole (Bodil et al., 2011).

The α-diversity patterns observed south of the GIF ridge, i.e., a decrease in $E(S_{20})$ in bivalves along the bathymetric gradient and a lack of trend in $E(S_{20})$ in gastropods, contrasts with previously described diversity patterns directly south of the GIF

TABLE 2 | Results from linear least squares regression models of Baselga (2010, 2012) pairwise β-diversity metrics as a function of depth separation between 300 and 1600 m.

Class	Region	Metric	*A*	*b*	Std. Error	*t*-value	R^2	*p*-value
Bivalvia	North	$\beta_{sør}$	0.28	0.00046	0.00004	10.9	0.57	***
		β_{sim}						ns
		β_{sne}	0.08	0.00057	0.00006	10.1	0.53	***
	South	$\beta_{sør}$	0.33	0.00029	0.00003	8.9	0.47	***
		β_{sim}	0.21	0.00017	0.00004	4.0	0.15	***
		β_{sne}						ns
Gastropoda	North	$\beta_{sør}$	0.43	0.00038	0.00003	12.5	0.67	***
		β_{sim}						ns
		β_{sne}	0.07	0.00047	0.00006	7.9	0.45	***
	South	$\beta_{sør}$	0.39	0.00018	0.00002	9.8	0.56	***
		β_{sim}						ns
		β_{sne}						ns

*Coefficients are based on the equation $y = a + b\,ds$ where a is the intercept and b is the slope which was statistically evaluated and "ds" stands for depth separation. ***$p < 0.001$; ns = $p > 0.001$.*

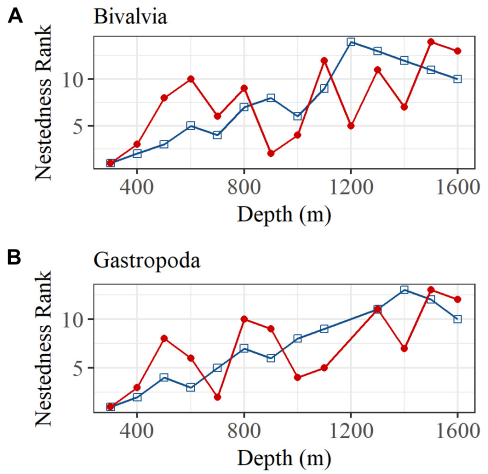


FIGURE 6 | The rank order of nestedness calculated using the BINMATNEST software for **(A)** bivalves and **(B)** gastropods, north (blue squares and line) and south (red dots and line) of the GIF ridge.

TABLE 3 | Bivalve and gastropod species that are suitable for monitoring ecological integrity of the benthic ecosystem north of the GIF ridge.

Class	Family	Species	No. samples[1]	Depth range	% samples within depth range
Bivalvia	Astartidae	*Astarte sulcate*	155	<50–1000	57
	Arcidae	*Bathyarca glacialis*	67	200–900	34
	Mytilidae	*Crenella decussata*	110	<50–750	50
	Cuspidariidae	*Cuspidaria subtorta*	197	<50–1150	71
	Mytilidae	*Dacrydium vitreum*	226	100–1400	82
	Nuculidae	*Ennucula corticata*	66	100–550	40
	Nuculidae	*Ennucula tenuis*	75	<50–750	34
	Nuculanidae	*Nuculana pernula*	114	<50–750	52
	Thyasiridae	*Thyasira dunbari*	205	50–1300	71
	Yoldiidae	*Yoldiella nana*	84	50–900	35
Gastropoda	Cancellariidae	*Admete viridula*	107	50–1100	39
	Capulidae	*Ariadnaria borealis*	113	<50–1000	42
	Cylichnidae	*Cylichna alba*	93	100–1300	34
	Lepetidae	*Lepeta caeca*	49	50–650	26
	Mangeliidae	*Propebela nobilis*	110	<50–1300	37

Species listed met the following criteria: (A) Detected in 40 or more samples; (B) At least 25% of samples included five or more individuals; (C) Detected in 25% or more samples collected within its observed depth range; (D) not observed beyond 1500 m depth in the BIOICE dataset. [1]Number of samples where a species was detected in a total of 366 samples.

ridge and in the broader North Atlantic (Rex and Etter, 2010). For example, Svavarsson (1997) report an significant increase in isopod $E(S_{200})$ directly south of the GIF ridge from 200 to 1500 m, but isopod diversity trends are known to deviate from general trends in other macrofauna as the order includes many species specifically adapted to the deep-sea (Hessler et al., 1979; Rex and Etter, 2010). In the broader North Atlantic, Bett (2001) and Narayanaswamy et al. (2005) also reported an increase in overall macrofauna and polychaete $E(S_n)$ between 200 and 2000 m depth in the Rockall Trough, south of the Wyville-Thomson ridge. Also, Brault et al. (2013a) described an increase in $E(S_{20})$ from the shelf toward depths exceeding 2000 m in bivalves in the western and eastern North Atlantic. The explanation for the observed deviation from the general trend directly south of the GIF ridge is unknown and requires comprehensive data on the environmental setting of the region. A likely explanation is that the oceanographic conditions directly south of the GIF ridge might affect biodiversity patterns (Gudmundsson, 1998), in particular, the relatively brisk current below ∼1500 m depth, carrying North Atlantic Deep Water (NADW) mixed with cool overflow water from the Nordic Seas westward at along the Icelandic continental slope (Dickson et al., 1990; Logemann et al., 2013). Current regimes can also impact upon sediment properties through resuspension of fine sediments, with sediment particle size recognized as an important driver of benthic diversity (Etter and Grassle, 1992; Gray, 2002). A numerical modeling study of sediments indicated that fine grained sediments or clay did not increase with increasing depth south of the GIF ridge as was observed north of the GIF ridge (Ostmann et al., 2014). However, due to the likely patchy sediment environments along the bathymetric gradient (Gray, 1981) and few benthic sampling localities (11) included in the study (Ostmann et al., 2014), the importance of sediment composition in driving diversity trends south of the GIF ridge remains uncertain.

Comparing Bivalves and Gastropods

General trends in bivalve and gastropod α- and β-diversity were similar north and south of the GIF ridge, but there were some marked differences between the groups. A difference is not unexpected as bivalves and gastropods have evolved independently for nearly 500 million years and have different habitat requirements and feeding mechanisms that should be considered (Ponder and Lindberg, 2008). Most bivalves have low mobility, include many infaunal species and are generally suspension or deposit feeders (Roy et al., 2000). Gastropods, on the other hand, are more species rich than bivalves, are functionally more diverse, operating as predators, grazers, omnivores, deposit feeders or carnivores, and are largely epifaunal (Hughes, 1986).

This considered, it is possible that the greater phylogenetic- and functional diversity of gastropods, could account for the larger unexplained variance in overall gastropod assemblages as compared to bivalve assemblages. Despite these differences, species assemblages of both taxonomic groups varied more as a function of water depth than region, indicating that water depth, and specifically the environmental changes associated with water depth, are a significant driver of β-diversity in both regions. This is in agreement with McClain et al. (2012), who described depth to be a better predictor of deep-sea bivalve β-diversity than geographical separation. Our exploration of the BIOICE data also found that a significant number of species were shared between regions to the north and south of the GIF ridge, despite environmental differences.

Beta Diversity

It is possible that the observed patterns in β-diversity could, in conjunction with the rapid decrease in α-diversity along the bathymetric gradient, reflect the geological history of the North Atlantic to some extent (Barry et al., 2013). During the last

glacial maximum, ice sheets covered the Nordic Seas, limiting surface primary production and the subsequent downward flux of organic matter to the seafloor. The benthic environment changed dramatically when the ice retreated ∼14 thousand years ago resulting in a significant increase in primary production at the surface and changes in water circulation (Smith et al., 1997; Müller et al., 2009). While Pleistocene glaciations likely eradicated much of the shelf and deep-sea fauna in the Arctic, other shelf fauna found refuge in the deep-sea and are considered the ancestral fauna of some of today's Arctic deep-sea fauna (Nesis, 1984). Thus, a large proportion of the fauna on the shelfs of the Nordic Seas is likely to have been introduced from the North Atlantic within the Holocene time-period.

Although the geological history of the North Atlantic is likely to play a significant role in shaping the species composition in the Nordic Seas, recent studies provide evidence supporting previous hypothesis indicating that energy dynamics, including chemical energy (i.e., food availability) and kinetic energy (i.e., temperature) are the most important drivers of both α- and β-diversity patterns in the benthic marine environment (Tittensor et al., 2010; Brault et al., 2013a; Woolley et al., 2016; Yasuhara and Danovaro, 2016). Temperature is a particularly important driver at temperatures below 5°C (Yasuhara and Danovaro, 2016) and thus the transition from ∼2 to 4°C south of the GIF ridge to a ∼−1°C north of the ridge undoubtably present many species with a physiological barrier. The physiological effect of hydrostatic pressure in conjunction with low temperatures could also explain the especially low diversity observed in the deep Nordic Sea basin (Brown and Thatje, 2014). Food availability, temperature and hydrostatic pressure are not mutually exclusive drivers but can influence species performance synergistically (e.g., Brockington and Clarke, 2001; Sebert, 2002). The ocean surface north and south of the GIF ridge exhibit significant seasonality in surface primary production, but there are notably shorter periods of phytoplankton blooms in the Iceland Sea, north of the GIF ridge (Pálsson et al., 2012; McGinty et al., 2016). Therefore, the benthic community in the deep Nordic Seas may be mostly composed of species who have successfully adapted to the extreme energy constraints in the region, i.e., sub-zero temperatures and highly pulsed availability of chemical energy.

Based on Baselga (2010) partitioning and the BINMATNEST rank order for bivalve and gastropod assemblages north of the GIF ridge, increasing community dissimilarity is largely due to the increase in nestedness, or species loss with depth, and relates to the decrease in α-diversity. Brault et al. (2013b) also reported lowered α-diversity, coupled with increasing nestedness from bathyal to abyssal depths in neogastropods. They argued that this pattern provides evidence of source-sink dynamics, i.e., that the abyssal populations are not self-sustaining due to the poor habitat quality at greater depths and require introduction of individuals from shallower habitats (Rex et al., 2005; Brault et al., 2013b). Similarly, the increase in nestedness north of the GIF ridge, in concert with the decrease in α-diversity, could indicate that at least some populations of bivalves and gastropods are not self-sustainable in the deeper part of their observed depth ranges, but instead require introduction from a "source"-population at shallower depths where food is more abundant and calcium carbonate saturation states (**Ω**) higher. For example, bivalve molluscs have been shown to require species specific **Ω** for successful larval development (Waldbusser et al., 2015). However, as pointed out by Brault et al. (2013b) such diversity patterns do not provide sufficient evidence to establish the existence of source-sink dynamics in a meta-population. Information regarding the genetic structure of "source" and "sink" populations is also required (e.g., Manier and Arnold, 2005).

The contribution of species turnover to β-diversity was considerably greater south of the GIF ridge where nestedness resultant dissimilarity was less significant. Nevertheless, the BINMATNEST analysis of nestedness indicated an increase in nestedness with depth south of the GIF ridge, albeit the correlation was relatively weak compared to that north of the GIF ridge. This was an unexpected finding as species turnover was expected to dominate β-diversity to a greater extent in this region. However, this finding likely relates to the unexpected decrease in α-diversity with increasing depth observed south of the GIF ridge, which again, possibly results from the special oceanographic regime directly south of the GIF ridge.

It is clearly of importance to increase understanding of the relative contribution of various environmental drivers associated with depth (e.g., hydrostatic pressure, food availability, temperature, **Ω**, and pH) to biodiversity patterns in the deep-sea. Research aimed to increase this understanding remains a challenge due to the significant correlation of multiple environmental parameters along the depth gradient. Recent studies have, however, recognized energy availability as a major driver of diversity patterns in the deep-sea (Brault et al., 2013a; Woolley et al., 2016). Nevertheless, it is likely that other environmental parameters also play a role in driving diversity patterns in distinct groups. For example, the decrease in **Ω** associated with depth could be a significant driver of biodiversity in the taxonomic groups investigated in this study and other calcifying taxa.

Identifying Indicator Species

Most of the bivalve and gastropod species sampled north of the GIF ridge were recorded at depths shallower than 500 m, with a few species showing extended distribution throughout the bathyal range. Interestingly, the epibenthic pectinid bivalve *Hyalopecten frigidus* was common in samples collected below 2000 m, suggesting that it is well adapted to the energy constrains of the deep Nordic Sea basin and low **Ω**. No gastropod species were observed in the few samples collected below 2000 m north of the GIF ridge.

The species considered suitable for monitoring early signs of changes in benthic communities under ocean acidification north of the GIF ridge were 15 in total. Samples collected for the BIOICE program were collected 10–27 years before this study, so it is important to realize that changes in the marine environment north of the GIF ridge are on-going and that environmental changes could already have induced changes in benthic communities in this region. Preferably, an establishment of a monitoring project would require a collection of

preliminary data on benthic communities and information on the natural (e.g., annual and seasonal) variability of benthic communities in the region.

SUMMARY AND CONCLUSION

Biodiversity patterns of bivalves and gastropods differed considerably between the bathymetric gradients north and south of the GIF ridge. A clear decrease in α-diversity and an increase in nestedness with depth were observed north of the GIF ridge, whereas a moderate decrease, and no decrease in α-diversity, was observed in bivalves and gastropods, respectively, south of the GIF ridge where species turnover is the dominant β-diversity component. Methods applied to the BIOICE dataset in this study were designed to address issues regarding the non-randomized sampling strategy and the lack of standardized sampling methods. Nevertheless, it is important to acknowledge these issues and the potential effects on the results of this study. As the limited amount of sample data from depths below 1600 m were largely excluded from analysis, this study does not address biodiversity patterns at these greater depths. It is recommended for future research to apply sampling strategies that are better designed to answer questions on biodiversity patterns to validate the findings of this study. Data presented here contribute significantly to the knowledge of molluscan biodiversity and species composition along bathymetric gradients in the high-latitude North Atlantic. This information is important in guiding future attempts to evaluate the degree of vulnerability in bivalve and gastropods communities in the Nordic Seas where environmental change related to ocean warming and acidification is observed and predicted (Olafsson et al., 2009; Bopp et al., 2013) and for efforts to predict the implications of these changes for deep-sea benthic communities more generally (Widdicombe and Spicer, 2008; Urban et al., 2016).

By adding to the general understanding of biodiversity patterns in the North Atlantic, including the Nordic Seas, our results provide an important baseline for future work aimed at quantifying ecosystem responses to rapid environmental changes taking place in the region – information vital for shaping conservation strategies that minimize the detrimental consequences of such changes in the future (Cavanagh et al., 2016).

DATA AVAILABILITY

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

HE wrote the manuscript and analyzed the data. NM took part in writing the manuscript and data analysis. GG edited the manuscript and provided advise about the species-data.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00129/full#supplementary-material

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Hydrodynamic Connectivity of Habitats of Deep-Water Corals in Corsair Canyon, Northwest Atlantic: A Case for Cross-Boundary Conservation

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Deep-water corals are significant ecosystem engineers that provide habitat complexity in the deep sea. They are indicator species of vulnerable marine ecosystems because of their slow growth and longevity, characteristics that can prolong recovery from disturbances such as fishing. For populations with discontinuous distributions, such as aggregations of deep-water corals, population connectivity is critical in regulating persistence and recovery and is one of the recommended elements in the design of area-based conservation measures. In this study, we assessed potential pathways of connectivity in the Corsair Canyon Conservation Area, off Nova Scotia, Canada, for populations of the deep-water corals *Paragorgia arborea* and *Primnoa resedaeformis* discovered in 2014 and afforded protection in 2016. Corsair Canyon located in the Canadian EEZ, ∼ 20 km from the border between Canada and the United States, is potentially receiving larvae from either the Canadian or US EEZ. In Corsair Canyon, *P. arborea* was very abundant at depths 484-856 m and some colonies of *P. arborea* were > 2 m high. These are the locally densest aggregations of *P. arborea* we have detected on the continental slope off Nova Scotia. We also recorded *P. resedaeformis* at similar depths. Colonies of both species were most often seen attached perpendicularly to a rock face, and into the current. We assessed hydrodynamic connectivity between Corsair Canyon and other canyons to the northeast and southwest along the continental slope with known occurrences of the two corals, using the ocean model Finite-Volume Community Ocean Model (University of Massachusetts-Dartmouth). Our results indicate that estimated hydrodynamic connectivity originates consistently from canyons to the southwest of Corsair Canyon, particularly Georges, and Heezen Canyons. Of these, only Georges Canyon is within Canada's EEZ and based on our data has very sparse populations of corals that can supply potential recruits. Predicted connectivity with the Northeast Channel Coral Conservation Area occurs in winter and spring, but the complexity of circulation in those seasons needs to be resolved to confirm the strength of this connection. Our results strongly suggest that cross-boundary coordination is essential in the conservation of aggregations of deep-water corals in the northwest Atlantic, by ensuring larval exchange and connectivity.

Keywords: deep-water corals, connectivity, area-based conservation, cross-boundary collaboration, submarine canyons, hydrodynamics, continental slope, fishery closures

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INTRODUCTION

Deep-water corals are distributed throughout the world's oceans and are important habitat engineers that provide structural complexity (Roberts et al., 2006; Buhl-Mortensen et al., 2010) and thus habitat for attachment, nursing and foraging to other invertebrates, such as crustaceans and echinoderms, and fish (Buhl-Mortensen and Mortensen, 2004; Auster, 2005; Du Preez and Tunnicliffe, 2011). Because deep-water corals are long-lived and have slow growth rates, their populations are expected to have slow recovery from natural or anthropogenic perturbations (Clark et al., 2015). For this reason, deep-water corals have been categorized as indicator species of vulnerable marine ecosystems, and their aggregations identified for conservation from fishing activities worldwide (FAO [Food and Agriculture Organization of the United Nations], 2009; ICES [International Council for the Exploration of the Sea], 2016). Some area-based protection has been afforded already to deep-water corals in several countries, including Norway, United Kingdom, Canada, United States, and New Zealand among others, and the level of protection varies from temporary fishing closures and permanent gear bans to Marine Protected Areas.

For area-based conservation actions to be effective, several ecological criteria must be met, including population persistence over space during natural (environmental) and anthropogenic (e.g., fishing) fluctuations (Sale et al., 2006). For spatially fragmented populations or sub-populations with discontinuous distributions, such as patches of dense aggregations of deep-water corals, persistence or recovery from perturbations of individual patches is regulated in part by the degree of population connectivity with other patches, as well as self-recruitment (Kool et al., 2013). For this reason, connectivity, and in particular population connectivity [i.e., the exchange of individuals (demographic) or genes (genetic) between patches or spatially distinct populations] is strongly recommended as one of the elements in the design of networks of Marine Protected Areas in international agreements (Convention on Biological Diversity, 2007) and the scientific literature (Gerber et al., 2003; Crowder and Figueira, 2006; White et al., 2010). For sessile species, such as deep-water corals, the main mechanism to achieve connectivity is through larval dispersal; patterns in connectivity can be used to identify larval sources and sinks, as well as potential stepping stones among patches. However, in the deep sea, measures of larval dispersal and population connectivity are largely lacking (Hilário et al., 2015), making the incorporation of these process in the design of marine reserves challenging. Because of this lack of data in this habitat, as well as in many others, connectivity is often estimated based on patterns of hydrodynamic flow (here termed hydrodynamic connectivity) (e.g., Kool et al., 2015). To our knowledge, population connectivity has been evaluated in the context of conservation in the deep-sea only on a few occasions. Examples include the scleractinian coral *Lophelia pertusa* in a network of deep-sea MPAs in Scotland (Fox et al., 2017), and deep-sea sponges and deep-water corals in a collection of closed areas by the Northwest Atlantic Fisheries Organization in the high-seas portion of the Grand Banks and Flemish Cap to protect vulnerable marine ecosystems (Kenchington et al., 2019).

The deep-water alcyonacean corals *Primnoa resedaeformis* and *Paragorgia arborea* have been a conservation focus for Canada in the northwest Atlantic Ocean in the last 15–20 years. Species distributions models have predicted areas of suitable habitat to occur on steeply sloping regions along the shelf break and shallow continental slope for *P. arborea*, but wider swaths that extend onto the shelf for *P. resedaeformis* (Bryan and Metaxas, 2007). In practice, the known locations of these two species along the continental margin off the coast of Nova Scotia and in the Gulf of Maine are fewer than predicted (Bryan and Metaxas, 2006). Within this region, some of the densest aggregations of these two taxa on the Scotian Slope are found in the Northeast Channel Coral Conservation Area (NECCCA) established specifically to protect them. Although abundance of these corals can vary greatly across different sections within the NECCCA, it generally increases with depth from an average of 4.8 and 0.6 colonies 100 m^{-2} for *P. resedaeformis* and *P. arborea,* respectively, at depths $<$ 500 m, to 12.8 and 2.5 colonies 100 m^{-2}, for each species, respectively, at depths $>$ 500 m (Mortensen and Buhl-Mortensen, 2004; Watanabe et al., 2009). Coral abundance within the NECCCA has increased slightly between 2001 and 2014 (Bennecke and Metaxas, 2017). Rates of recruitment vary across the NECCCA and are higher in shallower depths (658 – 671 m) amongst the coral thickets than on the floor of the canyon (860 m depth), where only a handful of colonies are present (Lacharité and Metaxas, 2013). The pattern could be the result of short dispersal distances and localized larval supply, gregarious settlement or hydrodynamics within the broader canyon. Within the coral thickets, recruitment rate was on the order of 300 colonies m^{-2} yr^{-1} (Lacharité and Metaxas, 2013), a rate that could result in abundances $>$ 6 orders of magnitude those observed for adult colonies in the NEC.

In addition to NECCCA, four other conservation areas have been designated in the Maritimes region by the Department of Fisheries and Oceans Canada, one Marine Protected Area and three fisheries closures (DFO [Fisheries and Oceans Canada], 2017). The Gully MPA was established in 2004 with one of its conservation objectives being to protect coral diversity. The Lophelia Coral Conservation Area was established in 2004 to protect the only known live reef complex of *Lophelia pertusa* in Atlantic Canada. The Jordan Basin Conservation Area was established in 2016 to protect high aggregations of *P. resedaeformis* and other sensitive filter-feeding invertebrate communities. Lastly, also in 2016, the Corsair and Georges Canyons Conservation Area was established to protect high densities of *P. arborea*. All conservation areas were established based on data on the distribution of corals. However, the potential for connectivity, and thus population persistence or recovery from disturbance, such as fishing, has not been assessed for any of these closures. Because *P. arborea* and *P. resedaeformis* are found in canyons and on the continental slope from New Jersey to Newfoundland (**Figure 1**), potential larval sources for the closures can be located on either side of the Canada-United States border, possibly introducing geopolitical constraints to their conservation.

In this study, we assess the potential pathways of hydrodynamic connectivity in the Corsair Canyon Conservation

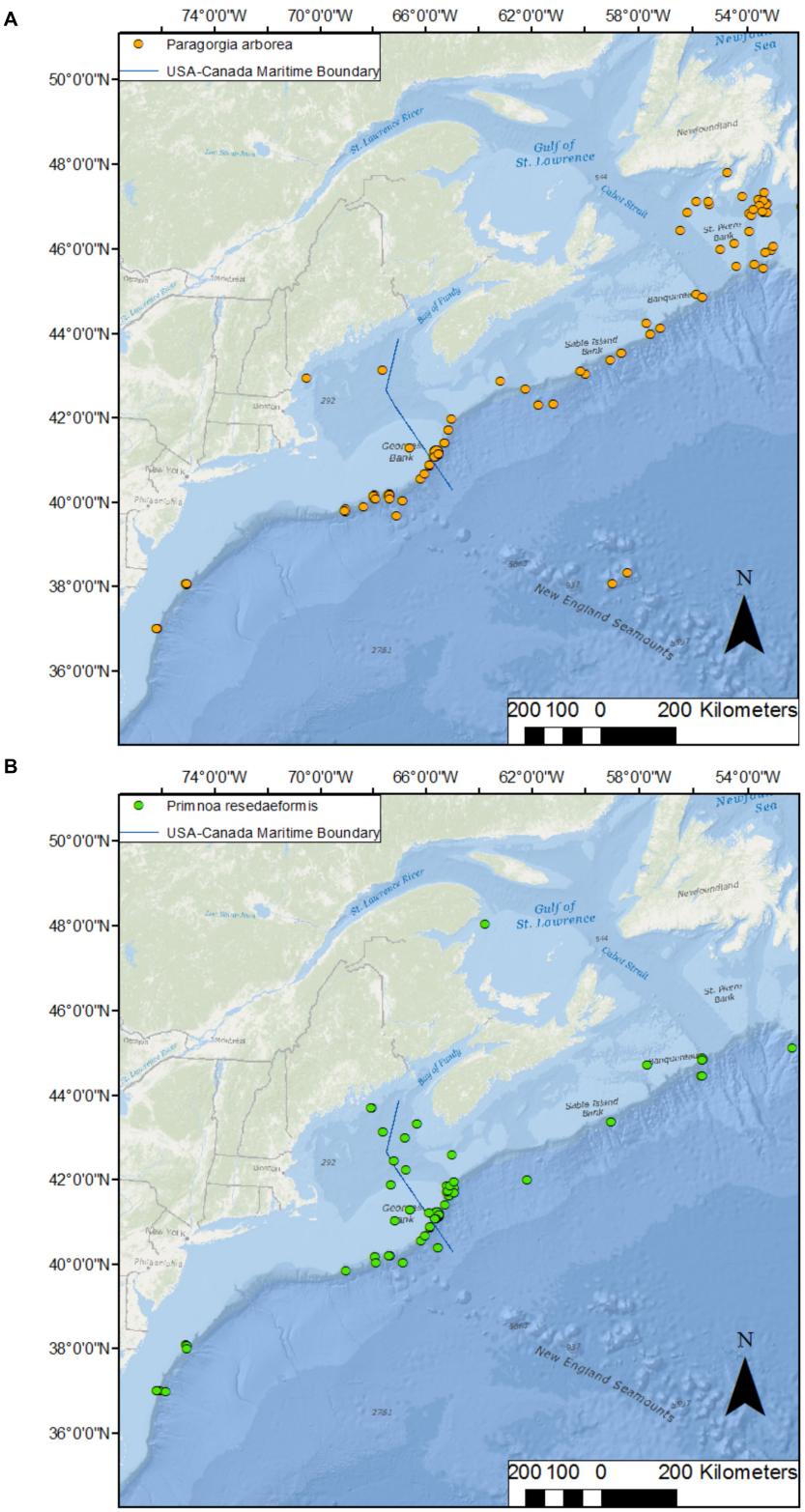


FIGURE 1 | Distribution of the deep-water corals *Paragorgia arborea* **(A)** and *Primnoa resedaeformis* **(B)** along the northwest Atlantic continental shelf break from New Jersey, United States, to Newfoundland, Canada. Data are: occurrences obtained from OBIS (http://iobis.org/), NOAA (https://deepseacoraldata.noaa.gov/), Quattrini et al. (2015), and this study; US-Canada boundary: NOAA's Ocean Service, Office of Coast Survey (OCS); bathymetry: World Ocean Base (Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors; World Ocean Reference (Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors).

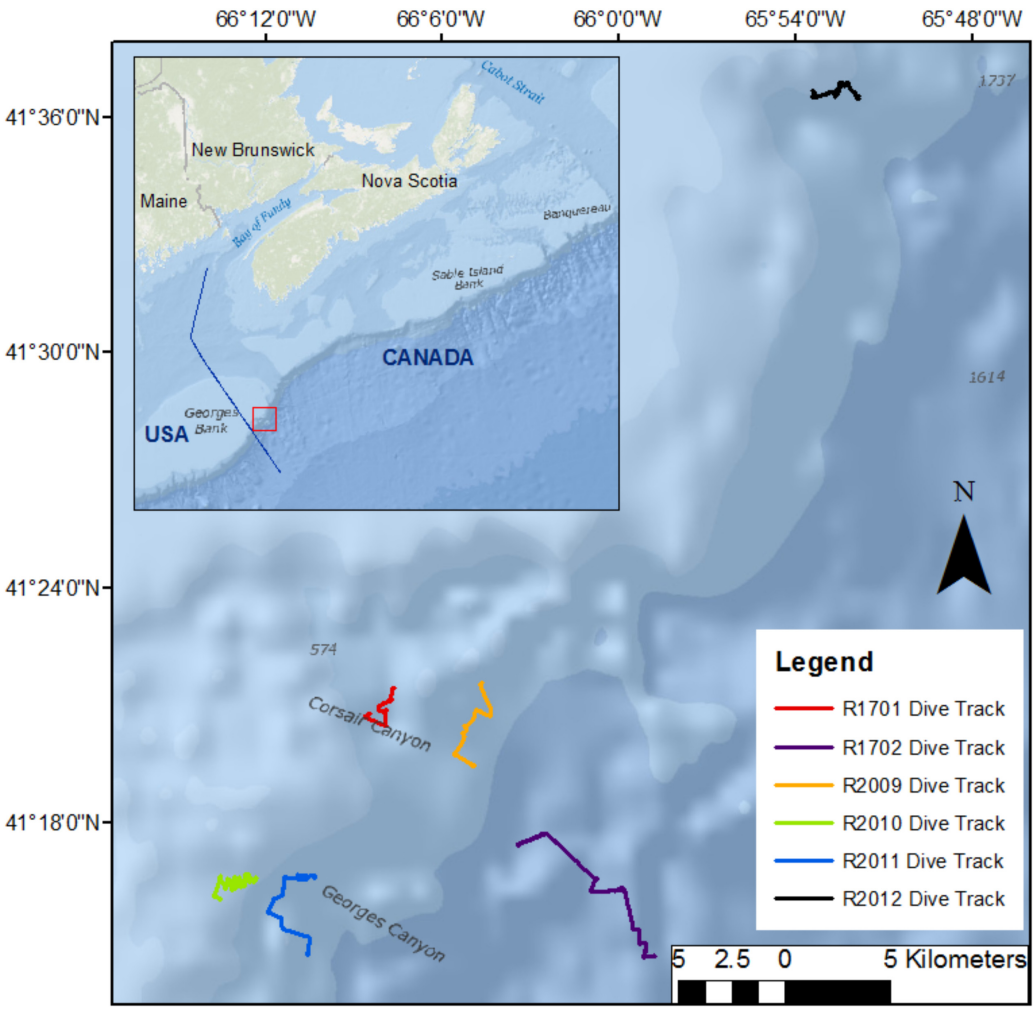


FIGURE 2 | Location of dive tracks followed by the remotely operated vehicle ROPOS in Georges Canyon in 2017 (R2010, R2011), Corsair Canyon in 2014 (R1701 and R1702) and in 2017 (R2009) and Fiddlers Cove in 2017 (R2012) on the Canadian continental shelf break and slope. Bathymetry data from: World Ocean Base (Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors; World Ocean Reference (Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors).

Area (CCCA) for the populations of *P. arborea* and *P. resedaeformis* discovered in 2014 and afforded protection in 2016. The reproductive patterns and larval ecology of both species remain mostly unknown and dispersal has not been measured for either species. *Primnoa resedaeformis* is presumed to be a broadcast spawner (which typically have large dispersal distances) with no evidence of periodicity in gametogenesis and presumed to have non-feeding larvae, which in turn may suggest short planktonic duration (Mercier and Hamel, 2011; Waller et al., 2014). Nothing is known about the reproduction or larval ecology for *P. arborea*. Based on population structure on the Scotian Shelf and Slope, *P. arborea* appears to be genetically mixed within individual sites on the western Scotian Shelf (i.e., where CCCA is situated) and thus was proposed to also have wide dispersal (Strychar et al., 2008). Regionally wide dispersal has been proposed as the reason for an absence of regional and bathymetric genetic structure for the species (Herrera et al., 2012). Here, firstly, we describe the distribution and size frequency of *P. resedaeformis and P. arborea* in Corsair Canyon, as well as in two other neighboring locations that have not been described before. Secondly, we use the Finite-Volume Community Ocean Model (FVCOM; Chen et al., 2003) to simulate broad patterns of hydrodynamic connectivity that can allow us to identify potential locations of allochthonous larval supply into Corsair Canyon. Because of the lack of knowledge on the reproduction and ecology of either species, we did not focus on particular spawning depths and seasons or larval durations for our simulations. We are using the populations in CCCA as a case study because: (1) they encompass local aggregations of some of the highest densities of *P. arborea* recorded to date in the Canadian northwest Atlantic; and (2) the canyon is located ∼20 km from the border between Canada and the United States and may be receiving larvae from aggregations in either Canadian or US national waters. Identifying the larval origin can

assist in the future selection of areas for protection to ensure the persistence of these uniquely dense aggregations and may lead toward cross-boarder collaboration in marine conservation.

MATERIALS AND METHODS

Study Sites

We conducted a total of 5 dives in two canyons (3 in Corsair Canyon and 2 in Georges Canyon) and 1 dive at another location on the continental slope (Fiddlers Cove) between Corsair Canyon and the Northeast Channel Coral Conservation Area with the ROV ROPOS (**Figure 2**). The dive tracks followed exploratory transects ascending the canyon walls and ranged in length between 3.7 and 8.9 km and in depth between ∼300 and ∼2200 m (**Table 1**). In 2014, the two dive tracks in Corsair Canyon were designed to cover a shallower section with steep topography (R1701) and a deeper section reaching the mouth of the canyon (R1702). The tracks included 6 and 7 transects, for R1701 and R1702, respectively, during which the ROV was flying at ∼1–5 m above the seafloor and at speeds of ∼ 0.3 knots allowing the detection and enumeration of epifauna (except when ascending vertical walls when measured altitude ranged from 1 to 16.1 m). The ROV transited between those transects in water, at altitudes > 8 m above the seafloor and speeds of 0.5–0.75 knots and detection of coral colonies was less reliable. In 2017, the dive track was designed to expand the spatial coverage in Corsair Canyon toward the eastern boundary of the fisheries closure. The 2 dive tracks in Georges Canyon and the 1 dive track at Fiddlers Cove were designed to explore the steepest sections of the most pronounced incisions on the continental shelf that neighbor Corsair Canyon. Except during brief periods of in-water transiting, the transects were generally done 0.5–4 m above the seafloor (7 m at one coral location) and at speeds of ∼0.3 – 0.5 knots.

Video Analysis

We estimated the distribution and size of colonies of *Paragorgia arborea* and *Primnoa resedaeformis* from video by a forward-facing HD camera [Insite Pacific Zeus-Plus HD camera (10x Zoom 5.2–52 mm) mounted on a pan and tilt with extend function]. For each dive, the video footage was split into intervals of 00:10:57:440 hh:mm:ss:msmsms during the initial recording on board ship, resulting in 64 segments for dives R1701, R2009, R2010 and R2011 and 53 segments for dive R2012. We linked video segments with the dive track (ROV heading, geographic coordinates and water depth) using Ocean Floor Observation Protocol (OFOP 3.3.5 by Scientific Abyss Mapping Services) based on synchronized time (Huetten and Greinert, 2008). ROPOS is fitted with a USBL system, allowing precision positioning of the vehicle on the seafloor. Although ROPOS relayed data 4 times per second, only a single datum per second was used for the track file in the OFOP program because of software limitations. Using the Seafloor Observation Window in OFOP, we entered observations of coral colonies and litter manually into the dive protocol along with the time and corresponding coordinates at which the observation was made. For every individual coral colony encountered by ROPOS, an observation identifying the coral species (e.g., *Primnoa*, *Paragorgia*), and whether it was alive, damaged or dead was recorded. Observations were georeferenced to produce a distribution of corals along the dive transect in ArcGIS. Observations of lost fishing gear and other debris were also recorded. We measured the size of the corals in ImageJ, using video frame grabs with 2 laser points, 10 cm apart as scale, if the scaling lasers were either on the coral itself or nearby on approximately the same plane as the coral. This requirement resulted in many fewer colonies measured than being encountered. Height was the maximum dimension of the coral protruding outward from the base or the substrate the coral was attached to, and width the maximum dimension approximately parallel to the base or substrate. We calculated median size, 50 and 75% quantiles using R (R Core Team, 2017).

Regional Ocean Circulation

Ocean circulation at the shelf edge of the Gulf of Maine is influenced in part by regional circulation patterns in the Northwest Atlantic, with the most dominant oceanographic feature in the region being the Gulf Stream. The positions of the north wall of the Gulf Stream and the shelf break delineate the Slope Sea, where subsurface flow is composed of different water masses (Gatien, 1976). Warm Slope Water flows northeastward adjacent to the Stream from the surface to ∼ 400 m depth. The Labrador Slope Water flows equatorward deeper (>100 m) and closer to the shelf break, as a continuation of the continental slope component of the Labrador Current originating in the Labrador Sea. At depths > 400–500 m, Labrador Slope Water is typically more common in the northern part of the shelf, progressively shallowing toward the south where North Atlantic Central Water dominates. Given this general pattern, a strong front separating cold fresh water from warm salty water is present along the shelf. North-south shifts are common, but on average, the front is located offshore on the shelf break from the tail of the Grand Banks of Newfoundland to approximately central Georges Bank, from where it follows the 200-m isobath to Cape Hatteras (Gatien, 1976; Townsend et al., 2015; Peterson et al., 2017). Interannual variability of regional oceanographic features, i.e., the location of the shelf-slope front and north wall of the Gulf Stream, and in the strength of the Labrador Current/Slope Water, has been consistently linked to atmospheric conditions, e.g., the North Atlantic Oscillation (Taylor and Stephens, 1998; Chaudhuri et al., 2009; Peterson et al., 2017).

In the vicinity of Georges Bank, shelf-slope water exchange is driven by the influx of Slope water through the Northeast Channel, the relative composition of which varies between the two Slope water masses (Townsend et al., 2006). Shelf-slope exchange is also influenced by warm-core rings (anticyclonic eddies) spawning periodically from the meandering Gulf Stream and inducing entrainment of shelf water onto the slope as they reach the shelf break (Garfield and Evans, 1987). On Georges Bank proper, circulation is dominated by strong M_2 tidal currents (semidiurnal) coupled with an anticyclonic residual circulation with summer intensification (Bigelow, 1927; Loder, 1980) and upwelling generally occurring around the edge of the bank

TABLE 1 | Transects done by the remotely operated vehicle in submarine canyons and continental slope in Atlantic Canada.

Location	Dive	Date	Start position	End position	Depth (m)	Dive track (m)	Transect length(s) analyzed (m)	Number of coral colonies
Georges Canyon	R2010	14 June 2017	41° 15.985′ N 66° 14.531′ W	41° 6.662′ N 66° 13.254′ W	375–638	8170	6140	Pa: 13; Pr: 13
	R2011	15 June 2017	41°14.502′ N 66° 11.662′ W	41° 14.470′ N 66° 11.610′ W	336–1121	8005	7740	Pa: 2; Pr: 0
Corsair Canyon	R1701	23 June 2014	41° 20.556′ N 66° 9.225′ W	41° 21.196′ N 66° 8.411′ W	480–870	3710	Transect 1: 1120 Transect 2: 1010 Transect 3: 460 Transect 4: 410 Transect 5: 160 Transect 6: 650	Pa: 33; Pr: 7 Pa: 136: Pr: 11 Pa: 19; Pr: 0 Pa: 0; Pr:0 Pa: 0; Pr: 0 Pa: 40; Pr: 96
	R1702	24 June 2014	41° 14.124′ N 65° 59.891′ W	41° 14.241′ N 66° 4.356′ W	788–2190	8920	Transect 1: 2520 Transect 2: 610 Transect 3: 970 Transect 4: 1820 Transect 5: 910 Transect 6: 1340 Transect 7: 760	Pa: 0; Pr: 0 Pa: 0; Pr: 0 Pa: 0; Pr: 0 Pa: 0; Pr: 0 Pa: 0; Pr: 0 Pa: 0; Pr: 0 Pa: 0; Pr: 0
	R2009	13 June 2017	41° 19.171′ N 66° 5.837′ W	41° 19.176′ N 66° 5.832′ W	366–984	6170	6170	Pa: 7; Pr: 13
Fiddlers Cove	R2012	16 June 2017	41° 35.885′ N 65° 52.005′ W	41° 36.065′ N 65° 53.501′ W	523–810	4480	3870	Pa: 9; Pr: 1

The dive tracks for R2009 was analyzed in its entirety. Some sections of R2010, R2011, and R2012 were omitted from the analysis because they were in-water transits. For dives R1701 and R1702, 6 and 7 transects, respectively, were done specifically to enumerate corals, while the remainder of the track was in-water transits between transects. Pa, Paragorgia arborea. Pr, Primnoa resedaeformis.

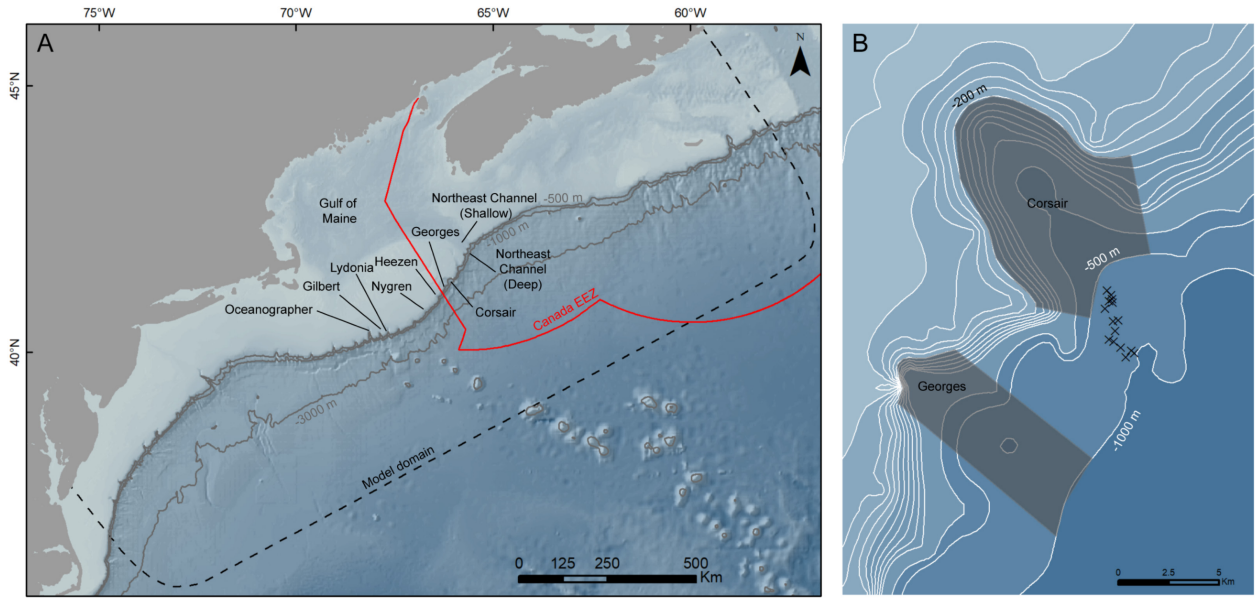


FIGURE 3 | (A) Nine zones of interest along the shelf edge between Northeast Channel ('NEC') and southwest Georges Bank. Geographic coordinates of approximate center locations of zones of interest are given in **Table 3**. Depth contours in meters. 'EEZ,' Exclusive Economic Zone. **(B)** Corsair and Georges Canyons zones of interest bounded by the 200-m and 1000-m depth contours. Endpoints of tracks (n = 15) are indicated. Geographic coordinates of endpoints are given in **Table 2**.

(Townsend et al., 2006). Because Corsair Canyon is located in a region of significant seasonal and interannual variability in ocean circulation, we explored potential allochthonous sources of larvae to the canyon over different seasons and years to capture this variability.

Assessment of Hydrodynamic Connectivity

We assessed hydrodynamic connectivity in Corsair Canyon offline, using advective velocity fields of the 3rd generation of the ocean model Finite-Volume Community Ocean Model held at the University of Massachusetts-Dartmouth (FVCOM-GOM3 30+ year hindcast; Chen et al., 2003). The model domain is built with an unstructured grid covering the Gulf of Maine, extending offshore of the shelf edge, and western Scotian Shelf. The model consists of 45 sigma layers and varying horizontal resolution between nodes, which increases close to shore and in areas of steep bathymetry. Hourly values of FVCOM from 1978 to 2015 are available online[1].

We estimated displacement of water at each time step (10 min) with a backward (implicit) Euler method based on the 3-dimensional advective flow fields. Backward displacement in the x, y, and z dimensions was determined with (opposite) velocity in the u (eastward velocity), v (northward velocity), and w (vertical velocity) flow components, respectively, estimated at the previous time step at this location. We extracted values of velocity components at the given depth of the track, at each position using 2-dimensional spatial (linear) interpolation from the nearest three resolved points (elements for the u, v, and w components) the seabed depth of which exceeded the depth of the track. Fewer than three available points led to early termination of the tracking algorithm. We extracted flow components from the nearest sigma layer at the given depth, with no explicit vertical spatial interpolation. To enhance computing efficiency, variability in sea surface height (height above the geoid) was not considered, although available from the model. Therefore, constant seabed depth (height below the geoid), and consequently vertical depth distribution of sigma layers, was used at all nodes. On and offshore of Georges Bank, the range of sea surface height is ∼1 m and increases to 1–2 m inshore of Georges Bank. If tracks reached within 100 km of the model boundary (coast and offshore), the tracking algorithm was terminated. Tracks were derived in the R computing environment, modified from freely accessible code written in the Python environment[2]. We examined patterns of connectivity on 5 days per month (11th–15th) for each of 3 months per year (January, May, and September) over 10 years (2004–2013). Each track was assumed to have terminated at 12 pm (UTC) at 500 m depth just offshore from Corsair Canyon (see below) and was temporally extended backward for a maximum of 60 days. Because the planktonic larval duration is not known for *P. arborea*, we chose this period to reflect a median value for larval duration for bathyal/deep-sea (cnidarian) species, as currently proposed in the literature (Hilário et al., 2015; Young et al., 2018).

Because bathymetric resolution in the ocean model is coarse, the canyon itself is only partially resolved. For this

[1]http://www.smast.umassd.edu:8080/thredds/hindcasts.html

[2]github.com/Particles-in-the-Coastal-Ocean

TABLE 2 | Geographic coordinates of **(A)** endpoints of hydrodynamic tracks in the vicinity of Corsair Canyon and **(B)** approximate center points of each zone of interest.

Zone of Interest	Latitude	Longitude
(A)		
Corsair Canyon	41° 18′ 43.4″ N	66° 7′ 50.7″ W
	41° 18′ 14.4″ N	66° 7′ 57.5″ W
	41° 17′ 53.5″ N	66° 7′ 41.7″ W
	41° 17′ 21.0″ N	66° 7′ 43.4″ W
	41° 16′ 59.9″ N	66° 7′ 01.1″ W
	41° 17′ 54.6″ N	66° 7′ 30.6″ W
	41° 17′ 38.1″ N	66° 7′ 38.8″ W
	41° 18′ 23.2″ N	66° 7′ 40.6″ W
	41° 18′ 25.7″ N	66° 7′ 47.9″ W
	41° 18′ 36.0″ N	66° 7′ 42.6″ W
	41° 18′ 28.7″ N	66° 7′ 40.8″ W
	41° 17′ 24.6″ N	66° 7′ 53.1″ W
	41° 17′ 10.5″ N	66° 7′ 29.1″ W
	41° 16′ 54.4″ N	66° 7′ 20.3″ W
	41° 17′ 04.8″ N	66° 7′ 07.2″ W
(B)		
Corsair Canyon proper	41° 20′ 42.0″ N	66° 09′ 43.2″ W
Georges Canyon	41° 15′ 14.4″ N	66° 12′ 21.6″ W
Heezen Canyon	41° 03′ 54.0″ N	66° 23′ 38.4″ W
Nygren Canyon	40° 46′ 55.2″ N	66° 41′ 20.4″ W
Lydonia Canyon	40° 25′ 33.6″ N	67° 39′ 57.6″ W
Gilbert Canyon	40° 21′ 21.6″ N	67° 52′ 26.4″ W
Oceanographer Canyon	40° 22′ 44.4″ N	68° 08′ 49.2″ W
NEC-Shallow	42° 06′ 25.2″ N	65° 46′ 12.0″ W
NEC-Deep	41° 59′ 02.4″ N	65° 35′ 16.8″ W

'NEC,' Northeast Channel.

reason, backward displacement was estimated from 15 locations (considered the endpoints of the track) offshore of Corsair Canyon (i.e., deeper than the 500-m depth contour; **Figure 3** and **Table 2**). This resulted in 150 tracks per endpoint based on day-month-year combinations, for a total of 2250 tracks. These locations were selected based on their potential to source Corsair Canyon in 'forward-tracking' mode (preliminary data, not shown). Since the algorithm estimates displacement (i.e., based on advective fields), and tracks are estimated in areas of relatively steep bathymetry at the shelf break, the depth of the seabed at its updated position was often shallower than its estimated depth (based on the w displacement), i.e., water 'hits' the seabed. To alleviate this, the depth of the track was adjusted to 1 m above the seabed depth at its updated position.

We assessed patterns of connectivity in 9 zones (**Figure 3** and **Table 2**): (1) 6 canyons to the south of Corsair Canyon along the edge of Georges Bank (in order of increasing distance from Corsair): Georges (∼40 km^2), Heezen (∼65 km^2), Nygren (∼43 km^2), Lydonia (∼94 km^2), Gilbert (∼105 km^2), and Oceanographer (∼144 km^2) Canyons (the latter 3 are part of the Northeast Canyons and Seamounts Marine National Monument established in 2016), bounded by the 200-m and 1000-m depth contours; (2) 2 contiguous zones at the mouth of Northeast Channel (NEC; northeast of Corsair Canyon), one in the shallow part of the channel proper ("NEC-Shallow"; ∼576 km^2) delimited by a straight cross-channel boundary at the 240-m and the 300-m depth contours, and another ("NEC-Deep"; ∼438 km^2) covering the 3 canyons present at the shelf edge seaward "NEC-Shallow" to the 1000-m depth contour; and (3) Corsair Canyon proper, between the 200-m and 500-m depth contours (∼65 km^2). Delimiting depth contours were based on the Gulf of Maine Bathymetric Data (MassGIS Data) similar to the bathymetry used in the ocean model.

For all 2250 tracks terminating at the 15 endpoint locations in Corsair Canyon, we determined hydrodynamic connectivity based on occurrence (recorded as binary, 0 or 1) of tracks passing through each zone over the track's full length. Individual tracks could be connected to multiple zones of interest based on spatial overlap between the track and each particular zone, depending on their temporal evolution; however, only connectivity with Corsair Canyon is described here. Tracks were pooled by month (n = 750 per month) to assess seasonal and interannual variability in hydrodynamic connectivity from zones of interest to Corsair. For each month, patterns in residence time (in hours) and transit time prior to reaching the mouth of Corsair Canyon (minimum, maximum, in days) were derived for each zone of interest. Beyond zones of interest, spatial patterns in tracks over the entire time period were determined using a raster grid with a horizontal cell size of 5 km covering the model domain. For each grid cell, the number of tracks passing through the cell was computed and expressed as a fraction of the total number of tracks (n = 750 for each month).

RESULTS

Physical Description of Sites

In Corsair Canyon, coarse sediment covered most of the seabed throughout the dive in the central region of the canyon (R1701). Ripples in the sediment were present in all except one transect, indicating oscillatory water motion, and ranged in size from 10 to 15 cm crest to crest. Low rock reliefs were often covered by consolidated sediment. Rock walls were encountered in all except one segment of the dive track. On the eastern margin of the canyon (R2009), the seafloor appeared relatively flat with very fine sediment and lacking visible megafauna on the southern deeper section of the dive, and more heterogeneous with some boulders without sediment cover, sometimes in clusters, along the northern shallower section, but without any rock wall outcrops. Some burrows were present throughout the dive, and one area also had distinct ripples in the sediment. During the deeper dive in the central region of the canyon (R1702), there were high concentrations of particulate organic matter in the water column. The seafloor was covered with soft sediment, and bioturbation (indicated by burrows and tracks) was evident. We encountered steep walls along the entire dive (20–60 m high), and pillars of bedrock in some of the transects. Many large rock outcrops were covered by thick layers of consolidated sediment. In Georges Canyon, there were only a few rock wall outcrops along both dive tracks, but boulders without sediment cover were scattered throughout the dives. In addition to the common relatively flat

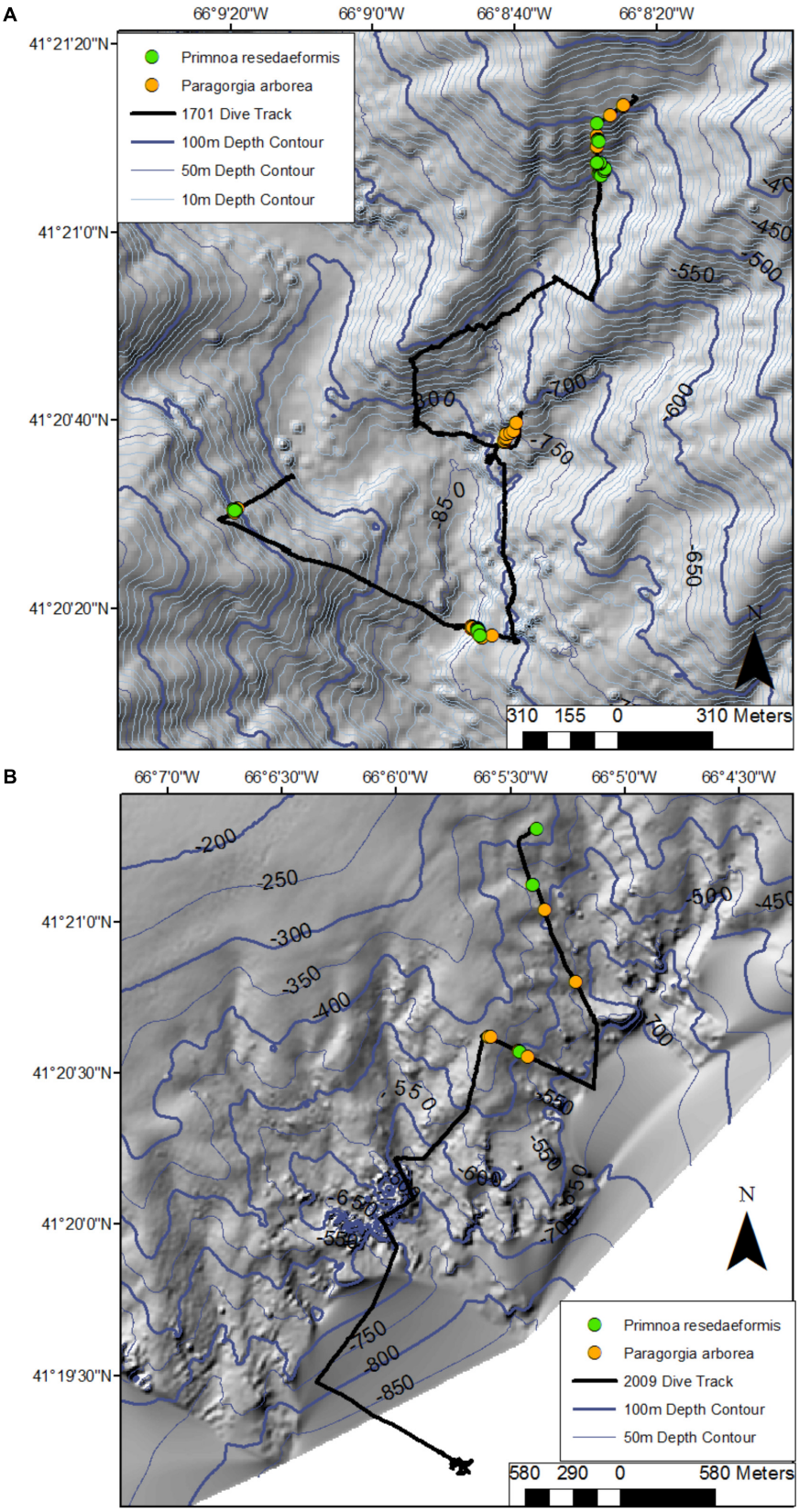


FIGURE 4 | Location of colonies of *Paragorgia arborea* and *Primnoa resedaeformis* along the dive tracks in Corsair Canyon in 2014 (R1701) **(A)** and 2017 (R2009) **(B)**. Bathymetric data provided by the Canadian Hydrographic Service, Fisheries and Oceans - Canada.

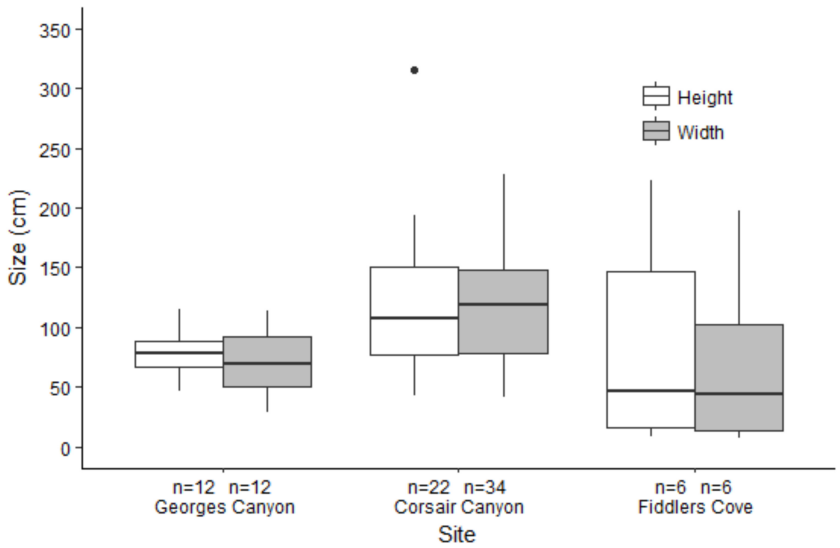


FIGURE 5 | Boxplots of height and width of measured colonies of *Paragorgia arborea* in Georges Canyon, Corsair Canyon and Fiddlers Cove. Boxes show 25 and 75% interquantile range, line shows median and whiskers are ± 1.5 IQR.

TABLE 3 | Sizes of colonies of *Primnoa resedaeformis* measured on dives in Georges Canyon, Corsair Canyon and Fiddlers Cove in 2014 and 2017.

Site	Dive	Height (cm)	Width (cm)
Georges Canyon	R2010	38.9	36.3
		48.1	32.7
	R2011	45.9	29.4
		70.0	52.1
		61.1	55
Corsair Canyon	R1701	105.3	64.5
		62.5	33.6
		–	57.3
		–	71.0
		–	74.1
		–	47.1
	R2009	72.6	99.4
Fiddlers Cove	R2012	64.6	83.2
	Mean	63.2	56.6
	SD	19.5	21.4

areas of fine sediment with burrows and tracks, there were a few steep sloping areas of either fine or consolidated sediment. In Fiddlers Cove, fine sediment covered the relatively smooth sloping walls for most of the dive track (R2012) with occasional boulders, rock walls, and outcrops of consolidated sediment. In some areas, many burrows and tracks were present, likely evidence of bioturbation.

Within Corsair Canyon, water temperature at the sea surface was 11.7°C (2017) to 14.3°C (2014) and decreased to 4.4°C at 1000 m (2017) and 3.5°C at 2000 m (2014). Oxygen concentration was 4.8–5.5 mL L^{-1} at the surface, decreased to a minimum of 3.5–3.7 mL L^{-1} at ∼ 200 m and then increased again to 6.1 mL L^{-1} at 2000 m. In Georges Canyon (2017), water temperature at the surface was 10.9°C and decreased to 4.1°C at 1100 m (R2010). Oxygen concentration was variable and unreliable at the surface but increased to 5.0–5.4 mL L^{-1} at depths of 600 and 1100 m, for each of R2010 and R2011, respectively. In Fiddlers Cove (2017), water temperature at the surface was 16.3°C and decreased to 4.4°C at 800 m. Oxygen concentration was 3.07 mL L^{-1} at the surface, decreased to a minimum of 0.05 mL L^{-1} at ∼240 m, and then increased to 5.1 mL L^{-1} at 800 m.

Coral Abundance

In Corsair Canyon, *Paragorgia arborea* was very abundant during dive R1701 (depths: 484–856 m) with a total of 228 live colonies recorded (**Figure 4**) and in three different color morphs (pink, white, and purple). We also recorded 97 live colonies of *Primnoa resedaeformis* at depths of 497–838 m. Colonies of both species were most often seen attached perpendicularly to the rock face, and into the current. Overall, coral colonies were more abundant in areas with rock walls, boulders and cobbles, in Transects 1, 2, and 6 (**Figure 4A** and **Table 1**). Some of these colonies were quite large for both species, and for *P. arborea,* in particular, 4 out of 36 colonies were > 2 m high (**Figure 5** and **Table 3**). The two corals were less abundant in the eastern region of Corsair Canyon where we only recorded 7 colonies of *P. arborea* and 13 of *P. resedaeformis* over the entire dive (R2009) (**Figure 4B**). These colonies were mostly attached to large boulders, and four *P. resedaeformis* were recruits < 5 cm in height attached to a fishing trap. No *P. arborea* or *P. resedaeformis* were recorded in the deeper sections in the eastern and middle regions of the canyon (R1702: 788 – 2190 m, R2009: > 548 m).

In Georges Canyon, we recorded few *P. arborea* and *P. resedaeformis* and most were found around a single location on dive R2010 (13 colonies of each species) with only 2 colonies of *P. arborea* recorded on R2011 (**Figure 6** and **Table 1**).

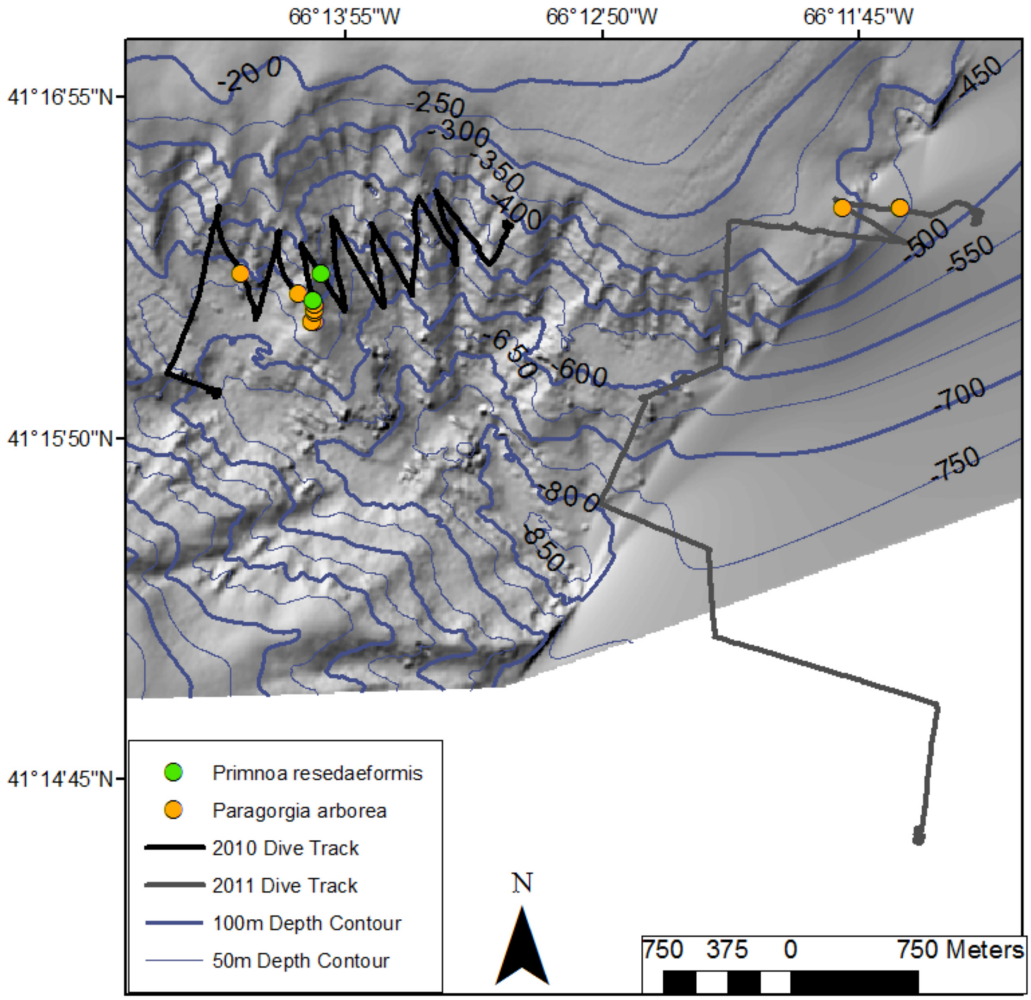


FIGURE 6 | Location of colonies of *Paragorgia arborea* and *Primnoa resedaeformis* along two dive tracks in Georges Canyon in 2017 (R2010 and R2011). Bathymetric data provided by the Canadian Hydrographic Service, Fisheries and Oceans - Canada.

Similarly, we only recorded 9 *P. arborea* and 1 *P. resedaeformis* in Fiddlers Cove, at depths between 620 and 691 m (dive R2012) (**Figure 7** and **Table 1**). The average size of the colonies at both sites was generally smaller than in Corsair Canyon, but still included some large colonies of *P. arborea* (**Figure 5** and **Table 3**). At both sites and all dives, the corals were attached to larger boulders or rock wall outcrops and were erect in the water column.

Coral Damage and Anthropogenic Litter

We only found damaged or dead colonies in Corsair and Georges Canyons. In Corsair Canyon, we recorded 1 damaged *Paragorgia arborea* (still attached to the substrate but only partially covered in living tissue) in dive R1701, and 5 colonies of *P. arborea* and 1 of *Primnoa resedaeformis* toppled and damaged (detached from their substrate but with some live polyps present). Eight dead colonies (consisting either of skeletons attached to their substrate with no live tissue or toppled skeletons with no live tissue present) of *P. arborea* were present in dive R1701, all of which were toppled. We also found one unrecognizable coral skeleton during dive R2009. In Georges Canyon, we found 10 coral skeletons which could not be identified to species.

Anthropogenic debris was present at all locations. The least amount was recorded in Corsair Canyon with 2 items in each of dives R1701 and R1702 (1 fishing line in each dive), and 4 pieces in R2009 (3 fishing lines and 1 lobster trap). At Georges Canyon, litter was abundant on both dives with 10 (3 fishing nets, 1 fishing line and 1 lobster trap) and 17 (1 fishing net and 10 fishing lines) items in R2010 (scattered throughout the dive track) and R2011 (concentrated in the northern section), respectively. At Fiddlers Cove, there were a total of 10 items of litter, clustered into a few locations near the middle section of the dive track, with 7 being fishing line.

Hydrodynamic Connectivity

Seasonal and inter-annual patterns of occurrence of predicted track origins that ended near the mouth of Corsair Canyon

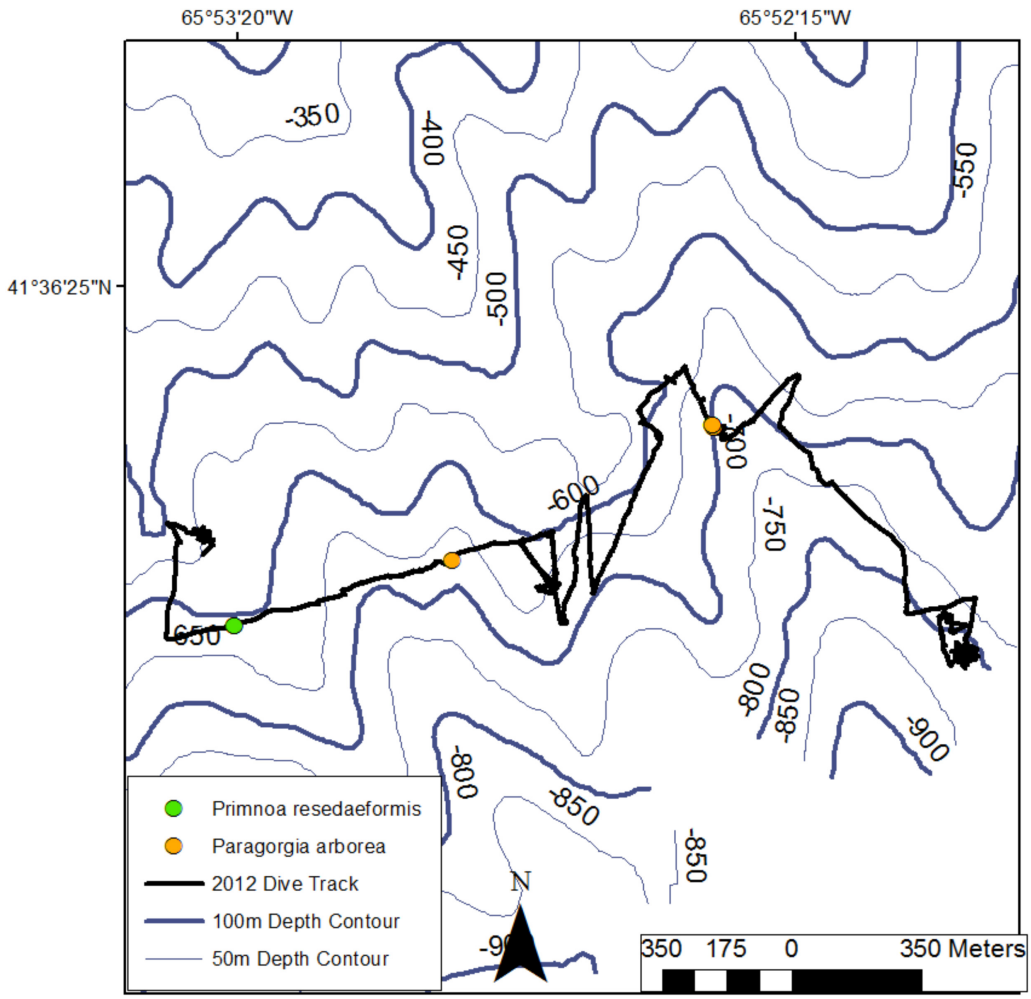


FIGURE 7 | Location of colonies of *Paragorgia arborea* and *Primnoa resedaeformis* along the dive track in Fiddlers Cove in 2017 (R2012). NRCan bathymetric data provided by Dr. Brian Kinlan (NOAA/NCCOS).

were most persistent from immediately adjacent areas: Corsair Canyon proper, Georges Canyon, and Heezen Canyon (**Figure 8** and **Table 4**). Occurrence in these areas among all assessed months and years was observed in 34.6, 65.8, and 29.0% of all predicted tracks, respectively. Estimated connectivity from sites in the Northeast Channel (northeast of Corsair Canyon) occurred in 18.4 and 11.2% of total tracks for the deep and shallow areas, respectively. When pooled, the Northeast Channel could thus be a potentially important source with a probability of occurrence of ∼30% within 60 days. Predicted connectivity from the deep area in Northeast Channel was clearly stronger in winter; for example 244 tracks occurred in January in 8 years, compared to 31 tracks in September in 6 years. Predicted connectivity from more distant canyons southwest of Corsair Canyon was more sporadic. Occurrence in these areas ranged from 5.3% of tracks with Lydonia Canyon to 9.6% of tracks with Nygren Canyon in 4–10 years. Despite its distance from Corsair Canyon, occurrence in Oceanographer Canyon was predicted to occur in 5.9% of all tracks. Predicted connectivity with these canyons was most evident in May and September, with tracks occurring in September in 7–8 years.

Mean residence time in each zone (calculated as the total time a track was located in that zone) was estimated at 16 h over all months and zones of interest (**Figure 9**). Short residence times were observed in areas southwest of Corsair Canyon, in Georges Canyon and Heezen Canyon, and particularly in Nygren Canyon (mean: 5.4, 7.9, and 9.0 h in May, January, and September, respectively). In contrast, mean residence times were longer in Lydonia Canyon, Gilbert Canyon and Oceanographer Canyon in September (19.1, 14.8, and 20.7 h respectively). Mean residence time was estimated to be consistently above the grand mean in January in the deep area of Northeast Channel (52.4 h), and in the shallow area (31.3 h). We attribute this pattern to the effect of tides in Northeast Channel. The longest residence times (> 200 h) were observed in January in the deep area of Northeast Channel and Oceanographer Canyon (single occurrence of 237 h).

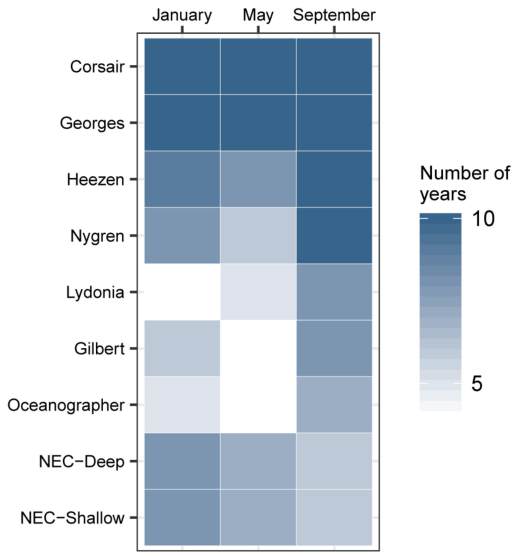


FIGURE 8 | Hydrodynamic connectivity based on occurrence (out of 10 years) observed between endpoints at the mouth of Corsair Canyon and zones of interest in January, May, and September between 2004 and 2013.

TABLE 4 | Number of tracks originating from each of the 9 zones of interest and ending at 15 endpoints offshore of Corsair Canyon (northwest Atlantic).

Zone of interest	January	May	September	Total
Corsair Canyon	389	185	205	779
Georges Canyon	462	469	549	1480
Heezen Canyon	193	250	210	653
Nygren Canyon	35	52	129	216
Lydonia Canyon	15	37	67	119
Gilbert Canyon	22	41	76	139
Oceanographer Canyon	26	50	56	132
NEC-Deep	244	138	31	413
NEC-Shallow	94	132	26	252

For each endpoint, tracks terminated on 5 days (11th – 15th) in January, May, and September from 2004–2013 at 12:00pm UTC (n = max. 750 tracks per month). 'NEC,' Northeast Channel.

Mean minimum transit time between the mouth of Corsair Canyon and zones of interest was estimated at 15.1 days prior to track end time across all years and months (**Figure 10**). As expected, areas nearer the mouth of Corsair Canyon (Corsair Canyon proper and Georges Canyon) showed short mean transit time, particularly in January for Corsair Canyon proper (1.8 days) and in May for Georges Canyon (0.9 days). Minimum transit time increased with increasing southwestward distance from Corsair Canyon at Heezen Canyon (3.7–8.0 days), Nygren Canyon (15.6–19.2), and Oceanographer Canyon (20.4–25.7). Estimated minimum transit times from Northeast Channel varied between 10.2 and 38.4 days and were generally faster for the deep than shallow area. Similar patterns were predicted for the maximum transit time from the zones of interest (data not shown). Maximum transit times reached ∼30 days in Gilbert and Oceanographer Canyons and 41 days in the shallow area of Northeast Channel.

The estimated position of tracks varied among months during the surveyed period (**Figure 11**). In January, most tracks straddled the upper continental slope at depths < 2000 m. To the southwest, the tracks extended at the farthest to Nygren Canyon, then diverting offshore into deeper waters. To the northeast, tracks were predicted to occur along the slope at the mouth of Northeast Channel, but rarely found northeastward of the Channel. In May, tracks originating from the northeast along the slope close to the shelf break appeared restricted by the 1000-m isobath. Estimated tracks reached further south than in January, most immediately offshore of Oceanographer Canyon, Gilbert Canyon and Lydonia Canyon, without penetrating into the canyons. Around the middle of Georges Bank, tracks extend further offshore down to the 3000-m isobath. In September, consistent with previous observations, no connectivity was predicted with areas northeast of Corsair Canyon. Most tracks originated from the southwest of Corsair Canyon, beyond Oceanographer Canyon. Most of these tracks, however, were confined to the 3000-m isobath, in the upper slope area extending immediately north of Corsair Canyon to Oceanographer Canyon. Overall, high interannual variability in spatial patterns was detected. The areas where > 50% of tracks were predicted to occur were restricted to the immediate adjacent region surrounding Corsair Canyon.

Overall, these patterns suggest that regional hydrodynamic connectivity from other zones of interest to Corsair Canyon is predicted to be strongest with nearby Georges Canyon and Heezen Canyon. Connectivity with canyons further to the southwest of Corsair Canyon is predicted to occur sporadically, and mostly in summer. At that time, currents flow predominantly northeastward, connecting Corsair Canyon to distant canyons close to the shelf edge, particularly Gilbert and Oceanographer Canyons in late summer (September). In contrast, predicted connectivity with the Northeast Channel (northeast of Corsair Canyon) is mostly observed in winter and spring, making it a potential source for Corsair at this time, with low potential for connectivity in summer. Tracks originating directly from the canyon proper were also observed at times, suggesting Corsair acts as a source, particularly in January.

DISCUSSION

The two deep-water corals *Paragorgia arborea* and *Primnoa resedaeformis* are widely distributed across the Atlantic continental margin of United States and Canada and into the Labrador Sea and spanning ocean basins. However, their distributions are fragmented, and corals are mostly found in canyons or regions of relative steep or heterogeneous topography that may include large boulders or vertical walls. This was the case in our study as well, where a single canyon, Corsair Canyon harbored dense aggregations of large colonies of *P. arborea*. Even within Corsair Canyon, these aggregations were found only at two locations with steep topography and large boulders.

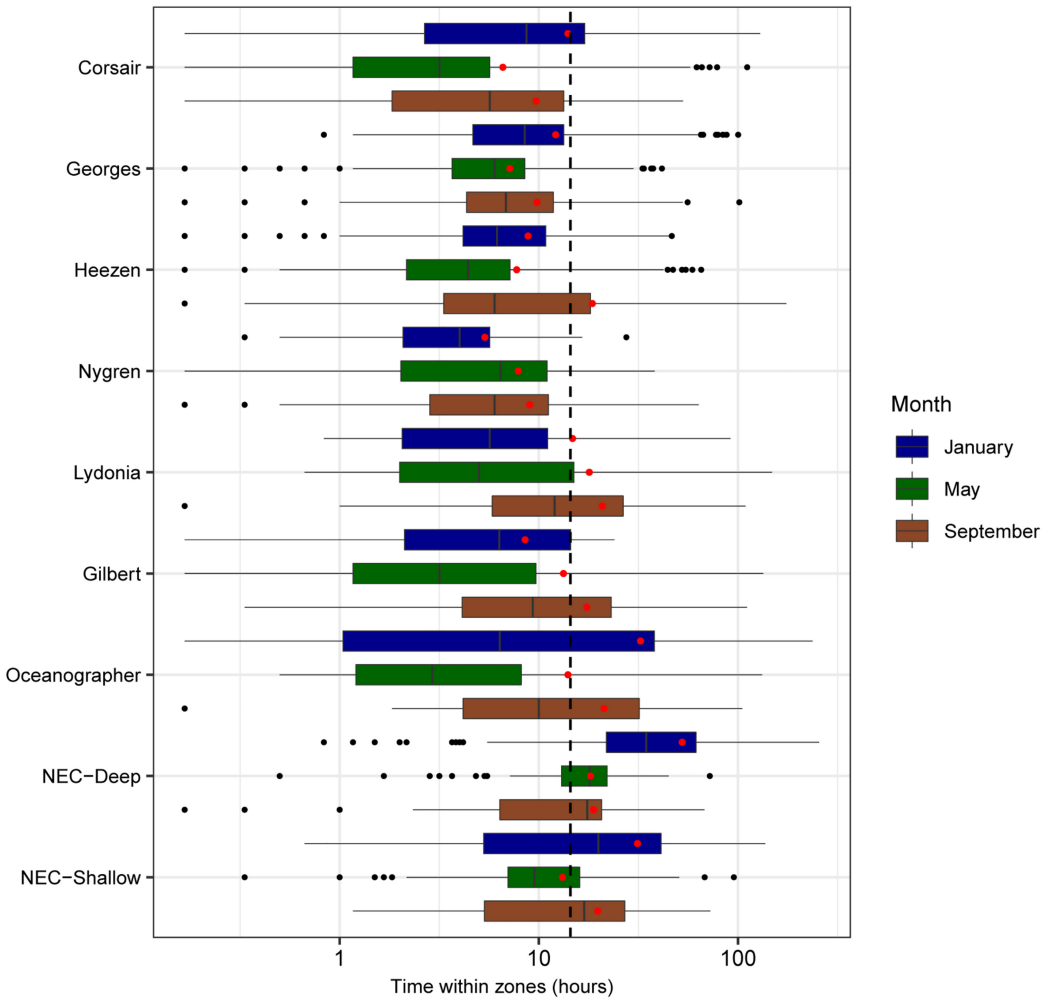


FIGURE 9 | Boxplots of residence time (h) for all tracks overlapping zones of interest segregated by month (sample sizes for the zone-month combinations are given in **Table 4**). Mean residence times for each month-zone combination are shown (red diamonds), as well as overall average (black dashed line).

These locations, in addition to providing hard substrate for attachment, likely experience relatively higher current flow than the surrounding flat seafloor and thus higher delivery of food particles. The densities of these coral aggregations were three times to an order of magnitude greater than at equivalent depths in the NECCCA and some of the colonies were very large (i.e., old) with a maximum height of > 3 m (100 s of years old; Bennecke et al., 2016). Corsair Canyon also had the largest number of damaged colonies (mostly from fishing activity) and most litter of all 3 canyons, underscoring the vulnerability of these dense coral patches to human activity. Because of their high abundance and their vulnerability, the coral aggregations in Corsair Canyon were afforded protection through a DFO fisheries closure.

Although the populations are protected, their viability and ability to recover from previous damage by human activity is not necessarily ensured. For spatially fragmented populations, population persistence (or recovery from fishing) depends in part on recruitment and colonization. Recruitment to a population can be either through self-seeding, or through dispersal from an allochthonous source and adequate connectivity with the source population. For coral populations in Corsair Canyon, allochthonous supply, as predicted solely by hydrodynamic connectivity, that originated from Georges and Heezen Canyons to the southwest of Corsair Canyon, was the most consistent during all seasons and most years. Of these, only Georges Canyon is within Canada's EEZ and based on our data has very sparse populations of corals that can supply recruits. The NECCCA, the only location with significant coral aggregations of *P. arborea* on the continental shelf break and slope within the Canadian EEZ, exhibited some predicted hydrodynamic connectivity with Corsair Canyon, particularly in winter and spring. Thus, NECCCA may be a source of recruits if winter and spring encompass the spawning season of *P. arborea*, which is currently unknown. However, based on our results in winter, downwelling and seaward offshore advection through Corsair Canyon may also be more frequent, arguably preventing flow into it and limiting its hydrodynamic connection with NECCCA.

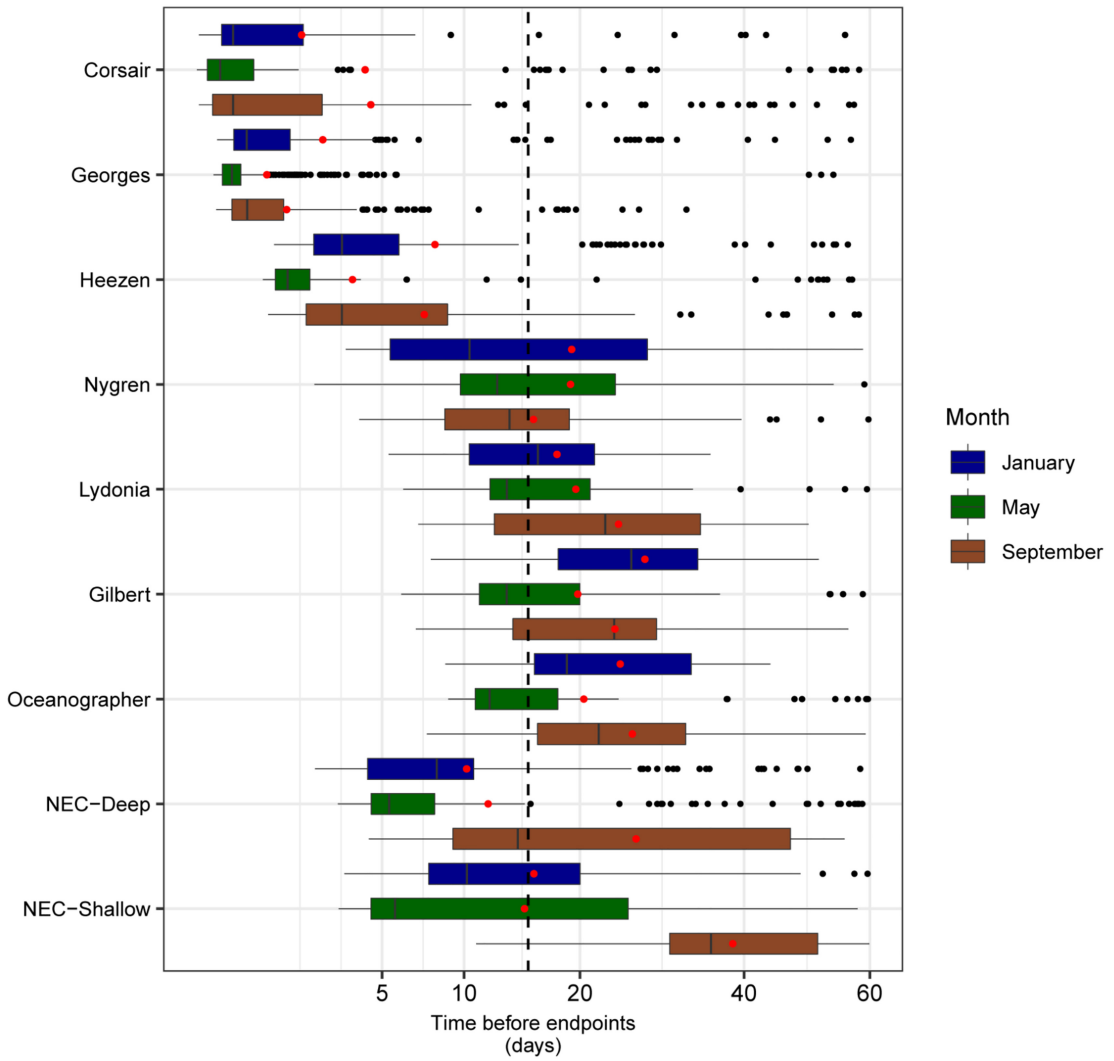


FIGURE 10 | Boxplots of mean minimum transit time calculated from all tracks overlapping each zone of interest, segregated by month (sample sizes for the zone-month combinations are given in **Table 4**). Mean transit times for each month-zone combination (red diamonds) and overall average (black dashed line) are also shown.

Our results suggest that Heezen Canyon, and to a lesser extent Nygren Canyon, which harbor high densities of *P. arborea* (Metaxas, personal observation), likely are the most consistent larval sources for the populations in Corsair Canyon. Predicted tracks ending in Corsair Canyon originate from regions in close proximity on the continental slope within 1–2 days, but more broadly over the shelf over periods of 30–35 days. These results suggest that the geographic range of potential larval sources will depend on larval duration, although likely restricted to the continental shelf and slope (and even the Gulf of Maine) because deep water corals are not found on the sedimentary habitats beyond the continental slope.

The predicted short transit times in reaching the end points in Corsair Canyon from the canyon proper may be indicative of low self-recruitment within the canyon. However self-recruitment may be higher in September, and less so in May, when longer transit times of up to 60 days were observed. Although these transit times may be indicative of currents bouncing in and out of the canyon, larvae trapped within those currents would be returned to the canyon on multiple occasions. Assuming a larval duration of < 60 days and passive dispersal (also currently unknown), these larvae would be positioned within the canyon at some point during their competency period. Both larval retention and larval return to their release points were demonstrated in simulations using ophiuroids in canyons in southwestern Australia (Kool et al., 2015). Corsair Canyon may act as a larval source to other locations along the slope; experiments using forward tracking can help elucidate this possibility, as well as explore the level of connectivity with NECCCA.

Population persistence of the coral aggregations in Corsair Canyon may require the preservation of coral aggregations

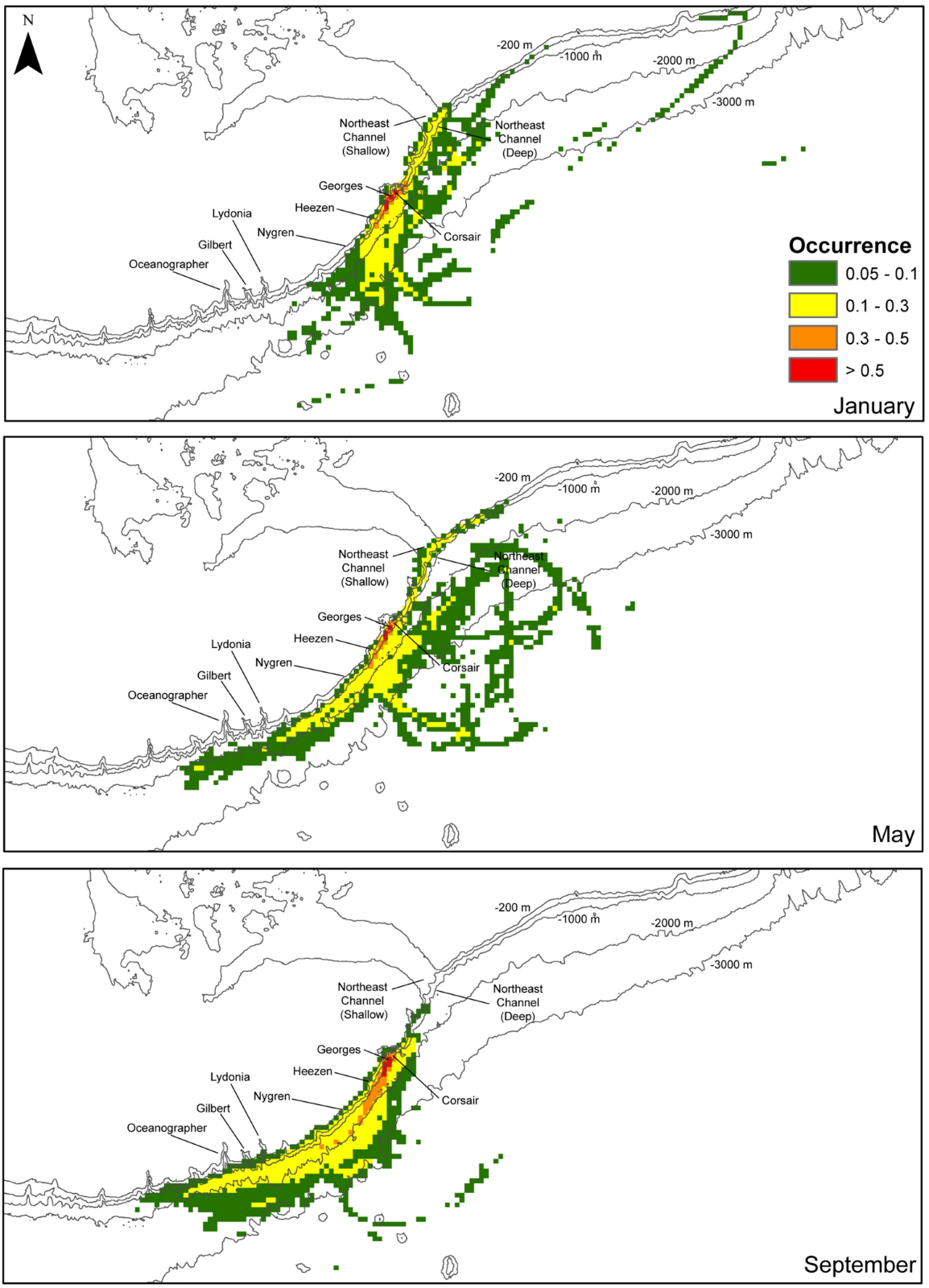


FIGURE 11 | Fraction of the total number of tracks (0–1) of all tracks in the region surrounding the mouth of Corsair Canyon over the maximum temporal length of release (60 d) segregated by month: January, May, and September (total of 750 tracks for each month). Densities were computed on a 5 km × 5 km grid. Fractions below 0.05 are not shown.

in Heezen and Nygren Canyons, i.e., within the EEZ of USA, as the most consistently emerging larval sources. The Northeast Canyons and Seamounts Marine National Monument, established in the USA in 2016, protects some canyons further south that do serve as minor source populations (particularly Oceanographer Canyon in autumn), but the boundary of the Monument does not extend as far north as Heezen and Nygren Canyons. In turn, given that Corsair Canyon may serve as a significant larval source to the southeast, its protection augments the probability of larval supply to canyons in the US EEZ. The broad geographic range over which tracks were predicted to occur over periods of 60 days indicate potential connectivity (however, of unknown magnitude) across the entire continental slope in the region and possibly the Gulf of Maine. Our results strongly suggest that cross-boundary coordination is essential in the conservation of aggregations of deep-water corals in the northwest Atlantic, for ensuring larval exchange and connectivity. The importance in transboundary considerations and cooperation in spatial planning and conservation is being advocated particularly for the marine realm, where few physical barriers to the movement of individuals and populations exist (Arafeh-Dalmau et al., 2017; Aburto-Oropeza et al., 2018). For example, Arafeh-Dalmau et al. (2017) illustrated the feasibility of a transboundary networks of MPAs in the Ensenadian ecoregion, linking the more poorly sampled marine habitats of Baja California, Mexico with the well-established network of marine reserves in California, USA. It is recognized that transnational efforts in marine conservation planning entail decisions complicated by multiple stakeholders, conservation targets and political climates. Including costs of conservation can facilitate the process as illustrated by a study on the crowded Mediterranean Sea (Mazor et al., 2014). Approaches, such as developing access to homogeneous data, promoting transboundary collaborations, developing joint management units, and improving monitoring and surveillance, have been proposed to overcome some of the considerable challenges in cross-boundary conservation (Katsanevakis et al., 2015).

Studies on ecological connectivity of canyons have addressed linkages of individual canyons with the continental shelf (e.g., marine litter originating in coastal zones, Ramirez-Llodra et al., 2013), and as conduits to the deep ocean beyond continental margins (Huthnance, 1995; Canals et al., 2006). Here, we estimated connectivity between canyon systems, a key area where research is currently lacking (Fernandez-Arcaya et al., 2017). To fully describe hydrodynamic connectivity between canyons, regional ocean models that accurately capture bathymetric features on continental margins are needed. In southwestern Australia, connectivity among a series of canyons was strongly influenced by the dominant circulation in the region and was correlated to the distance of the canyon from shore and the shape of the canyon (Kool et al., 2015), both of which affect local hydrography. In our study, the coarse resolution of the bathymetry in the ocean model prevented us from assessing hydrodynamics in the canyon proper because its bathymetry is poorly resolved. It is thus important that high-resolution bathymetric datasets be made readily available through online portals, in particular those held by national hydrographic agencies (see Mayer et al., 2018), to facilitate more realistic ocean modeling efforts. Further, these efforts can assist in the identification of patterns of connectivity which particularly for the offshore, remote areas are presently difficult to quantify accurately.

While we focused on hydrodynamic connectivity, estimates of larval dispersal and ecological connectivity may differ. Biophysical models are one way to estimate larval dispersal, which encompasses larval transport (in turn determined by advection and larval behavior), timing and location of spawning, planktonic larval duration, and larval settlement (Pineda et al., 2007). However, most of these factors remain unknown for most shallow-water species and for nearly all deep-sea species (Metaxas and Saunders, 2009; Hilário et al., 2015). Here, we have attempted to incorporate elements of the location and timing of spawning and larval settlement (by including canyons with known populations of deep-water corals and three different seasons) and planktonic larval duration (see Materials and Methods). We did not incorporate larval behaviors, such as diel or ontogenetic vertical migrations or responses to features in the water column, such as density structure or food layers, because there is absolutely no relevant data for larvae of our focal species. Other studies, using hypothetical but not quantified behaviors, have suggested that the vertical position of larvae of deep-sea species in the water column affects dispersal distance (e.g., Young et al., 2012; McVeigh et al., 2017). However, studies from shallow water species that examined the contributions of different factors in larval dispersal have suggested that site of larval release explains a much greater proportion of the variance than larval vertical migration (Daigle et al., 2016). The relative importance of these factors in modifying our observed patterns of hydrodynamic connectivity remains unknown.

Area-based conservation of deep-water corals is gaining momentum globally. On the northwest Atlantic, in the EEZs of Canada and United States, corals are abundant and diverse in canyons along the continental shelf break. However, their distribution is fragmented and maintaining population connectivity is paramount for sustaining the aggregations in the canyons. The hydrodynamics are complex and seasonally and annually variable, further complicating the identification of sources and sinks of potential coral recruits. We have shown that larval sources may occur across national boundaries and political jurisdictions. Ensuring the long-term preservation of vulnerable marine ecosystems, such as those formed by deep-water corals, requires transboundary collaboration in data collection and cooperation in management actions.

AUTHOR CONTRIBUTIONS

AM conceptualized the study and designed and led the ROV dives that collected the video. ML developed and conducted the analysis on hydrodynamic connectivity. SdM conducted the analysis of the video data on coral distributions. All authors contributed to the writing of the manuscript.

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frontiers in Marine Science

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Corrigendum: Hydrodynamic Connectivity of Habitats of Deep-Water Corals in Corsair Canyon, Northwest Atlantic: A Case for Cross-Boundary Conservation

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Keywords: deep-water corals, connectivity, area-based conservation, cross-boundary collaboration, submarine canyons, hydrodynamics, continental slope, fishery closures

A Corrigendum on

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In the original article, there were mistakes in **Figures 8–11** and **Table 4** as published. A mistake was made in the original tracking code during interpolation of the velocity fields from the ocean circulation model. Briefly, the fields were weighted by distance to the three nearest discrete points, rather than the *inverse* weight by distance to the same three nearest points (the proper approach). The outcome of this error is that velocities most resembled *distant* points rather than close ones. The corrected **Figures 8–11** and **Table 4** appear below.

In addition, in the original article, there was an error. To account for the above-stated mistake, a correction has been made to the ***Results***, ***Hydrodynamic Connectivity***, paragraphs 1–4:

"Seasonal and inter-annual patterns of occurrence of predicted track origins that ended near the mouth of Corsair Canyon were most persistent from immediately adjacent areas: Corsair Canyon proper, Georges Canyon, and Heezen Canyon (**Figure 8** and **Table 4**). Occurrence in these areas among all assessed months and years was observed in 34.6, 65.8, and 29.0% of all predicted tracks, respectively. Estimated connectivity from sites in the Northeast Channel (northeast of Corsair Canyon) occurred in 18.4 and 11.2% of total tracks for the deep and shallow areas, respectively. When pooled, the Northeast Channel could thus be a potentially important source with a probability of occurrence of ∼30% within 60 days. Predicted connectivity from the deep area in Northeast Channel was clearly stronger in winter; for example 244 tracks occurred in January in 8 years, compared to 31 tracks in September in 6 years. Predicted connectivity from more distant canyons southwest of Corsair Canyon was more sporadic. Occurrence in these areas ranged from 5.3% of tracks with Lydonia Canyon to 9.6% of tracks with Nygren Canyon in 4–10 years. Despite its distance from Corsair Canyon, occurrence in Oceanographer Canyon was predicted to occur in 5.9% of all tracks. Predicted connectivity with these canyons was most evident in May and September, with tracks occurring in September in 7–8 years."

"Mean residence time in each zone (calculated as the total time a track was located in that zone) was estimated at 16 h over all months and zones of interest (**Figure 9**). Short residence times

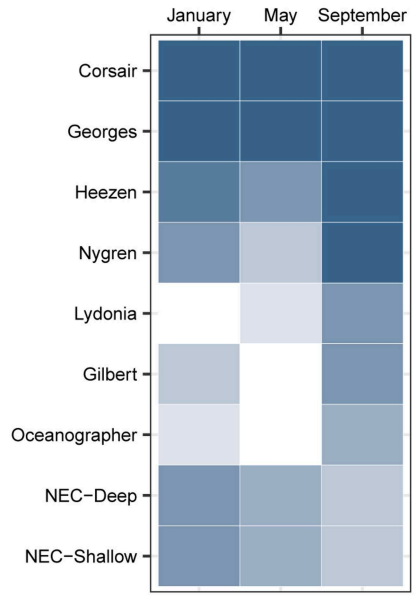


FIGURE 8 | Hydrodynamic connectivity based on occurrence (out of 10 years) observed between endpoints at the mouth of Corsair Canyon and zones of interest in January, May, and September between 2004 and 2013.

were observed in areas southwest of Corsair Canyon, in Georges Canyon and Heezen Canyon, and particularly in Nygren Canyon (mean: 5.4, 7.9, and 9.0 h in May, January, and September, respectively). In contrast, mean residence times were longer in Lydonia Canyon, Gilbert Canyon and Oceanographer Canyon in September (19.1, 14.8, and 20.7 h respectively). Mean residence time was estimated to be consistently above the grand mean in January in the deep area of Northeast Channel (52.4 h), and in the shallow area (31.3 h). We attribute this pattern to the effect of tides in Northeast Channel. The longest residence times (>200 h) were observed in January in the deep area of Northeast Channel and Oceanographer Canyon (single occurrence of 237 h)."

"Mean minimum transit time between the mouth of Corsair Canyon and zones of interest was estimated at 15.1 days prior to track end time across all years and months (**Figure 10**). As expected, areas nearer the mouth of Corsair Canyon (Corsair Canyon proper and Georges Canyon) showed short mean transit time, particularly in January for Corsair Canyon proper (1.8 days) and in May for Georges Canyon (0.9 days). Minimum transit time increased with increasing southwestward distance from Corsair Canyon at Heezen Canyon (3.7–8.0 days), Nygren Canyon (15.6–19.2), and Oceanographer Canyon (20.4–25.7). Estimated minimum transit times from Northeast Channel varied between 10.2 and 38.4 days and were generally faster for

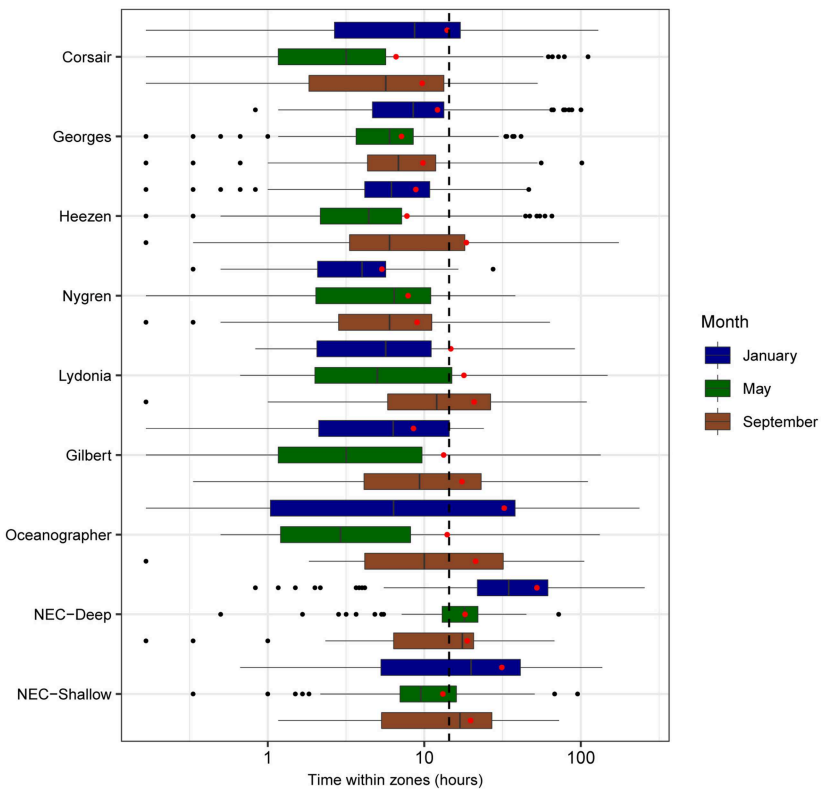


FIGURE 9 | Boxplots of residence time (h) for all tracks overlapping zones of interest segregated by month (sample sizes for the zone-month combinations are given in Table 4). Mean residence times for each month-zone combination are shown (red diamonds), as well as overall average (black dashed line).

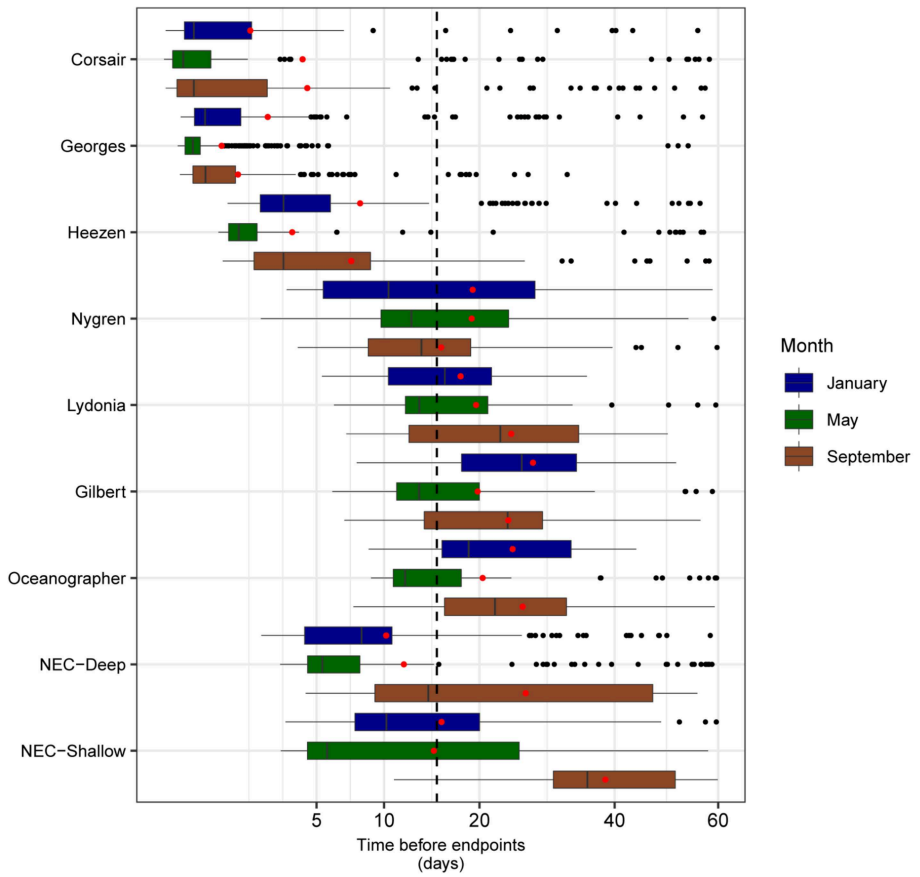


FIGURE 10 | Boxplots of mean minimum transit time calculated from all tracks overlapping each zone of interest, segregated by month (sample sizes for the zone-month combinations are given in Table 4). Mean transit times for each month-zone combination (red diamonds) and overall average (black dashed line) are also shown.

the deep than shallow area. Similar patterns were predicted for the maximum transit time from the zones of interest (data not shown). Maximum transit times reached ∼30 days in Gilbert and Oceanographer Canyons and 41 days in the shallow area of Northeast Channel."

"The estimated position of tracks varied among months during the surveyed period (**Figure 11**). In January, most tracks straddled the upper continental slope at depths < 2000 m. To the southwest, the tracks extended at the farthest to Nygren Canyon, then diverting offshore into deeper waters. To the northeast, tracks were predicted to occur along the slope at the mouth of Northeast Channel, but rarely found northeastward of the Channel. In May, tracks originating from the northeast along the slope close to the shelf break appeared restricted by the 1000-m isobath. Estimated tracks reached further south than in January, most immediately offshore of Oceanographer Canyon, Gilbert Canyon and Lydonia Canyon, without penetrating into the canyons. Around the middle of Georges Bank, tracks extend further offshore down to the 3000-m isobath. In September, consistent with previous observations, no connectivity was predicted with areas northeast of Corsair Canyon. Most tracks originated from the southwest of Corsair Canyon, beyond Oceanographer Canyon. Most of these tracks, however, were confined to the 3000-m isobath, in the upper slope area extending immediately north of Corsair Canyon to Oceanographer Canyon. Overall, high interannual variability in spatial patterns was detected. The areas where > 50% of tracks were predicted to occur were restricted to the immediate adjacent region surrounding Corsair Canyon."

Furthermore, a correction has also been made to the ***Discussion***, paragraph two:

"Although the populations are protected, their viability and ability to recover from previous damage by human activity is not necessarily ensured. For spatially fragmented populations, population persistence (or recovery from fishing) depends in part on recruitment and colonization. Recruitment to a population can be either through self-seeding, or through dispersal from an allochthonous source and adequate connectivity with the source population. For coral populations in Corsair Canyon, allochthonous supply, as predicted solely by hydrodynamic connectivity, that originated from Georges and Heezen Canyons to the southwest of Corsair Canyon, was the most consistent during all seasons and most years. Of these, only Georges Canyon is within Canada's EEZ and based on our data has

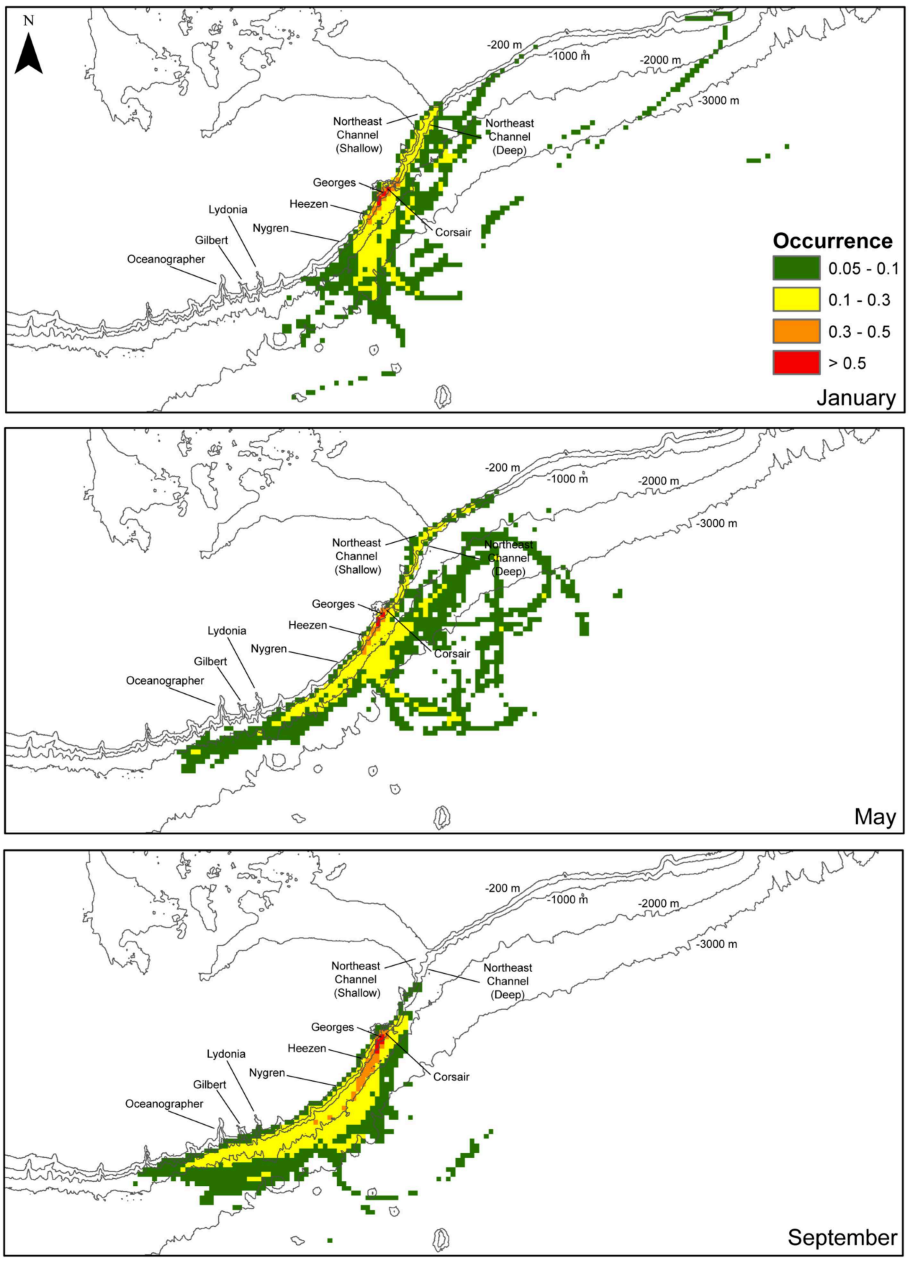


FIGURE 11 | Fraction of the total number of tracks (0–1) of all tracks in the region surrounding the mouth of Corsair Canyon over the maximum temporal length of release (60 d) segregated by month: January, May, and September (total of 750 tracks for each month). Densities were computed on a 5 km x 5 km grid. Fractions below 0.05 are not shown.

very sparse populations of corals that can supply recruits. The NECCCA, the only location with significant coral aggregations of *P. arborea* on the continental shelf break and slope within the Canadian EEZ, exhibited some predicted hydrodynamic connectivity with Corsair Canyon, particularly in winter and spring. Thus, NECCCA may be a source of recruits if winter and spring encompass the spawning season of *P. arborea,* which is currently unknown. However, based on our results in winter, downwelling and seaward offshore advection through Corsair Canyon may also be more frequent, arguably preventing flow into it and limiting its hydrodynamic connection with NECCCA. Our results suggest that Heezen Canyon, and to a lesser extent Nygren Canyon, which harbor high densities of *P. arborea* (Metaxas, personal observation), likely are the most consistent larval sources for the populations in Corsair Canyon. Predicted tracks ending in Corsair Canyon originate from regions in close proximity on the continental slope within 1–2 days, but more broadly over the shelf over periods of 30–35 days. These results

TABLE 4 | Number of tracks originating from each of the 9 zones of interest and ending at 15 endpoints offshore of Corsair Canyon (northwest Atlantic).

Zone of interest	January	May	September	Total
Corsair Canyon	389	185	205	779
Georges Canyon	462	469	549	1480
Heezen Canyon	193	250	210	653
Nygren Canyon	35	52	129	216
Lydonia Canyon	15	37	67	119
Gilbert Canyon	22	41	76	139
Oceanographer Canyon	26	50	56	132
NEC-Deep	244	138	31	413
NEC-Shallow	94	132	26	252

For each endpoint, tracks terminated on 5 days (11th – 15th) in January, May, and September from 2004-2013 at 12:00pm UTC (n = max. 750 tracks per month). 'NEC,' Northeast Channel.

suggest that the geographic range of potential larval sources will depend on larval duration, although likely restricted to the continental shelf and slope (and even the Gulf of Maine) because deep water corals are not found on the sedimentary habitats beyond the continental slope."

Lastly, a correction has been made to the ***Discussion***, paragraph 4:

"Population persistence of the coral aggregations in Corsair Canyon may require the preservation of coral aggregations in Heezen and Nygren Canyons, i.e., within the EEZ of USA, as the most consistently emerging larval sources. The Northeast Canyons and Seamounts Marine National Monument, established in the USA in 2016, protects some canyons further south that do serve as minor source populations (particularly Oceanographer Canyon in autumn), but the boundary of the Monument does not extend as far north as Heezen and Nygren Canyons. In turn, given that Corsair Canyon may serve as a significant larval source to the southeast, its protection augments the probability of larval supply to canyons in the US EEZ. The broad geographic range over which tracks were predicted to occur over periods of 60 days indicate potential connectivity (however, of unknown magnitude) across the entire continental slope in the region and possibly the Gulf of Maine. Our results strongly suggest that cross-boundary coordination is essential in the conservation of aggregations of deep-water corals in the northwest Atlantic, for ensuring larval exchange and connectivity. The importance in transboundary considerations and cooperation in spatial planning and conservation is being advocated particularly for the marine realm, where few physical barriers to the movement of individuals and populations exist (Arafeh-Dalmau et al., 2017; Aburto-Oropeza et al., 2018). For example, Arafeh-Dalmau et al. (2017) illustrated the feasibility of a transboundary networks of MPAs in the Ensenadian ecoregion, linking the more poorly sampled marine habitats of Baja California, Mexico with the well-established network of marine reserves in California USA. It is recognized that transnational efforts in marine conservation planning entail decisions complicated by multiple stakeholders, conservation targets and political climates. Including costs of conservation can facilitate the process as illustrated by a study on the crowded Mediterranean Sea (Mazor et al., 2014). Approaches, such as developing access to homogeneous data, promoting transboundary collaborations, developing joint management units, and improving monitoring and surveillance, have been proposed to overcome some of the considerable challenges in cross-boundary conservation (Katsanevakis et al., 2015)."

The authors apologize for these errors and state that they do not change the scientific conclusions of the article in any way. The original article has been updated.

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ORIGINAL RESEARCH
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The Diversity and Ecological Role of Non-scleractinian Corals (Antipatharia and Alcyonacea) on Scleractinian Cold-Water Coral Mounds

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Cold-water coral carbonate mounds, created by framework-building scleractinian corals, are also important habitats for non-scleractinian corals, whose ecology and role are understudied in deep-sea environments. This paper describes the diversity, ecology and role of non-scleractinian corals on scleractinian cold-water coral carbonate mounds in the Logachev Mound Province, Rockall Bank, NE Atlantic. In total ten non-scleractinian species were identified, which were mapped out along eight ROV video transects. Eight species were identified as black corals (three belonging to the family Schizopathidae, one each to the Leiopathidae, Cladopathidae, and Antipathidae and two to an unknown family) and two as gorgonians (Isididae and Plexauridae). The most abundant species were *Leiopathes* sp. and *Parantipathes* sp. 2. Areas with a high diversity of non-scleractinian corals are interpreted to offer sufficient food, weak inter-species competition and the presence of heterogeneous and hard settlement substrates. A difference in the density and occurrence of small vs. large colonies of *Leiopathes* sp. was also observed, which is likely related to a difference in the stability of the substrate they choose for settlement. Non-scleractinian corals, especially black corals, are an important habitat for crabs, crinoids, and shrimps in the Logachev Mound Province. The carrier crab *Paromola* sp. was observed carrying the plexaurid *Paramuricea* sp. and a black coral species belonging to the genus *Parantipathes*, a behavior believed to provide the crab with camouflage or potentially a defense mechanism against predators. More information on the ecophysiology of non-scleractinian corals and fine-scale local organic matter supply are needed to understand what drives differences in their spatial distribution and community structure.

Keywords: cold-water coral mounds, fine-scale spatial patterns, biodiversity, associated megafauna, Antipatharia, Alcyonacea, Logachev Mound Province

INTRODUCTION

Lophelia pertusa and *Madrepora oculata*, the dominant reef-forming scleractinian corals in the deep sea, have been widely studied over the last 20 years. However, due to the high biodiversity and the numerous symbiotic associates they have, non-scleractinian corals should not be overlooked (e.g., Buhl-Mortensen and Mortensen, 2005; Etnoyer and Morgan, 2005; Tazioli et al., 2007; Cerrano et al., 2010; Wagner et al., 2012; Corbera Pascual, 2015; Cúrdia et al., 2015; De Clippele et al., 2015). This is because non-scleractinian corals are known to be an important habitat for a diverse range of organisms providing, e.g., a feeding platform, a place to shelter or a substrate for fish to lay their eggs on (Buhl-Mortensen and Mortensen, 2004; Le Guilloux et al., 2010; Wagner et al., 2012; De Clippele et al., 2015). In this study, we will discuss the non-scleractinian corals belonging to the Antipatharia and Alcyonacea.

Antipatharia also referred to as black corals (Cnidaria: Anthozoa: Hexacorallia) encompass seven families (Wagner et al., 2012) with 75% (c. 180 species) found below 50 m depth (Cairns, 2007). The black corals' lifespan is greater than most other deep-sea coral species (Andrews et al., 2001, 2009; Roark et al., 2009). A *Leiopathes annosa* (Wagner and Opresko, 2015), colony from Hawaiian (United States) waters was estimated to be 4,265 years old with radial growth rates between 0.005 and 0.022 mm yr^{-1} (Roark et al., 2009; Sherwood and Edinger, 2009).

Gorgonians (Cnidaria: Anthozoa: Octocorallia) belong to the Order Alcyonacea can be found at virtually any depth, with records found as deep as 5850 m (Madsen, 1956). They can be found in most ocean basins and can live over 100 years (Hill et al., 2011; Watling et al., 2011; Lacharite and Metaxas, 2013). Octocorals grow faster and have lower lifespans than black coral species, with radial growth rates between 0.05 and 0.44 mm yr^{-1} (Watling et al., 2011).

Given their slow growth rates and great longevity, cold-water black corals and octocorals are particularly vulnerable to anthropogenic damage. Disturbance and removal through bottom fishing (Althaus et al., 2009) and exploitation for commercial therapeutic and jewelry/art use (Grigg, 2001) are significant threats. Deep-water black and octocorals are part of "Vulnerable Marine Ecosystems" (VME) as defined by United Nations General Assembly Resolutions 61/105 and 64/72 (Fuller et al., 2008).

This study focussed on the non-scleractinian corals that grow on the cold-water coral carbonate mounds in the Logachev Mound Province, Rockall Bank. While black corals and deep-sea gorgonians corals have been reported in this area in previous studies (Duineveld et al., 2007; Roberts et al., 2008; Henry et al., 2014) their community characteristics, ecology and functional roles have not been studied.

Cold-water coral carbonate mounds are topographic structures that owe their existence, partially or entirely, to the growth of scleractinian framework building corals, such as *Lophelia pertusa* and *Madrepora oculata* (Freiwald, 2002; Roberts et al., 2006). These mound structures have developed over glacial-interglacial time periods and vary widely in size and shape (Kenyon et al., 2003; Van Weering et al., 2003; Mienis et al., 2007; Wheeler et al., 2007). Both box core samples and video footage have revealed that cold-water coral carbonate mounds are associated with a high diversity of organisms (Raes et al., 2003; Raes and Vanreusel, 2005, 2006; Wheeler et al., 2005; Henry and Roberts, 2007). Corals are suspension feeders and have been shown to be more abundant on- vs. off-mound (Henry and Roberts, 2007). Soetaert et al. (2016) showed that at Rockall Bank, there is a significant interaction between tidal currents and cold-water coral formed mounds which induce downwelling events of surface water that brings the organic matter to 600 m deep. Therefore, the greater resuspension of particulate organic matter and the high currents keeping sedimentation rates low could explain why both filter and suspension feeders are more abundant on the mounds (Henry and Roberts, 2007). These characteristics make cold-water coral mounds important features to study regarding non-scleractinian coral presence and diversity. The dominant non-scleractinian fauna varies across European cold-water coral reef ecosystems with, for example, black corals dominating the Belgica Mound Province (Henry and Roberts, 2007), while gorgonians corals dominate reefs in Norwegian fjords (Mortensen et al., 1995). This difference could be a consequence of variability in hydrography, topography, and the biological traits of the species themselves, which is interrelated to the mound or reefs' size and complexity of the habitat (Ricklefs and Lovette, 1999).

Therefore, this study aims to: (1) document the diversity of these non-scleractinian corals on cold-water coral carbonate mounds, (2) determine what environmental conditions influence differences in their density, and (3) investigate their potential ecological role. The goal of this study is to provide more information on these non-scleractinian corals to ensure that better-informed decisions can be made to protect these long-lived organisms.

MATERIALS AND METHODS

Study Area

The Logachev Mound Province is located on the south-eastern slope of Rockall Bank in the northeast Atlantic (Kenyon et al., 2003; **Figure 1**). Within Rockall Trough, the upper layers down to 1,200–1,500 m are occupied by Eastern North Atlantic Water (ENAW) (Holliday et al., 2000). The cold-water coral carbonate mounds are between 5 and 360 m tall, up to a few kilometers long and located between 600 and 1000 m depth, which is within the boundaries of the ENAW (Kenyon et al., 2003; Mienis et al., 2007, 2009; de Haas et al., 2009). The ENAW circulates through an anticyclonic gyre in Rockall Trough with a net northward flow direction, while around the mounds there is a local residual current flow toward the south-west that ranges between 5 and 15 cm s^{-1} (Huthnance, 1986; Holliday et al., 2000; Mienis et al., 2007; White et al., 2007; Soetaert et al., 2016). There is also a stronger bottom-magnified diurnal tidal flow of 15–28 cm s^{-1}. It is these strong northwest-southeast directed currents that affect the growth direction of the mounds, which is perpendicular to the regional contours (Mienis et al., 2007; White et al., 2007).

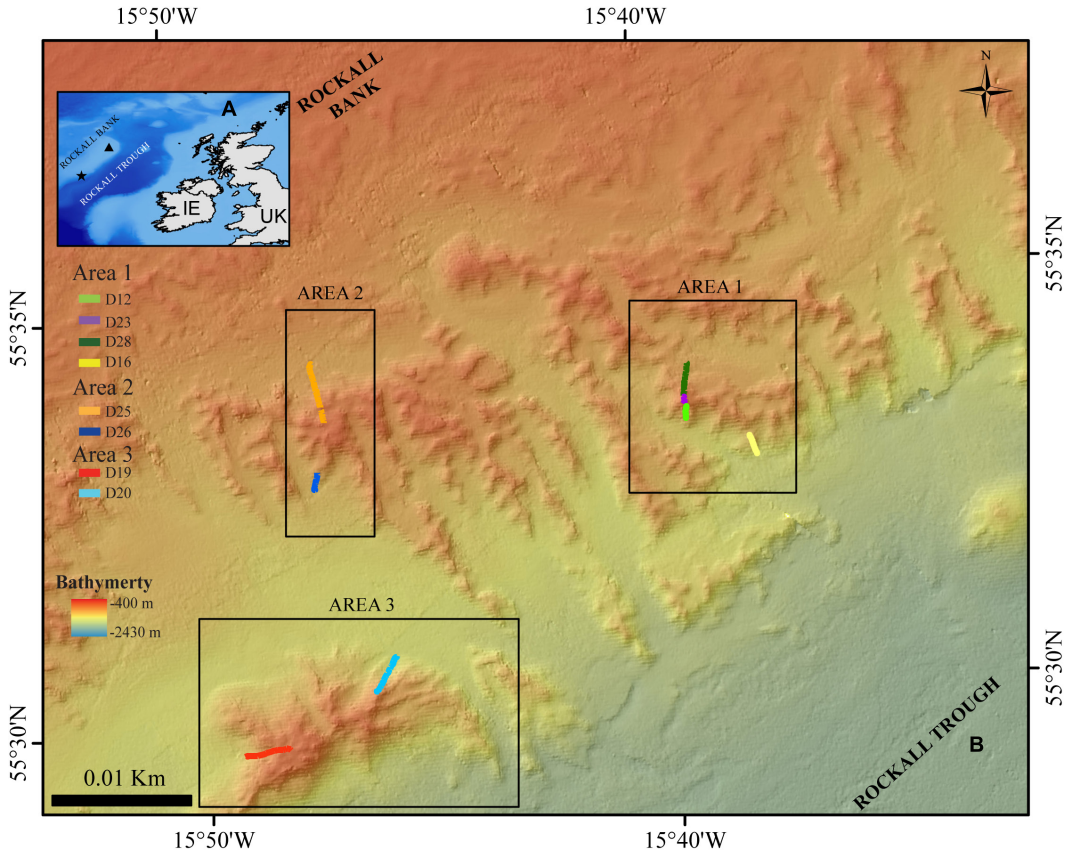


FIGURE 1 | (A) Location map of the Logachev Mound Province (star), and Rockall Island (triangle) on Rockall Bank. IE: Ireland **(B)** Location of the three study areas and ROV dives in the Logachev Mound Province on the south-east side of Rockall Bank.

The Logachev Mound Province consist of a cluster of mounds that are built of accumulated fine sediments baffled by coral reef framework, dead coral fragments and live coral on the summit. The mound bases are covered by bio- and siliciclastic sands with various amounts of pebbles, cobbles and boulders (de Haas et al., 2009). The flanks of the mounds are covered with patches of coral rubble, dead coral branches and living corals, while the summits of the mounds are characterized by dense *L. pertusa* patches at 500–600 m depth (Kenyon et al., 2003; Van Weering et al., 2003; de Haas et al., 2009).

Food is supplied to the suspension-feeding corals through different mechanisms. First, the presence of the coral framework will slow down the currents allowing the corals to gather food, but also trap sediments, which can then accumulate between the coral branches ensuring further growth of the mounds as a whole (Roberts et al., 2006; Dorschel et al., 2007; de Haas et al., 2009; Mienis et al., 2009; Roberts et al., 2009). Secondly, the interaction of the diurnal tidal currents with the slope of Rockall Bank and the topographies of the cold-water coral mounds themselves, induces downwelling of the productive Rockall Bank surface waters due to the formation of internal waves (Kenyon et al., 2003; Davies et al., 2009; Wagner et al., 2011; Findlay et al., 2013; Cyr et al., 2016; Soetaert et al., 2016). Thirdly, the interaction of internal waves and tidal currents with seabed sediments also causes nepheloid layers, which contain increased amounts of suspended seabed sediment that can supply the corals with food at deeper depths (Kenyon et al., 2003; Mienis et al., 2007). Intermediate Nepheloid Layers (INL) have been identified as turbidity clouds between 450 and 900 m depth and varied in depth and shape coincidingly with the diurnal cycle. The largest turbidity cloud can be found between 200 and 500 m depth, just above the carbonate mounds. A second smaller turbidity cloud can be found 25 km from Rockall Bank between 500 and 700 m depth (White et al., 2003; Mienis et al., 2006, 2007).

High-Definition Video Data

Video Data Acquisition

In the Logachev Mound Province, genera belonging to the Order Antipatharia Milne-Edwards and Haime (1857) (black corals), as well as the Order Alcyonacea Lamouroux 1816, were present and studied here using high definition (HD) video recordings from remotely operated vehicles (ROVs). High-definition video data were collected in the Logachev Mound Province in 2012 (RRS *James Cook* Cruise 073, May 18–June 15, 2012) as part of the Changing Oceans 2012 expedition, using the ROV *Holland-1*. The data were recorded with a combination of cameras mounted on the ROV: an HD Insite

mini-Zeus video camera with a direct HDSDI fiber output, a Kongsberg 14–208 digital stills camera, a Kongsberg 14–366 pan and tilt camera and an Insite Pegasus-plus fixed zoom camera. Four lights were used: two 400-W deep-sea power and light SeaArc2 HMI lights and two 25,000 lumen Cathx ocean APHOS LED lights. Two lasers spaced 10 cm were also mounted on the HD camera. The position and depth of the ROV were determined by USBL (Sonardyne) underwater positioning system and recorded using the OFOP (Ocean Floor Observation Protocol) software.

During the Changing Oceans Expedition, a total of eight video transects were recorded in the Logachev Mound Province with a total length of ∼3.4 km and an average width of 2.74 m ±0.5 m. These eight video transects only covered small parts, on alternating sides of three large clustered cold-water coral carbonate mounds within the Logachev Mound Province (**Figure 1** and **Table 1**). Since the transects only cover a section and not the whole of the clustered mound, they are referred to as area 1, 2, and 3. Based on Soetaert et al. (2016), it is known that the supply of organic matter varies with depth along the flank of Rockall Bank. It is therefore relevant to note that these three areas are located at different distances on the slope of Rockall Bank from the shallowest point, i.e., Rockall Island (**Figure 1**). Area 1, at 560–700 m depth, is located ∼26.1 km from Rockall Island, area 2 at 530–700 m depth is located ∼25.7 km and area 3 at 530–850 m depth is located ∼26.8 km from Rockall Island.

Substrate Classification

Substrate types were identified from the HD videos according to the classes listed in **Table 2** (see **Table 2** and **Figure 2**) and noted in Excel. The dominant substrate class was noted every meter from the HD videos for which the percentage cover for each substrate class were calculated per flank and area.

Coral Identification and Associated Fauna

The presences of non-scleractinian coral species were noted for every meter in Excel, alongside the notes on the dominant substrate class. Preliminary evaluation of the HD videos indicated a large number of occurrences of different size classes of the black coral species *Leiopathes* sp., which was therefore classified as small (<30 cm), medium (30–100 cm), or large (>100 cm).

The associated mobile megafauna was identified from the HD video and their location on the coral colonies specified as central branch versus the outer branch, and on the base, middle or top part of the colonies.

Analyses

The HD video dive transects that were used for analyses varied from 40 to 1040 m in length (**Table 1**). The video transects were systematically subsampled into a total of 84 groups located at a distance of 40 m to reduce the influence of spatial autocorrelation for statistical analyses (**Table 1**). The length of 40 m was chosen as this length gave the best representation of the substrate and species variability in relation to a changing bathymetry and rugosity. The ArcGIS "Join" function was used to calculate the total number of counts for each non-scleractinian coral species per sub-sample.

Diversity, Evenness, and Density

The species diversity, density, and evenness of all non-scleractinian corals were calculated in the PRIMER software (Clarke and Warwick, 2001). The data matrix composed of the sub-sample number (*y*-axis) and the counts of the non-scleractinian species found per 40 m sub-sample (x-axis). Two types of factors were added. A first identifying the location of the sub-sample (area 1, 2 or 3), and a second factor identifying the flank the sub-sample was located on (NE, S, NW, SW). Shannon diversity index (H′) and Pielou value were used to calculate the diversity and evenness of the non-scleractinian corals in the study area. The Pielou's evenness value can range from 0 to 1, and gives an indication of dominant species being present in a sample (∼0) or if there is an equal abundance of all species (∼1). Density was calculated for all the non-scleractinian corals together and for the species separately, by dividing their total counts by the total square meter which covered per 40 m sub-sample. When the video transects were recorded the ROV varied in height, affecting the average width, and thus the total area of the transect. The average width of the video transects can be found in **Table 1**. When a density calculation was made including two or more different video transects, their average width was used to calculate the total area covered. The number of different species counted per area and flank were also calculated in Excel.

TABLE 1 | Remotely operated vehicle dive information.

Dive (area)	Start Lon (decimal degrees)	Start Lat (decimal degrees)	End Lon (decimal degrees)	End Lat (decimal degrees)	Aspect/ flank	Depth range (min-max) (m)	Length/ Width (m)	No. Sub-samples
12 (1)	−15.65523	55.55799	−15.65557	55.55567	NE	(640–722)]	200/2.36	5
16 (1)	−15.63350	55.55119	−15.63142	55.547439	S	(758–874)	240/2.82	6
23 (1)	−15.65630	55.55847	−15.65571	55.55965	NE	(563–584)	40/2.55	1
28 (1)	−15.65585	55.56014	−15.65389	55.56674	S	(575–701)	240/2.91	6
25 (2)	−15.78718	55.57206	−15.78421	55.56013	NW	(547–705)	1040/3.37	26
26 (2)	−15.78795	55.55020	−15.78918	55.54672	SW	(702–768)	360/2.79	9
19 (3)	−15.82089	55.49419	−15.80442	55.49478	NE	(559–801]	880/2.62	22
20 (3)	−15.76447	55.51220	−15.77232	55.50529	NW	(610–873]	360/2.97	9

Average aspect represents the side of the area/clustered mound at which the video transects were collected.

TABLE 2 | Substrate classes identified in HD video data.

Substrate type	Abbreviation
L. pertusa thicket	LpT
Dead exposed *L. pertusa* framework with scarce live *L. pertusa* colonies	DEC
Coral rubble	CR
Lithified hardground	LiH
Fine sediment with pebbles, cobbles, and boulders (<100 cm diameter)	FS/P/C/B
Mixed sediment with large boulders (>100 cm)	MS/LB
Fine sediment	FS

Environmental Drivers of Spatial Variation in Density

The change in the density of the non-scleractinian species was studied in relation to the substrates and to environmental variables that were extracted from bathymetry data. Substratum information was obtained from video data (see section "Substrate Classification"). Terrain characteristics were extracted from a bathymetry dataset that was provided by the Irish National Seabed Survey programme (INSS) at a 20 m× 20 m resolution[1]. Several topographic variables were derived from the bathymetric grid using the ArcGIS 10.1, ESRI Software and the Benthic Terrain Modeler (Wright et al., 2012): slope, aspect (eastness and northness), rugosity (calculated at two spatial scales, using a square kernel window of respectively 3 × 3 and 9 × 9 pixels) and bathymetric positioning index (BPI; calculated at two spatial scales using an annulus kernel window with inner and outer radius of respectively 3 × 6 and 6 × 9 cells). More information on these variables can be found in De Clippele et al. (2017) and,

[1]www.gsiseabed.ie

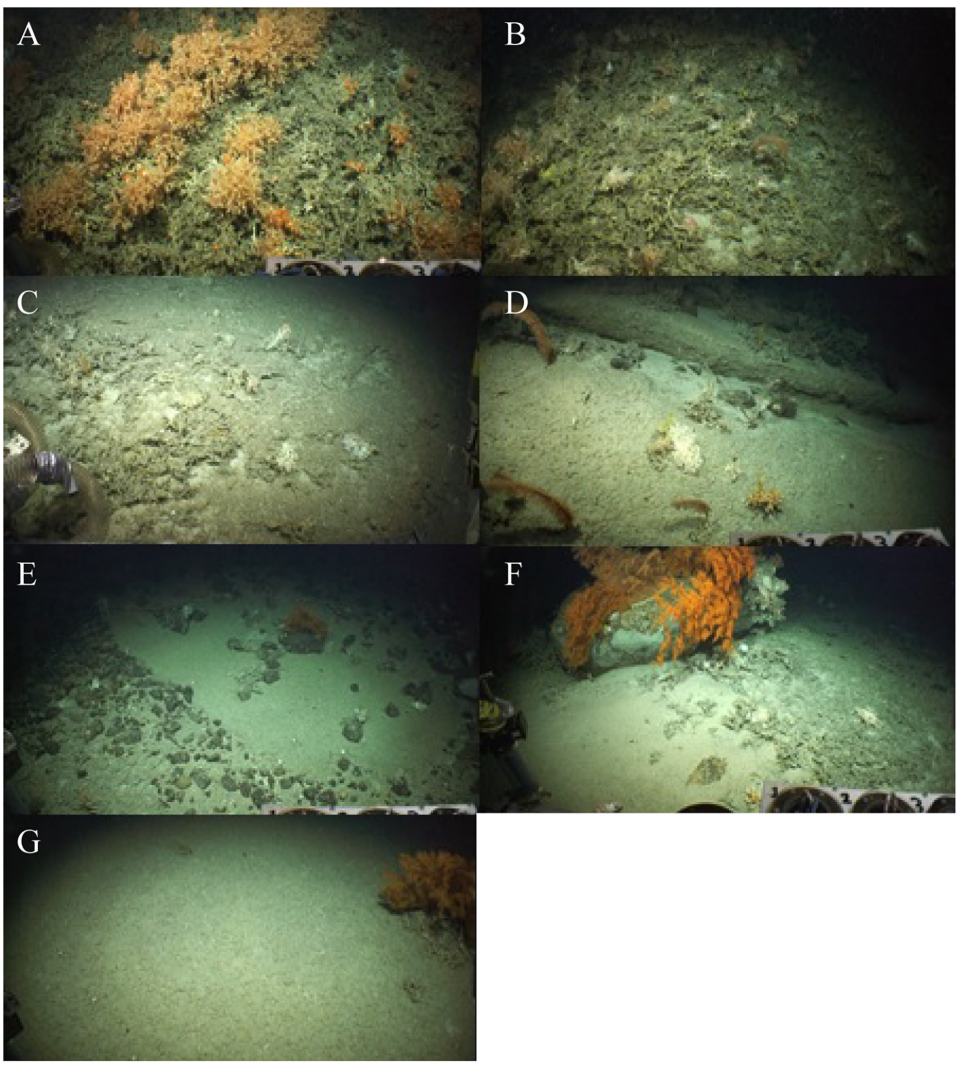


FIGURE 2 | Example photographs of substrate types identified in the Logachev Mound Province: **(A)** LpT, **(B)** DEC, **(C)** CR, **(D)** LiH, **(E)** FS/P/C/B, **(F)** MS/LB, **(G)** FS.

for example, in Wilson et al. (2007), Guinan et al. (2009), and Henry et al. (2010).

Because the response variables did not follow a normal Gaussian distribution, the more flexible Generalized Linear Modeling (GLM) approach was used. The probability distributions of the coral density data analyzed here belong to the exponential quasi-Poisson family (McCullagh and Nelder, 1989; Dobson and Barnett, 2008). The statistical software package R was used to perform the GLM (R Development Core Team, 2010).

Linear regression cannot include missing values. Hence sub-samples that had no abundances of the analyzed species present were excluded (McCullagh and Nelder, 1989; Dobson and Barnett, 2008). Backward stepwise regression decided what environmental variables (% occurrence of the seven substrate types and the variables derived from the bathymetry) contributed the most to the performance of the model. The best model was chosen based on the Akaike Information Criterion (AIC), which estimates if there is any uncertainty over the model (Cnaan et al., 1997; Symonds and Moussalli, 2011). Once the variables were selected, a GLM was performed. By taking the exponent of the coefficient values, the percentage change in the abundance of the coral per unit change of each explanatory variable was calculated. Species that had less than 50 individuals present were excluded from the statistical analyses due to the small sample size.

RESULTS

Substrate Types

Coral rubble (33.4%), dead exposed *L. pertusa* framework (25.7%), and fine sediment with pebbles, cobbles, and boulders (23.2%), were the most abundant substrate types recorded in the entire studied area (area 1, 2, and 3). *L. pertusa* thickets covered 10.8%, lithified hardground covered 4.2%, fine sediment covered 2.3% while mixed substrate with large boulders covered just 0.4%.

Dead exposed *L. pertusa* framework and coral rubble were present in high percentages in all the areas (**Table 3**). *L. pertusa* thickets were found predominantly in area 1 on the NE flank of the mound. A total of ∼39% of the terrain surveyed in area 2 and 3 were covered with the hard substrates (pebbles, cobbles, boulders, large boulders, and lithified hardgrounds), mostly on the NW flank of their mounds. Area 1 had only 4% of these hard substrates present.

TABLE 3 | Percentage contribution of the different substrates calculated from the HD video dive transects per area and per flank.

Area	LpT	DEC	CR	LiH	FS/P/C/B	MS/LB	FS
1 (total)	**31.92**	**38.72**	**20.16**	**1.59**	**1.66**	**0.24**	**5.71**
1 NE	24.93	19.84	1.40	0	0	0	0
1 S	6.99	18.88	18.76	1.59	1.66	0.24	5.71
2 (total)	**0.16**	**13.49**	**41.79**	**7.64**	**27.91**	**3.14**	**5.88**
2 NW	0.16	7.58	11.41	4.15	20.52	2.43	1.31
2 SW	0	5.92	30.37	3.49	7.39	0.71	4.56
3 (total)	**1.72**	**20.84**	**38.82**	**5.11**	**33.22**	**0.12**	**0.17**
3 NE	0.01	3.13	3.30	0	0	0.01	0.06
3 NW	1.71	17.70	35.52	5.11	33.22	0.11	0.12

*The dives included per flank and area can be found in **Table 1**.*

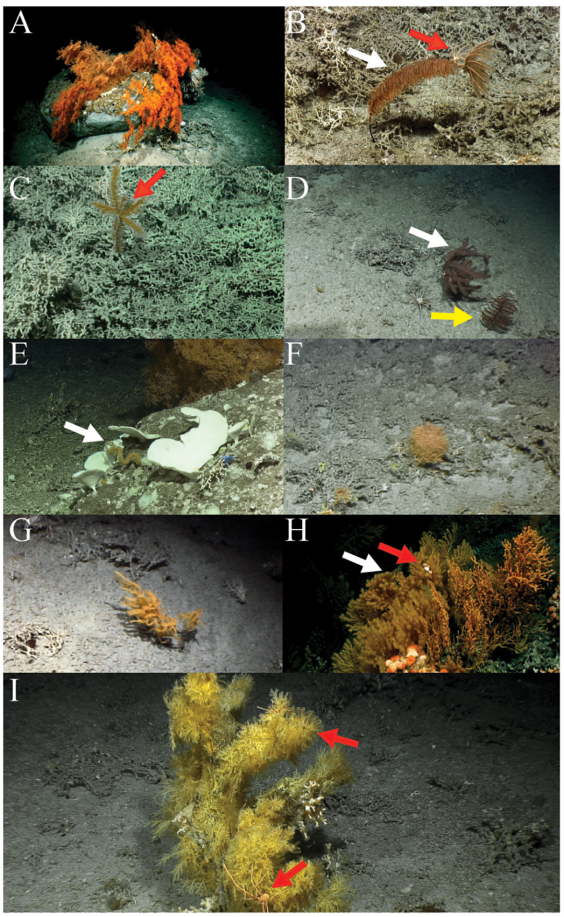


FIGURE 3 | (A) *Leiopathes* sp. **(B)** The white arrow points to *Parantipathes* sp. 1 and the red arrow points to two crinoids attached to the top of the coral. **(C)** *Parantipathes* sp. 2 with the red arrow indicating a shark egg case attached to it. **(D)** The white arrow points to *Trissopathes* sp. 1 and the yellow arrow to *Bathypathes* sp. **(E)** *Stichopathes* cf. *gravieri* indicated by the white arrow **(F)** *Acanella* sp. **(G)** Antipatharia sp. 2. **(H)** The white arrow points to *Paramuricea* sp. and the red arrow to a *Gorgonocephalus* sp. **(I)** Antipatharia sp. 1 with the top red arrow pointing to attached crinoids and the bottom red arrow pointing to a *Gastroptychus* sp.

Non-scleractinian Species

Ten non-scleractinian coral species with a total 1,707 specimens were counted across the three Logachev mound areas. Black corals were the most abundant non-scleractinian corals, overall, with 1,695 individual black corals recorded. In total eight different black coral species were identified: three species belonging to the family Schizopathidae (*Bathypathes* sp., *Parantipathes* sp. 1, *Parantipathes* sp. 2), one species belonging to the families Leiopathidae (*Leiopathes* sp.), Cladopathidae (*Trissopathes* sp.), and Antipathidae (*Stichopathes* cf. *gravieri*) and

two unidentified species which we refer to as Antipatharia sp. 1, Antipatharia sp. 2. Only two species belonging to the Order Alcyonacea were identified: one gorgonian coral belonging to the Isididae family (*Acanella* sp.) and one gorgonian belonging to the Plexauridae family (*Paramuricea* sp.). The different species are shown in **Figure 3**.

The black coral *Leiopathes* sp. was the most abundant antipatharian with a total of 1,583 individuals. The second most abundant coral was also a black coral species, *Parantipathes* sp. 1, with 60 individuals. The other non-scleractinian species were more rare, ranging between 1 and 11 counts and their densities varied with depth (**Table 4** and **Figure 4**).

Leiopathes sp. occurred in all three study areas and on all substrates except *L. pertusa* thickets (**Table 5**). The larger sized *Leiopathes* sp. colonies occurred mostly in areas with large boulders while the smaller sized colonies preferred dead exposed *L. pertusa* framework. Medium sized colonies occurred both on dead exposed *L. pertusa* framework and big boulders. *Leiopathes* sp. species has the largest depth range in the Logachev Province and was the deepest (874 m) recorded species (**Table 4**).

Like *Leiopathes* sp., *Parantipathes* sp. 1 was found in all three study areas, on all substrates, except for fine sediment. This species occurred mostly on dead exposed *L. pertusa* framework. Lower occurrences were found on large boulders and fine sediment with pebbles, cobbles, boulders (**Table 5**). This species had a much narrower depth range of 565–691 m depth (**Table 4**).

Parantipathes sp. 2 had a similar depth range (**Table 4**) and substrate preference to *Parantipathes* sp. 1 and also occurred in all the study areas. The only difference was that this species was also found in fine sediments (**Table 5**).

Stichopathes cf. *gravieri* was found in all the studied areas, on three substrates; mostly on large boulders, but also on dead exposed *L. pertusa* framework and *L. pertusa* thicket (**Table 5**). This species had the narrowest depth range and was only found between 663 and 696 m (**Table 4**).

Bathypathes sp. occurred mostly in areas with dead exposed *L. pertusa* framework, but also on large boulders and fine sediment with pebbles, cobbles and boulders (**Table 5**). This species occurs at greater depths between 678 and 859 m. This species was only found in area 1 and 2 (**Table 4**).

All four individuals of Antipatharia sp 1 together with one Antipatharia sp. 2 individual were found in one particular location in area 1 with coral rubble (**Table 5**) as a substrate at 860 m depth (**Table 4**).

All three *Trissopathes* sp. individuals were found within dead exposed *L. pertusa* framework (**Table 5**), at a wide depth range of 629–860 m, in area 1 and 2 (**Table 4**).

Only two records of *Acanella* sp. were made, one was located in an area with dead exposed coral framework, the other in coral rubble (**Table 5**). This species was only found at deeper depths of 772 m (area 2) and 860 m (area 1) (**Table 4**).

Seven of the *Paramuricea* sp. colonies were observed on dead exposed *L. pertusa* framework, while two were observed in *L. pertusa* thickets and one in coral rubble (**Table 5**). This species was found at depths of 546–796 m in all the study areas (**Table 4**).

Diversity, Evenness, and Density

The highest total diversity of non-scleractinian corals was recorded in area 2, with an H′ of 0.40 with a total of eight different species. The SW flank had a higher diversity of non-scleractinian corals compared to the transect on the NW flank. In area 1, a total of nine non-scleractinian coral species were recorded, but the overall H′ was slightly lower (0.33), with the S side of this area being higher in diversity. The lowest number of species and diversity was found in area 3, with, respectively, six species and an H′ of 0.11. Here, the highest diversity was found on the NW flank (**Table 6**). After calculating these parameters per area and the mounds' flank, these indices were also calculated per 40 m transect to reveal more fine-scale spatial variations. An H′ of 1.389 and 1.386 were recorded in area 1 at, respectively, 616 and 860 m depth. In area 2, the highest H′ of 1.175 and 1.039 were found at, respectively, 679 and 753 m depth.

The distribution of the most abundant and therefore dominant species, *Leiopathes* sp., also differed and affected the evenness on the different mounds. Area 3 had the lowest evenness with a value of 0.06, followed by area 1 with 0.15 and area 2 with 0.19. In area 1 an evenness of 1 was found at 616 and 655 m depth. Area 2 had an evenness of 1 at 663 and 728 m depth. The evenness in the different areas was always higher on the flanks, where a higher diversity of non-scleractinian species was found (**Table 6**).

Area 2 had a high average density of non-scleractinian corals with 0.136 ind. m^{-2}. Even though the diversity is low in area 3, it had the highest average densities of non-scleractinian corals (0.143 ind. m^{-2}) present, which was predominantly caused by the presence of a high density of *Leiopathes* sp. Area 1 had the lowest average density of corals present of only 0.034 ind. m^{-2} (**Table 6**). The density of non-scleractinian corals was highest on the flanks of the areas, which had a lower diversity and evenness.

As mentioned earlier, the black coral *Leiopathes* sp. is the most abundant non-scleractinian coral found in the Logachev Province (**Table 4**). Small sized colonies (<30 cm) were the most abundant size class, with the highest total density of 9.436 ind. m^{-2} recorded at depths between 546 and 874 m. Medium sized colonies (30–100 cm) were the least represented, had a density of 0.125 ind. m^{-2} and were found between 571 and 780 m depth. Large sized colonies (>100 m) were recorded at depths between 565 and 874 m. The large colonies had their highest densities of 0.364 ind. m^{-2}.

Environmental Drivers of Spatial Variation in Density

Statistical analyses to identify the environmental variables that cause differences in the density of non-scleractinian species were limited to the two most abundant species; *Leiopathes* sp. and *Parantipathes* sp 1. The analyses for *Leiopathes* sp. was performed for its most abundant size classes (small and large). Due to the small sample size of the remaining species, no significant results were found.

Leiopathes sp.: Percentage cover of dead exposed *L. pertusa* framework, depth and eastness ($p < 0.0001$) significantly affected the density of small-sized *Leiopathes* sp. When these variables increase with one unit (respectively percentage per 40 m, 40 m,

TABLE 4 | Observed recorded depth range and density (m^{-2}) of non-scleractinian species.

Species	Min depth	Max depth	Depth range	Density (m^{-2})									
				Total	Area 1			Area 2			Area 3		
						NE	S		NW	SW		NE	NW
	(m)	(m)	(m)										
Acanella sp.	772	860	88	0.013	0.022	0.000	0.030	0.018	0.000	0.000	0.001	0.034	0.000
Antipatharia sp. 1	860	860	0	0.025	0.087	0.000	0.120	0.000	0.000	0.000	0.002	0.000	0.000
Antipatharia sp. 2	628	628	0	0.006	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.000
Bathypathes sp.	678	859	181	0.082	0.152	0.000	0.211	0.018	0.112	0.090	0.004	0.000	0.000
Leiopathes sp. (all)	547	874	327	9.925	2.130	4.230	1.324	14.539	14.342	2.599	0.208	26.581	1.333
Leiopathes sp. (large)	565	874	309	0.364	0.152	0.078	0.181	0.090	0.989	0.448	0.009	0.000	0.070
Leiopathes sp. (medium)	571	780	209	0.125	0.022	0.078	0.000	0.090	0.292	0.090	0.003	0.136	0.035
Leiopathes sp. (small)	547	874	327	9.436	1.957	4.073	1.143	14.359	13.061	2.061	0.197	26.445	1.228
Paramuricea sp.	546	796	250	0.063	0.065	0.157	0.030	0.072	0.067	0.000	0.002	0.136	0.000
Parantipathes sp. 1	565	691	126	0.376	0.630	0.235	0.782	0.144	0.495	0.358	0.017	0.136	0.035
Parantipathes sp. 2	565	699	134	0.069	0.065	0.078	0.060	0.036	0.135	0.000	0.002	0.068	0.000
Stichopathes cf. *gravieri*	663	696	33	0.125	0.109	0.000	0.150	0.054	0.270	0.179	0.004	0.034	0.000
Trissopathes sp.	629	860	231	0.019	0.022	0.000	0.030	0.000	0.045	0.000	0.001	0.000	0.000

The total density and the densities for the three different areas and for the mound flanks are listed. The dives included per flank and area can be found in ***Table 1****. When more than one dive transect was recorded, as is the case for area 1 NE and Se and the areas overall, the average width of their transects were used to calculate the total area covered.*

degree per 40 m), the density of the colonies increased with, respectively, 2 and 0.8% and decreased by 48%. For large *Leiopathes* sp. individuals, only the mixed sediment with large boulders contributed significantly to changes in their density ($p < 0.001$). The density of large *Leiopathes* sp. individuals increases by 27% when mixed sediment with large boulders increases 1% per 40 m. This observation was also clear from the video observations.

Parantipathes sp. 1: Only lithified hardground contributed significantly to changes in the density of *Parantipathes* sp. 1 ($p < 0.01$). Its density increases 6% when the percentage cover of lithified hardground increases 1% per 40 m.

Associated Fauna

Depending on the speed and height of the ROV, species associated with non-scleractinian corals were not always visible. Therefore, no quantitative data are presented here. Instead, a qualitative overview is given describing which non-scleractinian coral species had associated organisms present, with notes of their location on the coral colonies.

On both small and large sized *Leiopathes* sp. colonies the anomuran crab *Gastroptychus* sp. were found on the middle and uppermost outer branches (**Figures 5A,B**). Small sized colonies would always host one specimen, while larger sized colonies hosted up to three specimens at the same time. On one occasion, a *Munida* sp. was found sheltering under a small *Leiopathes* sp. colony (**Figure 5H**). Ophiuroids and crinoids were only observed on larger sized colonies.

A close-up of a *Parantipathes* sp. 2 showed a small shrimp in between the branches (**Figure 5C**). But also *Gastroptychus* sp. (**Figure 5C**) and crinoids were found using this species (**Figure 5D**). On one occasion, a shark egg case was found attached to the top middle branch of a *Parantipathes* sp. 2 individual (**Figure 3C**).

One *Parantipathes* sp. 1 coral had two crinoids attached to the top central branch (**Figure 3B**). *Parantipathes* sp. 1 was found carried by three *Paromola* sp. crabs (**Figure 5F**). Two crabs were found carrying the plexaurid coral *Paramuricea* sp. (**Figure 5E**), ten crabs carried a sponge (**Figure 5F**), nine carried nothing, and on six occasions, it was unclear whether they were carrying something.

Antipatharia sp. 1 was only found in one location, where large numbers (∼10) of crinoids had attached themselves to it, together with one *Gastroptychus* sp. specimen (**Figure 3I**).

Finally, *Gastroptychus* sp. was also found on the top central branch of three *Bathypathes* sp. individuals (**Figure 5G**).

One large *Paramuricea* sp. was observed with a *Gorgonocephalus* ophiuroid attached to it in the central top branches (**Figure 3H**).

No large megafauna was visible on the corals *Acanella* sp., Antipatharia sp. 2, *Stichopathes* cf. *gravieri* and *Trissopathes* sp.

DISCUSSION

A total of ten different non-scleractinian coral species were identified in the ROV video data collected from the Logachev Province, Rockall Bank, NE Atlantic. Of these, eight belonged to the Order Antipatharia (Black corals) and two to the Order Alcyonacea. Even though it is accepted that, like scleractinian corals, non-scleractinian corals prefer areas where high current speeds enhance food availability and where hard substrate is available for settlement (Genin et al., 1986; Thiem et al., 2006; Davies et al., 2009; Roberts et al., 2009), their fine-scale spatial distribution is more complex and both the density and diversity

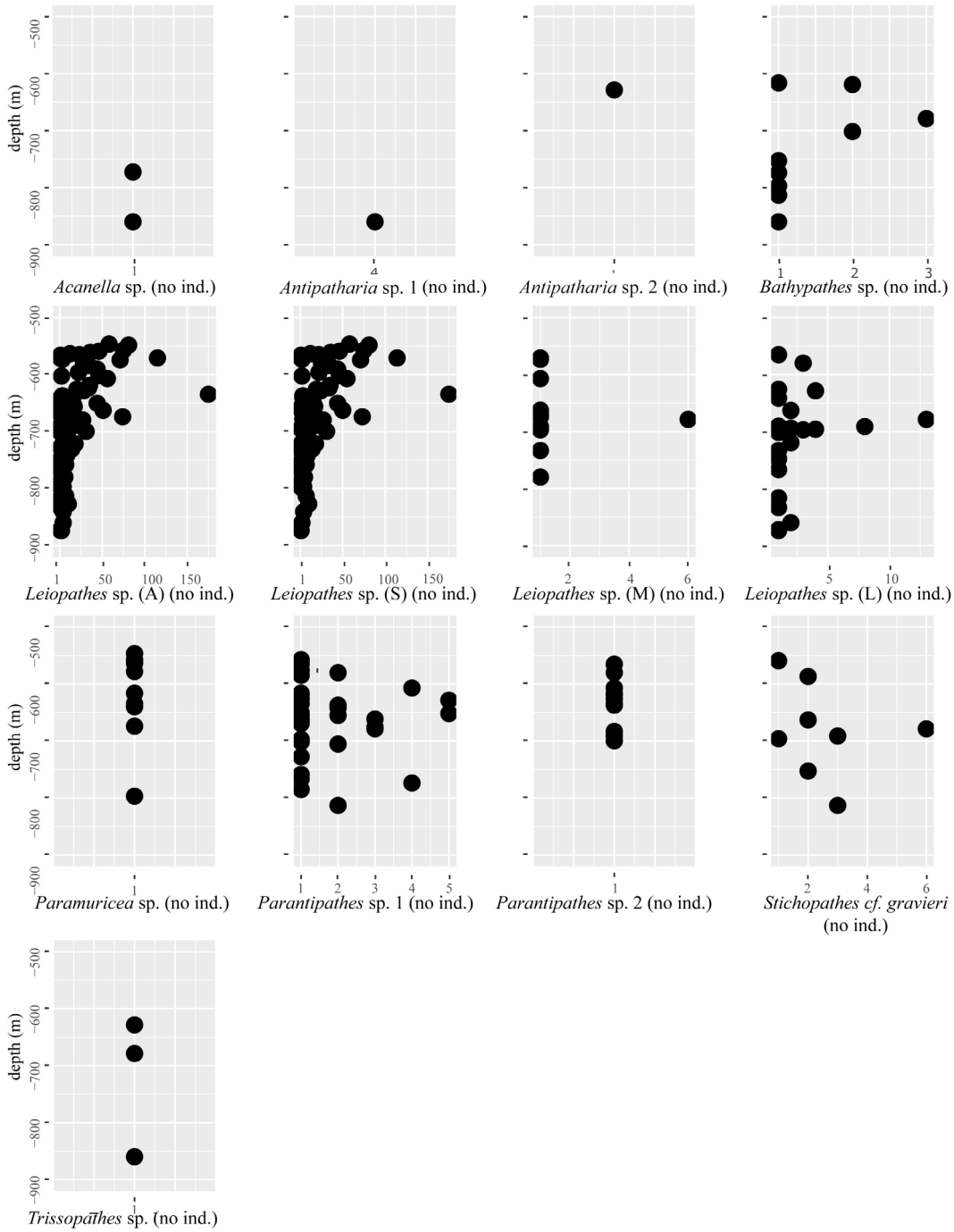


FIGURE 4 | The number of individuals (no ind.) of a certain species counted in the Logachev Mound Province (*X*-axis) plotted against depth (*Y*-axis). This gives an indication of the densities of certain species at certain depths. For *Leiopathes* sp., the abbreviations A, S, M, and L stand for, respectively, all, small, medium, and large.

of non-scleractinian corals varied within and between the areas examined in this study. It is important to note that it is likely that the depth range of the non-scleractinian corals studied in this area is wider than suggested here, as some could have been overlooked due small colony sizes or poor video quality.

High concentrations of organic matter (mixture of, e.g., dissolved organic matter, bacteria, marine snow, and small zooplankton) which are produced in the photic zone above Rockall bank, can be observed above the Logachev Mound Province, while off-reef seafloor areas at comparable depths are

TABLE 5 | Number of specimens found by substrate.

Species	LpT	DEC	CR	LiH	FS/P/C/B	MS/LB	FS
Acanella sp. (2 ind.)	0	1	1	0	0	0	0
Antipatharia sp. 1 (4 ind.)	0	0	4	0	0	0	0
Antipatharia sp. 2 (1 ind.)	0	0	1	0	0	0	0
Bathypathes sp. (13 ind.)	0	11	1	0	2	3	1
Leiopathes sp. (all) (1583 ind.)	0	2201	50	3	23	69	12
Leiopathes sp. (large) (58 ind.)	0	8	2	0	1	49	3
Leiopathes sp. (medium) (20 ind.)	0	12	0	1	1	11	0
Leiopathes sp. (small) (1505 ind.)	0	2181	48	2	21	9	9
Paramuricea sp. (10 ind.)	2	7	1	0	0	0	0
Parantipathes sp. 1 (60 ind.)	3	50	2	1	5	4	0
Parantipathes sp. 2 (11 ind.)	0	13	0	0	1	1	2
Stichopathes cf. *gravieri* (20 ind.)	2	9	0	0	0	12	0
Trissopathes sp. (3 ind.)	0	3	0	0	0	0	0

TABLE 6 | The diversity, evenness, average density, and number of different species counted per area and mound flank.

Area	Diversity (H′)	Evenness	Density (ind. m^{-2})	No. species
1	**0.33**	**0.15**	**0.034**	**9**
1 NE	0.29	0.26	0.046	3
1 S	1.48	0.67	0.028	9
2	**0.40**	**0.19**	**0.136**	**8**
2 NW	0.38	0.18	0.155	8
2 SW	0.67	0.48	0.032	4
3	**0.11**	**0.06**	**0.143**	**6**
3 NE	0.14	0.07	0.270	6
3 NW	0.49	0.35	0.014	4

depleted in suspended organic matter (Duineveld et al., 2007; Soetaert et al., 2016). When scleractinian cold-water corals, like *L. pertusa* and *M. oculata*, form mounds of a certain size, they can engineer the environment by altering the local hydrodynamics to their benefit. The clustered Logachev cold-water coral carbonate mounds have reached this size, and therefore induce tidal up- and downwelling, internal waves, and as a consequence also large INL, which supply the corals together with other filter feeders in their community with food (Mienis et al., 2007; Soetaert et al., 2016). This increased concentration of organic matter was reflected through healthy dense live *L. pertusa* thickets on the summits of the clustered mounds in our study area at a relatively shallow depth (between 560 and 610 m depth). These areas coincided with low densities and diversity of non-scleractinian corals even though this is precisely where organic matter concentrations are the highest (Soetaert et al., 2016). There are two explanations for this observation. Firstly, the permanent mucus layer (coenosarc) on the skeleton of live scleractinian corals prevents attachment of most epibiotic species (Freiwald, 2002; Buhl-Mortensen et al., 2010). Secondly, in our study area, the scleractinian corals might outcompete other filter and suspension feeders for food on mound summits. The food capture rates for different species can strongly depend on current velocity, seawater temperature and polyp size. High flow velocities can deform coral polyps reducing the exposed feeding surface area (Dai and Lin, 1993; Purser et al., 2010; Wijgerde et al., 2012; Gori et al., 2015). Higher flow speeds may also make the polyps less efficient at holding prey (Sebens et al., 1998; Orejas et al., 2011). Colder temperatures may cause the polyps to contract or affect nematocyst function (Gori et al., 2015). Warmer temperatures may increase the metabolism of corals, but can cause starvation if food supply is not met (Dodds et al., 2007; Davies et al., 2009). Some coral species with larger polyps can remove particles from their environment more efficiently compared to those with smaller polyps (Porter, 1976; Palardy et al., 2005; Wang et al., 2012). The effect of flow velocity, temperature and polyp size are unknown for the non-scleractinian corals described in this study. Since food supply is essential to maintain the basic physiological processes (Naumann et al., 2011), understanding what affects coral food capturing rates may help to explain the distribution pattern of the non-scleractinian corals in the Logachev Mound Province.

Dead exposed *L. pertusa* framework, and coral rubble become more abundant with increasing depth as the concentration of fresh organic matter decreases, and food becomes scarce toward deeper waters (Kenyon et al., 2003). Consequently, the first peak in non-scleractinian diversity was observed, right below the *L. pertusa* thickets in area 1. Food supply will still be relatively high at these depths, and an increased range of substrates such as coral rubble, dead *L. pertusa* framework and hard substrates (lithified hardgrounds, pebbles, cobbles, boulders) become available and can be used as settlement substrates (Mortensen and Fosså, 2006; Buhl-Mortensen et al., 2010). A significant correlation was found between lithified hardgrounds and the density of *Parantipathes* sp. Only a small percentage (22%) of the substrates in the study area consisted of these hardgrounds, but they are an important aspect of overall mound growth and development as they provide stability to the steep slopes of the mounds and can be used as substratum for mound-building invertebrates (Noé et al., 2006). Hardgrounds on the coral carbonate mounds

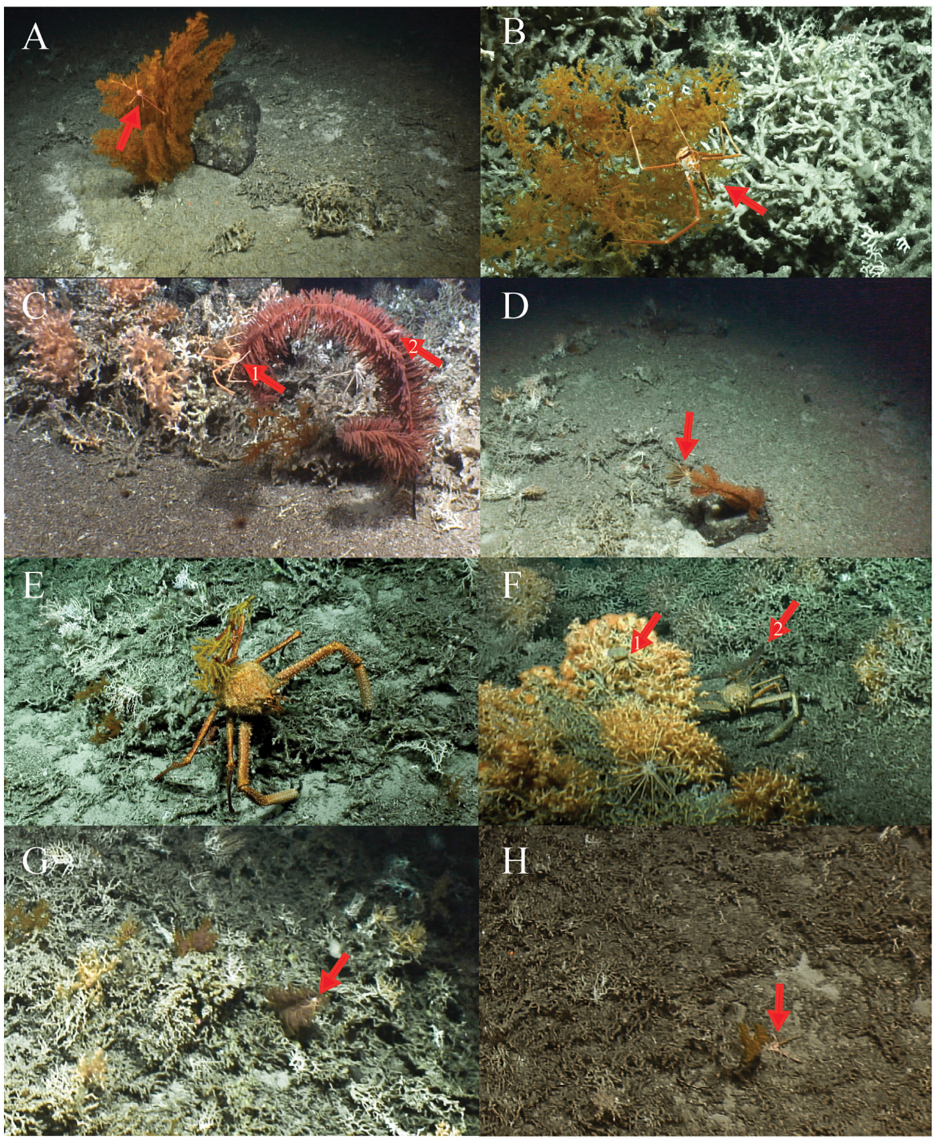


FIGURE 5 | (A,B) large and small-sized *Leiopathes* sp. colonies with the arrow pointing to a *Gastroptychus* sp. **(C)** *Parantipathes* sp. 2 with the first arrow pointing to a *Gastroptychus* sp. and the second arrow to a small shrimp. **(D)** *Parantipathes* sp. 2 with the arrow pointing to an attached crinoid. **(E)** *Paramuricea* sp. carried by *Paromola cuvieri*. **(F)** The first arrow points to *Paromola cuvieri* carrying a sponge and the second arrow points to *Paromola cuvieri* carrying a *Parantipathes* sp. 1. **(G)** The arrow points to a *Gastroptychus* sp. on the top central branch of *Bathypathes* sp. **(H)** The arrow points to *Munida* sp. sheltering under a small *Leiopathes* sp. colony.

in the Rockall area have been identified in the past (Van Weering et al., 2003). These hardgrounds can be completely exposed, showing signs of erosion by currents and sponge borings or can have different degrees of sediment cover with live and dead coral colonies (Wheeler et al., 2005, 2007). The exposure of these hardgrounds is associated with strong bottom currents (Noé et al., 2006), which could mean an increase in the food-encounter rate for cold-water corals that were able to settle there.

Differences observed in densities of non-scleractinian corals could be related to local variations in food supply. Soetaert et al. (2016) model's output of vertical current velocities and organic matter concentration in the water column of the Logachev Mound Province, appears to suggest that mounds that are located closer to Rockall Bank access more optimal food and hydrodynamic conditions. Therefore, the distance of the studied areas from the shallow bank to the deeper located mounds could affect the concentration of the organic matter reaching the corals. The lowest diversity and highest density of non-scleractinian corals was calculated for area 3. Even though the nutritional quality may not be so good, NLs could be an additional source of food, which could explain why we see high densities in area 3, which is located approximately ∼25 km from the bank (Mienis et al., 2007). From both shallow water

and land based ecosystems it is known that higher nutrient input can lead to a lower diversity and higher density for a rather low number of species (Hector et al., 1999; Chapin et al., 2000; Wiedenmann et al., 2013). This would suggest that area 3 is receiving higher concentrations of organic matter. The flanks of the areas with higher densities of corals were located perpendicular to the SW orientated residual current. It is likely that this current also facilitates the supply of additional food sources.

The most abundant non-scleractinian coral in our study areas is *Leiopathes* sp. Our data showed that *Leiopathes* sp. occupied all available substrates. From this observation, it seems this species is a generalist for settlement substrates, this could explain why it thrives in all our studied areas, even when the range of available substrates is low. *Leiopathes* sp. has a slow radial growth rate of 0.005–0.022 mm yr^{-1} and is one of the longest living species on earth (Roark et al., 2009; Carreiro-Silva et al., 2013). The slower radial growth rates and their longevity might be of an advantage in areas where food supply is scarcer.

An interesting difference in the density of the various size classes of *Leiopathes* sp. was observed. The vast majority (95%) of the colonies in our area were small sized (>30 cm), while 1% was medium (30–100 cm) and 4% were large (>100 cm). A high density of small-sized colonies could indicate a successful dispersal event with a high survival rate after settlement or that they are growing from regenerating fragments (Molodtsova, 2011). However, substrate stability might be another factor influencing the distribution of the different size classes. Small sized colonies were found in areas with dead exposed *L. pertusa* framework (95% of total individuals), while the large sized colonies were mainly found in areas with large boulders (78% of total individuals). Medium sized colonies were found in similar densities on both substrates. We suggest that this difference in survival could be related to the stability large boulders provide to a large colony. Colonies growing on dead exposed *L. pertusa* framework are inclined to fall over when exposed to high current speeds. Toward the summit of the cold-water coral mounds, large boulders become rare as they are covered with live and dead *L. pertusa* and therefore are unavailable as a stable substrate for large-sized *Leiopathes* sp. colonies. Therefore, the higher percentage cover of dead exposed *L. pertusa* framework versus large boulders could also explain why a difference in the densities of the different size classes is observed.

In past studies as well as here, shrimps, crabs, crinoids and ophiuroids were found to be using non-scleractinian coral species as a feeding platform and a place to shelter (e.g., Vytopil and Willis, 2001; Burkepile and Hay, 2007; De Clippele et al., 2015). No associates were observed visually on the corals *Acanella* sp., Antipatharia sp. 2, *Stichopathes* cf. *gravieri*, *Trissopathes* sp. and only one observation was made for the plexaurid *Paramuricea* sp. For *Paramuricea* sp. this was surprising as it has been found occupied abundantly by megafauna elsewhere (Rosenberg et al., 2005; De Clippele et al., 2015). Higher numbers of organisms occupied non-scleractinian coral colonies that were larger. This is expected as smaller sized colonies are unable to have more than one organism attached due to competition for perch sites. These associated organisms were mainly located on the top outer parts of the colonies, which increases their food encounter rate as their elevated position is further away from the slower current in the near-bottom boundary and therefore closer to the main flow (Fujita and Ohta, 1988). Generally, it is the corals' size, the number of branches and the availability of sufficient food that will impact the presence of associates on colonies. On one occasion, the squat lobster *Munida* sp. was found sheltering under a small *Leiopathes* sp. colony. This behavior was also observed under the sea pen *Kophobelemnon stelliferum* (De Clippele et al., 2015).

Even though non-scleractinian corals function as a habitat, only a minority of them had associated fauna present. This low occurrence of associated fauna could be caused by the lack of detailed surveying in our study, the high flexibility of the coral branches, and the relatively low availability of large-sized colonies. The non-scleractinian corals in our study have a more flexible skeleton compared to, e.g., the gorgonian *Paragorgia arborea* which commonly has abundant associated fauna present (Buhl-Mortensen and Mortensen, 2004, 2005; De Clippele et al., 2015). The skeleton of black corals is more flexible and chitinous, which is an adaptation for living in areas with very strong currents. To withstand strong currents, *P. arborea* grows much thicker branches compared to other corals (Mortensen and Buhl-Mortensen, 2004) which provide the associated organisms with a more robust and larger surface area to inhabit. A negative relationship between the presence of associated fauna and the flexibility and size of the colonies and branches has been shown before and therefore explains our lower presence of these associates (Buhl-Mortensen and Mortensen, 2004; Santavy et al., 2013).

Aside from functioning as a feeding platform and as a shelter, non-scleractinian corals were also used by the carrier crab *Paromola cuvieri* as camouflage or more likely, as anti-predator defense. In total, 30 carrier crabs were observed in this study, of which most were carrying a sponge, but also the black coral species, *Parantipathes* sp. 1 and the plexaurid *Paramuricea* sp. Antipatharians and alcyonaceans have previously been reported being carried by *P. cuvieri* between the dactyls and propodi of the fifth pereiopods (Wicksten, 1985; Guinot et al., 1995; Weaver et al., 2009; Braga-Henriques et al., 2012). Braga-Henriques et al. (2012) studied the behavior of 16 carrier crabs (*P. cuvieri*) in the Azores. The Braga-Henriques et al. (2012) study observed that damage of the fifth pereiopods could be a reason for when there was no object being carried. In the study presented here, no damage was observed, but this could be related to the distance between the ROV and seabed limiting the resolution of the video. The species that are carried by *P. cuvieri* varies depending on what species are available in the surrounding habitat. However, it will not necessarily be the most common invertebrates in that habitat (Braga-Henriques et al., 2012). The selection process of which species is carried is still unclear but is possibly related to weight, size and palatability (Braga-Henriques et al., 2012). In the Azores study, and in this study, camouflage-type behavior

was observed, as in some occasions the crab would lift the object above their carapace when disturbed by the ROV and its lights. However, Capezzuto et al. (2012) only observed such behavior as an adaptation to an anti-predator defense. At present, there are no indications of *P. cuvieri* using the carried species to attract other crabs or species. The sponges and cnidarians can distract predators, but also can protect the crabs with spicules and secondary metabolites against predators (Coll et al., 1982; Hill and Hill, 2002; Barsby and Kubanek, 2005; Hill et al., 2005).

CONCLUSION

Amongst the clusters of cold-water coral carbonate mounds, differences in the diversity and density of non-scleractinian corals were observed. In this study, the balance between food supplied by intermediate nepheloid layers and tidal downwelling, together with the presence of *L. pertusa* thickets and a variety of substrates seem to affect the diversity and density patterns observed. Substrate availability and stability is an important contributor to the differences observed in diversity and density, but also for the size class distribution of *Leiopathes* sp. The explanations that are given here for the differences in the fine-scale spatial distribution of non-scleractinian corals remain speculative. To fill in the gaps in our knowledge, more information on their ecophysiology and specific local organic matter concentrations for each area are needed.

AUTHOR CONTRIBUTIONS

LDC collected and analyzed the data. VH and JR supervised the study and reviewed the manuscript. TM identified the black corals and reviewed the manuscript.

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Distribution of Deep-Sea Sponge Aggregations in an Area of Multisectoral Activities and Changing Oceanic Conditions

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Discovery and understanding of fragile deep-sea habitats like sponge aggregations, are being outpaced by anthropogenic resource exploitation. Sustainable ocean development in the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA; northeast Atlantic), which harbors sponge aggregations, now requires adaptive management in the face of encroachment of multisectorial activities in this area (e.g., fishing, oil and gas, shipping) and climate change. We examined sponge morphotype composition, richness, diversity, density and body-size distribution inside and outside the FSC NCMPA, and the role of environmental variability and human impact in these sponge aggregations. Analyses were based on the examination of 465 high resolution images from 13 towed-camera transects. A catalog for regional sponge morphotypes was also developed and applied for these analyses. Analysis revealed that morphotype composition did not differ between inside and outside the FSC NCMPA but richness, diversity and densities of massive/spherical/papillate and flabellate/caliculate sponges were higher inside than outside the boundary. The sponge aggregations occurred within a narrow zone between 450 and 530 m depth, within relatively warm and saline water masses. Furthermore, multiple size cohorts of sponges were recorded inside the FSC NCMPA, in contrast to the single cohort outside. Distance-based linear modeling showed that demersal fisheries, substratum, salinity and temperature explained a statistically-significant amount of variation (48%, $p < 0.001$) of sponge density across the study area. Findings on density and size cohorts suggest that the FSC NCMPA boundary currently encloses the most vulnerable area, which also demonstrates normal ecosystem functions (e.g., recruitment). However, sponges were constrained to a narrow environmental niche shaped by fisheries and interactions of FSC NCMPA water masses with the slope that in turn likely determine, food supply to the sponge aggregations. Our study illustrated the vulnerability of the FSC NCMPA sponge aggregations to fisheries and changes to water mass properties over time. The morphotype catalog and suite of indicators (i.e., density and body-size

distribution) allow for baseline and future assessments of anthropogenic and climate change impacts on sponge aggregations' environmental status in the FSC NCMPA, thus guiding management as sectoral encroachment continues in this area.

Keywords: deep-sea sponges, marine protected area, fisheries, oil and gas, environmental health, climate change

INTRODUCTION

Sponges (Phylum Porifera) are widespread benthic organisms being found from the intertidal zone down to the abyss (Maldonado et al., 2017). Studies on shallow-water ecosystems have revealed the important role of sponges in habitat supply and nutrient cycling (e.g., Bell, 2008 and references therein). On the contrary, available information about sponges in the deep sea (i.e., generally areas below 200 m water depth), even for basic aspects like sponges' biogeographic distribution, biology and ecological roles, is very limited (Klitgaard and Tendal, 2004; Cathalot et al., 2015; Kazanidis et al., 2016, 2018).

Technological developments like the use of towed cameras, remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) can help us map the distribution of deep-sea sponges and the ecosystems they form i.e., deep-sea sponge grounds (Hogg et al., 2010). However, in order to maximize, the impact of these video/image-based methods, there is an urgent need to develop and establish common protocols and procedures (Henry and Roberts, 2014a,b). Method standardization (e.g., units used in reporting faunal density) will enable the comparability of findings among studies and will enable the identification of gaps, challenges, strengths, and opportunities for the exploration of sponge grounds and deep-sea ecosystems, in overall. Another important step for advancing our understanding on deep-sea sponge grounds is to unravel the environmental parameters that shape their distribution, which in turn will facilitate the development of efficient conservation strategies (Howell et al., 2016; Johnson et al., 2018). This is of uttermost importance as deep-sea sponges are slow-growing organisms which makes them particularly vulnerable to human activities such as bottom trawling (Kenchington et al., 2014; Pusceddu et al., 2014; Victorero et al., 2018) and oil and gas activities (Vad et al., 2018). Indeed, deep-sea sponge grounds fulfill the Food and Agriculture Organization of the United Nations (FAO) definition of Vulnerable Marine Ecosystems (VMEs) and have also been included in the Oslo/Paris Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) List of threatened and/or declining species and habitats in the northeast Atlantic (OSPAR, 2008). Existing studies (both modeling and observations) about the role of water mass properties on the environmental parameters shaping the distribution of deep-sea sponge grounds suggest important roles of hydrography and temperature (Rice et al., 1990; Bett, 2001; Murillo et al., 2012), ocean chemistry (e.g., salinity and silicate) (Beazley et al., 2015; Howell et al., 2016), and biological parameters such as the concentration of particulate organic carbon (Barthel et al., 1996; Howell et al., 2016).

The Faroe-Shetland Chanel (FSC, hereafter) in the northeast Atlantic hosts complex hydrographic and sedimentary features (Bett, 2003). Multisectoral collaborations between industry, government and academia have allowed detailed investigations of how the ecology of deep-sea benthic communities is shaped by the hydrography and sedimentary regimes in FSC (Bett, 2001; Henry and Roberts, 2004; Jones et al., 2006; Narayanaswamy et al., 2010), including the discovery of sponge aggregations within a narrow bathymetric zone (Bett, 2001; Axelsson, 2003). The area hosting these deep-sea sponge aggregations was designated in 2014 as the "Faroe-Shetland Channel Nature Conservation Marine Protected Area" (FSC NCMPA hereafter)[1]. Mixed sponge assemblages are recorded there including boreal "ostur" communities (Klitgaard and Tendal, 2004) a mixture of geodiid sponges such as *Geodia barretti*, *G. macandrewi*, *G. atlantica*, *G. phlegraei* (reported as *Isops phlegraei*) and several other flabellate, lobose, stipitate and encrusting species (Bett, 2001; Howell et al., 2010; Henry and Roberts, 2014a[2]). Sponge density ranged from 0.001 to 0.818 sponges/m^2 (Axelsson, 2003; Henry and Roberts, 2014a). More detailed information on density, bathymetric distribution and body size of different species is currently missing. Furthermore, how anthropogenic activities and environmental parameters shape the distribution of FSC NCMPA sponge aggregations is also unknown. This is an important knowledge gap because sponges in FSC NCMPA provide habitat for *Munida* crabs, the ophiuroid *Ophiactis balli* and sessile polychaetes (Howell et al., 2010) and also because of oil and gas, shipping and telecommunications[3] encroachment in the region. Oil exploration and production activities take place in the FSC since early 1990s (Vad et al., 2018). Investigations on the physical disturbance caused from drilling on the megafaunal communities in FSC have shown smothering of the seafloor in a radius of 50–120 m around the drilling site (Jones et al., 2006). This disturbance caused significant reduction in abundance, diversity and species richness of megafauna (e.g., sponges, cnidarians, molluscs) (Jones et al., 2006, 2007, 2012). Furthermore, studies on FSC have shown that a part of the fishing activity (8% of total time) is carried out sub-zero temperatures; however, best catches of Greenland halibut *(Reinhardtius hippoglossoides)* and Roughhead grenadier *(Macrourus berglax)* and most of the fishing activity were recorded in boundary waters (0–4°C) (Bullough et al., 1998). In addition, surveys in the area have revealed disturbance in sediments and sponges, assumed to result from trawling (Bett, 2000). Currently, there are no FSC NCMPA specific

[1]http://jncc.defra.gov.uk/page-6483

[2]http://jncc.defra.gov.uk/pdf/NEFSC_SACO_v1.0.pdf)

[3]https://marinescotland.atkinsgeospatial.com/nmpi/

management measures in place (e.g., for fisheries) and the statutory agency Marine Scotland is in the process of developing a joint recommendation to implement measures under the Common Fisheries Policy (Marine Scotland, 2017)[4].

Hátún et al. (2017) have shown a decline over the last 25 years in silicate concentrations in North Atlantic including the FSC NCMPA. Changes in the temperature and salinity profiles of FSC NCMPA water masses over the last two decades, have also been shown (Turrell et al., 1999; Sherwin et al., 2006; Berx et al., 2013; Broadbridge and Toumi, 2015; McKenna et al., 2016). Reduction in concentration of silicate can have detrimental effects on deep-sea sponges as silicate concentrations shape primary production (and thus food-supply) and also silicate is an integral compound of sponges' skeleton (Maldonado et al., 2011).

Deep-sea sponge aggregations of the FSC NCMPA are impacted by both human activities and climate change. Advancing, thus, our knowledge is essential for evaluating the existing FSC NCMPA boundary and for the development of conservation strategies for these VMEs (Johnson et al., 2018).

In the present study we have analyzed video/image material from inside and outside the FSC NCMPA to address three fundamental questions:

(1) Which sponge morphotypes are encountered inside and outside the NCMPA?
(2) How does sponge morphotype (a) richness and diversity, (b) density and (c) body-size distribution differ between inside and outside the FSC NCMPA?
(3) Which is the role of environmental variability and human activities in controlling the distribution and density of sponge morphotypes?

MATERIALS AND METHODS

Faroe-Shetland Channel Hydrography and Habitat Features

The Faroe-Shetland Channel (FSC) is characterized by complex hydrography as five water masses flow through it: North Atlantic Water (NAW), Modified North Atlantic Water (MNAW), Modified East Icelandic Water (MEIW), Norwegian Sea Arctic Intermediate Water (NSAIW), and Norwegian Sea Deep Water (NSDW) (Hansen and Østerhus, 2000). The distribution of these five water masses in the FSC is indicated by their characteristic temperature and salinity values which are accompanied by a specific spectrum of chemical and biological characteristics (see Table 1 in McKenna et al., 2016 for details). In the FSC, water masses above 400 m water depth are composed from NAW (9.5–10.5°C; 35.35–35.45 psu) or MNAW (7–8.5°C; 35.10–35.30 psu). NAW flows along the Shetland Shelf Edge while MNAW enters the FSC from the north of the Faroe Islands and recirculates within it. At greater depths (∼400–800 m) water masses are composed from MEIW (2–4.5°C; 34.76–34.99 psu) and NSAIW (−0.5–0.5°C; 34.89–34.91 psu). Bottom water mass NSDW (<−0.5°C; 34.91–34.92 psu) which has the greatest contribution in the southwards overflow through the Faroe Bank Channel and across the Wyville Thomson Ridge (Berx, 2012; Broadbridge and Toumi, 2015; McKenna et al., 2016). The boundary area occurring between the warm and cold-waters (found between ∼350–650 m) is particularly interesting as within it (∼550 m) rapid changes in seawater temperature (decrease up to 7°C within 1 h) have been recorded (Bett, 2001). These changes in seawater temperature are thought to be created by internal waves created by water flow across the Wyville Thomson Ridge. These internal waves propagate in the FSC at the boundary between warm and cold-water masses (Sherwin, 1991). Apart from the unusual temperature profile, the FSC is also interesting in terms of sedimentary habitat types that include areas of iceberg ploughmarks and North Sea Fan among others (Masson, 2001 for details; see also Bett, 2003; Narayanaswamy et al., 2010).

Visual Survey of Sponge Aggregations

In September 2014, a visual survey was conducted by Marine Scotland on board the MRV *Scotia* ("MoreDeep" cruise) to investigate the deep-sea sponge aggregations inside and outside the FSC NCMPA. The visual survey was conducted using a Seatronics[5] towed body hosting a Kongsberg Maritime OE14-366 PAL color zoom camera[6]. The system was also equipped with six high-intensity lights and sensors that measured at 1 s intervals, the altitude (the distance between the camera system and the seabed), depth (±0.1 m), and pitch and roll of the system (see McIntyre et al., 2013, 2016 for details). Seawater temperature was recorded (±0.01°C) through the sensor attached to the camera system. In total, 13 camera transects were conducted, which were grouped into one area inside (i.e., Area 2) and three areas (i.e., Area 1, Area 3, and Area 4) outside the FSC NCMPA (**Figure 1**). The average duration of each transect was ∼1 h 21 min at a speed of 1.5 m/sec. The altitude was 2–6 m. Because a camera positioning system was not available, positions recorded are those of the ship. Starting-ending points and depth range of the camera transects as well as values of temperature are given in **Table 1**. Sponge samples during the transects were not collected.

Image Analysis

The camera recorded continuous high definition (HD) video from which individual image frames were extracted every 20 s. Extraction was carried out with freely available software VLC. The frames were subjected to quality check with low-visibility frames been discarded. The resolution in images was 6544 × 3680 pixels in dimension with a 350 pixel/inch DPI. In total, 465 high quality image frames were subjected to further analysis (see below).

Sponge Morphotype Categories

Sponge morphotype categories were mainly based on the "Thesaurus of Sponge Morphology" (Boury-Esnault and Rützler, 1997) accompanied by studies on the distribution and structure of deep-sea sponge aggregations in the North Atlantic (Bett,

[4]https://www.gov.scot/Topics/marine

[5]http://www.seatronics-group.com

[6]www.km.kongsberg.com

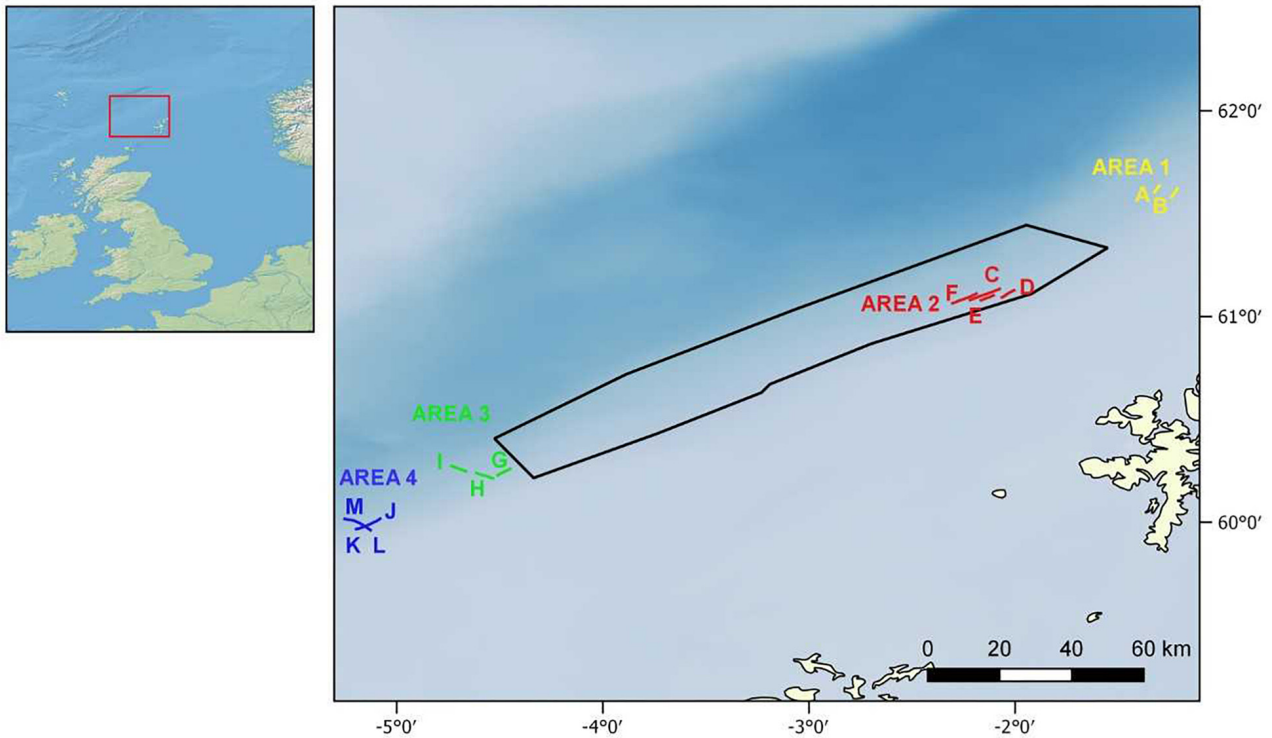


FIGURE 1 | Wider study area **(Left)** and camera transects inside (Area 2: transects C–F) and outside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA) (Area 1: transects A,B; Area 3: transects G–I; Area 4: transects J–M) **(Right)**. See also **Table 1**.

TABLE 1 | Coordinates and depth values for each of the transects inside (Area 2) and outside (Area 1, Area 3, Area 4) the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA).

Area	Transect	Min latitude	Max latitude	Min longitude	Max longitude	Min depth	Max depth	T (°C)	Salinity (psu)	Images per transect
1	A	61.60633	61.62217	−1.32350	−1.31133	529.5	532.9	3.12	34.89	19
1	B	61.58617	61.61350	−1.23833	−1.21850	431.4	440.5	5.61	34.90	50
2	C	61.08700	61.13350	−2.20250	−2.07733	492.0	500.6	8.51	35.13	93
2	D	61.09467	61.12117	−2.06200	−2.01800	449.8	454.0	8.98	34.91	32
2	E	61.07967	61.09950	−2.16433	−2.11283	467.7	473.0	8.55	34.95	44
2	F	61.06500	61.10667	−2.30267	−2.19767	516.0	523.3	6.52	35.00	65
3	G	60.23017	60.25433	−4.50783	−4.46117	497.4	501.1	8.01	35.16	40
3	H	60.21600	60.23167	−4.59000	−4.53883	502.0	574.6	7.92	35.22	19
3	I	60.24983	60.26617	−4.71200	−4.66933	661.5	715.1	2.41	34.89	11
4	J	59.98650	60.00900	−5.13933	−5.09250	498.7	511.8	8.49	35.19	93
4	K	59.96767	59.97567	−5.19300	−5.16500	482.5	496.3	9.29	35.24	32
4	L	59.99133	60.01183	−5.22533	−5.17100	547.1	631.3	5.67	35.21	44
4	M	59.96400	59.98950	−5.16850	−5.13017	452.4	534.9	8.73	35.24	65

Depth and temperature data were available for each of the images collected, while salinity data were available at lower spatial resolution. Average values (per transect) of temperature (T, °C), salinity (psu), number of images analyzed are given.

2001; Axelsson, 2003; Klitgaard and Tendal, 2004; Ackers et al., 2007; Cárdenas et al., 2013; Henry and Roberts, 2014a; McIntyre et al., 2016). The construction of the sponge morphotype catalog was also based on the examination of images collected by ROVs over several years in the wider FSC area. Five sponge morphotype categories were used (**Table 2**). Each sponge specimen recorded in the high-quality image frames of the present study was grouped in one of the five morphotype categories, and counted. Sponge morphotype categories were based on the "Thesaurus of Sponge Morphology" (Boury-Esnault and Rützler, 1997). Sponges were grouped in the five following categories: **Category 1:** encrusting (**Figure 2A**); **Category 2:** arborescent ("tree-like") (**Figure 2A**); **Category 3:** massive, spherical and papillate (**Figures 2B,C,G**); **Category 4:** flabellate

TABLE 2 | Categories of sponge morphotypes in the Faroe Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA).

Categories	Morphotypes	Genus/Species names
Category 1	encrusting	Possibly *Aplysilla sulfurea*, *Hymedesmia* spp.
Category 2	arborescent	"–"
Category 3	massive	*Geodia* spp. (e.g., *G. barretti*, *G. macandrewi*, *G. atlantica*, *G. phlegraei*)
	spherical	"–"
	papillate	Possibly *Oceanapia robusta*
Category 4	flabellate	Possibly *Phakellia ventilabrum*
	caliculate	Possibly *Axinella infundibuliformis*
Category 5	stipitate	Possibly *Stylocordila borealis*
	clavate	Possibly *Chondrocladia gigantea*

Genus/species names have tentatively been suggested for each category. "–" means lack of confidence.

("fan-shaped") and caliculate ("cup-shaped") (**Figures 2F,G**); **Category 5:** stipitate ("stalked") and clavate ("club-shaped") (**Figures 2D,E**).

Density and Body Size of Sponge Morphotypes

The surface of the seabed seen in each of the HD image frames (field of view) was quantified (in m^2) by matching the time point that a frame was captured with the relevant data (altitude and pitch angle of the towed camera system) provided by the sensor attached to the system. A detailed description of the methodology followed for measuring the field of view is given in McIntyre et al. (2013). In brief, altitude and pitch of the towed body were used in the survey area calculations using trigonometric equations. To correct for the effect of the distance on the visibility of the seabed, image analysis techniques in MATLAB[7] Image Processing Toolbox were used to construct a correction factor. The latter was a proportion of visible seabed in each image(see McIntyre et al., 2013 for details).

Using the number of sponge specimens from each morphotype Category recorded in each image and the surface of the seabed, values of sponge density were measured (sponge individuals per Category/m^2). These measurements of sponge morphotype density were carried out for categories 2, 3, 4, and 5 while specimens from sponge morphotype Category 1 ("encrusting") were logged in terms of presence/absence. Furthermore, using the camera's laser points as a reference (7.5 cm), we measured the width of flabellate sponges and the average value between "length" and "width" for the massive/spherical/papillate and the caliculate sponges (**Figure 3**). Body size measurements were grouped into 5 cm size classes following Bo et al. (2012) Measurements on body size were mainly carried out for transects A, B, C, D, E, F; unfortunately the position of the camera did not allow appropriate measurements to be taken in transects G, H, I, J, K, L, and M (**Figure 1**).

Fisheries and Environmental Data

The distribution of sponge aggregations inside and outside the FSC NCMPA was investigated in relation to water depth (m), type of substratum, temperature (°C), salinity (psu), water density (g/ml), oxygen saturation and demersal fisheries. Data on depth, type of substratum and temperature were available for each of the images collected during the visual survey of the present study. The type of the substratum in each of the 465 high quality image frames was grouped in one of the four categories (following Bett, 2003): (1) cobble (**Figure 4A**), (2) cobble with boulder (**Figure 4B**), (3) sand (**Figure 4C**), and (4) sand with boulder (**Figure 4D**). Data on salinity, water density and oxygen saturation (derived from equivalent temperature and salinity using a MATLAB routine[8]) from the FSC were supplied from Marine Scotland, at a coarser spatial scale. These data came

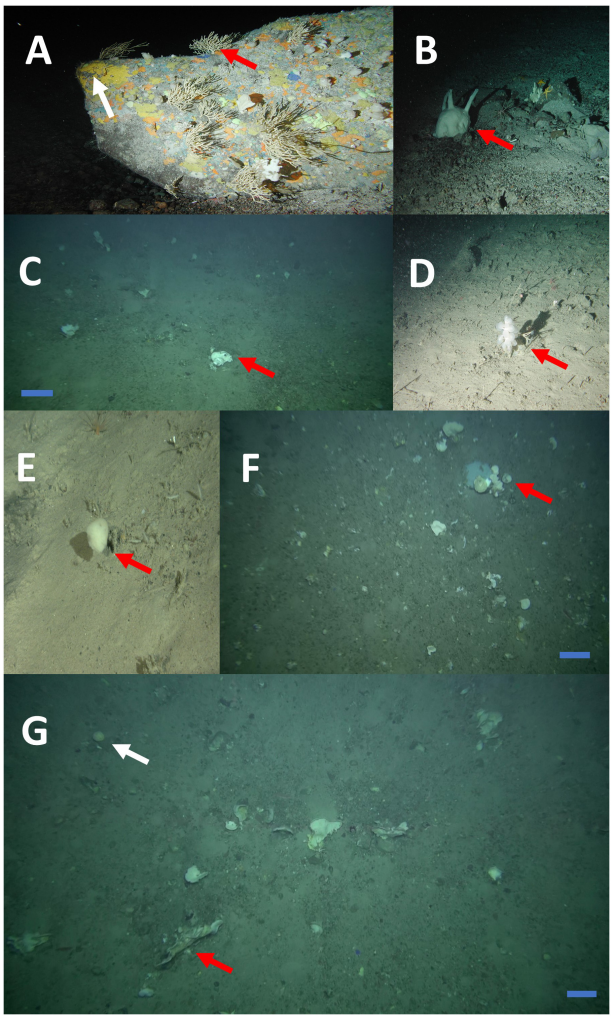


FIGURE 2 | Categories of sponge morphotypes from the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA). Category 1: encrusting (**A**, white arrow), Category 2: arborescent ("tree-like") (**A**, red arrow), Category 3: massive **(C)**, spherical (**G**, white arrow) and papillate **(B)**. Category 4: flabellate ("fan-shaped") (**G**, red arrow) and caliculate ("cup-shaped") **(F)**. Category 5: stipitate ("stalked") **(E)** and clavate ("club-shaped") **(D)**. All scale bars: 30 cm. See also **Table 2**.

[7] Release, 2017b; www.matlab.com

[8] http://mooring.ucsd.edu/software/matlab/doc/ocean/oxsat.html

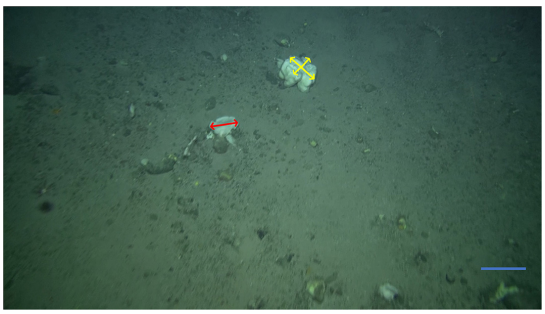


FIGURE 3 | Measurements carried out on the width of a flabellate ("fan-shaped" sponges, pointed with the red arrows) and "length" and "width" in a massive sponge (pointed with the yellow arrows). Scale bar: 30 cm.

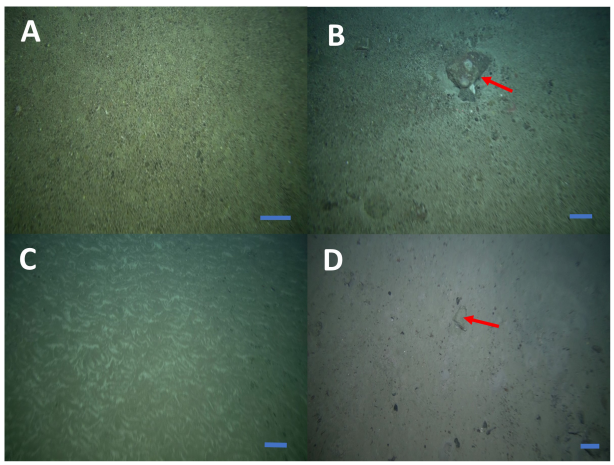


FIGURE 4 | Categories of substrate types inside and outside the Faroe-Shetland Channel Nature Conservation Marine Protected Area FSC NCMPA. Cobble **(A)**, cobble with boulder **(B)**, sand **(C)**, and sand with boulder **(D)**. Scale bars: 30 cm. Red arrows show boulders.

from locations inside the transects of the visual survey (**Table 1**) at similar depths.

Data on demersal fishing activity for Area 1, Area 2, Area 3, and Area 4, were extracted with qGIS[9] from the Marine Scotland MAPS NMPI (National Marine Plan Interactive) website using the layer entitled "Fishing statistics – Demersal landings (tons) from Scottish waters [per International Council for the Exploration of the Sea (ICES) statistical rectangle]"[10]. Data for this layer were available only for 5 years (2012–2016) enabling thus an assessment of recent demersal fishing impact on the sponge communities. For each of the ICES rectangles taken into account (i.e., rectangle 52E8 for Area 1; 51E7 for Area 2; 49E5 for Area 3; 48E4 for Area 4) an average value was calculated over the time period 2012–2016. The average value for the annual demersal landings were: 113 tons in Area 1, 64 tons in Area 2, 2836 tons in Area 3, and 3011 tons in Area 4.

Statistical Analysis

The number of sponge morphotypes (S) and Shannon's diversity index (H) were calculated using Primer-7 (Clarke et al., 2014) and these indices were compared between inside and outside the FSC NCMPA. Furthermore, the density of sponges was compared (1) inside versus outside the FSC NCMPA, (2) across the four areas (i.e., Area 1, Area 2, Area 3, and Area 4), and (3) across all transects. Sponge size was compared inside versus outside the FSC NCMPA. These comparisons were carried out in the software R (R Core Team, 2018). The Shapiro-Wilk test was applied to test for normality, followed by the Bartlett-test or the F-test to verify the equality of variances (for two or three groups, respectively). If the distributions were normal and the variances were equal, then the hypothesis that the groups have the same mean was tested using the two-sample *t*-test or the one-way ANOVA (for two or three groups, respectively). If distributions were normal but variances were not equal, the hypothesis that the means of the groups were the same was examined through the Welch's two sample *t*-test or one-way analysis of means (not assuming equal variances) (for two groups or three groups, respectively). If distributions were not normal, the hypothesis that the groups have the same median was tested through a Wilcoxon rank sum test or a Kruskal-Wallis rank sum test (for two or three groups, respectively). All values in the text are presented as mean ± standard error (*SE*).

The size-frequency distributions were analyzed applying the Bhattacharya analysis using the FISAT software package (Gayanilo and Pauly, 1997[11]). Size-frequency distributions were compared between inside and outside the FSC NCMPA; comparisons were carried out for morphotype Categories 3, 4 and for all morphotypes.

The grouping of the transects was analyzed in Primer-7. Specifically, non-transformed data on the density (individuals/m^2) of each sponge morphotype were used in the calculation of Bray–Curtis similarities and similarity matrices. Based on these matrices, clustering analysis was carried out. Finally, the role of environmental parameters and demersal fisheries in shaping the density of sponge morphotypes was analyzed through distance-based linear modeling ("Dist-LM" routine) in Primer 7.

RESULTS

Environmental Data

Preliminary investigation of environmental parameters (i.e., Draftsman Plots in Primer-7 software; see below for details) showed high correlations between salinity-density and between salinity-oxygen saturation and thus density and oxygen saturation data were not used further (see below for details).Average values of temperature ranged from 2.41°C (transect I) to 9.29°C (transect K) and average salinity ranged

[9]www.qgis.org/en/site/

[10]https://marinescotland.atkinsgeospatial.com/nmpi/

[11]http://www.fao.org/fishery/topic/16072/en

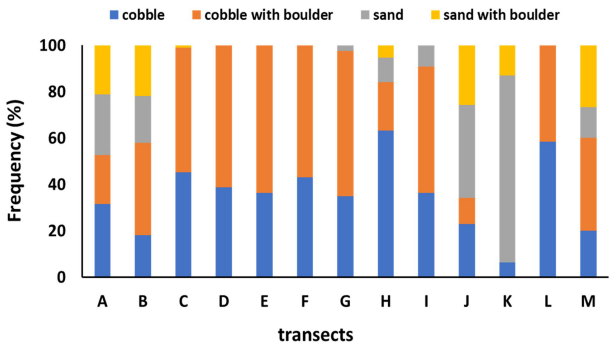


FIGURE 5 | Overview of substrate types in each of the thirteen transects.

from 34.89 psu (A, I transects) to 35.24 psu (transects K, M) (**Table 1**). Hard substrata (i.e., cobble, cobble with boulder) dominated most transects while soft sediments were the major type of substrate only in J and K transects (**Figure 5**).

Biological Data

Sponge Morphotypes Encountered Inside and Outside the FSC NCMPA

In the present study we recorded only three categories (Category 1, Category 3, and Category 4 in **Table 2**) out five previously recorded in FSC; there were no records of Category 2 or Category 5 (**Figures 2**, **6** and **Table 2**). Category 1 sponges were recorded in all transects except from transect I. Sponge morphotypes from Categories 1, 3, and 4 were found both inside and outside the FSC NCMPA (**Figure 6**). In Category 3, >90% of sponge specimens recorded were massive; similarly, in Category 4, >90% of sponges were flabellate. The number of sponge morphotypes (S) was significantly higher inside than outside the FSC NCMPA. Specifically, the number of sponge morphotypes (S) inside the FSC NCMPA was 1.2 ± 0.0 sponge morphotypes vs. 0.1 ± 0.0 sponge morphotypes outside the FSC NCMPA (Wilcoxon rank sum test = 46716, $p < 0.0001$; $n = 465$). Similarly, (H) was significantly higher inside than outside the FSC NCMPA. (H) inside the FSC NCMPA was 0.22 ± 0.01 while (H) outside the FSC NCMPA was 0.01 ± 0.00 (Wilcoxon rank sum test = 36628, $p < 0.0001$, $n = 465$).

Density of Sponge Morphotypes Inside and Outside the FSC NCMPA

Density of all sponge morphotypes was significantly higher inside than outside the FSC NCMPA (**Table 3**). Significant differences were also detected across the four areas (i.e., Area 1, Area 2, Area 3, and Area 4); higher values were recorded in Area 2 (**Table 3** and **Figure 6**). Clustering analysis using density values for each sponge morphotype revealed a higher level of similarity (∼50%) for transects in Area 2 (i.e., inside the FSC NCMPA) than transects in Area 1, Area 3, and Area 4 (i.e., outside the FSC NCMPA) (**Figure 7**). Finally, significant differences in density were recorded across all transects (**Table 3** and **Figure 6**). The highest density for Category 3 was found in transect F, for Category 4 in transect C and for all sponge morphotypes in transect F (**Table 3** and **Figure 6**).

Density of Sponge Morphotypes Across Depth

Density values for both Categories 3 and 4 showed a peak within a narrow zone (450–530 m) (**Figures 8A–C**). This peak was recorded inside the FSC NCMPA. The maximum values of density recorded for Category 3 was

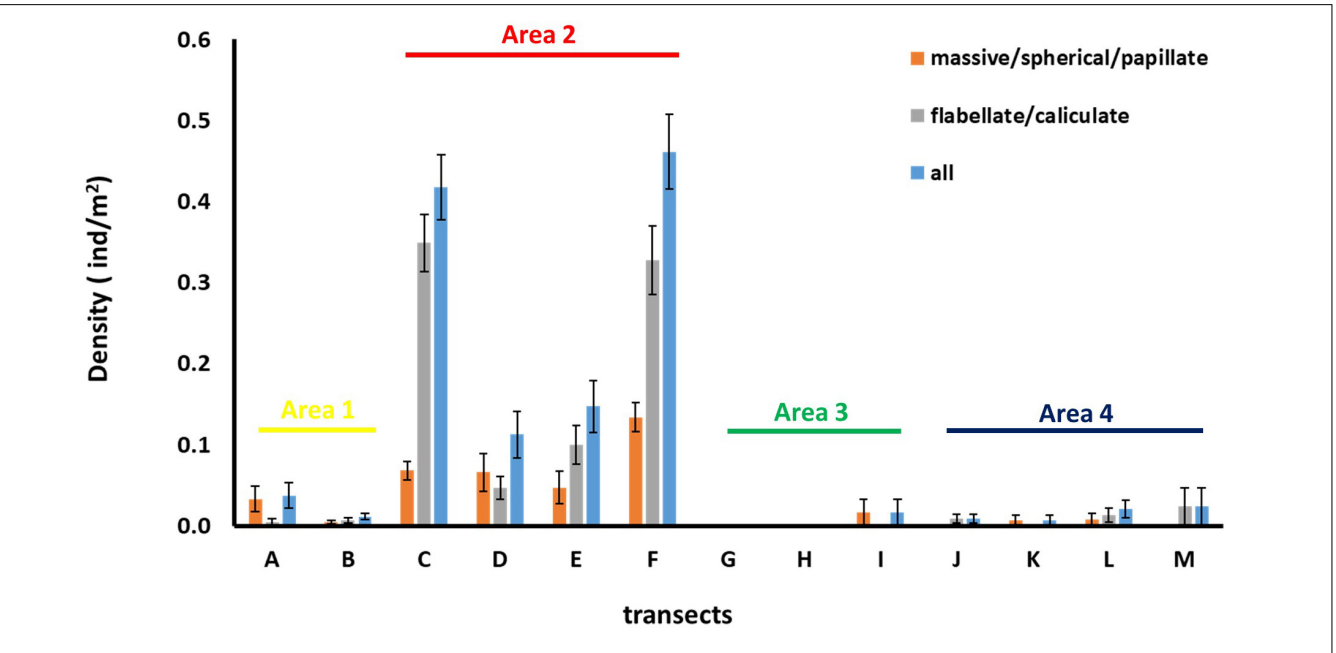


FIGURE 6 | Average ± standard error values of sponge density for each of the sponge morphotype categories across the thirteen transects.

TABLE 3 | Density of Category 3 (massive/spherical/papillate) and Category 4 (flabellate/caliculate) sponges inside and outside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA), across areas (Area 1, Area 2, Area 3, and Area 4) and across transects.

	Category 3 (massive/ spherical/ papillate) (average ± SE) (individuals/m^2)	**Category 4 (flabellate/ caliculate) (average ± SE) (individuals/m^2)**	**All morphotypes (average ± SE) (individuals/m^2)**
Inside FSC NCMPA	0.082 ± 0.009	0.256 ± 0.021	0.338 ± 0.024
Outside FSC NCMPA	0.006 ± 0.002	0.005 ± 0.002	0.011 ± 0.003
Analysis of variance inside vs. outside FSC NCMPA	Wilcoxon rank sum test = 37767, ***, *n* = 465	Wilcoxon rank sum test = 45800, ***, *n* = 465	Wilcoxon rank sum test = 47454, ***, *n* = 465
Area 1	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.01
Area 2	0.08 ± 0.01	0.26 ± 0.02	0.34 ± 0.02
Area 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Area 4	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.01
Analysis of variance across areas	Kruskal-Wallis chi-squared = 98.016, ***, *n* = 465	Kruskal-Wallis chi-squared = 218.71, ***, *n* = 465	Kruskal-Wallis chi-squared = 240.56, ***, *n* = 465
transect A	0.033 ± 0.015	0.005 ± 0.005	0.037 ± 0.016
transect B	0.005 ± 0.002	0.007 ± 0.003	0.011 ± 0.004
transect C	0.068 ± 0.011	0.349 ± 0.035	0.417 ± 0.040
transect D	0.066 ± 0.024	0.046 ± 0.014	0.112 ± 0.029
transect E	0.047 ± 0.020	0.100 ± 0.024	0.147 ± 0.032
transect F	0.134 ± 0.018	0.327 ± 0.042	0.461 ± 0.046
transect G	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
transect H	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
transect I	0.017 ± 0.017	0.000 ± 0.000	0.017 ± 0.017
transect J	0.000 ± 0.000	0.009 ± 0.005	0.009 ± 0.005
transect K	0.007 ± 0.007	0.000 ± 0.000	0.007 ± 0.007
transect L	0.008 ± 0.008	0.013 ± 0.009	0.021 ± 0.011
transect M	0.000 ± 0.000	0.023 ± 0.023	0.023 ± 0.023
Analysis of variance across transects	Kruskal-Wallis chi-squared = 133.07, ***, *n* = 465	Kruskal-Wallis chi-squared = 279.38, ***, *n* = 465	Kruskal-Wallis chi-squared = 289.18, ***, *n* = 465

*Mean values, standard error (S.E), results of statistical test, P values (***P ≤ 0.001, **0.001 < P ≤ 0.01, *0.01 < P ≤ 0.05, ns: no significant) and number of measurements (n), are given.*

0.79 individuals/m^2 (**Figure 8A**) and for Category 4 was 1.93 individuals/m^2 (**Figure 8B**).

Size of Sponge Morphotypes Inside and Outside the FSC NCMPA

The average size for Category 3 inside the FSC NCMPA was significantly higher than outside the FSC NCMPA i.e., 13.3 ± 0.8 vs. 9.2 ± 3.1 cm, respectively (Wilcoxon rank sum test = 944.5, $p < 0.05$, $n = 145$). In Category 4, there were no statistically-significant differences in the average size between transects inside and outside the FSC NCMPA i.e., 12.3 ± 0.4 vs. 11.7 ± 2.4 cm, respectively (Wilcoxon rank sum test = 2713.5, $p > 0.05$, $n = 469$). For all the sponge morphotypes, the average size inside the FSC NCMPA was not different from the average size outside the FSC NCMPA i.e., 12.6 ± 0.4 vs. 10.5 ± 1.9 cm, respectively (Wilcoxon rank sum test = 7621.5, $p > 0.05$, $n = 614$).

The analysis of the body-size distribution through the Bhattacharya method revealed clear differences between inside and outside the NCMPA. Specifically, in Category 3 there were two size cohorts in transects inside the FSC NCMPA and one size cohort outside the FSC NCMPA. In Category 4 there were three size cohorts inside the FSC NCMPA and one outside the NCMPA. The analysis of Categories 3 and 4 pooled together showed the existence of four size cohorts inside the FSC NCMPA and one size cohort outside the FSC NCMPA (**Table 4** and **Figure 9**).

Role of Fisheries and Environmental Parameters in Density of Sponge Morphotypes

Fisheries and environmental variability explained a total of 47.98% of the variation in the density of sponge morphotypes. Variables that explained significant amounts of variation included demersal fisheries pressure (29.75%), cobble with boulder (12.02%), salinity (4.89%) and temperature (1.07%) (**Table 5**). Inside the FSC NCMPA the density of Category 3 and Category 4 sponges was higher than outside the FSC NCMPA. Furthermore, the highest densities of Category 3 and Category 4 sponges were found in transects dominated by cobble with boulder substrata. The temperature and salinity values in transects with highest measured densities ranged from 6.52 to 8.98°C and 34.91 to 35.13 psu, respectively, indicating that the sponge aggregations were mainly sitting within the relatively warm and saline NAW, MNAW, and MEIW.

DISCUSSION

The present study showed that sponge morphotype composition did not differ between inside and outside the FSC NCMPA boundary, but richness, diversity and densities of Category 3 and Category 4 sponges (**Tables 2**, **3** and **Figures 2**, **6**) were higher inside than outside this boundary. Multiple size cohorts of sponges were recorded inside the FSC NCMPA, in contrast to the single cohort outside (**Table 4** and **Figure 9**). Variation in density of sponges was mostly explained by fisheries pressure: higher densities of sponges were found in the area- with lowest values of demersal landings (i.e., Area 2) while densities were significantly lower in the areas with higher demersal landings (i.e., Area 1, Area 3, and Area 4). Type of substratum explained also a significant amount of variation in sponge density: highest densities were found in cobble with boulder. Finally, water temperature and salinity explained also a significant (but lower compared to fisheries and substratum) amount of variation in sponge density: highest values were found in Area 2 where temperature and salinity ranged from 6.52 to 8.98°C and 34.91 to 35.13 psu, respectively, indicating that the sponge aggregations were mainly sitting within the relatively warm and saline NAW, MNAW, and MEIW.

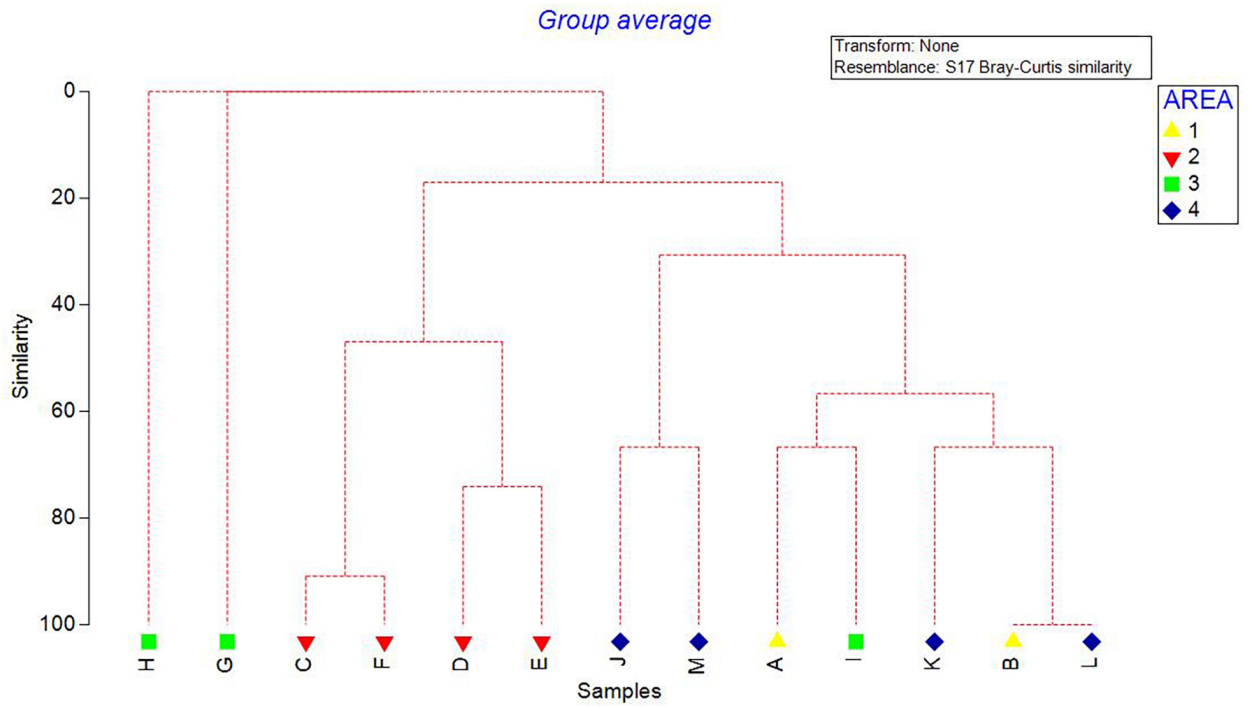


FIGURE 7 | Dendrogram showing the clustering of transects/areas (Area 1, Area 2, Area 3, and Area 4). Analysis was based on the density values (individuals/m^2) of sponge morphotype categories.

Richness/Diversity, Body-Size Distribution and Density of Sponge Morphotypes Inside and Outside the FSC NCMPA – The Role of Human Activities and Environmental Variability

Richness and Diversity of Sponge Morphotypes

Sponge aggregations inside and outside the FSC NCMPA were mainly composed of massive (most likely *Geodia* spp.) and flabellate (most likely *Phakellia ventilabrum*) sponges (**Table 2**). Unfortunately, biological samples were not collected during the transects and thus the taxonomic identification of specimens seen in images was not possible. Findings of the present study are in agreement with previous studies in the wider FSC that recorded *Geodia* and *Phakellia* in this area (Bett, 2001; Axelsson, 2003; Klitgaard and Tendal, 2004; Howell et al., 2010; Henry and Roberts, 2014a).

Although the same morphotypes were encountered inside and outside the FSC NCMPA, their richness and diversity were significantly higher inside than outside this boundary. Studies have shown that bottom fishing has an impact on the morphotypes of benthic organisms and the same may hold true for our findings on FSC NCMPA. Specifically, a photographic survey in the Georges Bank (northwest Atlantic Ocean) provided evidence that erect forms like hydrozoans, bushy bryozoans, sponges and sedentary polychaetes had higher cover in undisturbed sites while encrusting bryozoans were the only colonial group not affected by fishing (Asch and Collie, 2008). As regards the role of hydrography, Bell and Barnes (2000) have shown that massive and encrusting sponge morphotypes were more abundant at high-flow areas in the sublittoral zone, due to a high basal area to volume ratio which decreases removal from the substrates; on the contrary, pedunculate, papillate and arborescent morphotypes were more abundant at the low flow areas as these morphotypes may prevent sedimentation on sponges (see also Ginn et al., 2000; Bell et al., 2002; George et al., 2018). Bell and Barnes (2000) also showed that diversity of sponge morphotypes decreased with increasing flow due to the removal of delicate morphotypes. Studies on the hydrography of the FSC have shown the existence of active mesoscale variability (Sherwin et al., 2006). The role, however, of this hydrographic variability in shaping richness and diversity of FSC NCMPA sponge aggregations, is currently unknown.

Body-Size Distribution of Sponge Morphotypes

Our study showed that the number of body-size cohorts sponges was higher inside than outside the FSC NCMPA (**Table 4** and **Figure 9**). Although the available time series on demersal fisheries inside and outside the FSC NCMPA are limited the findings indicate the impact that fisheries can have on the FSC NCMPA sponge aggregations. However, due to this limited data availability, the impact of fisheries should be treated with caution. Actually, we did not observe trawl marks in any of the 465 images analyzed (see Figure 4 in Roberts et al., 2000). Hydrography, however, in FSC NCMPA is dynamic

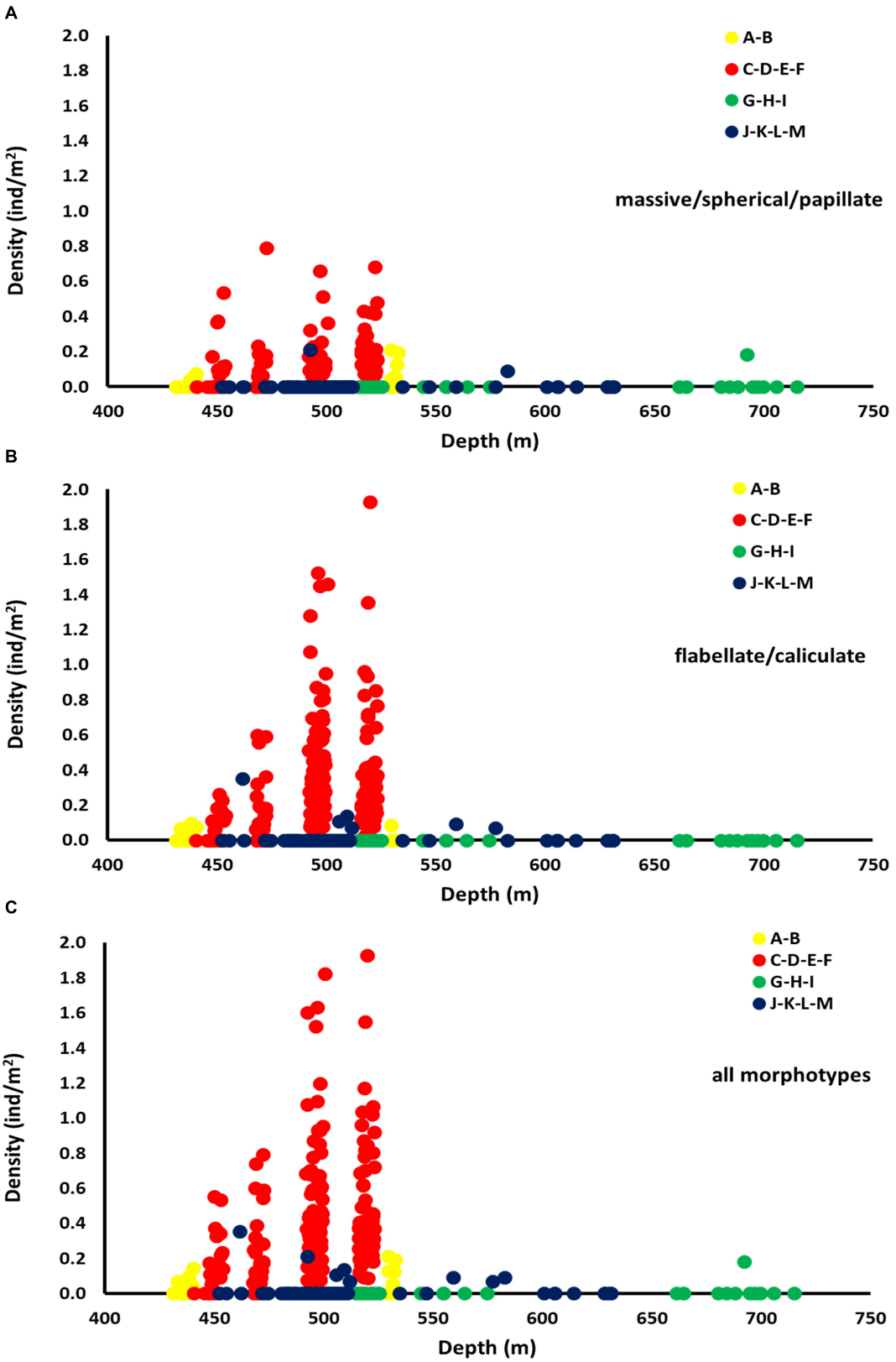


FIGURE 8 | Density (individuals/m^2) of sponge morphotypes across depth in each of the four areas: Area 1 (transects A-B), Area 2 (transects C-D-E-F), Area 3 (transects G-H-I), Area 4 (transects J-K-L-M). Data shown for Category 3 (massive/spherical/papillate) **(A)**, Category 4 (flabellate/caliculate) **(B),** and for all sponge morphotypes **(C)**.

TABLE 4 | Size cohorts (mean ± standard deviation for each cohort) in transects (a) inside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA), (b) outside the FSC NCMPA, and (c) across all transects.

Transects	Morphotype Category 3			Morphotype Category 4			Morphotype All categories		
	Size cohort	Mean	*SD*	Size cohort	Mean	*SD*	Size cohort	Mean	*SD*
Inside FSC NCMPA	1	12.8	7.1	1	9.9	4.6	1	9.0	3.9
	2	40.0	5.1	2	37.0	5.3	2	20.6	5.0
	3			3	50.0	4.9	3	37.9	4.3
	4			4			4	53.7	2.2
Outside FSC NCMPA	1	NA	NA	1	8.80	3.4	1	6.5	5.1
All transects	1	8.3	3.8	1	9.9	4.6	1	9.0	4.0
	2	40.0	6.0	2	36.3	5.6	2	20.9	4.8
	3			3	50.0	5.9	3	37.5	4.7
	4			4			4	50.0	4.3

"NA" refers to cases of limited data where Bhattacharya analysis could not be carried out. Category 3: massive/spherical/papillate sponges; Category 4: flabellate/caliculate sponges; All categories: Categories 3 and 4 pooled together. See also ***Figure 9****.*

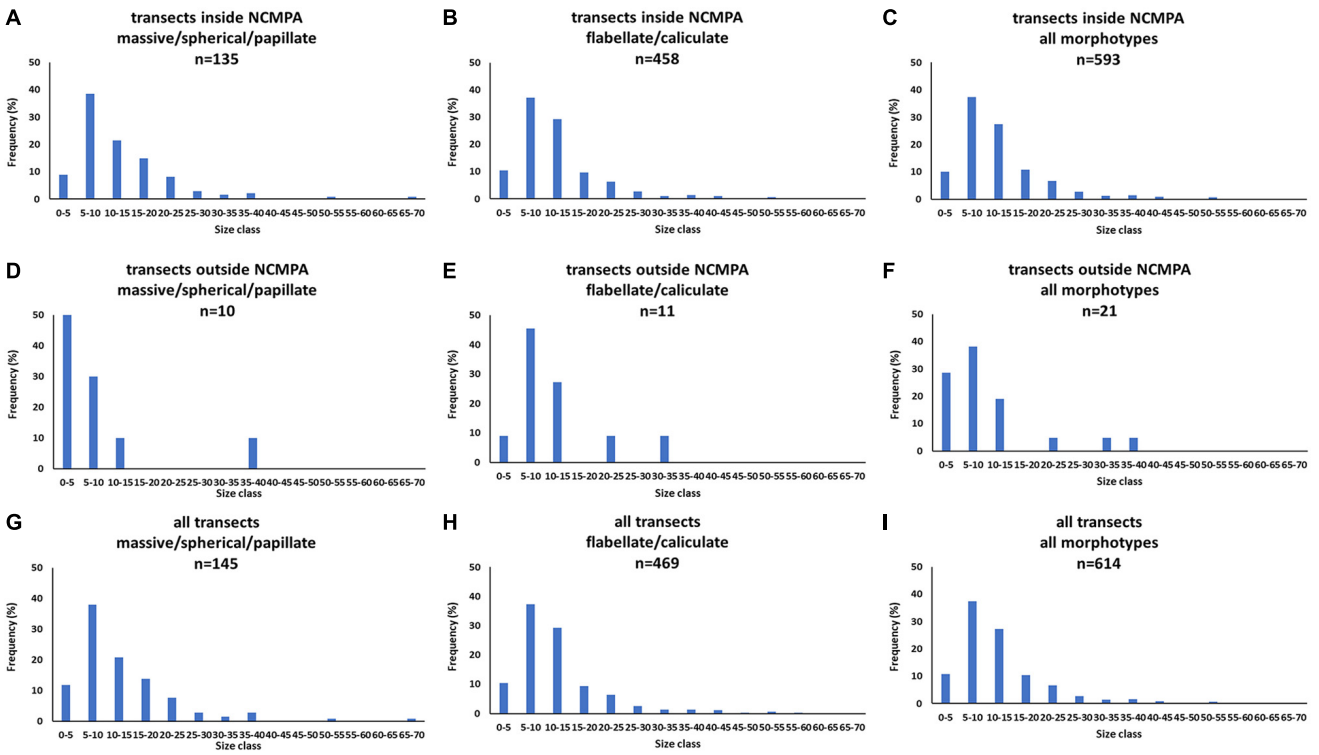


FIGURE 9 | Size-frequency distributions of sponge size (cm) for transects (i) inside the Faroe-Shetland Channel Nature Conservation Marine Protected Area (FSC NCMPA) **(A–C)**, (ii) outside the FSC NCMPA **(D–F)**, (iii) all transects **(G–I)**. Data are shown for Category 3 (massive/spherical/papillate), Category 4 (flabellate/caliculate), and for all sponge morphotypes.

(Sherwin et al., 2006) and trawl marks could have been erased. In addition, fishermen may intentionally now avoid the FSC NCMPA sponge aggregations in order to limit damage to fishing gear or due to relatively little fish biomass present in sponge aggregations (e.g., see Munoz et al., 2012; Kenchington et al., 2013; Kutti et al., 2014).

Present findings on sponge richness/diversity and body-size distribution are a strong indication about the presence inside the FSC NCMPA of more favorable conditions for reproduction, recruitment and growth of sponges. Data on these very important parameters, however, and their role in shaping deep-sea sponge aggregations are extremely limited (Witte, 1996; Fallon et al., 2010). Long-term studies in the abyssal northeast Pacific have shown a correlation between the increase in food supply and density of two glass sponges, suggesting that increased flux of particulate organic carbon

TABLE 5 | Outcome of distance-based linear modeling on the role of environmental parameters in the variation of density of sponge morphotypes.

Sequential tests					
Variable	**R^2**	**Pseudo-F**	***p***	**Individual proportion**	**Cumulative**
+Depth	0.0002	0.10	0.798	0.0002	0.0002
+Temperature	0.0109	4.98	0.018	0.0107	0.0109
+Cobble	0.0114	0.25	0.718	0.0005	0.0114
+Cobble with boulder	0.1315	63.65	0.001	0.1202	0.1316
+Sand	0.1329	0.71	0.448	0.0013	0.1329
+Sand with boulder	0.1334	0.26	0.793	0.0005	0.1334
+Demersal fisheries	0.4309	238.86	0.001	0.2975	0.4309
+Salinity	0.4798	42.86	0.001	0.0489	0.4798

may cause recruitment or regeneration in deep-sea sponges (Kahn et al., 2012). Furthermore, studies on reef-forming glass sponges in British Columbia showed that recruitment took place where hard substrate (sponge skeletons) was available (Kahn et al., 2016). Apart from the parameters shaping body-size distribution information on the number and structure of body-size cohorts themselves is also limited and when available, a detailed analysis like the one carried out here has not been completed. Available studies have shown unimodal distribution with long tails (e.g., in *Pachastrella monilifera* and *Poecillastra compressa* – Bo et al., 2012; various taxa – Rooper et al., 2016) and multimodal distributions (e.g., in *Pheronema carpenteri* – Rice et al., 1990; in *Geodia mesotriaena* – Klitgaard and Tendal, 2004).

Density

Density had significantly higher values inside than outside the FSC NCMPA (**Table 3** and **Figure 6**). The average value when all sponge morphotypes within the FSC NCMPA were summed, was 0.28 individuals/m^2 which is well within the range reported for deep-sea areas in the North Atlantic e.g., the Traena Coral Field (0.14 individuals/m^2 for geodiids and unidentified sponges – Cathalot et al., 2015), the Rosemary Bank Seamount Nature Conservation Marine Protected Area (1.2 individuals/m^2 for various demosponges – McIntyre et al., 2016), the Norwegian shelf (∼0.2 individuals/m^2 for various demosponges – Buhl-Mortensen et al., 1995), and Norwegian cold-water coral reefs (from 0.007 to 2.254 individuals/m^2 for *Mycale lingua*; from 0.011 to 0.139 individuals/m^2 for *Geodia barretti* – Purser et al., 2013) (see also Rice et al., 1990; Barthel et al., 1996; Kutti et al., 2013).

Densities of sponges peaked within a highly constrained depth zone of about 80 m (**Figure 8**) with substratum having a statistically-significant contribution. Highest values were recorded where cobble/cobble with boulder were the dominant or even the only type of substrate recorded (**Tables 2**, **3** and **Figures 5**, **6**). This finding is in agreement with available information about the presence of *Geodia* and *Phakellia* sponges on hard substrates (Hoffmann et al., 2003; Klitgaard and Tendal, 2004; Ackers et al., 2007; Gates and Jones, 2012; Tjensvoll et al., 2013).

Apart from fisheries pressure and substratum, a whole suite of other variables related to chemical oceanography exerted strong control over sponge aggregations in the FSC NCMPA in similar ways found in other North Atlantic regions. This suggests that these same factors shape distribution and structure of sponge grounds at the basin scale. These variables include water temperature, salinity and silicate concentrations (Murillo et al., 2012; Knudby et al., 2013; Beazley et al., 2015; Howell et al., 2016), topography, internal waves, current speeds, food supply (Rice et al., 1990; Klitgaard and Tendal, 2004; Knudby et al., 2013; Howell et al., 2016). Establishing a precise relationship between the contribution of each of the environmental parameters mentioned above and the distribution of deep-sea sponges/deep-sea sponge aggregations is still an open question given the limited availability of data on (a) species' physiological tolerances, (b) geographical/bathymetric distribution of these organisms and (c) measurements of environmental data at appropriate spatial scales (Tjensvoll et al., 2013; Beazley et al., 2015; Strand et al., 2017). In the present study, the values of temperature per transect inside the FSC NCMPA ranged from 6.5°C (transect F) to ∼8.9°C (transect D) and salinity values ranged from 34.9 psu (transect D) to 35.1 psu (transect C; **Table 1**); these values fall within the temperature and salinity range reported up to now for *Geodia* sponges in the North East Atlantic (Klitgaard and Tendal, 2004; Bett, 2012). Despite this agreement, it is not clear to what extent the high density of sponge aggregations recorded inside the FSC NCMPA is due to the physical/chemical parameters of the water masses *per se* and/or due to the outcome of the interaction of these water masses (i.e., NAW, MNAW, MEIW, NSAIW, NSDW) with the slope creating internal waves supplying food particles to deep-sea benthos (Mienis et al., 2009; Mohn et al., 2014). Taking into account, however, that (a) rapid changes in temperature have been recorded at the Faroe-Shetland Channel (up to 7°C within 1 h) at a depth of 550 m (Bett, 2001) and that deep-sea sponges feed mainly on particulate organic matter (e.g., Kazanidis et al., 2018 and references therein), it is likely that the hydrographic conditions (i.e., internal waves) play a more important role than temperature and salinity themselves in promoting the proliferation of sponges within the FSC NCMPA. Previous works have also highlighted the role of enhanced kinetic energy increasing the supply of food particles to sponges (Rice et al., 1990; Klitgaard and Tendal, 2004; Beazley et al., 2015).

Suggestions made above about the role of water mass characteristics and hydrography in promoting the proliferation of sponge aggregations within the FSC NCMPA gain further interest considering long-term changes in major chemical features in North Atlantic including the FSC NCMPA (Hátún et al., 2017). On top of changes in silicate concentration, long-term measurements (1994–2011) in the FSC NCMPA have also shown that surface layers (NAW and MNAW) have become warmer and more saline over the past two decades: temperatures have been increasing by 0.5°C per decade and salinities by approximately 0.07 (Berx et al., 2013). These temperature- and

salinity-relatedchanges in FSC water masses may pose additional pressures on the vulnerable sponge aggregations through changes like a decrease in oxygen concentration (e.g., Sweetman et al., 2017).

Conclusion and Suggestions Facilitating Adaptive Management in the FSC NCMPA

The present study provided evidence that the FSC NCMPA boundary currently encloses the most vulnerable area encompassing sponge communities with high richness, diversity, density and several size classes. Sponge communities were constrained to a narrow environmental niche shaped by relatively low fishing impact and the interactions of the five FSC water masses with the slope, supplying in this way food to sponges. This suggests that the deep-sea sponge aggregations are vulnerable not only to demersal fishing but could also be susceptible to changes in oceanic conditions over time.

The findings of the present study can contribute to the establishment of monitoring programs and efficient conservation strategies in the FSC NCMPA. Our study presents simple indicators that can be monitored during annual demersal camera surveys of the FSC NCMPA, including sponge richness/diversity, density, and body-size distribution. The present study serves both baseline and future assessments of anthropogenic and climate change impacts on deep-sea sponge ecosystem environmental status in the FSC NCMPA guiding thus adaptive management in FSC NCMPA.

AUTHOR CONTRIBUTIONS

FN designed and led the ship survey and collated the video footage. GK and JV processed the video/image material. GK, JV, and L-AH designed the statistical comparisons, while GK and JV analyzed the data with assistance from KG. BB provided oceanographic data from the FSC. All authors helped to write the manuscript.

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Expert Assessment of Risks Posed by Climate Change and Anthropogenic Activities to Ecosystem Services in the Deep North Atlantic

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Sustainable development of the ocean is a central policy objective in Europe through the Blue Growth Strategy and globally through parties to the Convention on Biological Diversity. Achieving sustainable exploitation of deep sea resources is challenged due to the huge uncertainty around the many risks posed by human activities on these remote ecosystems and the goods and services they provide. We used a Delphi approach, an iterative expert-based survey process, to assess risks to ecosystem services in the North Atlantic Ocean from climate change (water temperature and ocean acidification), the blue economy (fishing, pollution, oil and gas activities, deep seabed mining, maritime and coastal tourism and blue biotechnology), and their cumulative effects. Ecosystem services from the deep sea, identified through the Millennium Ecosystem Assessment framework, were presented in an expert survey to assess the impacts of human drivers on these services. The results from this initial survey were analyzed and then presented in a second survey. The final results, based on 55 expert responses, indicated that pollution and temperature change each pose a high risk to more than 28% of deep-sea ecosystem services, whilst ocean acidification, and fisheries both pose a high risk to more than 19% of the deep-sea ecosystem services. Services considered to be most at risk of being impacted by anthropogenic activities were biodiversity and habitat as supporting services, biodiversity as a cultural service, and fish and shellfish as provisioning services. Tourism and blue biotechnology were not seen to cause serious risk to any of the ecosystem services. The negative impacts from temperature change, ocean acidification, fishing, pollution, and oil and gas activities were deemed to be largely more probable than their positive impacts. These results expand our knowledge of how a broad set of deep-sea ecosystem services are impacted by human activities. Furthermore, the study provides input in relation to future priorities regarding research in the Atlantic deep sea.

Keywords: ecosystem services, climate change, anthropogenic impacts, risk, deep sea, North Atlantic Ocean, blue growth

INTRODUCTION

Although our oceans and seas are "out of sight, out of mind" according to much of society, we are becoming increasingly aware of the fact that marine ecosystems are highly impacted by climate change and our endeavors to exploit living and non-living marine resources (Halpern et al., 2008). Despite their remoteness and difficulty to access, the demise of the deep ocean is particularly noteworthy as it is the largest but least known biome on Earth. The deep North Atlantic Ocean has been studied for the last two centuries, and is now known to harbor ecosystems that support a biologically rich variety of life that perform key functions to global biogeochemical cycles, e.g., cycling of primary production, carbon and nutrients from the ocean surface to the deep seafloor (Oevelen et al., 2009; Vanreusel et al., 2010; Beazley et al., 2013). Complex three-dimensional ecosystems formed by cold−water corals, sponges, and topographically complex seamounts and hydrothermal vents not only support high and sometimes unique or endemic species, but these ecosystems also provide many ecosystem goods and services, which contribute to maritime economic activities that underpin the socio-economic wellbeing of Atlantic nations and their citizens (Galparsoro et al., 2014). These services include nutrient cycling and the biological pump, waste absorption and detoxification, fisheries and other deep ocean industries, bioprospecting and a number of cultural services related to education and science, aesthetic and inspirational contributions (Thurber et al., 2014). There is a lack of environmental baselines and assessments in relation to human interactions with the deep sea, but research points to three main impact contributors; the earlier days' disposal and dumping, current resource exploitation, and future climate change, impacting on natural resources and different habitat types, as described in some detail by Ramirez-Llodra et al. (2011). Deep sea habitats and services have undoubtedly been degraded by disposal and resource exploitation, and are now further challenged by unprecedented rates of climate change that will see the deep North Atlantic experience reduced oxygen levels and food supply to the seafloor, lower pH and a rise in deep ocean temperatures (Sweetman et al., 2017).

In addition to climate change and historic types of resource exploitation dating back to antiquity (fisheries) and into the last century (oil and gas), the European Commission Blue Growth Strategy seeks to support sustainable growth in the North Atlantic across five sectors: aquaculture, maritime and coastal tourism, blue biotechnology, ocean energy and seabed mining (EC, 2012). This strategy may pose a challenge to the business and policy objectives, seeking to balance societal needs with environmental sustainability.

One way to consider the balance between the blue growth economic agenda and sustainability is to assess the potential impacts or risks posed by different forms of human activity on the ecosystem services provided by the deep sea. It may also be assumed that an assessment of impacts and risks will inform marine spatial planning (MSP). MSP calls for due regard in relation to various pressures from human activities and climate change on marine ecosystems, their services and economic development (Ntona and Morgera, 2018). These impacts affect and pose risks in relation to services that the ecosystems provide to humans. To assess any form of risk, consequences and probability of hazard occurrences need to be identified. There is a multitude of studies assessing risks of specific activities, such as oil spills, aquaculture or shipping on specific resources, environments, ecosystems or their functions in marine ecosystems (Soares and Teixeira, 2001; Olita et al., 2012; Copp et al., 2016). However, there are few studies that integrate risk assessments and ecosystems services [see Nienstedt et al. (2012) for a terrestrial example], or at least these are mainly limited to discussion regarding the approach (Faber and van Wensem, 2012; Galic et al., 2012). There are several reasons for this gap. For one, the assessment of risks in relation to *natural environments* or *ecosystems* is often very demanding in itself. Knowledge is limited (particularly so in the deep sea), and the consequences can be highly diverse as well as controversial. Bringing the risk analysis one step further, to *ecosystem services*, can, therefore, be even more challenging. A second issue is; who are the experts that should assess the risk to ecosystem services? Although the scientific knowledge can provide expert input regarding risks to ecosystems, it is not clear which expert body can provide expertise in relation to ecosystem *services*, i.e., services from ecosystems that provide benefits to humans (MEA, 2005). Many economists assess values connected to ecosystem services (TEEB, 2010), but are they not necessarily the experts to assess unvalued risks, i.e., risks to ecosystem service provision as such? Though social scientists, in general, have not criticized the concept of ecosystem services to the same degree that others from different disciplines have (Morelli and Møller, 2015; Silvertown, 2015), they cannot be said to completely embrace it (Sullivan, 2010). Furthermore, social science in this domain has more often focused on the interaction between humans in nature, power structures and knowledge acquisition, rather than individual or societal beneficiary interactions with ecosystems. This is changing, however, with input from social sciences and the humanities increasingly finding its place, for instance in the intergovernmental science-policy panel on biodiversity and ecosystem services (IPBES) (Stenseke and Larigauderie, 2018). Nonetheless, our study links ecosystems and services via the risk aspect, making it acceptable to survey largely natural scientists.

Why is it of interest to assess risks to *ecosystem services*, rather than environments, ecosystems or ecosystem functions? Clearly, the drive within the EU for marine ecosystem-based management is central in the aim for a broader perspective on the use of marine resources (MSFD, 2008). The concept of ecosystem services, which has in recent years increasingly appeared in research, but also in policy and management (see for instance the MAES: Mapping and Assessment of Ecosystems and their services, under Action 5 of the EU Biodiversity Strategy to 2020, and the EU Blue Growth Strategy) brings nature's contributions to humans to the forefront. Assessing risks to these services brings the consequences of human drivers directly in contact with societal aspects, i.e., the risks are brought closer to the issues that managers and politicians are directly considering. Although risks to ecosystems and their functions are of course important, there is at least one layer of knowledge between the output of these kinds of assessments and the human dimensions that managers

and policy makers relate to. In going directly to the ecosystem services, we bring the risks of human drivers closer to home. Though there is mounting scientific evidence surrounding risks to ecosystems, the many linkages between ecosystems and the multitude of ecosystem services they provide are not always well known or clearly identified, especially in the deep sea. Identifying risks to ecosystem services that deep sea ecosystems supply illustrates more clearly the potential losses that society may experience if the human drivers of change in these environments are not taken into account. In addition, the deep sea is often both spatially and temporally distant to the services that humans value, and therefore, all the more important to identify the riskiest drivers, and from this provide input into where more work is required to mitigate or adapt to the risks involved.

In this paper, we use a Delphi survey approach to assess *risks* to deep sea ecosystem services within the North Atlantic. This is in contrast to previous work which has considered effects on ecosystems and their functions (Ahnert and Borowski, 2000), effects by single drivers (Gornitz et al., 1994) and the effects on ecosystem services in coastal areas (Hayes and Landis, 2004), which has most often been the focus in the literature. The Delphi approach is an iterative expert-based survey approach, in order to see whether perceptions may reach greater consensus based on information about the choices of peers in a previous round of the survey. Due to the lack of specific experts in this matter, we have chosen to use a broad set of expertise to assess the risks to ecosystem services in the deep sea. Our Delphi study respondents are members of two EU Horizon 2020 projects, consisting of a large variety of mostly biological and oceanographic expertise in relation to the North Atlantic deep-sea. The experts span physical oceanography, ecosystem modeling, deep sea ecology and genetics, natural resource economics and social science, as well as marine policy. We assess risks of human activities or drivers on ecosystem services in the deep sea, using expert elicited risk assessments in a Delphi format. The results expand our knowledge of how a broad set of ecosystem services from the deep-sea are impacted by human activities. Furthermore, the study provides input in relation to future priorities, regarding research in the North Atlantic. The remainder of the paper follows this structure: The methodologies are discussed in the next section. The results are presented in section "Results", with discussions and conclusions in section "Discussions".

MATERIALS AND METHODS

We used a Delphi survey to assess the risks of human drivers to deep-sea ecosystem services. The Delphi method has its origins from the RAND Corporation in the 1950s and 1960s and was largely motivated by the need for improved forecasting and securing some form of judgment convergence (Dalkey, 1968). Over the years it has been utilized in a multitude of different assessments spanning from health issues (Steen et al., 2014; Keller et al., 2015) to challenges in the pulp and paper industry (Toppinen et al., 2017). The method is largely used to obtain some form of opinion consensus, whilst avoiding the influence of dominant individuals. In recent years, Delphi surveys have increasingly been applied to environmental issues, such as valuation (Strand et al., 2017), and especially in relation to issues where there is limited knowledge, either in relation to the ecology (Filyushkina et al., 2018) or the values (Scolozzi et al., 2012; Filyushkina et al., 2018).

The Delphi method relies on a panel of experts to gather information; on a subject with limited knowledge. This expert opinion is gathered through an iterative, anonymous survey with feedback. The survey is sent around twice or more, and information regarding the results of the previous round is distributed to allow the experts to evaluate their assessment and to see if there may be some agreement or convergence regarding the issue surveyed. The objective is to allow information produced by an expert group to be evaluated, building consensus over time (see the stages in the Delphi approach in **Table 1**).

Though the Delphi process is considered to be more reliable than a single survey, the method has been critiqued for group pressure, rather than knowledge development, leading to consensus in repeated surveys (Woudenberg, 1991). However, the Delphi approach is also roundly defended, especially in relation to complex issues (de Loë et al., 2016) and topics where information is not easy to come by Landeta (2006). Also, in other fields where surveys are used, giving respondents time to reflect, discuss and gather information is seen as a way to secure responses that are more reliable (MacMillan et al., 2006).

Risk Assessment Survey

The risk assessment survey was developed based on literature on ecosystem services in the deep sea (Armstrong et al., 2012; Galparsoro et al., 2014; Thurber et al., 2014), and determination of relevant human drivers within the research group (see **Table 2**).

Ecosystems Services

Ecosystem services are described as those services that ecosystems provide for human wellbeing. There exists a number of different ecosystem service frameworks that have been developed over the last 15 years. We apply the Millennium Ecosystem Assessment's (MEA, 2005) framework in our analysis (**Figure 1**). This framework includes supporting services that feed into the direct services to humans; the provisioning, regulating and cultural services. A number of newer frameworks,

TABLE 1 | Stages in the Delphi survey approach.

Steps	
1	Definition of problem
2	Selection of experts
3	Survey instrument development
4	Testing of survey instrument
5	Distribute 1st survey
6	Analysis of 1st round results, and development of presentation for 2nd survey
7	Distribute 2nd survey
8	Analysis of 2nd round results, comparison to 1st round, develop report

such as TEEB (The Economics of Ecosystems and Biodiversity), CICES (The Common International Classification of Ecosystem Services) and IPBES, do not include supporting services explicitly in their service portfolio (TEEB, 2010; CICES, 2013; IPBES, 2017). The motivation for not including the supporting services is largely due to the issue of double counting values. When monetarily estimating the value of ecosystem services, supporting services cannot be valued separately, as their values are inherently included in the value of the direct services that they feed into. Since we do not undertake valuation in this study, double counting is not an issue we need to consider. Furthermore, in our study area (the deep sea), most ecosystem services are removed in time and space from humans, hence very many services are of the supporting type (Armstrong et al., 2012).

Human Drivers

The human drivers of risk to ecosystems and their services were identified through discussions with experts and include some of the key areas identified for development within the EU Blue Growth Strategy (**Table 2**) (aquaculture was not considered a risk to the study area).

TABLE 2 | Human drivers identified for the Delphi survey risk assessment.

Identified Human Drivers
Temperature Change
Ocean Acidification
Fishing
Pollution
Oil and Gas
Mining
Tourism
Blue Biotechnology

Defining Risk

Risk is the product of two entities, consisting of (1) some measure of the consequences of an occurrence and (2) the likelihood that the occurrence will take place. Usually, the occurrence is defined as some hazard. However, occurrences need not be hazards causing negative effects, though this is usually what we worry most about and are most interested in identifying. In our case, the hazards are presented as a number of different human drivers or their combination, impacting on ecosystem services. These drivers need not always lead to negative effects on all ecosystem services and in some cases provide positive effects, or there may indeed be reasons to believe some drivers may have both positive and negative effects. Our study involves a large number of ecosystem services and human drivers across the North Atlantic Ocean. It is recognized that there is currently limited knowledge of the deep sea and this leads to increased uncertainty in the study. As such, experts could note both positive

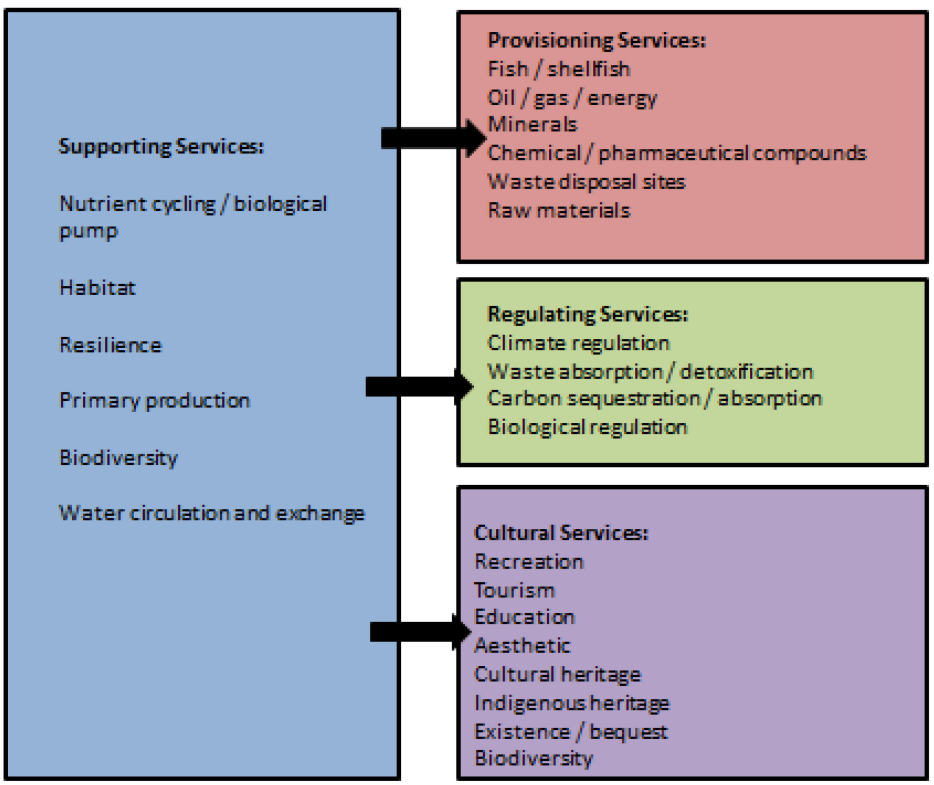


FIGURE 1 | Ecosystem services in the deep sea, using the Millennium Ecosystem Assessment framework.

and negative effects in our assessment. Hence, the assessment allows for positive and negative effects, with a scale of 1–5 (from very low severity to very high severity), or alternatively neither being applicable for some drivers in relation to some ecosystem services. The likelihood of the effect occurring is also measured on a scale of 1–5 (very low probability to very high probability). Ideally, we should have included probabilities and specified severities. However, in order to keep the survey as brief as possible, we kept to these simplifying descriptions. Such a presentation of risk may, however, be problematic, and must be used with caution (Cox, 2008). However, we do not estimate a risk measure, but rather present the graphical combination of likelihood and severity. Risk assessment, in general, can also be critiqued based on normative aspects and in relation to problems of aggregation (Stirling, 1998). However, caution is largely suggested in relation to decision-making in high-risk situations. For the use of assessing risk aspects in relation to broad categories of ecosystem services, such as we are carrying out here, many of the cautions are less problematic.

It is, however, worth noting the choice of grid lines in the risk matrix (i.e., where the high, moderate and low risk is assigned) is highly subjective. Clearly, these lines should be determined by some aim to "minimize the maximum loss of misclassified risks" (Cox, 2008, p 510), but this requires a lot more knowledge regarding consequences than is available for our study and is seldom problematized in risk assessments.

The Survey

An initial survey was developed and pre-tested. Following revisions to the survey, the first round of the Delphi ecosystem service risk assessment was held at the 2nd EU Horizon 2020 project ATLAS' General Assembly in April 2017. The session included a brief introduction to the aims of the work, the Delphi method and ecosystem services. The participants were given explanatory material (see **Appendix 1**) and the survey in an Excel sheet via email (see **Appendix 2**). Anonymity was guaranteed, as no data was collected that could identify the respondents. All respondents could pull out of the survey at will. While some surveys were returned during the project meeting, the majority were submitted in the following weeks. A total of 30 surveys were submitted and included for analysis. The responses to the first round survey were analyzed; figures were produced to present relevant results for the next round and a new survey using results from the first survey was developed using SurveyMonkey[1] (see **Appendices 3** and **4** for the second survey and an example of the online survey). In our presentation of the results from the first survey, we show first the perceptions of *negative* effects, as these are of most interest in relation to policy, research, mitigation and adaptation. We presented the risk reporting matrices in the fashion of likelihood and effect as shown in **Figure 2**, where the two axes are represented by rank numbers. This representation is not uncommon (see for instance FAO guidelines for Ecosystem Approach to Fisheries[2]).

[1]https://www.surveymonkey.net/

[2]http://www.fao.org/fishery/eaf-net/eaftool/eaf_tool_4/en#EAFTool-EAFToolSynergy

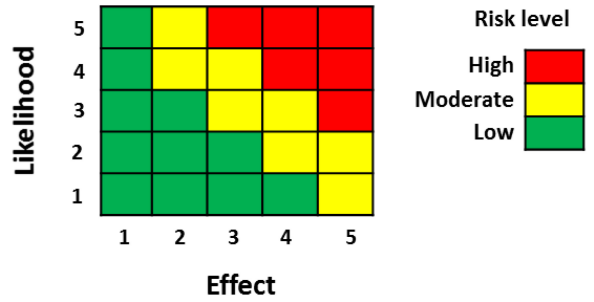


FIGURE 2 | Risk reporting matrix.

The second survey was distributed, by e-mail, to the ATLAS project members at the end of October 2017, and two reminders were sent out. By mid-November, 20 surveys from participants who had taken part in the first round were received. In April 2018, a special session was held for all project members at the EU Horizon 2020 project SponGES' General Assembly. The project members were asked to complete the second version of the Delphi ecosystem service risk assessment online, using SurveyMonkey. Prior to completing the survey, respondents received a brief presentation about the Delphi method, ecosystem services and structure of the survey, including the results from the first survey. These initiatives resulted in a total of 55 responses. The results from the ATLAS second round and the SponGES assessment were pooled and analyzed, and compared to the first round, as presented in the Results section below.

RESULTS

The results presented focus on the second round of the Delphi survey. The first round was employed as an initial information gathering exercise, which provided information for use in the second round. Results from the first round of the Delphi survey are available in **Appendix 3** and equivalent results from the second round are presented in **Appendix 5**. We focus on the results from the second survey, which is reasonable given a Delphi approach, where the second survey includes more assessment by the respondents. In some cases, the results may appear different in the two surveys, but we find hardly any statistically significant difference, and hence only present the figures from the second survey in this section (see the **Appendices** for results from the first survey).

In the following we present the results from two forms of risk; (1) the risk resulting from anthropogenic activities (human drivers) on each ecosystem service identified to the deep sea and (2) the perceived level of risk associated with each human driver. As discussed previously, both positive and negative effects were surveyed, but in this section, we focus on the negative effects.

Fifty-five (55) responses were received from experts participating in the ATLAS and SponGES projects to the second survey, out of which 47% (all from the ATLAS project) participated in the first round. For each ecosystem service, the number of human drivers that pose high, medium and low risks

are identified. The *median* severity and the *median* likelihood of the negative effects are presented for all services and drivers, as the data gathered is at the ordinal level. The high, medium and low risks connected to the negative effects of human drivers on different ecosystem services are presented in **Figure 3**. It is shown that habitat and biodiversity, both supporting ecosystem services, are at high risk from six out of nine human drivers. Biodiversity, when it is considered a cultural ecosystem service, is at high risk from five human drivers. The provisioning ecosystem service of fish/shellfish is at high risk from four of the human drivers. Resilience is at high risk from two human drivers while the remaining ecosystem services are at high risk from at most one human driver, if any at all.

The ecosystem services at low risk from a high number of human drivers are waste disposal and raw materials (both provisioning ecosystem services) and a supporting ecosystem service of primary production. None of these three ecosystem services are at high risk from human drivers.

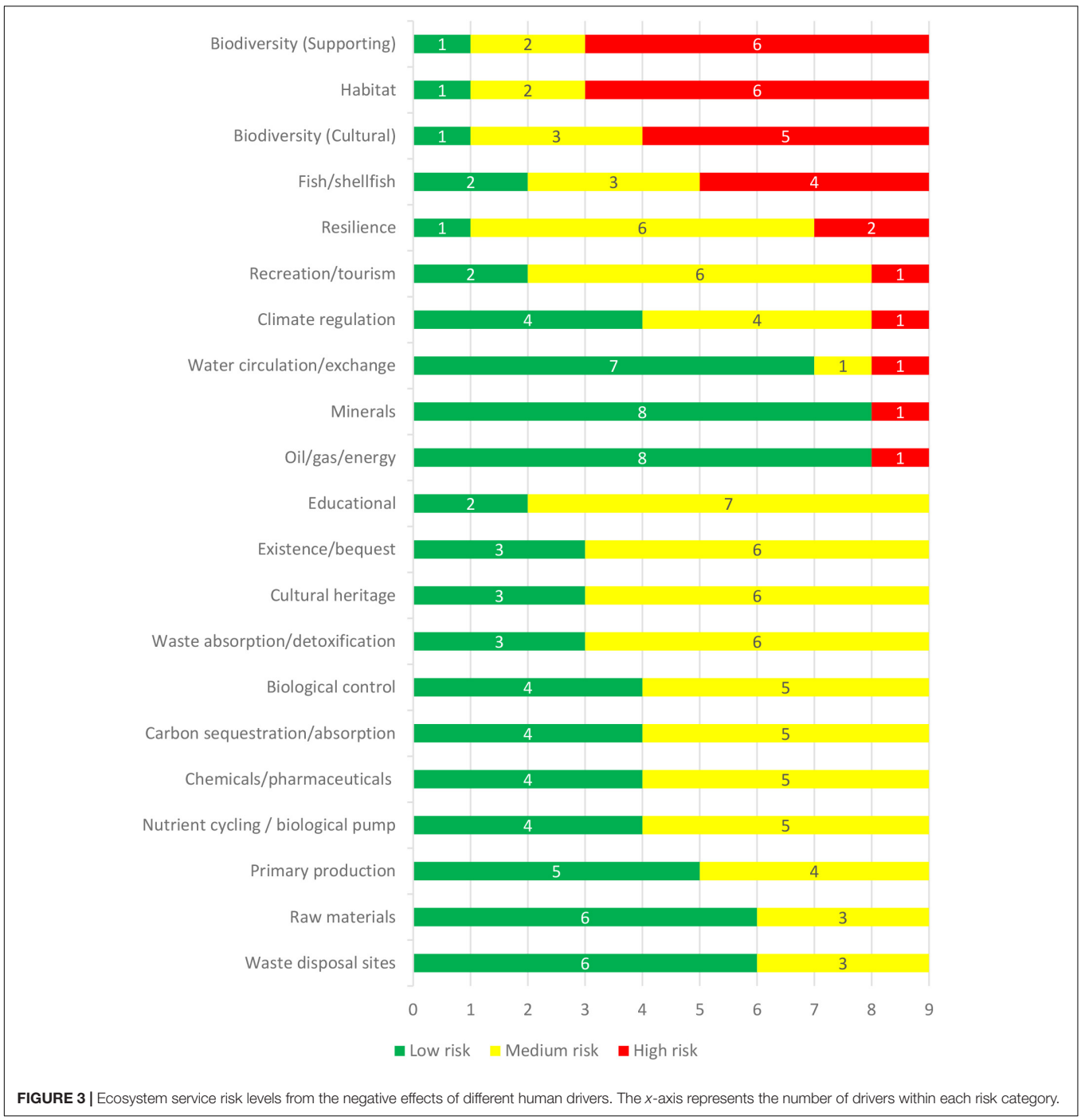


FIGURE 3 | Ecosystem service risk levels from the negative effects of different human drivers. The *x*-axis represents the number of drivers within each risk category.

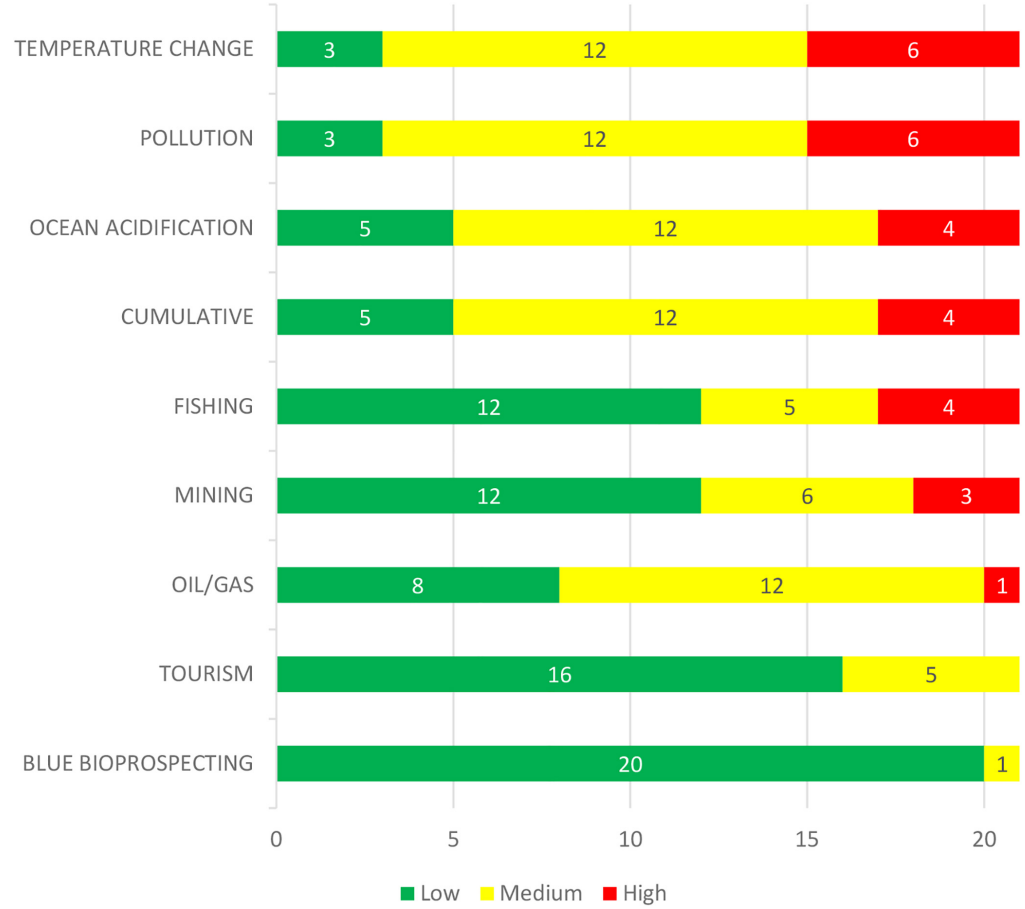


FIGURE 4 | Human drivers risk levels upon ecosystem services. From the assessment of negative effects of human drivers on ecosystem services. The *x*-axis represents the number of ecosystem services within each risk category (low, medium and high).

The second objective was to assess the level of risk associated with the human drivers specifically. In **Figure 4**, we illustrate the different human drivers and how they impact on the 21 ecosystem services as regards to high, medium and low risks. This is used to identify the anthropogenic activities (human drivers) that are perceived to have the highest level of risk to ecosystem services.

In **Figure 4**, pollution and temperature change both cause high risk to five ecosystem services. This means that pollution and temperature pose high risk to 28% each for the ecosystem services identified. Ocean acidification, fishing and the cumulative impacts cause high risk to four ecosystem services each. This corresponds to about 19% of the identified ecosystem services. These are followed by mining, causing high risk to three ecosystem services. Tourism and blue biotechnology are not perceived to have any high risk impacts on ecosystem services, and oil/gas activities are only perceived to be high risk in relation to oil/gas/energy as provisioning services.

The rankings of human drivers remain the same in both the first and second surveys, except for temperature change which replaces ocean acidification as the greatest risk in the second survey. In addition, the risks of the six high risk human drivers increase. For instance, in the first round, pollution posed high risk to four ecosystem services and this increases to six in the second survey. Adverse impacts of tourism remain the same, but risk perceptions of blue biotechnology declined in the second survey. There is, however, no statistical difference between the average number of ecosystem services at high, medium and low risk in the first and second surveys as can be seen in **Table 3**. We also observe that the variation only declined in the second round for the medium risk case. This may be due to the difference in the number of participants who responded to the two rounds. It is worth noting that there is large variation in the high-risk ecosystem services, as well as for the human drivers.

In **Figure 5**, the *positive* effects of the different human drivers on different ecosystem services are presented, in order to compare the expectation of positive versus negative effects of different human drivers. We chose not to develop a single risk measure (for instance by using the product of the two digits from effect and likelihood), despite this not being uncommon in the literature (Staples et al., 2014), as products of ranked measures may give spurious and therefore unreliable results when compared (Cox, 2008; Hubbard and Evans, 2010). Each separate figure shows the positive and negative effects, using green and red colored bubbles, respectively. The size of the

TABLE 3 | Mean number of human drivers posing high, medium and low risk to ecosystem services, and mean number of ecosystem services at high, medium and low risk from human drivers, in the first and second survey.

	Human drivers			Ecosystem services		
	First survey	Second survey	*T*-values of mean differ-ence test	First survey	Second survey	*T*-values of mean difference test
High risk	0.81 (1.03)	1.33 (2.06)	−1.04	2.00 (1.73)	3.11 (2.31)	−1.15
Medium risk	3.90 (2.07)	4.57 (1.75)	1.13	10.44 (4.42)	8.55 (4.30)	0.92
Low risk	3.52 (1.57)	3.72 (2.23)	−0.40	8.33 (6.08)	9.33 (6.04)	−0.35

Numbers in parenthesis are standard deviations. T-values of mean difference test between the two surveys.

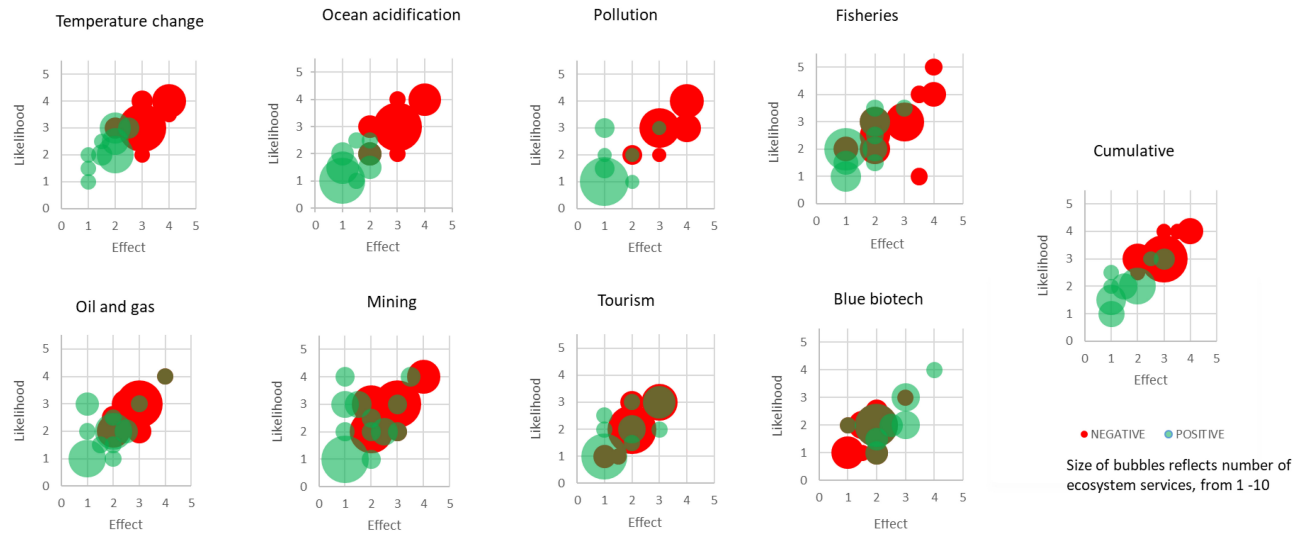


FIGURE 5 | Risk assessment for different ecosystem services: Median likelihood, positive (green) and negative (red) median effect of different human impacts.

bubble illustrates how many services are represented at each point of likelihood and severity of effect. Here we observe that for temperature change, ocean acidification, pollution, fisheries, oil/gas activities and cumulative effects, the negative effects come at far higher risk levels than the positive. This can be seen from the red bubbles concentrating to the upper right of the figures, while the green are more to the left. For mining and tourism, this effect is less clear. We can observe that for blue biotechnology, the positive effects come at far higher risk levels than the negative.

Comparison of the First and Second Survey, and Respondent Certainty

Comparing the first and second surveys, risk perceptions regarding human drivers give some appearance of worsening in the second survey relative to the first (for graphical comparison, see **Figure 3** above for the second survey and **Figure A4** in **Appendix 5** for the first survey). The number of human drivers that pose high risk increases from three to six for biodiversity (as a supporting service), two to six for habitat, three to five for biodiversity (as a cultural service) and two to four for fish/shellfish. However, using simple *t*-tests we find no statistically significant difference between the average of number of human drivers classified as high, medium and low risk to deep-sea ecosystem services, identified in the first and second surveys, as can be seen in **Table 3**. We also observe that the variation only declined in the second round for the medium risk case. This may be due to the difference in participants in the two rounds. It is worth noting the large variation in the high-risk human drivers.

We also assessed whether perceptions differed from the first survey to the second, regarding the average number of human drivers posing high risk to ecosystem services, for those services that are perceived to be at high risk from at least one human driver, as shown in **Table 4**. Using *t*-tests, we reject the

TABLE 4 | Conditional mean number of human drivers posing high risk to ecosystem services, for those services that are perceived to be at high risk from at least one human driver.

	First survey	Second survey	*T*-values of mean difference test
High risk	1.7 (0.8232726)	2.8 (2.20101)	−1.4803
Medium risk	3.6 (1.074968)	2.7 (2.162817)	1.1784
Low risk	3.6 (1.429841)	3.5 (3.02765)	0.0944

Numbers in parenthesis are standard deviations. T-values of mean difference test between the two surveys.

null hypothesis that the two conditional means are different, at the 5% level.

Although the rankings of ecosystem services in terms of high risk remain almost the same in both the first and second survey, there were some changes in rankings of ecosystem services that are low risk. Risk perceptions of human drivers to educational services increased in the second survey but waste absorption, carbon sequestration, chemicals/pharmaceuticals and nutrient cycling were ranked lower in the second survey than in the first survey. However, the ecosystem services' risk levels show similarly small changes as observed for the human drivers (see **Table 3**).

After the risk assessment, we asked about respondents' certainty in their responses using a scale from 1 to 5 (with 1 being very uncertain and 5 being very certain). The median level of the certainty score is 3 for both surveys, but the average certainty increased slightly from 2.56 in the first survey to 2.82 in the second round. A *t*-test found no statistical difference (at 5% level) between the expressed certainty in the two surveys.

We also asked the respondents to identify which ecosystem services that they are certain about. The main ecosystem services identified here include biodiversity, climate regulation and habitat. The cascading effects of these on other ecosystem services, especially under the supporting and regulating ecosystem services, were also noted. Instead of ecosystem services, some of the respondents indicate the impacts of human drivers that they are certain about. The human drivers cited include temperature change, ocean acidification, mining, pollution, tourism, biotechnology and fishing.

We also offered the respondents an opportunity to identify which ecosystem services they were most certain about. Although not all respondents responded to this query, the main ecosystem services identified included biodiversity, climate regulation and habitat. Some of the ecosystem services that respondents were uncertain about, regarding how they will be impacted by human drivers, include carbon cycle, oceanographic and water circulation, in addition to the combined effects of the undergoing changes in ecological functions on regulating services. Some of the respondents mention issues, such as the ecosystem services framework, the political will to take actions that are required to address the effects of human drivers and the scoring and monetary valuation of these effects.

During the survey, we asked the experts to give opinions on the validity and usefulness of the ecosystem services framework for understanding human dependence on the marine environments. The general impressions from these responses indicate that the majority of experts think that the ecosystem services framework is very useful. However, they also believe that it can be improved, especially strengthening the scientific basis of the framework. Some reservations are expressed about the intangible nature of some of the ecosystem services, such as cultural and supporting services, as well as the fact that ecosystem service frameworks can mask the importance of natural processes and functions that underpin the framework itself. Some propose that other frameworks should be developed to provide alternative perspectives.

DISCUSSION

The survey points to four perceived high risk human drivers: pollution, temperature change, ocean acidification and fisheries, in addition to the cumulative effects. These results are similar to the findings of Halpern et al. (2008), who, using a number of databases combined with an expert judgment based area assessment, showed how Northern Atlantic ecosystems, especially in the east, are highly impacted. The authors show that the climate drivers (sea temperature, UV and ocean acidification), impact the largest ocean areas. However, though fishing covers far less area, different aspects of fishing (different types of by-catch as well as habitat modification), were perceived to pose similar threat levels as that of the climate factors. Pollution was given far less attention in the Halpern et al. (2008) study than it has been in our results. This may be due to further knowledge about the extent of marine pollution over the last 10 years, or because pollution is perceived to have a greater impact on ecosystem services than on marine ecology, the latter which was the focus of the Halpern et al. (2008) study. Interstingly, in our study, oil/gas and mining are considered to be far less risky in relation to ecosystem services than the four main high risk drivers. Blue biotechnology and tourism are perceived to provide the greatest positive effects and likelihoods, with oil/gas and mining following them. In conclusion, newer blue growth industries do not seem to involve the greatest risk to ecosystem services. Indeed, it seems to be the larger global problems of climate, pollution and fisheries that are perceived to pose the highest risks to marine ecosystem services.

The main contribution of this study is to focus on risk to ecosystem services, rather than marine ecology or ecosystems, which is what are usually studied. Here we observe that the ecosystem services perceived to be most threatened, i.e., services with high risk levels in relation to most human drivers, are fish and shellfish, biodiversity (both as a supporting and a cultural service) and habitats. Provisioning (fish/shellfish), cultural (biodiversity) and supporting services (biodiversity and habitats) are therefore believed to be at risk from the largest number of human drivers. The only regulating service understood to be at risk was climate regulation, due to temperature change. Indeed, supporting services were perceived to be the most at risk. This is noteworthy, as when focusing on ecosystem services, most of the newer frameworks (TEEB, 2010; CICES, 2013; IPBES, 2017) largely do not include supporting ecosystem services, but rather focus on the final provisioning, regulation, and cultural services. An important message is that if the focus is only given to the three ecosystem service types that directly impact humans, we may clearly ignore important impacts and their risks. This is particularly meaningful in the deep sea.

This study has several qualifications worth mentioning. One is that the numbers of responses are limited and having more respondents in the first version would have been advantageous. Furthermore, organizing the likelihood in a different fashion, for instance in probabilities rather than ranks, would allow a more multiplicative presentation (probability multiplied by effect), though as mentioned earlier, this is not without its problems. Giving the respondents more information would be good but

must be evaluated against the time needed to carry out the survey. Yet more information in the second survey, regarding the variance in the results, could have been informative. The survey is very large and demands a lot of the respondents. One option could be to limit a follow-up survey to the most high risk drivers and ecosystem services, in order to probe these further. Though a qualitative assessment of respondent uncertainty was included, a more systematic uncertainty assessment related to risks would benefit a future study, providing extra input on knowledge gaps and further research needs.

The study underlines a number of issues. For one, there seems to be large degree of uncertainty around the level of high risk that different human drivers pose. Though pollution, temperature change, ocean acidification and fisheries, and the cumulative effects are, on average, deemed to pose high risk to several ecosystem services, there is substantial variation in this perception. This points to a need for further study in relation to these drivers and their linkages to ecosystem services. There is also considerable variation amongst the respondents, regarding the ecosystem services perceived to be at high risk. The fact that it is the high-risk drivers and services that show the greatest variation is concerning, and stresses the need for more research into the pressures and their responses, especially in the deep sea. Furthermore, the focus on supporting services being at risk is notable. The fact that most of the respondents were natural scientists may be one explanation for this result, and points to the need for greater inclusion of other disciplinary fields in surveys that involve ecosystem services. However, it should not be surprising that supporting services are central services in the deep sea, and that their importance may well surpass many other services that receive more attention in shallower and coastal waters.

Achieving sustainable exploitation of deep sea resources is challenged by the huge uncertainty around the many risks posed by human activities on these remote ecosystems and the goods and services they provide. This study contributes to the blue growth development and MSP in the deep sea by identifying human activities and climate change effects that may have an impacts on ecosystem services. The identification of the levels of risk associated with different human activities, and the perceived level of risk to ecosystem services will help inform future development and potentially maintain ecosystems in the deep sea.

AUTHOR CONTRIBUTIONS

GV and CA analyzed the data. CA initiated the writing of the manuscript. All authors were substantially involved in the survey development and data collection, contributed to development of the results used and the final product in significant ways, and provided approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00158/full#supplementary-material

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Characterization and Mapping of a Deep-Sea Sponge Ground on the Tropic Seamount (Northeast Tropical Atlantic): Implications for Spatial Management in the High Seas

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Ferromanganese crusts occurring on seamounts are a potential resource for rare earth elements that are critical for low-carbon technologies. Seamounts, however, host vulnerable marine ecosystems (VMEs), which means that spatial management is needed to address potential conflicts between mineral extraction and the conservation of deep-sea biodiversity. Exploration of the Tropic Seamount, located in an Area Beyond National Jurisdiction (ABNJ) in the subtropical North Atlantic, revealed large amounts of rare earth elements, as well as numerous VMEs, including high-density octocoral gardens, *Solenosmilia variabilis* patch reefs, xenophyophores, crinoid fields and deep-sea sponge grounds. This study focuses on the extensive monospecific grounds of the hexactinellid sponge *Poliopogon amadou* (Thomson, 1878). Deep-sea sponge grounds provide structurally complex habitat, augmenting local biodiversity. To understand the potential extent of these sponge grounds and inform spatial management, we produced the first ensemble species distribution model and local habitat suitability maps for *P. amadou* in the Atlantic employing Maximum Entropy (Maxent), General Additive Models (GAMs), and Random Forest (RF). The main factors driving the distribution of the sponge were depth and maximum current speed. The sponge grounds occurred in a marked bathymetric belt (2,500 – 3,000 m) within the upper North Atlantic Deep Water mass (2.5°C, 34.7 psu, O_2 6.7–7 mg ml^{-1}), with a preference for areas bathed by moderately strong currents (0.2 – 0.4 ms^{-1}).

GAMs, Maxent and RF showed similar performance in terms of evaluation statistics but a different prediction, with RF showing the highest differences. This algorithm only retained depth and maximum currents whereas GAM and Maxent included bathymetric position index, slope, aspect and backscatter. In these latter two models, *P. amadou* showed a preference for high backscatter values and areas slightly elevated, flat or with gentle slopes and with a NE orientation. The lack of significant differences in model performance permitted to merge all predictions using an ensemble model approach. Our results contribute toward understanding the environmental drivers and biogeography of the species in the Atlantic. Furthermore, we present a case toward designating the Tropic Seamount as an Ecologically or Biologically Significant marine Area (EBSA) as a contribution to address biodiversity conservation in ABNJs.

Keywords: deep-sea, sponge grounds, seamount, species distribution models, biogeography, ABNJ, EBSA

INTRODUCTION

Most of the deep seabed lies in areas beyond national jurisdictions (ABNJ), areas where the biogeography of vulnerable marine ecosystems (VMEs) has received relatively little attention and where governance is limited. Such ecosystems are often characterized by slow-growing, long-lived and late-maturing species, traits that limit their potential for resilience and recovery from human disturbances such as bottom-contact fishing and, in the future, deep-sea mining (Ramirez-Llodra et al., 2011). Consequently, the United Nations General Assembly (UNGA) (Resolution 61/105) called all Member States to take management measures in the high seas to protect VMEs (UNGA, 2006; FAO, 2009). The resolution made regional fisheries management organisations (RFMOs) responsible for identifying VMEs in their regulatory areas and implementing management measures to regulate impacts from bottom trawling. In the case of deep-sea mining applications, the International Seabed Authority (ISA)—the body that regulates activities on the seabed in ABNJs—is to develop policy tools on the exploitation of minerals that consider VMEs and ecologically or biologically significant marine areas (EBSAs) that may include VMEs (Miller et al., 2018). However, little is known about the distribution of most VMEs, and every effort to improve the understanding of marine VME biogeography may lead to better ocean governance.

Seamounts can host numerous VME indicator species (Schlacher et al., 2014; Watling and Auster, 2017). These underwater mountains provide hard substrata for VME indicator taxa such as corals, sponges and other species to settle and grow (Rogers et al., 2007; Samadi et al., 2007; Clark et al., 2012). Seamounts are often characterized by particular hydrography, enhancing the flow of currents and ultimately, the availability of food to suspension feeders (Watling and Auster, 2017). Flow enhancement is often more pronounced on elevated features on the seamount, such as a ridges or pillars that raise from the surrounding seafloor (Ramirez-Llodra et al., 2010; Watling and Auster, 2017). High densities of corals and sponges can be found on those features (Genin et al., 1986; Rogers et al., 2007; Roberts et al., 2009; Henry et al., 2013; Victorero et al., 2018), although benthic assemblages and biomass may vary among seamounts in less productive regions, where substratum is not suitable, or where seamounts are not adjacent to continental slopes (Rowden et al., 2010). VMEs on seamounts are threatened by human activities, especially from bottom-trawling fishing and, in the future, from the expected impacts of deep-sea mining (Clark et al., 2010) as they are a potential resource for scarce elements used in the generation of low-carbon technologies. Since VMEs are abundant on seamounts and there is a lack of distributional data that prevents their mapping before any activity occurs, Watling and Auster (2017) suggested managing seamounts as VMEs as a precautionary measure.

In the North Atlantic, VMEs formed by deep-sea sponges are sometimes encountered on seamounts, ridges, continental slopes and in fjords (Rice et al., 1990; Klitgaard, 1995; Barthel et al., 1996; Murillo et al., 2012; Knudby et al., 2013; Cárdenas and Rapp, 2015; McIntyre et al., 2016). Classed as VME indicator taxa because of their often slow rates of growth and long lifespans (Murillo et al., 2016), deep-sea sponge grounds are especially vulnerable to mechanical disturbances on the deep seafloor. A type of animal forests (Rossi et al., 2017), sponge grounds are known to occur in areas where local currents enhance food supply (Klitgaard and Tendal, 2004; Hogg et al., 2010), often forming along distinct bands that follow bathymetric contours (Hogg et al., 2010). As habitat-formers, sponges are drivers of biodiversity in deep-sea ecosystems (Beazley et al., 2013, 2015) and play a significant role in ecosystem function by recycling dissolved organic matter into particulate matter that becomes available to detritivores and ultimately, to organisms at higher trophic levels (de Goeij et al., 2013; Rix et al., 2016). Sponges also contribute significantly to the silicon cycle by acting as a silicon reservoir (Maldonado et al., 2011). Despite remaining poorly mapped in the North Atlantic (Klitgaard and Tendal, 2004; Murillo et al., 2012), Distribution Models (DMs) may provide the understanding that is currently lacking by predicting sponge habitats beyond surveyed areas and offering information for the development of conservation measures (e.g., Knudby et al., 2013; Howell et al., 2016).

In the high seas of the northeastern Atlantic, the Tropic Seamount lies within the Western Sahara Seamount Province, along the northwestern African continental margin. Although its

composition and volcanic origin is well studied (Schmincke and Graf, 2000; van den Bogaard, 2013), little is known about its fauna apart from a few reports of deep-sea corals (Schmincke and Graf, 2000; Vázquez et al., 2011). A recent dedicated geological survey, led by the National Oceanographic Centre (NOC, Southampton, United Kingdom), part of the MarineE-tech project, focused on assessing controls on the formation, distribution and composition of seafloor ferromanganese crust deposits and impacts of their future potential exploitation by the deep-seabed mining industry. Part of the exploration mission was to survey the seamount using a remotely operated vehicle (ROV) to characterize the biological communities on Tropic Seamount, both by providing video and stills imagery and by sampling organisms for taxonomy using a combination of molecular and classical morphological-based classifications. Preliminary video analysis revealed the existence of a diverse set of VME indicator taxa, as found and described from other seamount ecosystems. However, one of the most distinctive observation was the occurrence of dense aggregations of the hexactinellid sponge *Poliopogon amadou* Thomson (1877), which formed extensive areas of sponge grounds in the deeper flanks of the seamount.

Poliopogon amadou, the only member of its genus in the Atlantic, is a large, fan-shaped pheronematid sponge that reaches up to 35 cm in height (Xavier et al., 2015). Its distribution and the factors that drive its occurrence remain poorly understood, but appears rather biogeographically limited. It has been recorded southwest of the Canary Islands (HMS *Challenger* expedition, 1878); on the Mid-Atlantic Ridge (MAR) at the equatorial region (between 15° and 23°N) and south of the Azores over a depth range of 2480–4022 m (Tabachnick and Menshenina, 2002); at asphalt seeps in the southwest Atlantic off Brazil (Fujikura et al., 2017); on the Caribbean Sea (Reiswig and Dohrmann, 2014); and the Vema Fracture Zone (Victorero and Xavier, personal observations). Xavier et al. (2015) also reported dense populations on the MAR at the Great Meteor Seamount in 2,675–2,765 m. The aim of the present study was to identify the environmental factors associated with its occurrence and predict the distribution of this VME indicator sponge on the Tropic Seamount. The distribution of *P. amadou* was modeled using three different DMs algorithms and for the purpose of management applications, a forecast ensemble map was produced to account for the predictions and uncertainties of the three modeling techniques (Araújo and New, 2007). This information can then be used to inform on-going high seas management efforts such as maritime spatial planning, environmental impact assessments, conservation of biogeographically unique provinces, and UN negotiations of a new treaty to protect biodiversity beyond national jurisdiction (BBNJ).

MATERIALS AND METHODS

Study Area

The Tropic Seamount (**Figure 1**), located in the northeastern Atlantic (23°55′ N, 20° 45′W), is a four-armed, star-shaped guyot dated to 91.1 ± 0.2 Ma (van den Bogaard, 2013). With a flat-topped summit (slope of 0.5°–4°) sitting at approximately 1,000 m water depth with its base rooted at approximately 4,200 m depth, the seamount presents a truncated cone slightly elongated along a north-south axis, measuring about 42 km in length and 37 km in width (Palomino et al., 2016). The flanks of the seamount are divided by four ridges 10–13 km in length with slopes ranging from 5° to 45°. Radiating from the summit, the flanks also exhibit gullies measuring 3–10 km in length (Palomino et al., 2016). The seamount is thought to have once been an oceanic island that eroded and subsided to its present depth at 1,000 m (Schmincke and Graf, 2000).

This seamount sits between the seasonally productive waters off the NW African coast and the more oligotrophic waters of the North Atlantic subtropical gyre (Henderiks, 2001). The surface waters are supplied by the Canary Current (CC), which flows south-westward along the African coast, turning west to join the North Equatorial Current at 20°–25° N. Below the seasonal thermocline and waters influenced by coastal upwelling (<100 m), the North Atlantic Central Water (NACW) and South Atlantic Central Water (SACW) lie above ∼700 m. The NACW is characterized by a higher level of dissolved oxygen than the SACW. Intermediate depths, 700–1,600 m, are ventilated by the lower salinity Antarctic Intermediate Water (AAIW). Deeper layers from ∼1,600 m to the seafloor, are defined by the Upper North Atlantic Deep Water (NADW), which is the shallowest deep water mass influenced by the Mediterranean Water (MW) (Hernández-Guerra et al., 2001; Knoll et al., 2002; Hernández-Guerra et al., 2005; Pastor et al., 2012; Bashmachnikov et al., 2015; Pastor et al., 2015). The influence of the MW decreases southward and seasonally, stretching south in winter (Pastor et al., 2012). Phytoplankton-enriched waters from upwelling events extend offshore to the study area (Hernández-Guerra et al., 2005). Dissolved oxygen levels at the seamount drop to 2.5–3.5 $\mu g\ ml^{-1}$ in the core of the oxygen minimum zone in ∼750 m and rise to 5 $\mu g\ ml^{-1}$ at 3,000 m (Koschinsky et al., 1996).

Data Collection

Exploration of the Tropic Seamount was conducted from October 29th to December 8th 2016 during the research cruise JC142 on the RSS *James Cook* in support of the MarineE-tech project, one of four large projects part of UK's NERC (Natural Environment Research Council) research program 'SoS Minerals.' During the cruise, the entire seamount was mapped with an EM120 multibeam echo-sounder, three moorings were deployed and 37 conductivity-temperature-depth (CTD) stations were occupied. There were also 28 ROV dives using the ROV *Isis* (Murton et al., 2017).

Biological Data

Remotely operated vehicle operations were mainly directed at rock sampling and drilling of ferromanganese crusts. Video and photographic surveys were conducted to characterize the biological communities on the seamount. The ROV was equipped with a mini Zeus HD video and SCORPIO digital stills camera, with scaling lasers 10 cm apart (Murton, 2016). The ROV maintained a mean altitude of 2.24 m from the seabed to ensure a consistent field of view. Voucher specimens of most

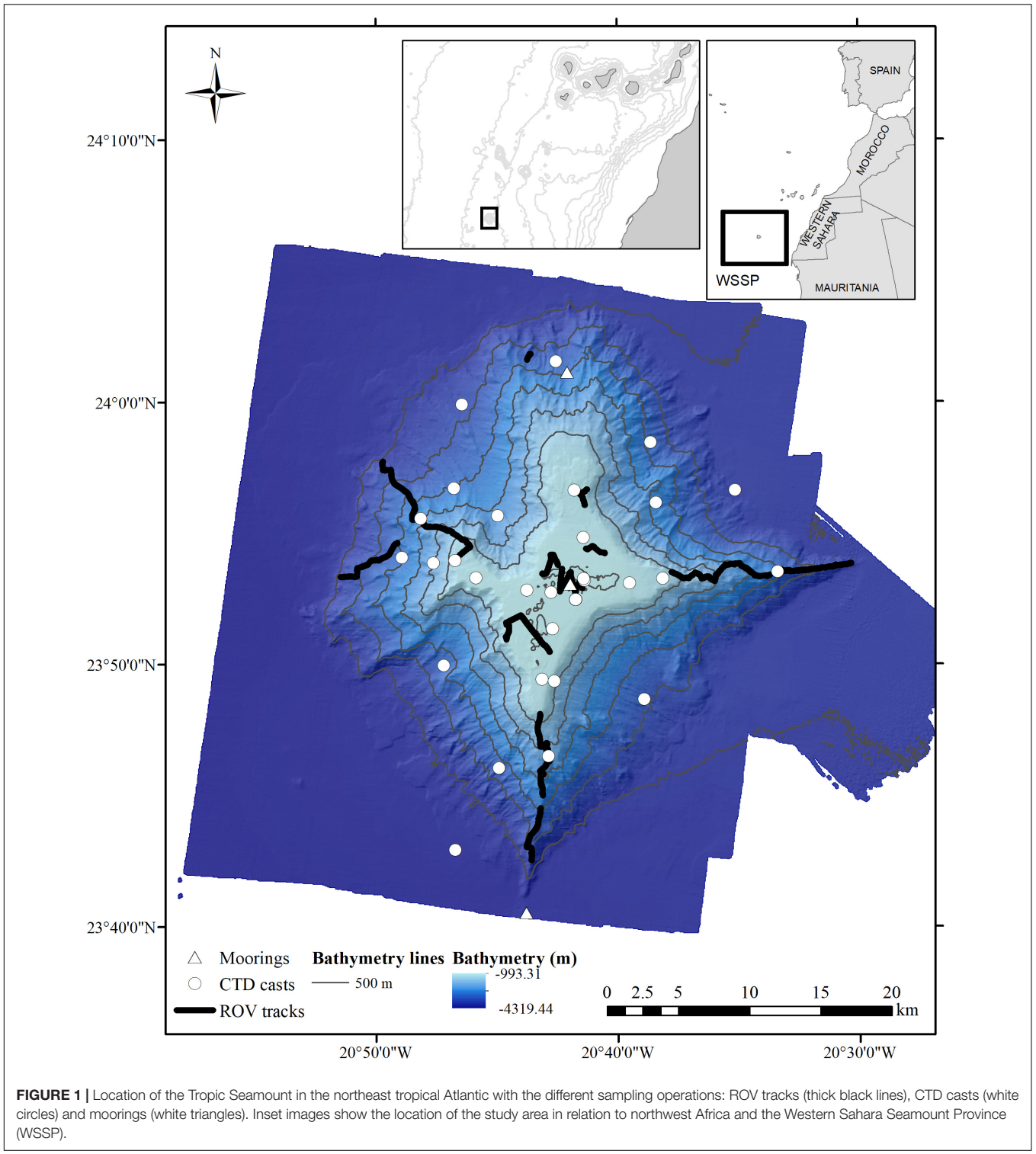


FIGURE 1 | Location of the Tropic Seamount in the northeast tropical Atlantic with the different sampling operations: ROV tracks (thick black lines), CTD casts (white circles) and moorings (white triangles). Inset images show the location of the study area in relation to northwest Africa and the Western Sahara Seamount Province (WSSP).

abundant organisms were collected to confirm identifications from imagery. **Figure 1** shows the sampling effort.

Organisms were identified and counted in video still images generated from the SCORPIO (12 M pixel) camera. Frames were extracted using Quicktime 7 Pro at a rate of one still per minute (every 15 m) to yield a total of 19,654 images. Species were identified down to the lowest possible taxonomic level based on visual observation (**Table 1**). The sponge *P. amadou* was one the most commonly observed habitat-forming VME indicator species in the study area, forming extensive monospecific sponge grounds. The final image databank for the analysis of the distribution of *P. amadou* contained 7,547 images after removing

TABLE 1 | VME indicator taxa observed on the images analyzed from the Tropic Seamount.

Types of VME indicators	Observations
Cold water coral reefs	
Solenosmilia variabilis (Duncan, 1873)	Patchily present in ledges, but no large reefs.
Coral gardens	
Acanella arbuscula (Johnson, 1862) *Acanella* sp. *Narella bellissima* (Kükenthal, 1915) *Narella* sp. *Thouarella* sp. *Corallium tricolor* (Johnson, 1899) *Corallium* sp. cf. *Swiftia* sp. *Acanthogorgia armata* (Verrill, 1878) *Chrysogorgia* sp. *Metallogorgia melanotrichos* (Wright and Studer, 1889) *Iridogorgia* sp.	Coral gardens of various types included different identified and unidentified octocoral species. A coral garden of the Family Isididae hosted deep-sea squid eggs indicating a potential spawning ground.
Black corals	
Parantipathes sp. *Bathypathes* sp. *Leiopathes* sp. cf. *Sticopathes* sp.	Other unidentified antipatharian species were also observed.
Sponges	
Poliopogon amadou (Thomson, 1877) *Pheronema carpenteri* (Thomson, 1869) *Stylocordyla pellita* (Topsent, 1904) *Hertwigia falcifera* (Schmidt, 1880) *Euplectella* sp. *Aphrocallistes beatrix* (Gray, 1858) *Hyalonema* sp. *Caulophacus* sp. *Asconema* sp. *Phakellia* sp.	Sponges recorded during the dives were mainly hexactinellids, but also demosponges (*Phakellia* sp.), and other undetermined and encrusting sponges.
Crinoid fields	
Endoxocrinus (Diplocrinus) wyvillethomsoni (Thomson, 1872) *Koehlermetra porrecta* (Carpenter, 1888)	In addition to the two species contributing to crinoid fields, the thalassometrid *Thalassometra lusitanica* (Carpenter, 1884) was also seen in numbers in some areas. Other species included a small 5-armed stalked crinoid, either *Gephyrocrinus grimaldii* (Koehler and Bather, 1902) (Hyocrinidae), or *Porphyrocrinus* sp. (Phrynocrinidae), and possibly *Zenometra columnaris* (Carpenter, 1881) (Zenometridae) (only the second record of this species from the NE Atlantic).
Other VME indicators	
Xenophyophore beds	
Brisingids	

duplicates, images with 'video-error' messages or with poor visibility, and images with no associated environmental data to match. Abundance was not enumerated because the ROV lasers were not visible in the majority of the images, and the camera tilt angles varied constantly, both of which prevented accurate calculation of the field of vision, thus only presence–absence of sponges were used in the present study.

Environmental Variables

Multibeam echosounder and backscatter data were acquired using the ship mounted Kongsberg EM122. Processing was done using Caris HIPS and SIPS for the bathymetry and the QPS FM Geocoder Toolbox v7.6.3 for the backscatter. Final grids and mosaics were produced with a grid spacing of 50 m. This resolution was applied in the distribution models after resampling (if needed) all the environmental variables used for the analysis. Acoustic backscatter strength measured the acoustic energy reflected back from the seafloor and is itself a function of slope, acoustic hardness and seafloor roughness. For flat seafloor, it can be considered a proxy for substrate type. High backscatter seafloor represents hard substratum while low reflectivity typically indicates soft-sediment. Substrate type influences the distribution of benthic organisms, and previous studies have related backscatter intensity to the distribution of sponges and other deep-sea species (e.g., González-Irusta et al., 2015; Rowden et al., 2017). A set of additional seafloor variables was derived from the bathymetric data, as quantitative seabed descriptors, using the terrain function in the R package 'raster' (Hijmans et al., 2013) and the Benthic Terrain Model tool in ArcGIS 10.1 (Environmental Systems Research Institute [ESRI], 2015). These variables were Aspect (measured in terms of northness and eastness), Slope, Roughness, and fine (3/25 radius) and broad-scale (25/250 radius) Bathymetric Position Index (BPI).

Water column properties were recorded from 37 CTD casts and the temporal dynamics of the water masses investigated through the deployment of three moorings along the longitudinal axis of the seamount for 30 days (**Figure 1**) and shipboard acoustic Doppler conductivity profiler (ADCP). The mooring data together with the CTD casts were used to produce a hydrodynamic model of the seamount (Cooper and Spearman, 2017). The model domain extended over an area of 500 km × 500 km; all runs were done including tide and real-time wind values. Model outputs included a time series of salinity, temperature and current velocity at 49 layers through the water column (with higher resolution near the seabed and surface) at a horizontal resolution over the seamount of 100–800 m. Model simulations were used to obtain the maximum near-bed velocity of currents (at 1 m above the bed) to include in the distribution models. The current information was derived at a variable resolution from 500 to 600 m, changing across the study area. The layer was then interpolated (using ordinary kriging) to the same resolution as the bathymetric data and rest of the variables using the function "krige" from the 'gstat' package (Pebesma, 2004).

Before starting data analysis, collinearity between variables was checked using Spearman's rank correlation coefficient and the Variance Inflation Factors (VIFs) (Zuur et al., 2009).

Roughness and broad-scale BPI were highly correlated with slope and depth, respectively (Spearman's rank correlation values > 0.7 and VIFs > 3) and were removed from the analysis. Consequently, seven variables were retained for the construction of the models to explore the factors controlling the distribution of *P. amadou*: water depth, slope, fine-scale BPI, eastness, northness, backscatter and maximum current speed (**Figure 2**).

Data Analysis

The distribution of *P. amadou* at Tropic Seamount was modeled using three algorithms widely used in species distribution modeling (González-Irusta et al., 2015): Maxent (Phillips et al., 2006), GAMs (Hastie and Tibshirani, 1986) and Random Forest (Breiman, 2001) using R (R Core Team, 2018). The Maxent algorithm estimates species distribution by minimizing the distance between the probability density of species occurrence and the probability density of the covariates as they occur in the geographic space (Elith et al., 2011). Although it was developed as a new machine-learning algorithm, Renner and Warton (2013) demonstrated that it is actually equivalent to an inhomogeneous Poisson process. Recently, Phillips et al. (2017) have developed a new R package named 'maxnet' (Phillips, 2017), which uses this feature to fit Maxent models using the 'glmnet' package for regularized generalized linear models (Friedman et al., 2010). The main advantage of the 'maxnet' package is that it allows one to fit a point process model while keeping all the derived feature classes (especially hinge features) and default tuned regularization values of the Maxent Java application (Phillips et al., 2017). This means that the raw output of Maxent can be used directly as a model of relative abundance. In this work we used all the default parameters of 'maxnet' but using real absences derived from the ROV data instead of pseudo-absences.

General Additive Models (GAMs) are an extension of General Linear Models (GLMs) which allow one to model non-linear relationships between the response variable and the explanatory variables, using a smoothing function to link both. The distribution of many marine species and habitats have been successfully modeled using this non-parametric approach (e.g., González-Irusta and Wright, 2016; Parra et al., 2017; Serrano et al., 2017). The GAM models were fitted using the function "gam" in the 'mgcv' package (Wood, 2011). We used a binomial GAM with logit function and constrained the smoother curves to 4 knots to avoid overfitting.

The third model applied was Random Forest (RF) using the package 'randomForest' (Liaw and Wiener, 2002). This modeling framework builds multiple classification trees, each generated with subsets of random data and using a randomly smaller set of the predictor variables (Breiman, 2001). Unlike GAMs, RF offers the advantage of lacking any underlying assumption of the distribution of the response variable.

The variable selection differed for each algorithm. Maxent was fitted using all the variables previously selected after checking for collinearity, whereas for GAMs the variable selection was performed using the Akaike Information Criteria (AIC) and the function "dredge" from the package 'MuMIn' (Barton, 2018). For Random Forest the function "VSURF" from the package 'VSURF' (Genuer et al., 2010) was used to select the variables. The relationship between the environmental layers and the predicted probability of presence was analyzed using response curves and produced using the methodology described by Elith et al. (2005). We kept all the variables constant except the

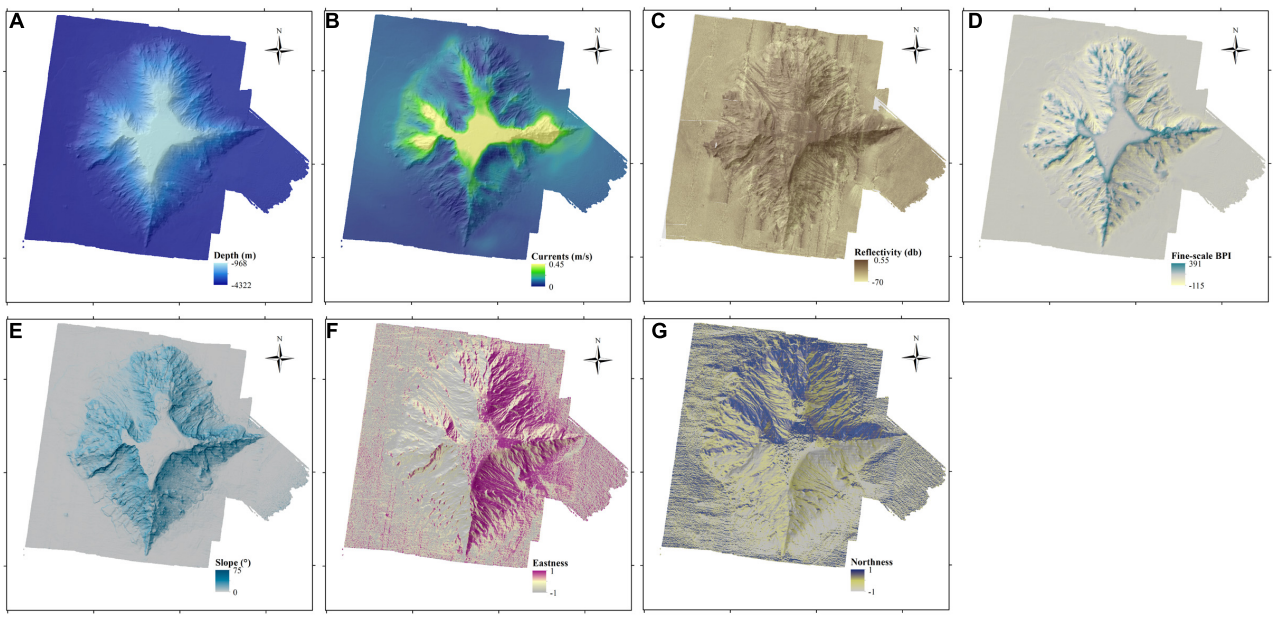


FIGURE 2 | Maps illustrating the spatial patterns of the seven bathymetry-derived variables, which were used as explanatory variables in the models. **(A)** Depth, **(B)** Maximum speed of currents at the seabed, **(C)** Fine-scale Bathymetric Position Index (BPI), **(D)** Slope, **(E)** Reflectivity, **(F)** Northness, and **(G)** Eastness aspects of the seabed.

target variable, which was varied at 500 points across its range. Then, the prediction of each algorithm was computed for each of the 500 values of the target variable and used to produce the response curves. The importance of each variable in the final output was computed using the methodology described by Thuiller et al. (2009), which enables direct comparison across models. The spatial autocorrelation of residuals was analyzed for each model using the "variogram" implementation in the 'gstat' package (Pebesma and Graeler, 2018). The semi-variance of the residuals did not show any trend with distance between each point and therefore spatial autocorrelation in the models' residuals was rejected.

Model Evaluation

The performance of the models was assessed by cross-validation using the function "get.block" from the 'EnMEVAL' package (Muscarella et al., 2014). This function finds the latitude and longitude that divides the number of occurrence localities into four similar groups. The objective of this method is to provide a larger level of spatial independence between the training and the evaluation data, reducing overestimation of model performance caused by a lack of spatial independence in the data (Fourcade et al., 2017). From the four original spatial blocks, we randomly selected one to evaluate the model (test subsample) and used the other three to build the models (training subsample). The ability of the training subsample to predict the probability of presence was tested using the test subsample in 10 runs. To avoid identical sample selection when the same block was selected, a random selection of only 80% of the data was used on each iteration.

The performance of the models was estimated using four different statistics: Sensitivity, Specificity, the True Skill Statistic (TSS) (Fielding and Bell, 1997), and the Area Under the Curve (AUC) of the receiver operating characteristic (ROC). Sensitivity is the proportion of observed presences that are predicted as such, whereas specificity is the proportion of observed absences that are correctly predicted. The TSS is the result of summing sensitivity and specificity and then subtracting one from the value. Allouche et al. (2006) suggested that TSS is a better option than the kappa statistic to evaluate distribution models, because it corrects kappa's dependence of prevalence while still keeping all the advantages of this statistic. These three metrics need to convert the continuous prediction of the models (with values ranging from 0 to 1) into binomial values (0 and 1) using a threshold. In the present study we have used the value which maximizes the sum of sensitivity and specificity as threshold, following the recommendations by Liu et al. (2013). The last metric (AUC) was developed to overcome the potential subjectivity in the threshold selection. The ROC curve plots the sensitivity as a function of commission error (1-specificity). The area under the curve (AUC) provides a single number in the range of 0 to 1 as a metric of model performance independent of threshold selection, where AUC values $\geq$ 0.9 indicate excellent performance, values between 0.7 and 0.9 indicate good performance, and values $\leq$ 0.5 indicate better than random performance. Although Lobo et al. (2008) questioned the effectivity of AUC to measure model performance, it is still one of the preferred metrics to evaluate models performance and, together with the other three metrics, it ensures an adequate evaluation of the applied models. Differences between the models for the four statistics were tested using Tukey's HSD *post hoc* test (p-value < 0.05).

Ensemble Models

Ensemble models are an effective solution to provide unique management advice by homogenizing the outputs of different SDMs techniques (Araújo and New, 2007; Robert et al., 2016; Rowden et al., 2017), usually achieved by computing the weighted averages of the different model outputs. Ensemble models also permit uncertainty caused by the different predictions to be calculated. In this study, we estimated an ensemble of all models as the weighted average of the GAM, Maxent and RF models (after Oppel et al., 2012; Anderson et al., 2016; Rowden et al., 2017) and integrated the spatial uncertainty of each of the three models in the estimation. Confidence levels for the prediction of each modeling approach were addressed using a bootstrap technique following Anderson et al. (2016) and Rowden et al. (2017). Accordingly, a random subset of the presence-absence data, in equal proportions, was drawn with replacement, and the three models built with their original settings. Predictions were then made for the study area. This process was repeated 200 times for the GAM, Maxent and RF models, which resulted in 200 estimates for each cell. Model uncertainty was then calculated as the coefficient of variation (CV) of the bootstrap output, i.e., the standard deviation divided by the mean. The weighted averages were calculated as the mean of the weighted averages of the TSS and AUC statistics.

RESULTS

VME Indicator Taxa

Remotely operated vehicle images showed high diversity of VME indicator taxa on Tropic Seamount (**Figure 3**). Coral debris was observed in still images mainly on the summit dives but also on some of the ridges to a depth of 1,800 m. Fifteen cold-water coral species were observed, including one scleractinian, twelve octocorals and two black corals (**Table 1**). The main scleractinian coral identified from the images was *Solenosmilia variabilis* (Duncan, 1873), which was normally present on ledges, forming patches at depths from ∼1,000 to 1,800 m. Octocoral composition varied with depth, with *Acanella arbuscula* (Johnson, 1862), *Metallogorgia melanotrichos* (Wright and Studer, 1889), *Corallium tricolor* (Johnson, 1899), and species from the genus C*hrysogorgia* (Duchassaing and Michelotti, 1864), *Iridogorgia* (Verrill, 1883), and *Thouarella* (Gray, 1870) generally present at depths of ∼1,010–3,000 m on rocky substrates. The octocorals *Narella bellissima* (Kükenthal, 1915), *Acanthogorgia armata* (Verrill, 1878) and cf. *Swiftia* (Duchassaing and Michelotti, 1864) were commonly observed at depths up to 3,600 m associated to volcanic substrates. Unidentified black coral species belonging to the genus *Parantipathes* (Brooke, 1889) and *Bathypathes* (Brooke, 1889) were also observed. Extensive coral gardens, another type of animal forests (Rossi et al., 2017), dominated by bamboo corals (Familiy Isididae) tentatively

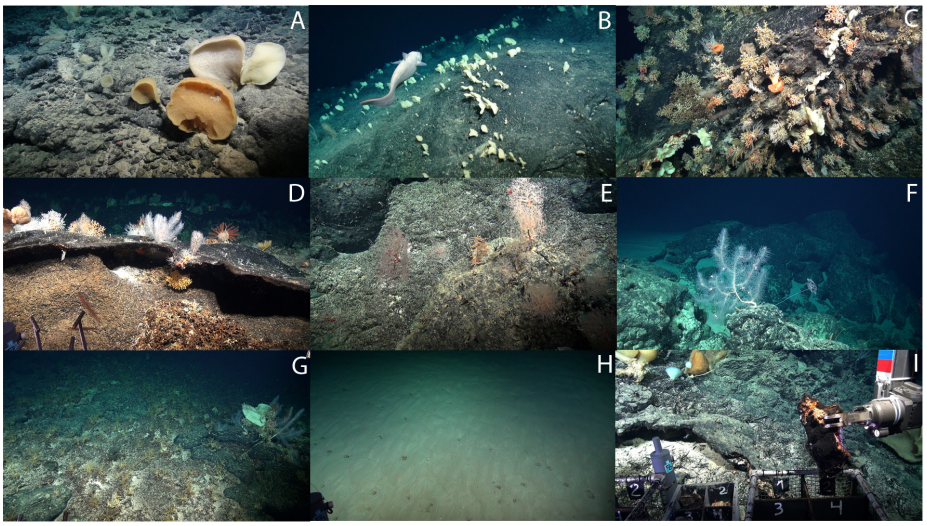


FIGURE 3 | Seabed photographs showing some of the VME indicator taxa observed on the Tropic Seamount. **(A)** Specimens of *Poliopogon amadou*. **(B)** Sponge ground of *Poliopogon amadou*. **(C)** Coral garden on a ledge with diverse octocorals and patches of *Solenosmilia variabilis*. **(D)** Octocoral garden and coral rubble. **(E)** Antipatharian species, *Metallogorgia melanotrichos* and *Chrysogorgia* sp. **(F)** Unidentified black coral. **(G)** A crinoid field of possibly *Thalassometra lusitanica*. **(H)** Field of xenophyophores. **(I)** ROV *Isis* sampling ferromanganese crust.

assigned based on branching patterns to the genus *Keratoisis* (Wright, 1869) and *Lepidisis* (Verrill, 1883) based on ROV images were recorded at 2,500–3,500 m depth.

Deep-sea squid eggs from an unidentified species were observed laying on bamboo corals on several occasions, indicating a potential spawning and/or nursery ground. Cold-water coral composition for Tropic Seamount is comparable to the reported for the la Concepción Bank and El Hierro ridge (Northern Seamounts group WSSP) and to the Canary Island slopes, with dominance of octocorals (Brito and Ocanña, 2004; Almón et al., 2014; Álvarez et al., 2016). Dense assemblages of bamboo corals of the genus *Keratoisis* have also been reported for Cape Verde seamounts between 1,900 and 3,699 m (Hansteen et al., 2014).

Besides *Poliopogon amadou*, other sponges seen included the hexactinellid *Pheronema carpenteri* (Thomson, 1869), *Stylocordyla pellita* (Topsent, 1904), *Hertwigia falcifera* (Schmidt, 1880), *Aphrocallistes beatrix* (Gray, 1858), and species from the genus *Euplectella* (Owen, 1841); *Hyalonema* (Gray, 1832); *Caulophacus* (Schulze, 1886); *Asconema* (Kent, 1870); and *Phakellia* (Bowerbank, 1862). Demosponges and other undetermined massive and encrusting sponges were also observed.

Xenophyophore and crinoid fields were also observed (**Table 1**). Among crinoids, the most common species were fields of stalked *Endoxocrinus (Diplocrinus) wyvillethomsoni* (Thomson, 1872) (Isselicrinidae), and two thalassometrid feather stars: *Koehlermetra porrecta* (Carpenter, 1888), an orange species with 20 or more arms, and a yellow species, perhaps *Thalassometra lusitanica* (Carpenter, 1884). The stalked species, *E. wyvillethomsoni*, is the only member of order Isocrinida found in the NE Atlantic occurring along the eastern Atlantic margin from west of Ile d'Ouessant, France (49°N) to south of the Canary Islands off the coast of Morocco (25°N) at depths from 1,246 to 2,070 m (Roux, 1985). *Koehlermetra porrecta* occurs in the eastern Atlantic from George Bligh Bank (NE end of the Rockall Plateau) to Ascension Island, over a depth range of at least 768–1,448 m (possibly 755–1,769 m) (Carpenter, 1888; Bullimore et al., 2013; Narayanaswamy et al., 2013). Stevenson et al. (2017) reported large populations of *K. porrecta* in 778–941 m in the Bay of Biscay. Records of *Thalassometra lusitanica* range from the Canary Islands and Morocco to off Cape Carvoeiro, Portugal, at depths of 1,229–1,716 m (possibly 914–1,912 m), with one record in 2,165 m (Clark, 1950, 1980).

Species Data

From the initial dataset of 7,547 pictures distributed across the study area, 923 showed at least one specimen of *P. amadou*. The mean number of *P. amadou* sponges in the images in which they occurred was 11 individuals with a maximum of 121 individuals. The sponge seemed to be distributed throughout the four ridges sampled on the seamount. Analysis of the still frames showed wide presence of *P. amadou* in the eastern, southern and western ridges of the seamount. A brief ROV dive on the northern crest of the seamount recorded one specimen of *P. amadou*. The sponges occupied a distinct bathymetric belt ranging from 1,960 to 3,660 m. Different body sizes ranging from ∼5 to 55 cm in length were observed across all the stills. The sponges were found only on hard substrates corresponding to rocks, of which the majority had a ferromanganese crust.

Hydrography

For the depths where *P. amadou* was recorded (1,960 – 3,660 m), the CTD casts registered temperatures ranging from 2.5 to 4°C, salinity values between 34.91 and 35.05 psu, and oxygen levels between 6.5 and 6.9 $\mu g/ml^{-1}$. The casts showed an

inflection point in these parameters at ∼2,500 m, where oxygen reached values of 6.8 $\mu g/ml^{-1}$, the temperature was ∼3.25°C and salinity 34.99 psu. Hydrodynamic modeling revealed a strong influence of tides on surface and bottom currents, with a NE-SW current rotating anticlockwise over the diurnal tidal cycle. The elongated ridges extending outward from the star-shaped seamount cause high current variability. The eastern and western flanks dissipate higher energy, whereas the northern and southern spurs dissipate less energy. The distribution of sediment-covered and sediment-poor areas coincided with this energy distribution, which is observable on the ROV videos and the backscatter intensity. The summit had a variable layer of biogenic silty fine sand forming ripples aligned with the (varying) peak current velocity. Numerical modeling indicates the presence of a weak Taylor Cap on the summit of the seamount (Cooper and Spearman, 2017).

Variable Influence

The importance of the environmental variables varied across the modeling algorithms, although depth was the most influential, followed by the maximum velocity of currents, for all three (**Table 2**). While the RF model considered only depth and the maximum velocity of currents as important for the prediction of suitable habitats, Maxent and GAM models included all environmental variables as predictors of *P. amadou*. The variables slope, backscatter, eastness and northness had some effect on the probability of presence in the GAMs and Maxent, although their influence was low (**Table 2**).

For all environmental variables, Maxent predicted higher probabilities of presence for *P. amadou* relative to the GAM and RF models (**Figure 4**). In general, Maxent, GAM and RF models showed similar response patterns in the environmental variables (depth and maximum velocity of currents) included in the three models. Modeling returned a marked bathymetric belt for the sponge in 2,000–3,500 m, with a peak of higher probably around 2,800 m, which was observed in the response curves of the three models. This trend corresponded well with the observed depth range of the occurrence records. For the variable maximum current speed, the three models showed a similar trend and predicted an increased probability of presence of *P. amadou* at speeds up to 0.2 m sec^{-1} for Maxent, 0.25 m sec^{-1} for GAM, and 0.28 m sec^{-1} for the RF model. Following similar response patterns, Maxent and GAM models predicted that *P. amadou* would occur on areas elevated from surrounding environments (with a peak in the probability of presence around a fine-scale BPI of 75) and with low values of slope, which followed a slightly different trend. The trend in the GAM was constantly negative with two different intensities (slightly negative from 0 to 30° and very negative for values ≥ 30°), whereas the trend for Maxent it was only negative for slope values > 20°. For the aspect variables, Maxent and GAM models predicted the highest probability of presence for values equal to 1 (northeast) and the lowest for values equal to −1 (southwest) for both variables (eastness and northness), but differed for intermediate values. Finally, *P. amadou* seemed to have a predisposition for hard substrata (high reflectivity values ≤ −30 db), with a linear increase of backscatter values for the range from −50 to −35/30 db.

TABLE 2 | Index of importance of each predictor variable for the GAM, Maxent and Random Forest models.

Variables	Maxent	GAM	RF
Depth	0.948	0.961	0.853
Slope	0.064	0.071	–
Fine-scale BPI	0.114	0.120	–
Maximum current speed	0.181	0.215	0.482
Eastness	0.069	0.034	–
Backscatter	0.054	0.045	–
Northness	0.037	0.025	–

Values reflect an index calculated as one minus the coefficient of correlation between the prediction performed by the model and a bootstrapped prediction. If the correlation between both models is high (close to 1), the index is close to 0, since the effect of the variable in the model is low. If the importance of the variable is high, then the model with real values and the bootstrapped model will be very different and therefore the correlation will be low and the index high.

Comparison of Model Performance

The distribution of *P. amadou* was mapped using binomial GAMs, Maxent and RF models. The performance of the models was good for each measure of accuracy calculated, with high values of explained deviance, AUC, sensitivity, specificity and TSS values (**Figure 5**). All four models had a good ability to discriminate between areas where *P. amadou* was present and absent (all AUC mean values ≥ 0.8), with GAM, Maxent and Ensemble the best performers. All models showed sensitivity and specificity values in the range of 0.75 – 1.0. For sensitivity, all models had values between 0.9 and 0.95, indicating high accuracy in the prediction of correctly assigned observed presences, although GAM performed slightly worse. In contrast, specificity values—the proportion of observed absences correctly predicted—were lower between 0.7 and 0.8, with GAM being the best performer and Maxent the worst. For the TSS metric, the GAM had the highest performance with a TSS value of 0.69. The Maxent model, however, had the lowest TSS value (0.64). *Post hoc* Tukey's HSD comparisons between the models for the four statistics (Tukey test; $P < 0.05$) did not show any significant difference between models for any of four statistics.

Predicted Species Distribution

Figure 6 shows the probability of presence for *P. amadou* based on GAM, Maxent and RF. Besides the bathymetric range of the distribution, the topographic variables also influenced the predicted habitat. Generally, the Maxent model predicted the distribution of suitable habitat for *P. amadou* to be more extensive, although two areas of high probability of occurrence were consistent across all three models. The Maxent model predicted suitable habitat along the northern, eastern, southern and western spurs of the seamount and along the NE and SE flanks, where it reflected the topography of the gullies. The GAM model predicted suitable habitats in the same areas as the Maxent model, but with lower probability of occurrence on the NE and SE flanks. Both the Maxent and GAM models displayed similar predicted distributions, as both included the same environmental variables in the model construction and

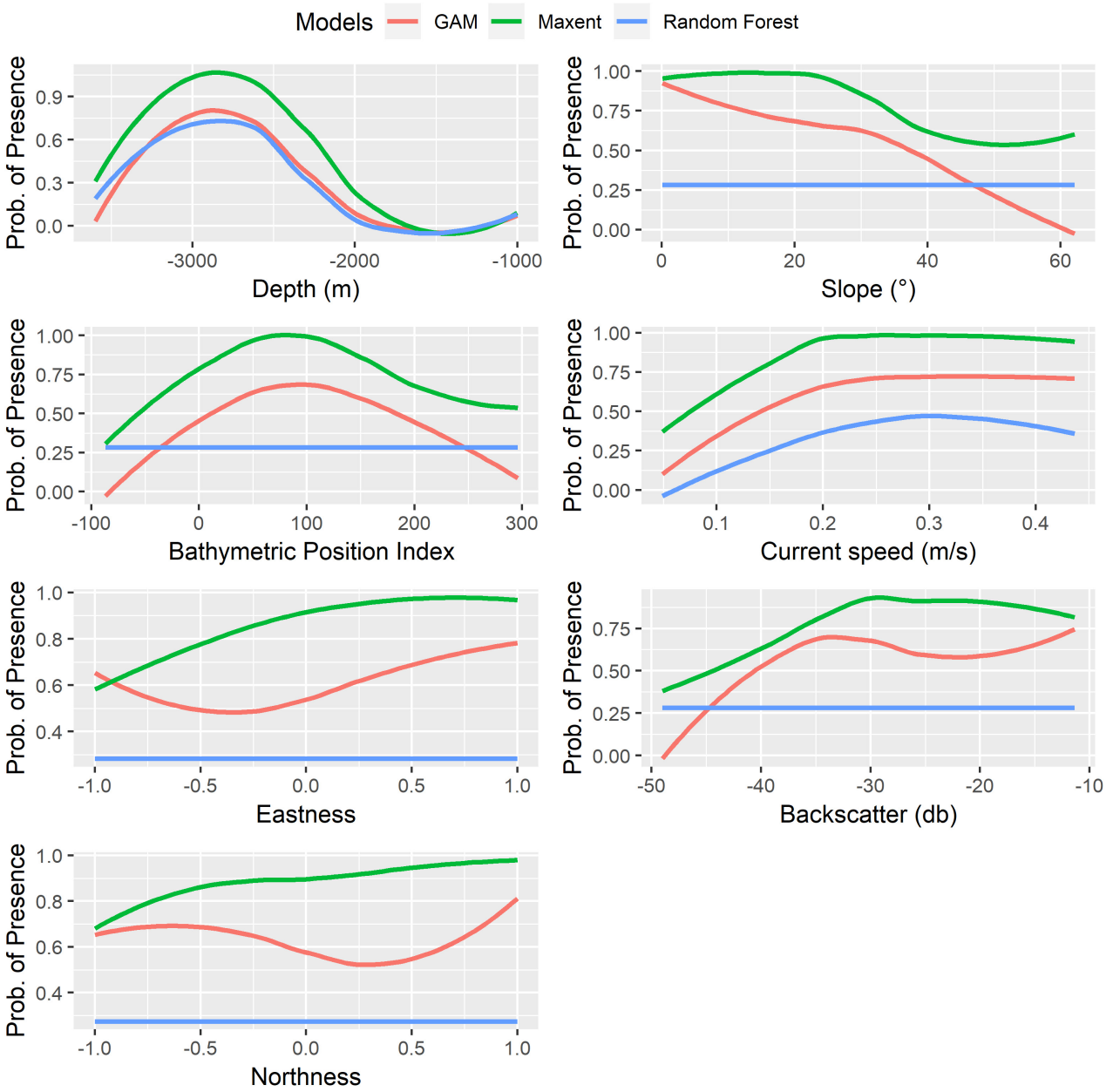


FIGURE 4 | Response curves of the probability of presence of *Poliopogon amadou* for each predictor variable for the GAM, Maxent and Random Forest prediction of the probability of presence. The response curve is the dependence of the probability of the presence on one predictor variable after averaging out the effects of the other predictor variables in the model.

exhibited similar response curves. Besides the bathymetric range of the distribution, the topographic variables also influenced the predicted habitat. In contrast, the RF model predicted suitable habitat for *P. amadou* along a bathymetric belt around the seamount, but only with high probability of occurrence on marked contours on the eastern and western spurs, similarly to the GAM prediction. This predicted distribution reflected the distribution of the environmental variables included in the model, namely depth and maximum current speed. At ∼3,000 m, a continuous band of less suitable habitat around the seamount marks the lower depth limit of the predicted suitable habitat.

The predicted suitable habitat by the ensemble model reflected the average of all three models weighted accordingly by the results of the evaluation process (**Figure 7A**). *Poliopogon amadou* was widely distributed mainly on the eastern and western ridges and less concentrated on the northern spur, NE and SE flanks and the southern spur. Although the bathymetric imprint of the RF model was observed on the NW and SW flanks of the seamount, the probability of presence on these areas was low.

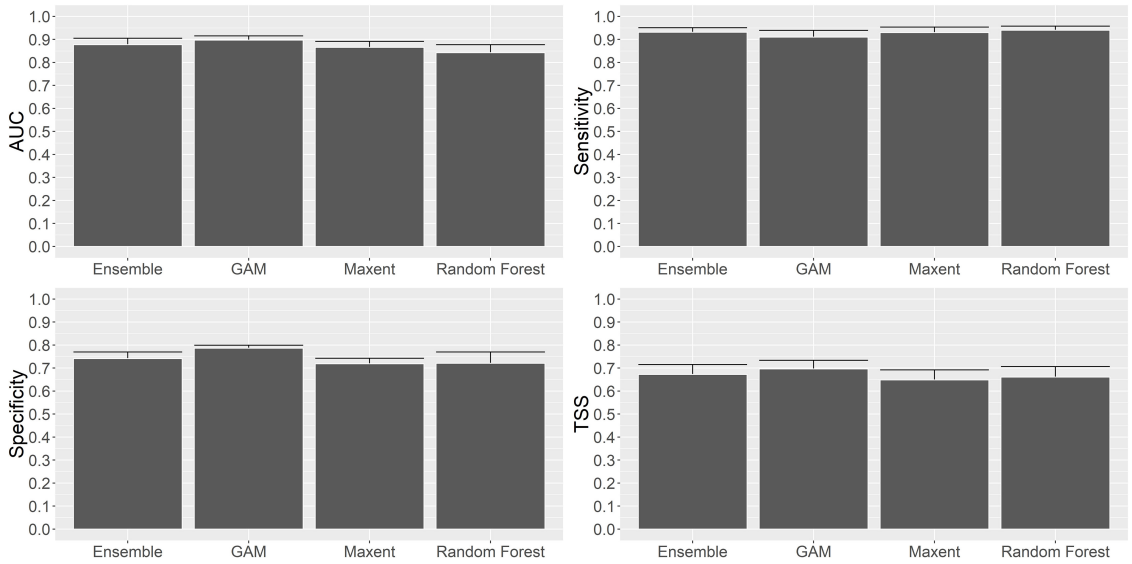


FIGURE 5 | Comparison of performance statistics (AUC, Sensitivity, Specificity and TSS) for the Ensemble, GAM, Maxent and Random Forest models.

The spatial patterns of high-modeled uncertainty corresponded to the main areas predicted as highly suitable habitat on the eastern and western spurs, together with a bathymetric belt of high uncertainty across the seamount (except for a patch on the SE flank) that reflected again the RF model imprint (**Figure 7B**).

DISCUSSION

The Tropic Seamount harbors diverse and near pristine benthic communities that include several VMEs such as reef-building coral species *Solenosmilia variabilis*, several species of octocorals and black corals that formed diverse animal forests, crinoid fields, and sponge grounds. This diversity is most likely related to the specific oceanographic characteristics and hydrography of the Tropic Seamount. The phytoplankton-enriched waters from the Sahara upwelling events extend offshore reaching the Tropic Seamount (Hernández-Guerra et al., 2005), that is fed by the iron-rich dust coming from the Sahara desert making the NW waters off Morocco a very productive oceanographic area (Henderiks, 2001). The existence of a Taylor Cap on the seamount may be affecting the distribution of particulate organic carbon keeping organic matter suspended and circulated within certain depth ranges (Clark et al., 2010).

In this study we focused on an important VME, the sponge grounds formed by *P. amadou,* to produce predicted DMs that could have implications for High Seas conservation, and support the designation of the Tropic Seamount as an EBSA with extensive coverage of a diverse set of pristine and, in the case of *P. amadou*, biogeographically unique VMEs. Deep-sea sponge grounds have international conservation and management significance because of their low resilience. These habitats and their associated communities are particularly vulnerable to anthropogenic impacts such as fishing and deep-sea mining due to their slow growth (Hogg et al., 2010), proving their recovery very slow or inexistent (Klitgaard, 1995). However, the conditions responsible for the formation of sponge grounds remain poorly understood, with the exception of a few studies in the northwest Atlantic (e.g., Beazley et al., 2018) and the Antarctic (e.g., Gutt and Koltun, 1995; Dayton et al., 2019), where different environmental and physical factors play a role in their distribution and persistence. Our work adds to the growing literature on the potential use of high-resolution DMs for deep-sea conservation and management of VMEs, and is the first to investigate the environmental drivers of the distribution of a biogeographically unique VME formed by *P. amadou*.

Environmental Drivers

All three DMs included depth as the most important explanatory variable. *Poliopogon amadou* occurred in a wide bathymetric range across the seamount, from 1,960 to 3,660 m depth, but with a marked preference for 2,500 and 3,000 m depth, as confirmed by the presence of more sponges in ROV images from these depths. This finding agrees with previous work. Xavier et al. (2015) found *P. amadou* aggregations at the Great Meteor Seamount and collected specimens between depths of 2,675 – 2,765 m. They collected another specimen at the Closs seamount at 2,761 m. Similarly, and at the closest location to our study site, the *P. amadou* holotype was collected at 2,790 m depth southwest of the Canary Islands (station 3, 25°24′ N 20°14′ W) during the HMS *Challenger* expedition (Thomson, 1878). As suggested by Xavier et al. (2015), the similarity in depth ranges between these records supports the idea that *P. amadou* occurs in bathymetrically constrained bands. However, depth is a proxy for other environmental variables including temperature, salinity, oxygen, food availability, pressure, near-bottom current speed and sediment type (Harris and Whiteway, 2009). In this study, available data from the CTD casts included temperature, salinity

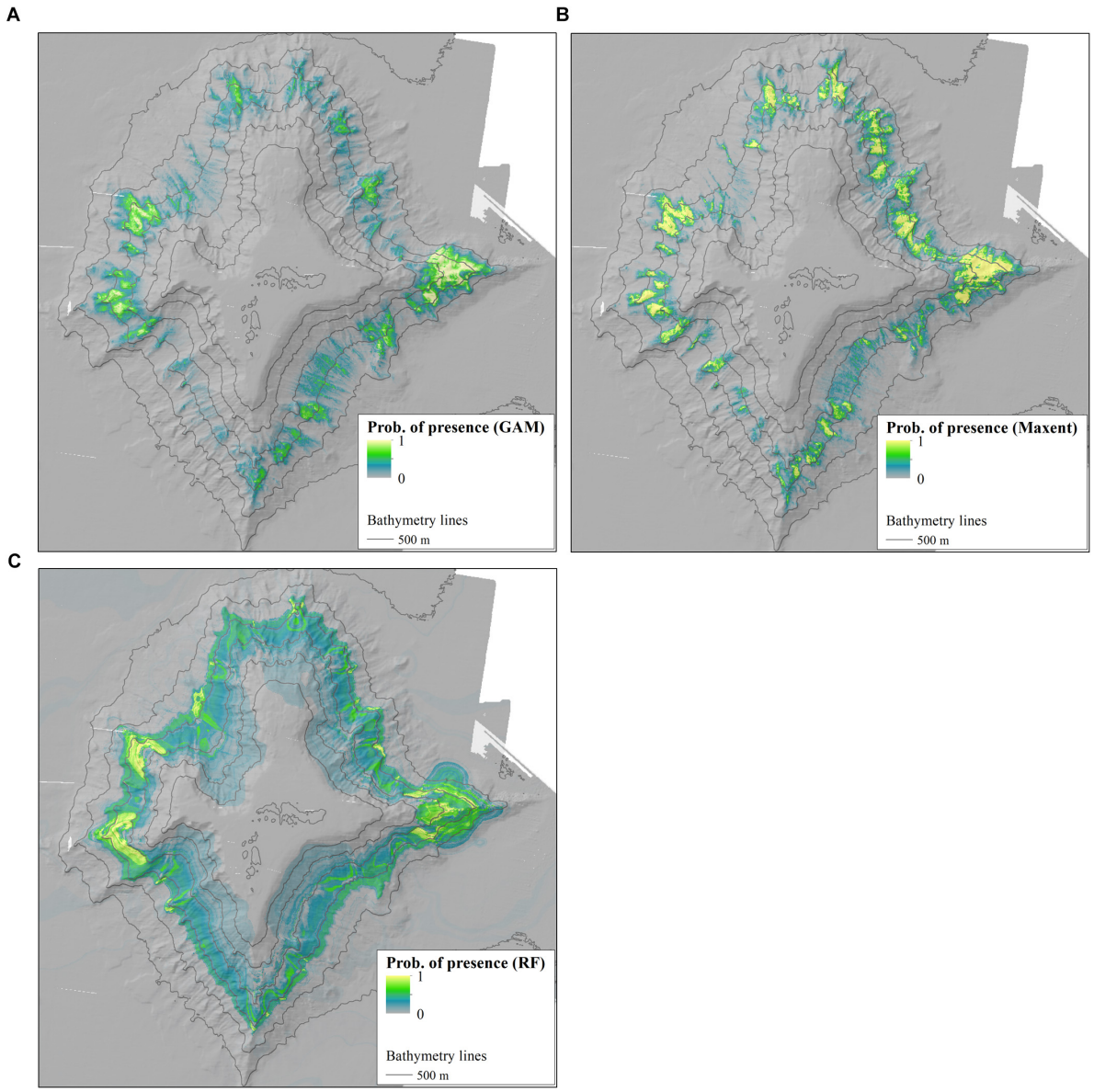


FIGURE 6 | Distribution maps of *Poliopogon amadou* using **(A)** GAM, **(B)** Maxent, and **(C)** Random Forest models. The figures show the probability of presence of the sponge on the Tropic Seamount and the seamount bathymetry.

and oxygen. Although these variables were not suitable to be included in the model because of their high level of correlation with depth and higher level of uncertainty (only 36 points for the whole seamount), they can be used to help explain the observed depth range of *P. amadou* on the Tropic Seamount. For instance, the predicted distribution of the sponge grounds of the hexactinellid *Vazella pourtalesi* on the Scotian Shelf, off Nova Scotia, Canada, was driven by minimum bottom temperature. The sponge grounds occurred in a warm and saline water mass with low oxygen, but high in nutrient concentration, Warm Slope Water (Beazley et al., 2018). In a similar way, Howell et al. (2016) also found bottom temperature as the second most important variable (after depth) explaining the distribution of *Pheronema carpenteri* in the North Atlantic. Although the depth range was well defined by the DMs on the Tropic Seamount and agreed with the depth distribution observed in the species in surrounding areas, it is not possible to establish a depth limit for *P. amadou* across the Atlantic given the proxy nature of this variable and the few records in the literature. The variable nature of the depth range for benthic species is well known and it has been previously described for other species (e.g., Dullo et al., 2008; Radice et al., 2016).

The bathymetric range where *P. amadou* was more frequent (2,500 – 3,000 m) corresponded with an inflection point in temperature, salinity and oxygen across the seamount. The temperature and salinity in that band ranged between 2.75

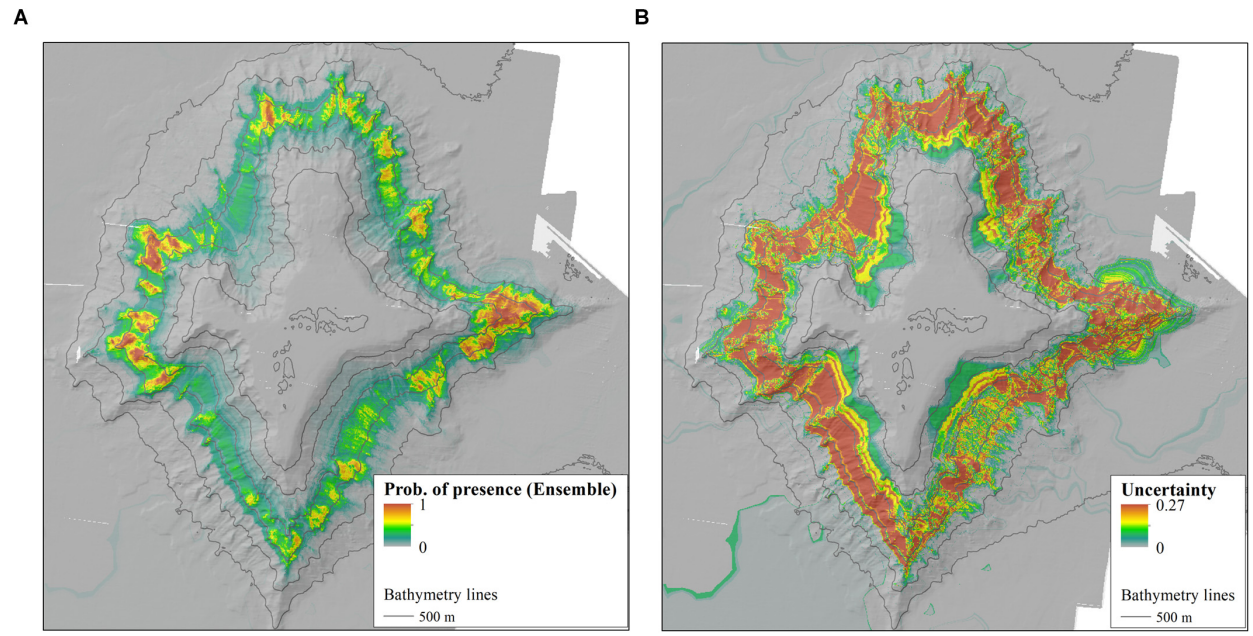


FIGURE 7 | Prediction of *Poliopogon amadou* presence for the ensemble distribution model **(A)** and **(B)** uncertainty (CV) for the ensemble distribution model.

and 3.25°C and 34.94 and 35.04 psu, respectively. Dissolved oxygen ranged between 6.8 and 6.9 $\mu g\ ml^{-1}$. This band matches the intermediate level of the Upper NADW (2.5°C, 34.5 psu, O_2 6.7–7 $\mu g\ ml^{-1}$) that seems to be well developed at approximately 2,000 m depth (Hernández-Guerra et al., 2005). This water mass, together with the hydrography of the area, seem to be controlling the distribution of *P. amadou* in the Tropic Seamount. To date there are no studies characterizing the water masses where *P. amadou* occurs, however, observations from the Vema Fracture Zone at 2,940–2,230 m occurred inside the NADW too, with temperatures ranging between 2.7 and 3.3°C and salinity of 34.9 psu (L. Victorero, personal communication). If the general oceanographic conditions of seamounts are comparable, these results may be extrapolated to similar seamounts occurring along the path of the NADW mass, as suggested by Roberts et al. (2018) for the deep-sea sponge grounds found on the Schultz Massif Seamount of the Arctic Mid-Ocean Ridge.

Maximum speed of currents at the seafloor was the next most important environmental predictor in the three DMs. Sponges are normally found where local currents enhance food supply but are not able to withstand direct exposure to very strong currents (Rice et al., 1990). As non-selective filter feeders, large quantities of sediment in the water column can clog a sponge's filtering apparatus (Hogg et al., 2010; Tjensvoll et al., 2013). This agrees with the observed response curves, which show increased probability of sponge presence at current speeds $\leq$ 0.2–0.28 m sec^{-1}, but no effect at greater speeds. The reason for the lack of a negative response at the highest current speeds could be explained because this value is not exceptionally high (especially since they are maximum and not mean current speeds).

Fine-scale Bathymetric Position Index, slope, aspect and backscatter were the other variables included in the GAM and Maxent models. Substrate type is thought to influence the distribution of sponges by facilitating larval settlement (Knudby et al., 2013). However, the biological relevance of backscatter intensity in this study was minimum. This could be due to the fact that most of the area of the seamount was hard substrate, with lower reflectivity values on the southern ridge, and consequently not a discriminant factor in the model. The homogeneity in the backscatter intensity is probably because these data cannot distinguish between clean hard substrate and hard substrate covered by a thin layer of sediment (<50 cm, Lo Iacono et al., 2008), which reduces its usefulness in DMs approaches in such environments. BPI (i.e., the relative elevation of the seabed in comparison to neighboring areas) could partially resolve this limitation, as areas with high BPI generally correspond to regions of hard substrate; however, the importance of this variable in the final model is uncertain. The aspect of the seabed, in terms of northness and eastness, predicted the highest probability of presence of *P. amadou* on the northern, eastern and western slopes, which coincided with the direction of the modeled currents on the seamount. In the ROV images, the specimens could be seen oriented in one direction, probably reflecting both the need to respond to flow and grow in an area that allowed maximization of the suspended resource.

Model Comparison

The three models used to predict the distribution of *P. amadou* showed good performance, with no significant differences between them for any of the statistics analyzed. The three models predicted the highest probability of presence of the sponge on the eastern and western ridges and certain patches

on the northern spur. The selection of the variables in the model construction was the main driver of the differences found among the models, namely on the areas where data were not available. Random Forest was built using only two variables (depth and maximum current speed), whereas GAM and Maxent also included the rest of the environmental variables (backscatter, fine-scale BPI, slope, eastness and northness). The inclusion of these other variables in the model construction of GAM and Maxent allowed us to take into account microscale effects related to the geomorphology of the seabed. This resulted in less-broad predictions across the depth band suitable for *P. amadou* than the Random Forest probabilities. The differences are especially clear in the southwest slope of the seamount, mainly unsuitable for the GAM and Maxent prediction, but suitable for Random Forest. Despite the inclusion of these variables in the construction of the models, GAM and Maxent did not show statistically significant differences in any of the evaluation statistics and therefore the RF model was retained for the ensemble forecast, although its impact in the final ensemble model was weighted by the results of the evaluation process.

The library used in the variable selection for the RF model could have driven the main differences between the models. The library 'VSURF' for RF models selected only depth and currents as predictors, and this was reflected in the output of the RF model which displayed a continuous bathymetric belt of probability of presence for *P. amadou* on the seamount. Other methodologies for RF variable selection are available and it would be interesting to see how the selection process results would differ. This highlights the usefulness of ensemble models, which average all model outputs and so take into account uncertainties and performance of different algorithms. The resulting ensemble model is thought to provide a more robust predicted distribution of *P. amadou* than any of the individual models and thus have clearer value for spatial management measures. The ensemble model maintains areas of high probability of presence in the same areas predicted by the individual models. However, it also maintains high the probability of presence of *P. amadou* across its suitable bathymetric range regardless of slope orientation, which is an effect of the inclusion of Random Forest in the model.

The uncertainty of the ensemble model was higher along a bathymetric belt from approximately 2,000 to 2,800 m depth across the seamount, with a patch of lower uncertainty on the SE flank. This depth is within the range where the highest probability of *P. amadou* occurring is predicted (2,500 – 3,000 m) and where the maximum velocity of currents at the seabed is lowest. Model uncertainty is difficult to estimate, but the bootstrap procedures applied to the GAM, Maxent and RF models provided a measure of internal consistency across the models (Anderson et al., 2016). Uncertainty maps are a key resource when applying predictions of distribution models to management measures (Vierod et al., 2014), as they can incorporate some level of confidence to the predictions and management actions (Anderson et al., 2016). Sources of uncertainty not accounted for in our models might be other key driving factors of habitat suitability for the sponge including oceanographic variables such as silicate, phosphate and nitrate availability, and POC flux (Howell et al., 2016).

Habitat Importance and Implications for Conservation

The sponge grounds of *P. amadou* were one of the most frequent and extensive VMEs observed on the Tropic Seamount, with different body sizes (from approximately 5 cm up to 55 cm) indicating a stable population with on-going recruitment. Although we did not model abundance of the sponge directly, it has been demonstrated that, in general, the outputs of DMs can be used as proxies for abundance (Weber et al., 2017). In this study we modeled the probability of presence to find a sponge in a ROV picture for each grid cell, a probability which is directly correlated with the abundance of the sponge inside a grid cell. The higher the abundance in the grid cell, the higher the probability to find a presence. This is especially accurate for Maxent models since, as explained by Phillips et al. (2017), "the interpretation of Maxent as an inhomogeneous Poisson process allows Maxent's 'raw' output format to be used directly as a model of relative abundance." Therefore, it is possible to predict that the highest concentrations of *P. amadou*, and therefore of sponge grounds, will be in modeled areas of highest probability of presence.

The distribution models presented here are relevant to the Fishery Committee for the Eastern Atlantic (CECAF), which is the Regional Fishery Body responsible for the identification, description and mapping of VMEs or indicator species in their regulatory areas in ABNJs. By mapping and understanding the ecological variables that are related with the VME indicator species in the CECAF area, we are able to provide expert advice on the occurrence of deep-sea sponge grounds and other VME indicator taxa in efforts to limit anthropogenic threats from future marine resource exploitation. The depths of most VME indicator taxa on Tropic Seamount make these seamount habitats de facto refuges from bottom fisheries impacts, as supported by a lack of evidence for any contact with bottom-fishing gear from the ROV images and from fishing records across the wider CECAF area (Fao Fiaf/R1184, 2016).

Tropic Seamount could in future become vulnerable to other types of deep-water exploitation. The latest survey on the area by the MarineE-Tech project found deposits of ferromanganese crusts at all depths. In particular, the thickest crusts (<20 cm) are located at the greatest depths of the seamount (3,000 – 4,000 m) on the eastern and western ridges, while the summit generally hosts the thinnest crusts (Murton et al., 2017). These crusts hold significant resources of tellurium and cobalt, making this underwater feature of interest to future deep-sea mining. Specimens of *P. amadou* were found only on hard substrates corresponding to rocks, of which the majority had a ferromanganese crust. Deep-sea mining will very likely cause some extent of biodiversity loss (Van Dover et al., 2017), and much recent research has addressed this conflict between industry and conservation (e.g., Shirayama et al., 2017; Dunn et al., 2018; Van Dover et al., 2018).

The ISA, together with new legally binding policy instruments for BBNJ (Long and Chaves, 2015), can help address these threats and sustainably manage VMEs on Tropic Seamount if a robust evidence base on VME occurrence can be constructed based on ground-truthed and predictive models. The present study offers the first biological study to ground-truth the occurrence of potential VMEs on Tropic Seamount, alongside predictive models to increase the spatial coverage beyond ROV and AUV surveys. Predicted habitat for *P. amadou* was found to be favorable on the deep flanks of the seamount within a very narrow oceanographic regime. Thus, any deep-sea mining operation on these flanks should consider sediment deposition throughout the water column and potential for sediment plumes to spread from adjacent non-flank areas including those on the shallower summit. Other VME taxa observed on Tropic Seamount, such as coral gardens and patches of *S. variabilis* are also likely to provide important ecosystem functions on the seamount, indeed one type of coral garden hosted a nursery ground for deep-sea squid: here too, predictive species and habitat models could greatly aid in building the evidence base for VME occurrences.

Combined with the multiple ground-truthed records of VME taxa, new classes of predictive habitat models may provide powerful new lines of evidence to help sustainably manage seamounts in the High Seas from impacts of resource exploitation as these new data can help verify VME occurrences and/or identify marine protected areas (MPAs), for which there are some management and avoidance measures for industries to take. Additionally, the high deep-sea biodiversity cataloged in the present study and predicted spatial extent of *Poliopogon* sponge grounds, the importance of coral gardens for early life history stages of deep-sea squid, and the unique biogeographic affinities of some VME taxa are now being used to build a case to nominate Tropic Seamount as a candidate EBSA (CBD, 2008) and as a large VME itself (Watling and Auster, 2017). Operationalizing EBSAs as an additional management consideration for industry in the same way that VMEs and MPAs do is still its infancy, but first a robust evidence base for why an area meets EBSA criteria is critical to lay these foundations.

AUTHOR CONTRIBUTIONS

BR-S, JG-I, and L-AH conceived the biological study. BM was the chief scientist of the MarineE-Tech project and designed the program, led the cruise and collected the data. IY provided images and survey data. LV directed the collection of biological observations and voucher specimens. JS provided data from the hydrodynamic model. BR-S and JC analyzed image data. GK helped with sponge classification. JX, MC-S, ÍS, and CM provided taxonomic expertise on the identification of species from images. BR-S and JG-I undertook the modeling and interpreted the data. BR-S led the writing, and drafted text for the manuscript. JG-I, JX, LV, ÍS, CM, MC-S, and JS contributed draft text to the manuscript. All authors revised and approved the final version of the manuscript.

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Benthic Oxygen and Nitrogen Exchange on a Cold-Water Coral Reef in the North-East Atlantic Ocean

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Cold-water coral (CWC) reefs are distributed globally and form complex three-dimensional structures on the deep seafloor, providing habitat for numerous species. Here, we measured the community O_2 and dissolved inorganic nitrogen (DIN) flux of CWC reef habitats with different coral cover and bare sediment (acting as reference site) in the Logachev mound area (NE Atlantic). Two methodologies were applied: the non-invasive *in situ* aquatic eddy co-variance (AEC) technique, and *ex situ* whole box core (BC) incubations. The AEC system was deployed twice per coral mound (69 h in total), providing an integral estimate of the O_2 flux from a total reef area of up to 500 m^2, with mean O_2 consumption rates ranging from 11.6 ± 3.9 to 45.3 ± 11.7 mmol O_2 m^{-2} d^{-1} (mean ± SE). CWC reef community O_2 fluxes obtained from the BC incubations ranged from 5.7 ± 0.3 to 28.4 ± 2.4 mmol O_2 m^{-2} d^{-1} (mean ± SD) while the O_2 flux measured by BC incubations on the bare sediment reference site reported 1.9 ± 1.3 mmol O_2 m^{-2} d^{-1} (mean ± SD). Overall, O_2 fluxes measured with AEC and BC showed reasonable agreement, except for one station with high habitat heterogeneity. Our results suggest O_2 fluxes of CWC reef communities in the North East Atlantic are around five times higher than of sediments from comparable depths and living CWCs are driving the increased metabolism. DIN flux measurements by the BC incubations also revealed around two times higher DIN fluxes at the CWC reef (1.17 ± 0.87 mmol DIN m^{-2} d^{-1}), compared to the bare sediment reference site (0.49 ± 0.32 mmol DIN m^{-2} d^{-1}), due to intensified benthic release of NH_4^+. Our data indicate that the amount of living corals and dead coral framework largely contributes to the observed variability in O_2 fluxes on CWC reefs. A conservative estimate, based on the measured O_2 and DIN fluxes, indicates that CWC reefs process 20 to 35% of the total benthic respiration on the southeasterly Rockall Bank area, which demonstrates that CWC reefs are important to carbon and nitrogen mineralization at the habitat scale.

Keywords: cold-water coral, biogeochemistry, benthic respiration, nitrogen cycling, carbon cycling

INTRODUCTION

Benthic solute exchange and carbon mineralization have been studied extensively in the past decades (e.g., Glud, 2008). However, the importance of reef structures, including cold-water corals (CWCs), for benthic carbon and nitrogen cycling is still poorly resolved. CWC reefs are topographically complex structures supporting high biomass and species richness of macro- and megafauna (Jonsson et al., 2004; Roberts et al., 2006). These CWC reefs can trap and mineralize large amounts of particulate organic matter (POM) and are presumed to act as carbon cycling hotspots (van Oevelen et al., 2009; Cathalot et al., 2015). However, quantification of mineralization rates remain few due to the complications of sampling and incubation intact CWC communities.

Most studies on the metabolism and nitrogen cycling of CWCs investigate individuals or nubbins of corals that are incubated *ex situ* in experimental chambers (Purser et al., 2010; Maier et al., 2011; Orejas et al., 2011). These approaches have concluded that CWCs act as a deep-sea source of dissolved inorganic nitrogen (DIN) as NH_4^+ and, presumably due to an active nitrifying community associated with the CWC microbiome, NO_3^- (Khripounoff et al., 2014; Middelburg et al., 2015). These observations hint at the presence of a dynamic nitrogen cycle on CWC reefs, especially given the identification of archaea in the microbial assemblage of CWCs (Van Bleijswijk et al., 2015). Assessments of community-based nitrogen fluxes in these habitats, however, have yet to be performed.

Upscaling results from laboratory incubations to the scale of CWC reefs is problematic given (i) the natural complexity and the spatial heterogeneity in faunal density and biomass distribution, and (ii) potential recovery/sampling effects on community performance. Only three quantitative studies on O_2 fluxes at CWC reefs have been conducted, and these were focused on relatively shallow CWC communities at ∼100–200 m depth (White et al., 2012; Cathalot et al., 2015; Rovelli et al., 2015). These studies have suggested that the organic carbon turnover at CWC reefs is enhanced compared to soft-sediment habitats at equivalent depths, but also show extensive variations in reef activity. The drivers of such variability are still poorly constrained, and it is currently unknown to what extent the resolved range can be extrapolated to other and deeper CWC reef communities.

Here, we combine two methodologies to quantify the O_2 and DIN flux of CWC reef communities, located in the North East Atlantic between 500 – 900 m depth. We used the non-invasive Aquatic Eddy Covariance (AEC) technique to quantify the *in situ* O_2 flux at CWC reef communities and *ex situ* whole-box core incubations to measure the O_2 and DIN flux of CWC reef communities and at a bare sediment reference site. Our primary aims are to (i) provide robust measurements of the O_2 flux of a CWC reef community, (ii) compare the invasive versus the non-invasive methodology (iii) provide a first estimate of DIN solute exchange of a CWC reef community and iv) quantify the importance of sediment, dead coral framework and living CWC in driving the whole CWC reef community O_2 and DIN flux.

MATERIALS AND METHODS

Study Site and Sampling

The Logachev mound province is located on the SE slope of Rockall Bank, approximately 500 km NW of Ireland (N 55.55, W 15.80, **Figure 1A**). In this area, coral mounds are present in a 90 km × 60 km area between 500 and 1000 m water depth (Kenyon et al., 2003; Mienis et al., 2006). The CWC communities on the mound consist of framework-building *Lophelia pertusa* and *Madrepora oculata* with associated macrofaunal such as polychaetes (e.g., *Eunice norvegica)*, sponges (e.g., *Hexadella dedritifera*), and crinoids (Van Weering et al., 2003; Van Soest and Lavaleye, 2005). Ambient bottom water temperatures on the coral mounds vary between 7–9°C. The area is characterized by high bottom current velocities, internal tidal waves and hydraulic jumps (Mohn et al., 2014; Van Haren et al., 2014; Cyr et al., 2016).

This study targeted three sites: the Haas mound, which is 360 m high and the largest carbonate mound in the region; the Oreo mound, a smaller carbonate mound SW of the Haas mound with the summit at 750 m water depth; and an off-mound bare sediment reference site at 500-m water depth further upslope Rockall Bank (**Figures 1B–D**; Mienis et al., 2006). Previous work on the Logachev mound province showed a large habitat heterogeneity on the CWC reefs; with patchy distribution of live coral, bare sediments and coral rubble on the summit of the Haas mound, and a dense thriving CWC reef on the southern flank of the Haas- and Oreo mound (Duineveld et al., 2007; de Haas et al., 2009; Van Bleijswijk et al., 2015).

During the R/V Pelagia research cruise 64PE420[1] (30/04/2017 to 07/05/2017), twelve box cores were collected along with two parallel deployments of the NIOZ ALBEX lander (Duineveld et al., 2004), equipped with the AEC system. To cover the above-mentioned habitat heterogeneity of the CWC reef communities in the region, AEC deployment and box core sampling was performed at the following sites (**Table 1**): (i) two box cores and one AEC deployment at the summit of the Haas mound, (ii) four box cores and no AEC deployment at Southern flank of the Haas mound, (iii) three box cores and one AEC deployment at the summit of the Oreo mound and (iv) three box cores at the bare sediment reference site (**Figures 1B–D**). Eight of the eleven box cores were used for the incubation experiments, while six were subsampled to characterize the surface sediment. **Table 1** provides an overview of the applied methodological approaches at the respective stations.

Aquatic Eddy Covariance (AEC) Technique

The AEC system consisted of an Acoustic Doppler Velocimeter (ADV Vector, Nortek, Norway), an underwater amplifier (see McGinnis et al., 2011) with two fast Clark-type O_2 microelectrodes and a dedicated battery canister allowing up to 5 days of continuous sampling at 64 Hz. The AEC system was mounted on a leg of the NIOZ ALBEX lander using a metal extension (**Figure 2**). This design ensured that the

[1] Cruise report doi: 10.5281/zenodo.1454465.

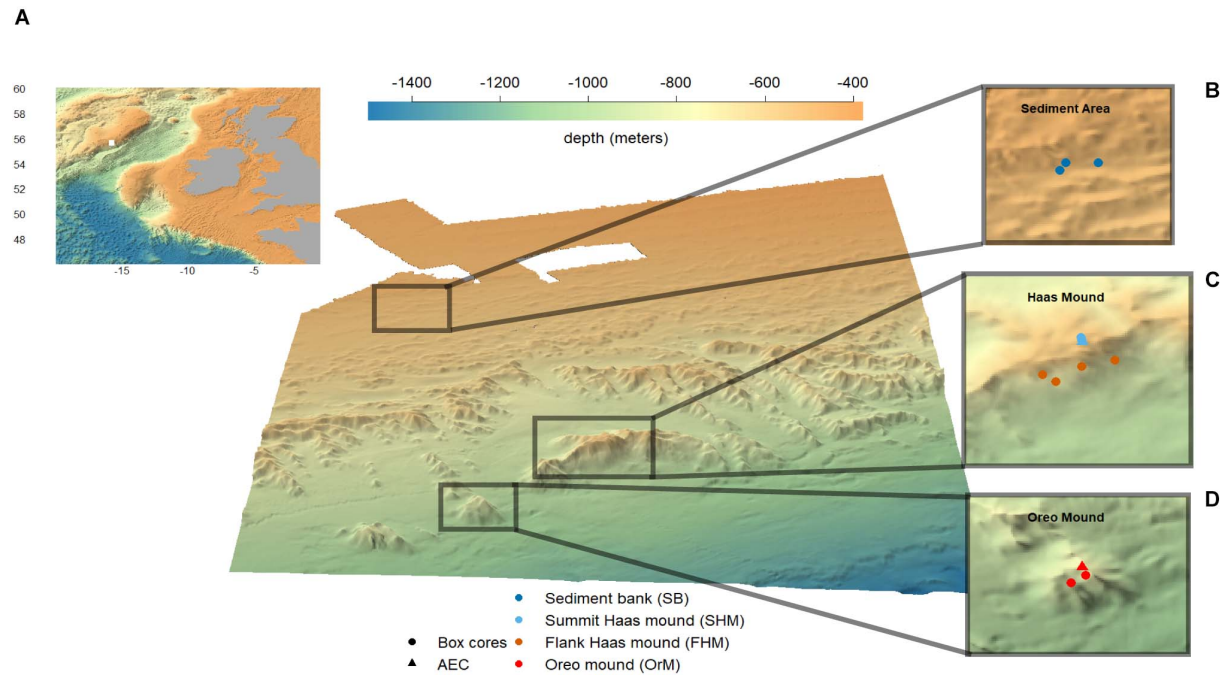


FIGURE 1 | Multibeam map of the Logachev mound province with as insets: **(A)** Location of Logachev mound province at the SE Rockall Bank, NE Atlantic (GEBCO, 2013), **(B)** sampling locations at the bare sediment reference site, **(C)** sampling locations at Haas mound, **(D)** sampling locations at Oreo mound. Plot produced with R package *plot3D* (Soetaert, 2017).

TABLE 1 | Station characteristics; date, depth, latitude, longitude, and applied methods.

Station	Date	Depth (m)	Latitude	Longitude	Method
SHM 1	30/04/2017	536	N 55° 29.71′	W 15° 47.98′	BC
SHM 2	30/04/2017	539	N 55° 29.74′	W 15° 47.99′	BC; SC
SHM 3	30/04/2017	536	N 55° 29.69′	W 15° 47.98′	AEC
FHM 1	04/05/2017	747	N 55° 29.16′	W 15° 48.30′	BC; SC
FHM 2	05/05/2017	639	N 55° 29.25′	W 15° 48.47′	BC
FHM 3	06/05/2017	616	N 55° 29.36′	W 15° 47.98′	SC
FHM 4	06/05/2017	719	N 55° 29.45′	W 15° 47.57′	SC
OrM 1	06/05/2017	838	N 55° 26.89′	W 15° 52.43′	BC; SC
OrM 2	07/05/2017	757	N 55° 27.01′	W 15° 52.22′	BC; SC
OrM 3	07/05/2017	744	N 55° 27.14′	W 15° 52.28′	AEC
SB 1	02/05/2017	495	N 55° 38.30′	W 15° 55.94′	BC; SC
SB 2	02/05/2017	501	N 55° 38.19′	W 15° 56.03′	BC; SC
SB 3	02/05/2017	503	N 55° 38.29′	W 15° 55.48′	SC

SHM, summit Haas mound; SB, sediment bank reference site; FHM, flank Haas mound; OrM, Oreo mound; BC, box core incubation; SC, sediment characteristics; AEC, aquatic eddy covariance technique.

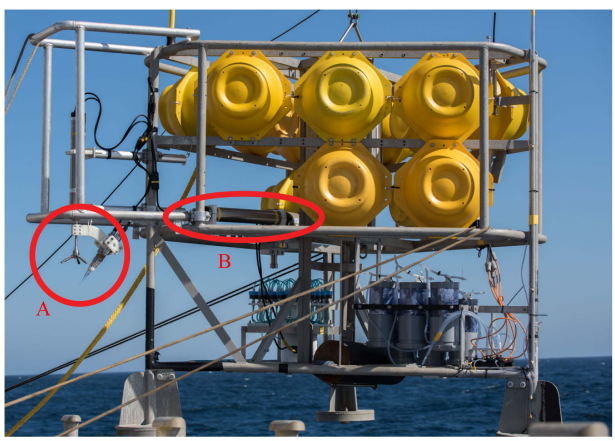


FIGURE 2 | The ALBEX lander (Duineveld et al., 2004) equipped with **(A)** the AEC instrument; **(B)** fluorescence sensor.

system was positioned 0.5 m outside the lander frame to minimize any potential flow disturbance by the frame itself. To protect the AEC system, an aluminum caging was mounted around the ADV (**Figure 2**). The ADV sampling volume was positioned at a measurement height (h) of 80 – 86 cm above the sea bed. This ensured that AEC measurements were performed well above large coral patches which could otherwise damage the sensors and lead to local disturbance of the flow field.

The O_2 and velocity time series were processed following established AEC protocols as outlined in detail in Attard et al. (2014) and Rovelli et al. (2015). Key steps included (i) sensor reading calibration, (ii) data averaging and despiking, (iii) rotation of the flow velocity coordinate system, (iv) computation of the turbulent fluctuations, (v) alignment of the O_2 and vertical velocity fluctuations, and (vi) quantification of O_2 fluxes. Raw

readings from the O_2 microelectrodes were *in situ* calibrated based on concurrent O_2 measurements from a factory-calibrated Rinko optical dissolved O_2 meter (JFE Advantech Co., Ltd., Japan). Each flow velocity time series was screened to identify periods where the ambient flow measured by the AEC had been disturbed by the lander frame and these were removed from subsequent processing. Turbulent fluctuations of O_2 and vertical velocity were obtained over a time interval of 5 min using linear detrending, which was found to be the most suitable for the given bottom roughness. Both fluctuation time series and O_2 fluxes were computed using the Fortran program suite Sulfide-Oxygen-Heat Flux Eddy Analysis (SOHFEA) version 2.0 (available from www.dfmcginnis.com/SOHFEA; McGinnis et al., 2014). To relate the O_2 flux rates to the respective benthic communities and their heterogeneity, the footprint area of the AEC was estimated for each deployment based on h and the bottom roughness length scale (z_0) (Berg et al., 2007). Mean values for z_0 were derived assuming Law-of-the-Wall as described in Inoue et al. (2011).

Box Core (BC) Incubations

Box cores (BCs) were taken from the reef framework and bare sediment with a NIOZ- designed box corer (**Figure 3A**). The BC consisted of a cylindrical barrel of 50 cm diameter and 55 cm height and sampled an area of 0.2 m^2. A camera was mounted on the BC and recorded the seafloor just before sampling. After collection, the cores, with reef community and bottom water, were sealed with plexiglass lids, placed in a temperature-controlled water reservoir to maintain *in situ* temperature, covered in black plastic sheets, and subsequently incubated after an acclimatization period of ∼2 h (**Figures 3A,B**). *In situ* temperatures were recorded by repeated CTD casts during the cruise. PreSens© O_2 and temperature sensors were installed in the lid, along with a magnetic stirrer (**Figure 3C**). The mixing efficiency of the stirring device was tested prior to the cruise by adding ∼10 ml of a uranine solution (1 g L^{-1}) to a BC with dead coral framework. Uranine fluorescence was measured with a Cyclops® seven fluorescence sensor (Turner Designs, Inc.) and revealed homogeneous mixing already after ∼3 min (data not shown). The BCs taken at the bare sediment reference site were subsampled with a 12 cm diameter- plexiglass incubation core, and incubated in a temperature-controlled room (8–10°C). The use of smaller subsampled incubation cores for bare sediment reference site was preferred since the porous marine sediment caused problems in closing the base of the large BCs during incubation.

In both procedures the O_2 concentration of the overlying water was measured continuously at 30 s intervals. The O_2 saturation did not drop by more than 20% of the start O_2 value during the incubation. Samples for DIN, i.e., NH_4^+, NO_3^- and NO_2^-, were taken in triplicate by 10 ml syringes through a sampling port in the lid at the start and at the end (∼24 h later) of each incubation. In six of the nine incubations a third intermittent measuring point was included. DIN samples were filtered through 0.45 μm cellulose membranes filters (Acrodisc® 25 mm filter, 0.45 μm HT Tuffryn® membrane) and frozen (−20°C) until analysis 8 weeks later in the laboratory at NIOZ. Sampled water was replaced by bottom water retrieved with the CTD rosette from the respective sampling station. After the incubation, the water was drained, and the living CWC and dead coral framework stored frozen (−20°C). Dead coral framework is here defined as dead coral branches with associated biofilm, epifauna and endofauna. A sediment sample of the top cm layer was taken by a plastic liner (i.d. 5 cm) for analysis of grain size and organic carbon and nitrogen content (**Figure 3C**). Due to large amounts of coral fragments in the sediment layer, it was not possible to sample the sediment of stations SHM 1 and FHM 2.

Concentration of DIN was measured using a SEAL QuAAtro analyzer (Bran + Luebbe, Norderstedt, Germany). Corals were freeze-dried, and dead coral framework was oven-dried at 55°C, to constant weight. Corals and dead coral framework were weighed (i.e., dry weight) and subsampled for organic carbon analysis. Subsamples (∼2 g, 3 per incubation) were ground and homogenized to fine powder using a ball mill at a 30 s^{-1} frequency (MM301, Retsch). About 20 mg of coral powder was subsampled into silver measuring cups, exposed to hydrochloric acid fume (HCl, 37%) for 3 days, and subsequently acidified with increasing levels of concentrated HCl (2, 5, and 30%) until all inorganic carbon was removed (Maier et al., 2019). Another set of tin cups was filled with ∼20 mg of coral powder for total organic nitrogen analysis and was not acidified. The acidified and non-acidified cups were pinch closed and, respectively, analyzed for total organic carbon and total organic nitrogen with an element analyzer (Thermo Electron Flash EA 1112 Analyzer). To determine the sediment grain size distribution, sediment samples were freeze-dried, sieved through a 2 mm mesh to remove small coral fragments, and analyzed by laser diffraction technique (Mastersizer 2000; Malvern Instruments Ltd., Malvern, United Kingdom; measurement range 0.02–2000 μm). In addition, ground sediment samples were analyzed for organic carbon and nitrogen content as described above.

Absolute O_2 concentrations were calculated with the *marelac* R package from the percent O_2 air saturation measured by the O_2 sensors (Weiss, 1970; Soetaert et al., 2016). The O_2 and DIN fluxes (mmol m^{-2} d^{-1}) were subsequently calculated from the slope of a linear regression fitted to the observed concentration change and corrected for box core volume and surface area (Glud, 2008). To unravel the contribution of living corals, dead coral framework and sediment to the total O_2 and DIN flux, we performed a planar regression of the observed benthic flux from the box core incubations against the predictor variables "living coral biomass" (kg dry weight m^{-2}) and "dead coral framework" (kg dry weight m^{-2}) ($n = 6$), of which the intercept is interpreted as sedimentary benthic flux. Specifically, we resolved the regression model: $flux = a \cdot CWC + b \cdot Framework + c$, in which *flux* is the measured flux of O_2 or DIN (mmol m^{-2} d^{-1}), a is the parameter representing the dry-mass-specific benthic flux for living corals (i.e., mmol kg DW^{-1} d^{-1}), *CWC* is the dry weight of living CWCs in the box core scaled up to m^{-2} (kg DW m^{-2}), b is the dry-mass-specific flux for dead coral framework (mmol kg DW^{-1} d^{-1}), *Framework* is the dead coral framework density (kg DW m^{-2}), and c is the sediment flux (mmol m^{-2} d^{-1}). Hence, we actually used the differences in the living coral biomass and dead coral framework in each box core to quantify the contribution of "living coral biomass", "dead coral

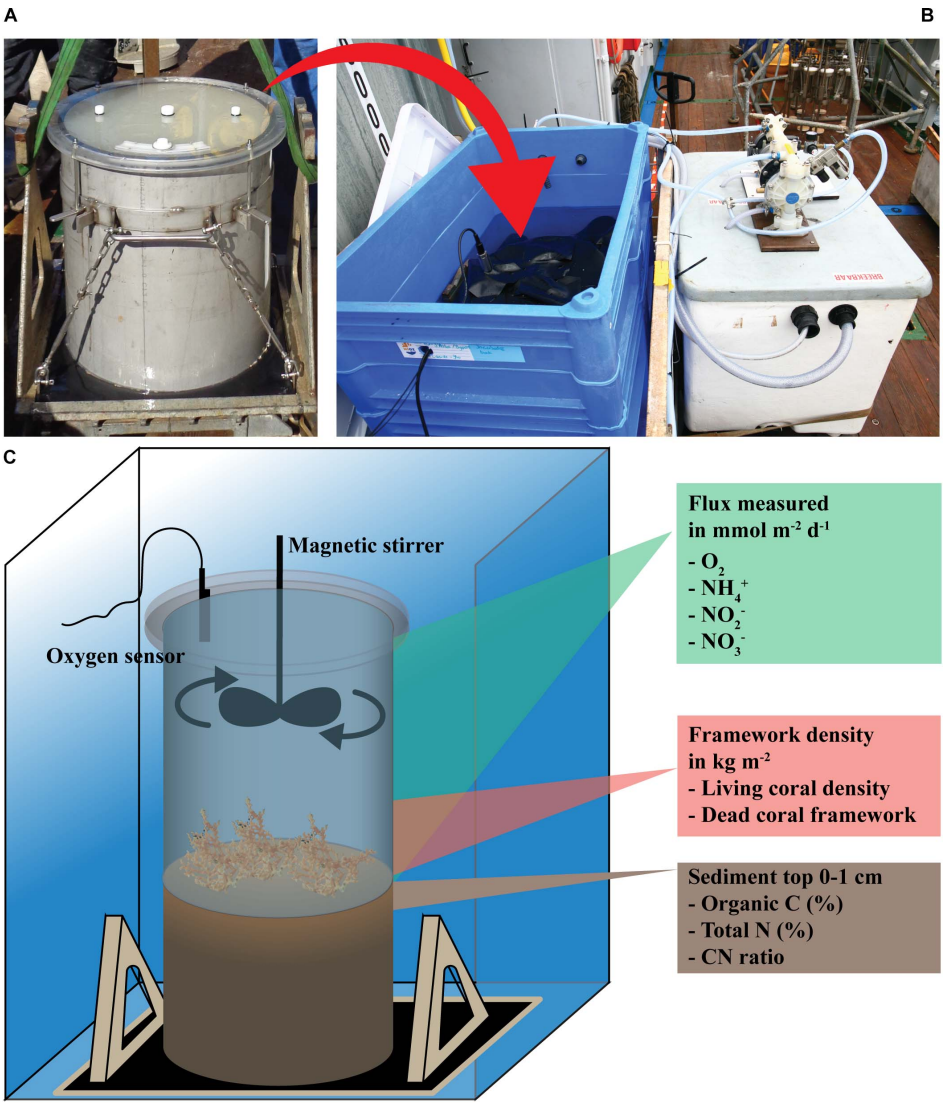


FIGURE 3 | (A) Box core after closure with lid, **(B)** incubation set-up, **(C)** schematic view of incubation set-up and measured variables.

framework" and "sediment" to the total flux in each incubation. All statistics were performed in the statistical software program R (R Development Core team, 2018). Plotting methodology mentioned in caption of the respectful plot.

RESULTS

Site Description

The bare sediment sites were characterized by a smooth surface with occasional drop stones (**Figure 4A**). In contrast, recordings at the summit of the Haas mound showed a patchy distribution of coral colonies, dead coral framework and bare sediment patches (**Figure 4B**). On the southern flank of the Haas and Oreo mounds, a thick framework of thriving coral reef was observed (**Figures 4C,D**).

Sediment Characteristics and Coral Density of Box Core Incubations

The surface sediment at the reference site was mainly composed of fine to medium sand (grain size between 63 – 630 μm), with a low organic matter content (i.e., 0.19% organic carbon and 0.03% organic nitrogen) (**Table 2**). Surface sediment on the coral mounds was substantially finer than at the reference site and was composed mainly of silt and very fine sand (grain size between 2–200 μm). Consistent with the finer particle sizes, the organic nitrogen and carbon content was higher on the mounds as compared to the reference site. The [molar] CN ratio of the sediments was similar among the four sampling sites (**Table 2**).

In all box cores used for incubations, the density of dead coral framework was substantially (on average 27 times) higher than the density of living coral (**Table 3**). Three scleractinian CWC

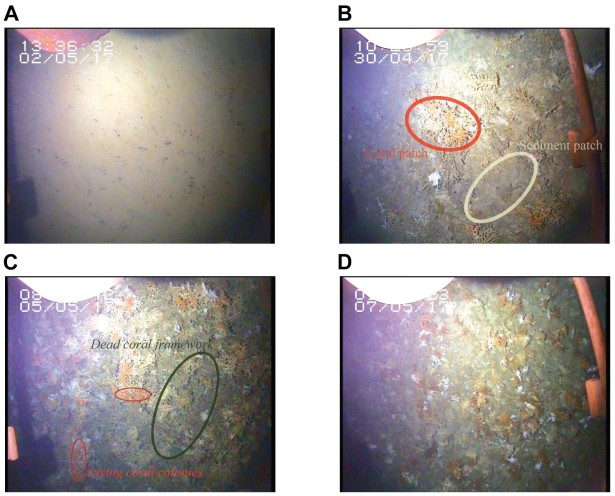


FIGURE 4 | Stills extracted from the video that was mounted on the boxcore displaying the four habitats sampled by box core. **(A)** Reference site on Rockall Bank, **(B)** the summit of Haas mound, note the patchy distribution of coral framework and sediment and **(C,D)** southern flank of Haas and Oreo mound, respectively, showing a thick layer of living coral and dead coral framework.

species were present in the six box cores: two colonial species of *Lophelia pertusa* and *Madrepora oculata*; and the solitary *Desmophyllum dianthus*. The organic carbon and nitrogen content of the dead coral framework was three to four times lower as compared to the living corals. The Haas mound summit showed the largest range of living coral density (0.01 – 3.31 kg DW m^{-2}). The Haas mound flank was characterized by a low living coral density (0.00 – 0.08 kg DW m^{-2}) and comparatively high dead framework (19.59 – 85.97 kg DW m^{-2}). On the Oreo mound, only living corals of the species *M. oculata* and small amounts of *D. dianthus* were found (0.45 – 0.98 kg and 0.01 – 0.05 kg DW m^{-2}, respectively). The amount of dead coral framework on the Oreo mound (5.00 to 9.54 kg DW m^{-2}) was comparable to that of the summit of the Haas mound.

O_2 Fluxes Measured by the AEC Technique

The two AEC deployments provided a total of 28 h and 41 h of unobstructed useful measurements, respectively. During the 28-h deployment on the summit of Haas mound (i.e., SHM3, **Table 1**), the lander was deployed diagonally to the main flow axis and the lander structure affected 25% of the measurements, which were therefore excluded from the analysis. Undisturbed flow velocities ranged between 0 and 23 cm s^{-1} (average 9.8 cm s^{-1}). The dominant flow direction changed during the deployment (**Figure 5A**), suggesting that the O_2 flux measured with the AEC technique is representative of different CWC community patches. This was confirmed by particle path analysis (data not shown), and by the fact that the cumulative flux analysis found distinctly different integrated O_2 fluxes [11.5 ± 3.6 (mean ± SE) and 22.35 ± 5.6 mmol m^{-2} d^{-1}, respectively] for the different footprints (**Figure 5B**). The site-representative bottom roughness length scale (z_0) was 3.1 cm for both AEC footprints.

The AEC deployment on top of Oreo mound (OrM 3, **Table 1**) revealed a strong directional flow with velocities ranging from 0.047 m s^{-1} up to 1.8 m s^{-1} (average 0.89 m s^{-1}). The lander structure affected 42% of the measurements, but the values obtained during unobstructed flow came from one distinct AEC footprint and gave an O2 flux of 45.3 ± 11.7 mmol m^{-2} d^{-1}. The site-representative z_0 was 5.1 cm, reflecting a rougher benthic surface than at the summit of Haas mound.

O_2 Fluxes Measured by BC Incubations

Temperature during the box core incubations ranged between 7.6 and 9.4°C, which corresponds well to the range of *in situ* water temperature (8.7 – 9.0°C). Leakage at the base of the box corer created an occasional air bubble under the lid of the core, and the ship movement caused the air bubble to mix with the incubation water, and induced periods of O_2 perturbation (**Figure 6**). When an air bubble was observed, it was eliminated by adding bottom water. The period during which the O_2 concentration was visually perturbed was omitted from the linear regression. After removal of the air bubble, the O_2 decreased continued in a comparable way to before the presence of the air bubble (**Figure 6**).

The O_2 flux at the reference sediment site ranged from 0.6 to 3.2 mmol O_2 m^{-2} d^{-1} (mean ± SD: 1.9 ± 1.4 mmol O_2 m^{-2} d^{-1}) (**Table 4**). The O_2 flux of the CWC reef communities ranged from 5.7 to 28.4 mmol O_2 m^{-2} d^{-1} (mean ± SD: 14.6 ± 8.4 mmol O_2 m^{-2} d^{-1}). The variability in CWC reef community O_2 flux was higher on the summit of the Haas mound than on the flank and at Oreo mound (Summit Haas = 17.0 ± 16.0 mmol O_2 m^{-2} d^{-1}, Flank Haas = 15.5 ± 6.9 mmol O_2 m^{-2} d^{-1}, Oreo = 11.2 ± 2.8 mmol O_2 m^{-2} d^{-1}) (**Table 4**).

Nitrogen Fluxes Measured by BC Incubations

During all incubations, the concentration and flux of NO_2^- were negligible, hence we present only the results for NH_4^+ and NO_3^-. The initial NH_4^+ concentrations ranged from 0.3

TABLE 2 | The sediment characteristics median grain size (μm), organic nitrogen content (%), organic carbon content (%) and molar C/N ratio.

	Sediments	Summit Haas	Flank Haas	Oreo mound
Median grain size (μm)	224.9 ± 28.8	41.6 ± –	62.8 ± 6.1	74.1 ± 17.4
Organic nitrogen	0.03 ± 0.00	0.09 ± –	0.06 ± 0.00	0.06 ± 0.00
Organic carbon	0.19 ± 0.01	0.51 ± –	0.32 ± 0.05	0.32 ± 0.06
C/N ratio	6.77 ± 0.71	6.26 ± –	6.08 ± 0.83	6.15 ± 0.77

Values are presented in mean ± SD, SD only if n > 1.

TABLE 3 | The density (kg dry weight m^{-2}), organic carbon content (%) and organic nitrogen content (%) of the living corals and dead coral framework for box core.

		Summit Haas mound		Flank Haas mound		Oreo mound	
		SHM 1	SHM 2	FHM 1	FHM 2	OrM 1	OrM 2
L. pertusa	Density	n.d.	3.31	0.05	n.d.	n.d.	n.d.
	Organic carbon	–	0.67 ± 0.09	0.34	–	–	–
	Organic nitrogen	–	0.17 ± 0.02	0.11	–	–	–
M. oculata	Density	0.01	0.09	0.01	n.d.	0.98	0.45
	Organic carbon	0.79	0.71 ± 0.08	*	–	1.43 ± 0.35	1.27 ± 0.18
	Organic nitrogen	0.19	0.19 ± 0.03	*	–	0.33 ± 0.08	0.31 ± 0.05
D. dianthus	Density	n.d.	n.d.	0.02	n.d.	0.01	0.05
	Organic carbon	–	–	1.14 ± 0.01	–	1.16	2.11
	Organic nitrogen	–	–	0.24 ± 0.01	–	0.25	0.41
Dead framework	Density	5.85	6.95	19.59	85.97	9.54	5.00
	Organic carbon	0.12 ± 0.04	0.19 ± 0.08	0.14 ± 0.01	0.14 ± 0.02	0.14 ± 0.01	0.22 ± 0.03
	Organic nitrogen	0.06 ± 0.01	0.08 ± 0.02	0.07 ± 0.02	0.07 ± 0	0.06 ± 0.01	0.09 ± 0.01

*mean ± SD, SD only if n > 1, n.d., not detected, *not measured due to technical error.*

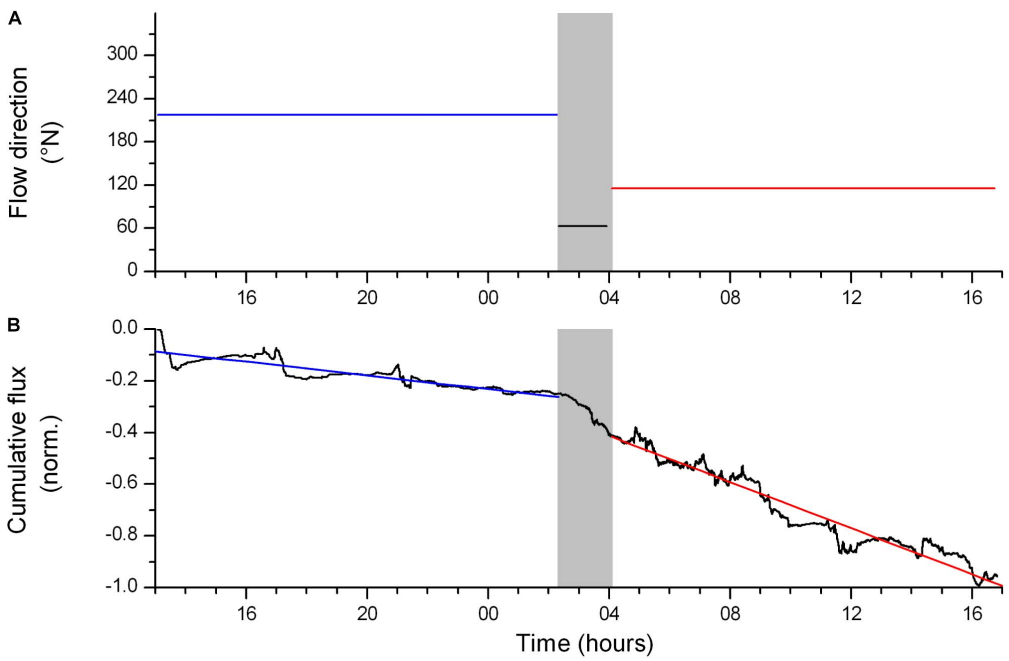


FIGURE 5 | (A) Dominant flow direction during the deployment at summit of Haas mound (i.e., SHM3), **(B)** normalized cumulative O_2 flux at summit of Haas mound (SHM3). Note that a linear change of the cumulative flux over time indicates stable conditions and thus well-developed fluxes. Linear sections (red and blue lines) indicate the main flux contributions from the two AEC footprints. The shaded time frame represents a transitional period in the flow direction which resulted in flow disturbances by the lander structure and overall unstable flux conditions. Deployment time is in hours after 30-Apr 00:00 UTC.

to 0.5 μmol L^{-1} while values at the end of incubation were between 0.3 and 2.0 μmol L^{-1} and NO_3^- concentrations during incubations increased from 10.0 – 17.0 μmol L^{-1} to 11 – 20 μmol L^{-1}. Due to the occasionally high variation within the triplicate samples, the calculated fluxes were not always significant (**Table 4**). However, the average DIN ($NO_3^- + NH_4^+$) flux of CWC reef communities (1.17 ± 0.87 mmol N m^{-2} d^{-1}) was around two times higher than that of bare sediment reference site (0.49 ± 0.32 mmol N m^{-2} d^{-1}). At the bare sediment reference site, NO_3^- fluxes were relatively more important than the NH_4^+ fluxes for the overall DIN flux. Generally, the DIN fluxes of box core incubations were mainly driven by NO_3^- except for incubations containing CWC colonies, in these cores the NH_4^+ fluxes were a significant part of the DIN fluxes.

Unraveling the Biogeochemical Fluxes

Planar regression of the box core O_2 fluxes against living coral and dead coral framework, with the intercept representing the

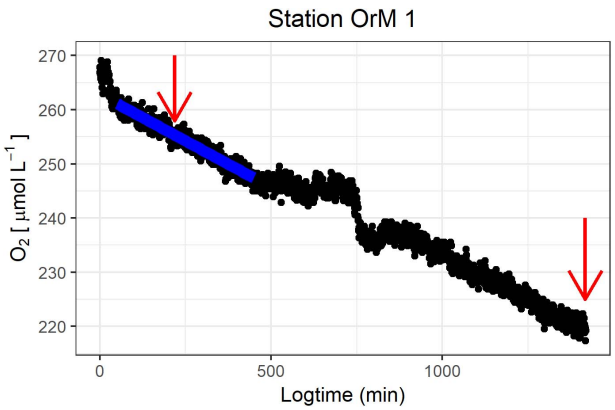


FIGURE 6 | Representative O_2 concentration series during a boxcore incubation (OrM 2), with the black dots representing the O_2 concentration ($\mu mol\ L^{-1}$) and the blue line the resulting linear regression which was used to calculate the O_2 flux. The red arrows indicate sampling of DIN. The disturbance caused by air bubble development is visible between minute 500 and 800. Plot produced with R package *ggplot2* (Wickham, 2016).

contribution of the sediment, showed a robust relation (R^2-adj: 0.99, **Figure 7** and **Table 5**), indicating that the dry-mass-specific O_2 flux of living coral is >30 times higher than that of the coral framework. For the NH_4^+ flux, living coral density was the only significant descriptor (R^2-adj = 0.94, **Table 5**) and contributions from the sediment and dead coral framework were non-significant. The NO_x flux was not significantly related to the amount of live or dead coral framework, and only the intercept (i.e., sediment activity) was significant. Note that the regression could only be based on the box core incubations, as data on the coral and dead coral framework density in the AEC footprint are lacking.

DISCUSSION

Constraining O_2 Exchange Rates at CWC Reefs

This study provides the first concurrent O_2 flux measurements from box core (BC) incubations and aquatic eddy-covariance (AEC) and contributes to the small database for O_2 fluxes of whole CWC reef communities (**Table 6**). The mean O_2 flux derived by AEC generally aligns well with the flux derived by chamber incubations for homogenous cohesive sediments in shallow water and deep sea settings (Berg et al., 2003, 2009; Glud et al., 2016). In complex benthic habitats such as permeable sand, maerl beds, reefs or megafauna enriched sediments, the O_2 exchange obtained by the two approaches often diverges (Glud et al., 2010; Attard et al., 2014, 2016). This discrepancy has been ascribed to mesoscale heterogeneity that might be poorly represented during chamber deployments, or to changes of flow characteristics or food availability during chamber enclosure (Attard et al., 2015). However, deep water AEC deployments in complex habitats such as CWC reefs come with logistical challenges and often require access to a work-class remotely operated vehicle for accurate positioning (Rovelli et al., 2015), which limits the applicability of the approach. Moreover, in dynamic settings such as CWC reefs, the AEC approach requires a relatively long deployment time of 12 – 24 h to integrate the inherent short-term variations associated to changes in flow direction and velocity (Holtappels et al., 2013; Glud et al., 2016).

Our study measured the O_2 flux at sites that visually differed in their density of living coral and dead coral framework. While the BC incubations showed no site differences, the regression analysis showed that two variables, namely the quantity of living coral and dead coral framework, explained most variability in

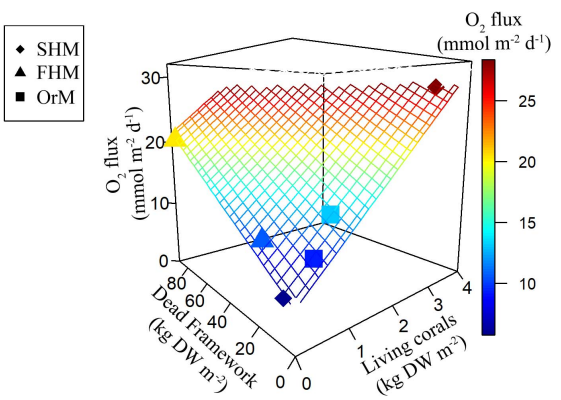


FIGURE 7 | Planar regression of the O_2 flux (mmol m^{-2} d^{-1}) against the predictor variables living coral density (kg dry weight m^{-2}) and dead coral framework density (kg dry weight m^{-2}), of which the intercept is interpreted as sedimentary O_2 flux. The six incubated boxcores are plotted as individual datapoints and plane represents results of the regression model. Note that the symbols in the plot are shape according to their location (see legend) and colored according to the observed O_2 flux. Plot produced with R package *plot3D* (Soetaert, 2017).

TABLE 4 | Benthic O_2 and DIN fluxes measured from the BC incubation experiments expressed in mmol m^{-2} d^{-1}.

	Summit Haas		Flank Haas		Oreo mound		Sediment		
	SHM 1	**SHM 2**	**FHM 1**	**FHM 2**	**OrM 1**	**OrM 2**	**SB 1**	**SB 2A**	**SB 2B**
O_2	**5.7 ± 0.3**	**28.4 ± 2.4**	**10.7 ± 0.9**	**20.5 ± 0.8**	**13.1 ± 0.7**	**9.2 ± 1.2**	**3.2 ± 0.0**	**1.9 ± 0.0**	**0.6 ± 0.0**
NH_4^+	0.02 ± 0.02	**0.98 ± 0.16**	0.16 ± 0.10	0.00 ± 0.02	**0.22 ± 0.02**	**0.06 ± 0.02**	0.01 ± 0.06	−0.11 ± 0.10	−0.02 ± 0.02
NO_3	**0.93 ± 0.09**	**2.04 ± 0.30**	**1.12 ± 0.10**	**0.54 ± 0.05**	**0.58 ± 0.09**	**0.38 ± 0.08**	**0.15 ± 0.04**	**1.04 ± 0.23**	0.40 ± 0.22

Values are reported as flux ± SD, values in bold are significant fluxes ($p < 0.05$).

TABLE 5 | Planar regression of the benthic flux, i.e., *flux = a · CWC + b · Framework + c* (n = 6), with *a,* "Living coral" rate, *b,* "Dead coral framework" rate and *c*, "Sediment" rate.

	Living coral (mmol kg^{-1} DW d^{-1})	Dead coral framework (mmol kg^{-1} DW d^{-1})	Sediment (mmol m^{-2} d^{-1})	Model fit (R_2 – adj)
O_2	**6.39 ± 0.32**	**0.18 ± 0.01**	**5.32 ± 0.59**	0.99
NH_4	**0.28 ± 0.03**	0.00 ± 0.00	0.01 ± 0.06	0.93
NO_3	0.36 ± 0.17	0.00 ± 0.01	0.64 ± 0.32	0.37

Significant model parameters are highlighted in bold.

TABLE 6 | Overview of O_2 fluxes (mmol m^{-2} d^{-1}) of CWC communities based on various methods.

Site	Depth (m)	O_2 flux	Method	SCOC[a]	References
Summit Haas mound, Rockall Bank	539	17.0[b]	AEC	2.7/7.1	this study
	536 – 539	17.0 ± 16.0	BC		
Flank Haas mound, Rockall Bank	639 – 747	15.5 ± 6.9	BC	2.1/6.4	this study
Oreo mound, Rockall Bank	744	45.3 ± 11.7	AEC	2.1/6.4	this study
	757 – 838	11.2 ± 2.8	BC		
Mingulay reef complex (Scotland)	128	27.8 ± 2.3	AEC	7.8/9.2	Rovelli et al., 2015
Stjernsund (Norway)	220	24.8 ± 2.6	AEC	5.2/6.4	Rovelli et al., 2015
Traena marine protected area (Norway)	280	121.5 ± 9.9[c]	AEC	4.2/5.8	Cathalot et al., 2015
	280	81.7 ± 9.8	*In situ* incubation and upscaling		
Guilvinec & croisic canyons (France)	850	7.7	*In situ* incubation and upscaling	1.9/4.4	Khripounoff et al., 2014
Tisler reef (Norway)	102 – 150	37.1	Water retention time combined with O_2 change	7.9/9.6	White et al., 2012

For comparison, mean sediment community oxygen consumption (SCOC) for soft sediments for the respective depth is provided from published regressions. [a]Global regression of O_2 flux for soft sediment at comparable depths after Glud (2008) and Andersson et al. (2004). Note that Glud (2008) only included O_2 fluxes obtained in situ, while Andersson et al. (2004) included both in situ and ex situ data. [b]Average of two AEC footprints, 22.4 ± 5.6 and 11.5 ± 3.6 mmol m^{-2} d^{-1}, respectively. [c]Based on two short AEC deployments of 2 h each.

the O_2 flux at all three investigated coral sites. The congruence of the O_2 fluxes by the AEC and BC method for the summit of Haas mound, which showed a patchy distribution of living corals and bare sediment, suggests that the habitat variability of the ∼500 m^2 large AEC footprint was reasonably represented by the replicate ∼0.2 m^2 large BC incubations. In contrast, at the deeper (∼750 m) Oreo mound we encountered a higher near-bottom flow velocity, and the average O_2 flux derived by the AEC technique was four times higher than that obtained with the BC incubations. Data on the density of living coral and dead framework in the AEC footprint is unfortunately not available, so it remains difficult to judge what caused the high AEC O_2 flux at Oreo mound. As the AEC data from Oreo mound were of high quality and represented a large footprint (∼500 m^2), we believe that the AEC value presumably provides the more robust O_2 flux estimate on a CWC community scale and that the two box core incubations poorly represented the natural habitat variability or compromised the natural flow conditions. It should also be noted, that a higher O_2 flux at Oreo mound was *a priori* anticipated given the higher coral density previously observed on video transects and on the boxcore videos (**Figures 4B–D**).

The measured O_2 fluxes of the summit of Haas mound compare well with those reported for the shallower CWC communities at the Mingulay Reef Complex and Stjernsund (Norwegian glacial sound) (Rovelli et al., 2015). The AEC-based O_2 flux at Oreo mound is, however, ∼3 times higher, which underlines the large spatial metabolic variability that may exist between mounds of the same mound province. The highest O_2 flux reported for CWC reefs was reported for a "cigar-shaped" reef at the Traena marine protected area in Norway (Cathalot et al., 2015). That O_2 flux, however, is representative for the head section of these reefs, which are known for having a very dense cover of live *Lophelia pertusa* (Cathalot et al., 2015) and this may not be directly comparable to the other CWC mounds. Furthermore, the measurements at the Traena marine protected area were based on a short measuring period of a few hours (∼2 h) and may thus not fully represent average flux conditions at the measuring site. Excluding that value, the available AEC-based O_2 uptake rates of CWC communities converge toward 28.7 mmol m^{-2} d^{-1}, which is a factor of 5 higher than the O_2 uptake for soft bottom systems at similar depths (Andersson et al., 2004; Glud, 2008).

The dry-mass-specific O_2 flux for living corals (inferred from planar regression model) of 6.39 ± 0.32 mmol O_2 kg^{-1} DW d^{-1} compares well with O_2 fluxes measured for *L. pertusa* or *M. oculata* obtained during laboratory incubations (Dodds et al., 2007; Larsson et al., 2013; Khripounoff et al., 2014), suggesting limited disturbance induced by the sampling. The coral framework consists of eroding dead branches that provide a substrate for biofilm, consisting of microbial biomass, and sessile and mobile fauna. Fauna encountered in the box cores (data not shown) belonged to the classes/phyla: Echinoidea, Polychaeta, Porifera, Crustacea, Actiniaria, which also previously have been identified as dominant in NE Atlantic CWC communities (e.g., Duineveld et al., 2007;

Henry and Roberts, 2007). The inferred dry-mass-specific O_2 flux for dead coral framework (0.2 mmol O_2 kg^{-1} DW d^{-1}) was more than 30 times lower than the flux for living corals. However, as all box cores contained substantially more framework than living corals, especially at the southern flank of the Haas mound, the framework still contributed significantly, ranging from 10 to 75% of the total benthic O_2 flux.

The organic carbon content (∼0.35%) and median grain size (∼ 63 μm) of sediment on the coral mounds is in line with previous work in the same area (Mienis et al., 2009a,b), while being slightly lower than found in sediments underneath a CWC reef in Norway (Wehrmann et al., 2009). The dominance of fine and comparatively organic-rich sediment below the CWC framework is presumably caused by baffling of the water flow by the coral branches that leads to the accumulation of fine sediment particles between the coral framework (Dorschel et al., 2005; de Haas et al., 2009). Mienis et al. (2019) recently showed with a laboratory flume study that the current velocity was strongly reduced within and behind (i.e., wake effect) coral framework patches, inducing the settlement of inorganic and organic particles. In addition, the enhanced trapping of suspended organic matter by the filter-feeding faunal community, and subsequent deposition as (pseudo)feces, may additionally enrich the organic carbon concentration on coral mounds (Maier et al., in review). The reference site in contrast, lacks the baffling effect of the framework and (most of) the filter-feeding activity, which leaves a coarser sediment with lower organic carbon content.

To date, little is known on O_2 flux mediated by the sediment underneath a CWC reef. Microbially mediated processes are presumably more active in sediment underlying a CWC reef as compared to bare sediments (Wehrmann et al., 2009). Our findings support this idea in two ways. Firstly, the sediment on the coral mounds consists of finer and more organically rich material than the reference site, likely due to the baffling effect of the coral framework discussed above, suggesting that mineralization will be higher. Secondly, from the planar regression we inferred an O_2 flux of 5.3 mmol m^{-2} d^{-1} for the sediment underlying the coral framework, which is indeed a factor ∼3 higher than the average O_2 flux measured at reference site. The O_2 flux of the CWC-sediment inferred in this study is substantially lower than the O_2 flux of 33.2 ± 10 mmol m^{-2} d^{-1} (mean ± SD) that was measured in a food web model of the CWC community at Rockall Bank (van Oevelen et al., 2009). This might reflect a true difference among sites, but in addition to spatial and temporal variability, methodological differences may contribute to this difference, as the latter authors measured the O_2 flux in a core that was taken from a box core after the overlying coral and dead framework was removed.

Cold-water coral reef communities appear to be hotspots of carbon mineralization on the seafloor. A habitat suitability model suggest a CWC habitat cover of 4.7% for the Logachev mound province (areal extent of 60 × 90 km) (Rengstorf et al., 2014). Assuming the remaining 95.3% in the area consists of soft-sediments, we can calculate the benthic soft-sediment respiration with the depth-dependent power equation developed by Glud (2008). Using the median CWC community O_2 uptake rate obtained from the BC incubations (11.9 mmol O_2 m^{-2} d^{-1}), and the AEC technique (24.8 mmol O_2 m^{-2} d^{-1}), we estimate that CWC reefs are responsible for 20 to 35% of the total benthic respiration in the Logachev mound province, depending on which median O_2 uptake rate is used. This percentage is in line with calculations of the relative importance of CWC reefs in benthic OM cycling on the Norwegian Margin (36% of total benthic respiration; Cathalot et al., 2015) and indicates that the CWC mounds in the Logachev mound province play an important role in regional carbon cycling.

Nitrogen Fluxes of a CWC Reef Community

The present study reports the first nitrogen flux measurements of intact CWC communities and allows a comparison with sediment communities. The nitrogen fluxes measured from the bare sediment reference site incubations showed a variable release of NO_3^- into the overlying water and negligible NH_4^+ efflux. This pattern is consistent with many earlier studies on nitrogen cycling in deep water, aerobic sediments, which have shown that NH_4^+ produced by organic matter mineralization generally is oxidized by different nitrifying microorganisms to NO_2^- and subsequently to NO_3^- which diffuses out of the sediment (Thamdrup and Dalsgaard, 2008; Libes, 2009).

The inorganic nitrogen fluxes from the incubations including a CWC reef community are markedly different. Firstly, the 2.4 times higher NO_3^- efflux by the CWC reef community, compared to the sediment, is consistent with its higher O_2 flux/consumption. The significant production of NH_4^+ by the CWC reef community indicates that the NH_4^+ typically produced by the reef fauna (Wright, 1995), like sponges (Hoffmann et al., 2009; Leys et al., 2017) and *Lophelia pertusa* (Middelburg et al., 2015), is only partly nitrified, presumably by reef-associated micro-organisms including archaea (Van Bleijswijk et al., 2015). CWC reef communities, in contrast to soft sediment communities, hence increase the NH_4^+ concentration of the bottom water. This modification of the nitrogen cycle by CWC reef communities is consistent with the observations of elevated NH_4^+ concentrations in the water column above the CWC mounds at Rockall Bank (Findlay et al., 2014).

The inferred dry-mass-specific NH_4^+ release rate for living corals in our study (0.29 ± 0.03 mmol NH_4^+ kg^{-1} DW d^{-1}) compares favorably with the reported *in situ* values and *ex situ* rates of 0.10 – 0.40 mmol NH_4^+ kg^{-1} DW d^{-1} (Khripounoff et al., 2014; Middelburg et al., 2015; Maier et al., 2019). Our results also show that the living CWCs are primarily responsible for the observed NH_4^+ release, as the dry-mass-specific dead coral framework DIN fluxes are found to be negligible. This is consistent with the planar regression of the O_2 flux data, which showed that the dry-mass-specific O_2 flux of living corals is >30 times higher than that of dead coral framework.

CONCLUSION

In conclusion, we show that the O_2 flux of CWC reef communities in the North-East Atlantic Ocean is on average ∼5 times higher than that of soft sediments from comparable depths. This implies that also deep CWC reefs, in addition to earlier findings for relatively shallow (<200 m depth) CWC reefs, are hotspots of carbon cycling on continental margins. Moreover, despite a dominance of dead coral framework in the reef community, the living CWCs appeared to be the major driver of this high O_2 flux. The first CWC reef community-based DIN fluxes to-date show that the CWC reef community, specifically the living CWCs, alter benthic nitrogen cycling compared to bare sediment, by largely circumventing nitrification and releasing NH_4^+ directly into the ambient water. This implies that CWC reefs are not only hotspot of carbon cycling, but are also hotspots of nitrogen cycling.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

DO, GD, FM, ML, LR, and RG designed the study. DO, GD, FM, and LR coordinated the lander deployment and box core sampling. EF and SM ran the on-board incubations and processed samples. All authors contributed to the data analysis and writing of the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Ocean Circulation Over North Atlantic Underwater Features in the Path of the Mediterranean Outflow Water: The Ormonde and Formigas Seamounts, and the Gazul Mud Volcano

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Seamounts constitute an obstacle to the ocean circulation, modifying it. As a result, a variety of hydrodynamical processes and phenomena may take place over seamounts, among others, flow intensification, current deflection, upwelling, Taylor caps, and internal waves. These oceanographic effects may turn seamounts into very productive ecosystems with high species diversity, and in some cases, are densely populated by benthic organisms, such corals, gorgonians, and sponges. In this study, we describe the oceanographic conditions over seamounts and other underwater features in the path of the Mediterranean Outflow Water (MOW), where populations of benthic suspensions feeders have been observed. Using CTD, LADPC and biochemical measurements carried out in the Ormonde and Formigas seamounts and the Gazul mud volcano (Northeast Atlantic), we show that Taylor caps were not observed in any of the sampled features. However, we point out that the relatively high values of the Brunt–Väisälä frequency in the MOW halocline, in conjunction with the slope of the seamount flanks, set up conditions for the breakout of internal waves and amplification of the currents. This may enhance the vertical mixing, resuspending the organic material deposited on the seafloor and, therefore, increasing the food availability for the communities dominated by benthic suspension feeders. Thus, we hypothesize that internal waves could be improving the conditions for benthic suspension feeders to grow on the slope of seamounts.

Keywords: seamounts, Mediterranean Outflow Water, Taylor columns/caps, internal waves, cold-water corals

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INTRODUCTION

According to the Staudigel et al. (2010) definition, seamounts are any geographically isolated topographic feature taller than 100 m. Either forming clusters or alone, seamounts constitute an obstacle to the free ocean flow, modifying the pattern of circulation not only locally but also globally (Lavelle and Mohn, 2010). As a result of these alterations, a variety of hydrodynamical processes and phenomena, such as flow intensification, current deflection, upwelling, turbulence, trapped waves, jets, Taylor caps, or internal waves, can take place (Noble and Mullineaux, 1989; Eriksen, 1991; Roden, 1991; Dower et al., 1992; Beckmann and Mohn, 2002; Mohn and Beckmann, 2002; Coelho and Santos, 2003). Besides, seamounts play an important role in the generation, breakdown, and even trapping of eddies (Royer, 1978; Roden, 1986; Bashmachnikov et al., 2009; Sokolovskiy et al., 2013).

These oceanographic processes induced by the topography may provoke the enhancement of the primary production and retention of plankton (Xavier and van Soest, 2007; Denda et al., 2016), turning seamounts into ecosystems with high biomass, biodiversity and sometimes with a considerable level of endemism (Boehlert and Genin, 1987; Beckmann and Mohn, 2002; O'Hara, 2007; Pitcher et al., 2007; Clark et al., 2010; Miller and Gunasekera, 2017), which offer particularly good conditions for the settlement of benthic suspension feeders like corals and sponges (Koslow et al., 2001; Xavier and van Soest, 2007; O'Hara et al., 2008). Cold-water corals (CWC) have been described along the path of the Mediterranean Outflow Water (MOW) in several locations: at the Gazul mud volcano (Rueda et al., 2016), the Galicia Bank (e.g., Duineveld et al., 2004; Serrano et al., 2017), and the Porcupine Seabight (De Mol et al., 2002), among others.

The MOW is an intermediate water mass, salty, and warm, found between 800 and 1,500 m depth (Daniault et al., 1994). It is formed when the dense Mediterranean water reaches the Gulf of Cadiz through the Strait of Gibraltar and mixes with the lighter Atlantic water flowing over, forming a less salty water mass (Bozec et al., 2011). After leaving the Gulf of Cadiz, around Cape St. Vincent, the MOW spreads in two directions: northwards, following the continental slopes of the Iberian Peninsula, and westwards, to the central-North Atlantic (Iorga and Lozier, 1999).

Some studies have suggested a possible Mediterranean origin for CWC in the pathway of the MOW through the eastern Atlantic (De Mol et al., 2005; Henry et al., 2014), supported by the stepping stone role largely attributed to seamounts (Brenke, 2002; Gubbay, 2003; Samadi et al., 2006; O'Hara, 2007). However, in spite of the importance of those seafloor elevations for the spread and settlement of CWC and other benthic organisms (Koslow et al., 2001; Brenke, 2002; Gubbay, 2003; Samadi et al., 2006; O'Hara, 2007), there are few studies addressing the ocean circulation and hydrographic conditions over seamounts in the pathway of the MOW.

In this paper, we investigate the role of the hydrographic conditions over several underwater features in the pathway of the MOW to determine the dynamics that likely boost the settlement of benthic suspension feeders in these areas. Specifically, we address whether the well-known Taylor caps are the phenomenon governing the dynamics of the Ormonde and Formigas seamounts and the Gazul mud volcano (**Figure 1**). We also address the importance of the water mass distribution in establishing the dynamical conditions on the slope of these features. We hypothesize that the presence of the MOW lead to relatively high values of the Brunt–Väisälä frequency in its halocline, which, together with the steep slope, will set up conditions for the breakout of internal waves and the amplification of currents at the bottom, favoring the presence of benthic suspension feeders near the seabed.

This paper is organized as follows: the section "Materials and Methods" describes the data acquisition and processing methodology. The section "Results" presents the results of the dynamics and hydrography of each region of study. Lastly, section "Summary and Discussion" summarizes and briefly discusses the results obtained.

MATERIALS AND METHODS

Area of Study

Following the path of the MOW through the eastern Atlantic, three seafloor elevated features, where CWC have been described (WWF, 2004; Oceana, 2005; Rueda et al., 2016), were selected as target regions for this study: the Gazul mud volcano and the Ormonde and Formigas seamounts (**Figure 1**). Both Gazul and Ormonde are directly in the pathway of the MOW after it outflows through the Strait of Gibraltar, while Formigas, located further away in the middle of the Atlantic, is influenced by the westward branch of the MOW (Bashmachnikov et al., 2015).

The Gazul mud volcano is located in the continental slope of the Gulf of Cadiz (Palomino et al., 2015). Gazul is sculpted by the MOW, which has carved two downstream depressions at both sides of the structure, whereas its rear sector has a peculiar saddle shape as result of the low velocities that enable sedimentation (Rueda et al., 2012; Palomino et al., 2016). The Ormonde seamount forms part of the Gorringe Bank at around 125–150 miles west-southwest of Cape St. Vincent. It presents a steep southeastern flank with gullies and incipient canyons and a northwestern flank without remarkable incised features. At the southwestern, it is separated of the Gettysburg seamount by a passage of a maximum depth of 800 m. The Formigas seamount is at the southeastern part of the Azores. Its western section is occupied by a 1,800 m depth flat abyssal plain, with a few of incipient gullies, and at the northeastern side, around twenty knolls are spread on an area of 130 km^2.

Data

In order to characterize hydrographically and dynamically the Gazul mud volcano and the Ormonde and Formigas seamounts, both climatological and *in situ* field data were used. The climatological data include mean annual temperature, near-surface current velocities, mean winds and Sea Surface Temperature. The mean annual temperature was obtained from the Roemmich-Gilson Argo Climatology, generated using Argo temperature and salinity data interpolated with a weighted

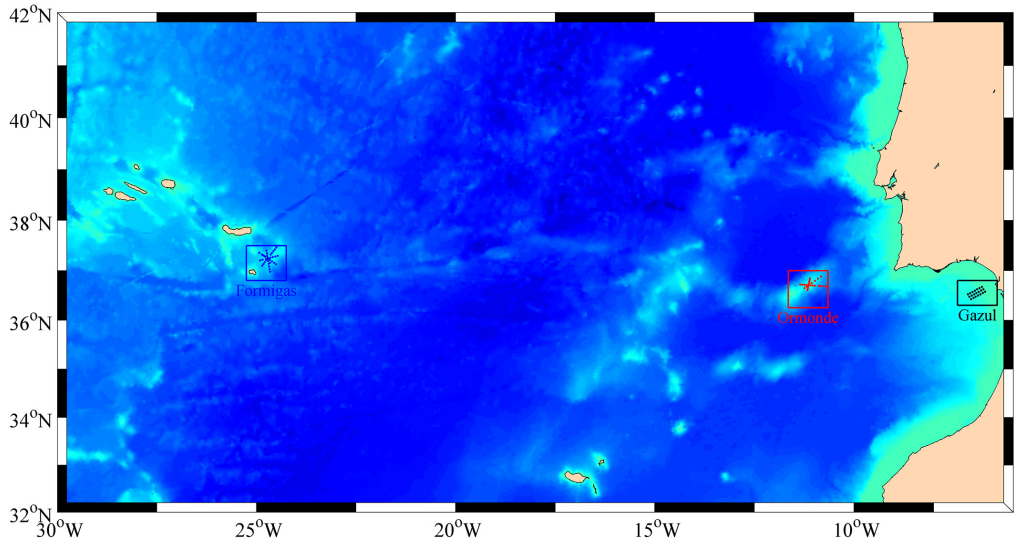


FIGURE 1 | Distribution of the stations for the three regions of the MEDWAVES Atlas Cruise contemplated in this study: the Formigas (in blue) and Ormonde (in red) seamounts, and the Gazul mud volcano (in black).

least-squares fit, as described in Roemmich and Gilson (2009). The near-surface current velocities were derived by the NOAA Atlantic Oceanographic and Meteorological Laboratory using observations from surface drifting buoy observations (Lumpkin and Johnson, 2013), and the mean wind and Sea Surface Temperature data were produced by the NOAA Earth System Research Laboratory. Sea Surface Temperature was obtained from the daily High-Resolution-Blended satellite Analyses product (Reynolds et al., 2007). The mean wind, interpolated using a wide range of observing systems, was obtained from the International Comprehensive Ocean-Atmosphere Data (ICOADS). A more detailed description of the datasets used can be found in **Table 1**.

Data from the TPXO7.2 model was used to describe the barotropic tidal regime in each of the regions of study. This model uses a generalized inverse method, which assimilates altimeter data to predict tide height and currents (Egbert and Erofeeva, 2002).

The *in situ* field data were gathered during the MEDWAVES cruise carried out between the 21st of September and the 25th of October 2016, on board the RV Sarmiento de Gamboa, as part of the H2020 ATLAS Project. In each of the three features (**Figure 1**) a specifically designated sampling grid was carried out. In the Gazul mud volcano, located in the continental slope of the Gulf of Cadiz, three hydrographic sections, perpendicular to the flow, were carried out, with 21 hydrographic stations in total. In the Ormonde seamount, which is part of the Gorringe Bank, 25 hydrographic stations were carried out in a radial grid perpendicular to the bathymetry. In the Formigas seamount, southeastern of the Azores, 41 hydrographic stations were carried out in a radial grid perpendicular to the bathymetry.

In each station, conductivity, temperature, oxygen concentration, and pressure were measured with redundant temperature and salinity sensors from a Seabird 9111 CTD. Additionally, at each hydrographic station, velocity data were acquired from a Lowered Acoustic Doppler Current Profilers (LADCP) system composed of a dual 300 kHz LADCP. The LADCP data were processed according to Fischer and Visbeck (1993). LADCP data were used to estimate the velocity in the assumed layer of no-motion by comparing the LADCP with the geostrophic velocity profile at each station as indicated in Comas-Rodríguez et al. (2010). The data were acquired at each station from the surface down to 10 m above the bottom. Distance intervals between stations were approximately 5 km to resolve mesoscale. Temperature and pressure sensors were calibrated at the SeaBird laboratory before the cruise. On board salinity calibration was carried out with a Guildline Autosal model 8400B salinometer with a precision better than 0.002 for single samples.

In addition, a total of 17 video transects were also recorded in the three target features using the ROV Liropus. Positioning of the ROV was achieved using the HYPACK software. The ROV was equipped with a HD color zoom video camera illuminated by Sealite Spheres, an underwater photo still camera and a pair of parallel laser pointers mounted 10 cm apart (see specifications in Orejas et al., 2017). A set of geo-referenced still images extracted from the ROV video transects at 5 m intervals was used to characterize the benthic communities. To allow comparison between the different features, only those images within 1.5–2.5 m width range were retained for analyses. Low quality images that prevented from fauna identification were also excluded. Benthic organisms larger than 5 cm were identified to the lowest possible taxonomic level and the abundances were aggregated for total invertebrates and the phyla Porifera and Cnidaria. The Formigas seamount is the largest of the studied features, hence surrounded by several water masses, and also covers a large depth range (from 500 to 1,500 m depth). That makes this feature the most suitable one to study the influence of different water

TABLE 1 | Climatological data.

Data	**Argo temperature climatology**
Source	Scripps Institution of Oceanography: http://sio-argo.ucsd.edu/RG_Climatology.html
Time period	From 2004 to 2014
Spatial coverage	1/6 × 1/6 degree
Measurements	Mean temperature (degree Celsius)
References	Roemmich and Gilson, 2009
Data	**Annual means of drifter data**
Source	NOAA/AOML and NOAA/PMEL: http://www.aoml.noaa.gov/phod/dac/dac_meanvel.php
Time period	From 1979 to 2015
Spatial coverage	1/2 × 1/2 degree
Measurements	Zonal and meridional current velocity coefficients (m/s)
References	Lumpkin and Johnson, 2013
Data	**Climatological monthly means of drifter data**
Source	NOAA/AOML and NOAA/PMEL: http://www.aoml.noaa.gov/phod/dac/dac_meanvel.php
Time period	From 1979 to 2015
Spatial coverage	1/2 × 1/2 degree
Measurements	Zonal and meridional current velocities (m/s)
References	Lumpkin and Johnson, 2013
Data	**NOAA High Resolution SST Data**
Source	NOAA/OAR/ESRL PSD: http://www.esrl.noaa.gov/psd/
Time period	From 1981 to 2017
Spatial coverage	1/4 × 1/4 degree
Measurements	Daily mean Sea Surface Temperature (degree Celsius)
References	Reynolds et al., 2007
Data	**ICOADS 1-degree enhanced**
Source	NOAA/OAR/ESRL PSD: http://www.esrl.noaa.gov/psd/
Time period	From 1960 to 2014
Spatial coverage	1 × 1 degree
Measurements	Zonal and meridional wind monthly mean at surface (m/s)
References	ICOADS website publications page: http://icoads.noaa.gov/publications.html

masses in the presence of benthic communities dominated by suspension feeders. From seven video transects conducted in the Formigas seamount, a total of 801 images were analyzed. Abundances for the whole invertebrate community (including five phyla), porifera and cnidarians were averaged in 2 m bins along the depth gradient of Formigas seamount.

RESULTS

Overview

All the study targets are located in the area of influence of the east side of the North Atlantic Subtropical Gyre. The surface temperatures in this area decrease northward (**Figure 2**), reaching annual mean temperatures between 18 and 20°C. At the latitudes of the sampled features, between 38 and 36°N, the temperature also decreases toward mainland; with a temperature difference of around 1°C between Formigas and Gazul (**Figure 2**). This temperature difference is the result of the near-surface currents governing in this area: the Azores Current and the branch it splits near Madeira, which meanders toward the Strait of Gibraltar (Johnson and Stevens, 2000; Sala et al., 2016), prone to form cyclonic meanders at its north side and anticyclonic ones at the south (Juliano and Alves, 2007), and the Portugal Current, which flows southwards along the Iberian shelf (**Figure 3**), until it reaches the Azores Current, which acts as boundary between the north and south circulation of the North Atlantic Subtropical Gyre (Relvas et al., 2007).

These near-surface currents are not constant all year round and in fact they show strong seasonal variability (**Figure 3**). Thus, in winter (**Figure 3A**), the eastward branch of the Azores Current (34°N) is intense and well defined, flowing directly to the Strait of Gibraltar. In autumn (**Figure 3D**), the Azores current is still observed, although weaker. However, during both, spring and summer (**Figures 3B,C**), the surface current flowing to the east at the surface, almost disappears, and it turns southward, toward the Canary Current, due to the intensification of the trade winds during those seasons. Similarly, there is a shift in the currents north of the Azores. In winter and autumn (**Figures 3A,D**), the current flows eastwards, while in spring and most of the summer (**Figures 3B,C**) there is a southward flow perpendicular to the islands (25°W). The Azores islands, islets and seamounts act as a barrier that weaken the flow and alter its course; hence the current barely reaches the area surrounding the Formigas seamount.

In the Ormonde area, the Portugal Current flows over the seamount all year long. Although, it can be observed a slight decrease in intensity as the flow goes between the seamounts. In general, this current gets weaker as it goes south. The Portugal Current is stronger in summer, remaining considerably constant for the rest of the year, and it produces a cyclonic gyre in winter and, to a lesser extent, in autumn, when it reaches the eastward Azores Current.

In the region where the Gazul mud volcano is located, there is a strong current to the south-southeast that eventually goes through the Strait of Gibraltar. During the months of winter and autumn, this flow is also fed by the Azores Current. However, as this current does not reach the Gulf of Cadiz in spring and summer, the additional input of water is smaller and comes from the Portugal Current.

Similar seasonal patterns were found in the monthly mean winds. In Formigas (**Figure 4A**) the winds vary both in intensity and direction. During the winter months, the winds are predominantly from the southwest, while in summer the north component is more important and the winds are also more intense. In Ormonde (**Figure 4B**) the winds do not change much in direction, but they do change in intensity, with maximums in July. Finally, in Gazul (**Figure 4**) the winds are also more intense in summer, and they shift from northeast in winter to northwest in summer. The variation of the winds also affects the sea surface temperature. It seems very similar in the three areas, with a minimum of temperature around March, and a maximum that shifts from September–October in Formigas and Ormonde (**Figures 4D,E**) to August–September in Gazul (**Figure 4F**).

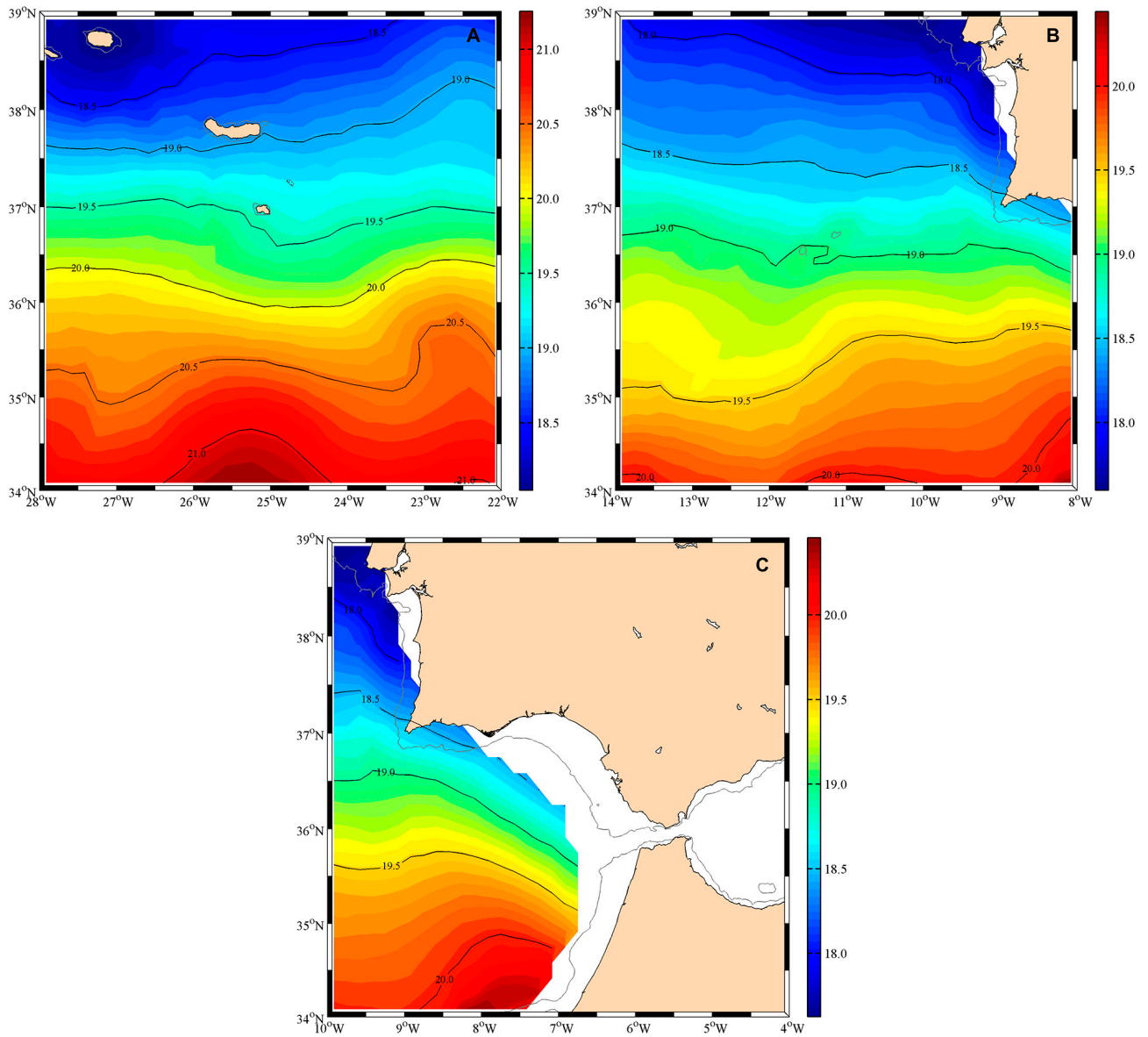


FIGURE 2 | Mean annual temperature in degrees Celsius in the Formigas **(A)** and Ormonde **(B)** seamounts, and the Gazul mud volcano **(C)**.

However, the temperature is around 1°C lower in Ormonde, with values between 15°C and 22°C, than in Formigas and Gazul, both in winter and in summer. This is probably consequence of the strong north-northwest winds present in the Ormonde region all year round.

In summary, the mean ocean circulation in the region of study is subject to high seasonal variability, and therefore do not provide permanent favorable conditions for the development of Taylor caps, which require a unidirectional steady current to be formed (Lavelle and Mohn, 2010). However, in spite of the unsteadiness, Taylor caps could still be generated (Beckmann and Mohn, 2002). In order to identify the hydrodynamical phenomena governing the circulation over the these underwater features in the path of the MOW, and, in particular, to verify if Taylor caps are formed, we will analyze, in the next section, the regional dynamics over the three features.

Dynamics

As it was pointed out in the previous section, the mean ocean over the three underwater features in the pathway of the MOW does not meet the conditions for the formation of Taylor caps. To evaluate whether, in spite of the unsteadiness, Taylor caps could still be generated, in this section, we will describe the dynamics over the Ormonde and Formigas seamounts and the Gazul mud volcano found during the MEDWAVES cruise.

In the Gazul mud volcano the upper ocean circulation is characterized by a two-layer flow, with the lighter North Atlantic Central Water (NACW) on top of the heavier MOW, as it can

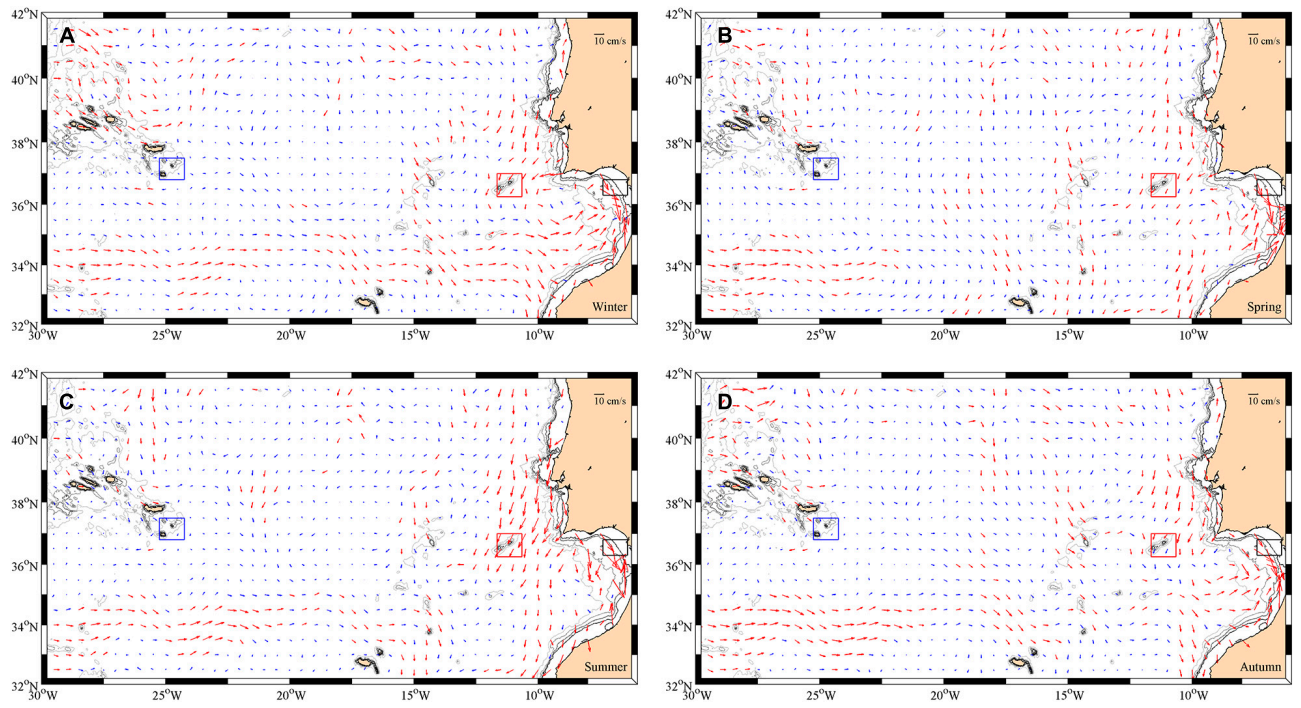


FIGURE 3 | Seasonal near-surface current velocities. The blue arrows correspond to velocity values under 5 cm/s and the red arrows to values from 5 to 40 cm/s. The squares are the areas of study: the Formigas (in blue) and Ormonde (in red) seamounts, and the Gazul mud volcano (in black). Each panel corresponds to a different season: **(A)** winter, **(B)** spring, **(C)** summer, and **(D)** autumn.

be observed in the horizontal distribution of LADCP velocities (**Figure 5**). The upper layer (**Figure 5A**) flows eastward along the first 400 m of all the region of Gazul, transporting the Atlantic waters into the Strait of Gibraltar. On the other hand, the MOW exits through the Strait close to the bottom (**Figure 5B**). This deep outflow moves westward close to the slope of the Gulf of Cadiz. It is interesting to notice the disruption of the current on its path close to 36°30′N 6°90′W, which turns the flow to the north at both the upper and the deeper level.

Over the Ormonde seamount, the strong influence of the Azores Current lead the predominant flow to the east, as it is shown in the horizontal distribution of velocities (**Figure 6**). Thus, between the 40 and 540 m (**Figure 6A**), there is a strong eastward current; however, in the intermediate layer (560–1,000 m) (**Figure 6B**) the seamount disrupts the flow. This disruption causes a constant flow around the southwest part of the seamount, resulting in a weak anticyclonic circulation around Ormonde.

The circulation in the Formigas area does not follow a well-defined pattern (**Figure 7**), since the presence of the seamount and the islets greatly disrupts the flow. In the top 800 m (**Figures 7A,B**) the flow is deflected to the northeast, while at the intermediate layer (560–1,000 m) the flow is diverted, surrounding both flanks of the seamount. At greater depths, the northern branch of the flow is blocked by the San Miguel Island, and the main flow surrounds the Formigas seamount by its south flanks, describing a weak anticyclonic circulation.

The analysis of the barotropic tidal regime shows a different behavior in each of the areas studied. For the Gazul mud volcano the tide has velocities of about 2 cm/s in the northeast-southwest direction (**Figure 5A**). However, in both the Ormonde (**Figure 6A**) and Formigas (**Figure 7A**) seamounts the tides are stronger, reaching the 5 cm/s, but in opposite directions, with a northwest-southeast tide for Ormonde and a northeast-southwest one for Formigas.

Hydrography

The Mediterranean water, after outflowing through the Strait of Gibraltar flows westward over the Gazul mud volcano. After that, the MOW continues its spread into the Atlantic, reaching the Ormonde seamount, which diverts the flow toward the southwest, forcing it to surround the seamount, and finally it reaches Formigas.

Hence, the three regions are characterized by the presence of the MOW at mid-depths. In fact the θ/S diagrams (**Figure 8**) for the areas sampled show a similar vertical distribution of water masses. In particular, all of them have a relative salinity minimum around γ^n 27.160 kg/m^3, indicative of the presence of the NACW, and a relative maximum of salinity at γ^n 27.630 kg/m^3, distinctive feature of the MOW. This maximum shows an intensity decrease from Gazul to Formigas which characterizes the propagation of the MOW into the Atlantic.

Specifically, the Gazul mud volcano (**Figures 9A–C**) shows a vertical distribution divided in three layers. In the first 10–20 m there is a mixed layer in which the temperature

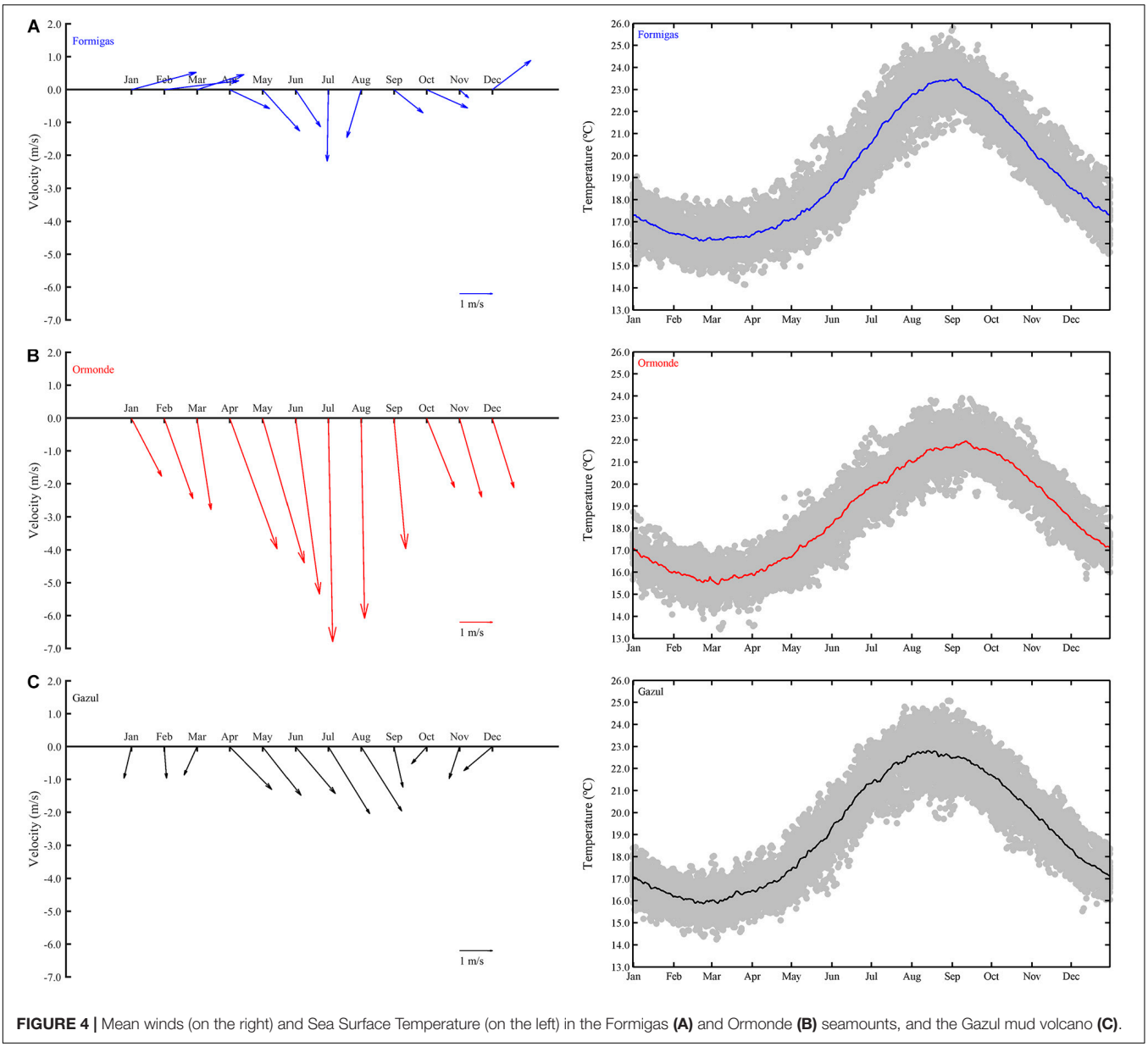


FIGURE 4 | Mean winds (on the right) and Sea Surface Temperature (on the left) in the Formigas **(A)** and Ormonde **(B)** seamounts, and the Gazul mud volcano **(C)**.

and the salinity are almost constant, followed by the seasonal thermocline that reaches 50 m in the stations located away from the coast. Just below the surface layer, it is located the NACW, which is characterized by an almost linear relationship between temperature and salinity, reaching its minimum (11.87°C and 35.67) between 300 and 450 m. Finally, separated from the NACW, by the isohaline of 35.75 and the 27.162 kg/m^3 isopycnal (and the 12.50°C isotherm), the MOW occupies approximately the deepest 150 m from the bottom. In this layer, there is an increment in both temperature and salinity, with maximum values of 36.57 and 13.64°C, and a relative minimum in the oxygen concentration (**Figure 9D**).

Regarding the Ormonde seamount (**Figures 10A–C**), the surface layer is located above the isopycnal of 26.850 kg/m^3, and the surface waters are divided among a mixed layer that goes down almost 50 m and the seasonal thermocline, reaching depths less than 100 m. Between the 100 and 400 m (isopycnals of 26.850 and 27.200 kg/m^3), the NACW shows its characteristic linear decrease of temperature and salinity. Below the NACW, and between the 27.380 and 27.820 kg/m^3 isopycnals, there is a sharp increase in salinity consequence of the presence of the MOW. The temperature is practically constant, with a small increase until 900 m, where it reaches a relative maximum of 12°C. However, the increase of salinity continues until depths of 1,200 m, with values up to 36.44. There is a second core around the 800 m, near the 27.620 kg/m^3 isopycnal, where a less noticeable maximum of salinity can be found. The influence of the MOW is noticeable from 500 to 1,400 m, with values of oxygen concentration reaching the characteristic

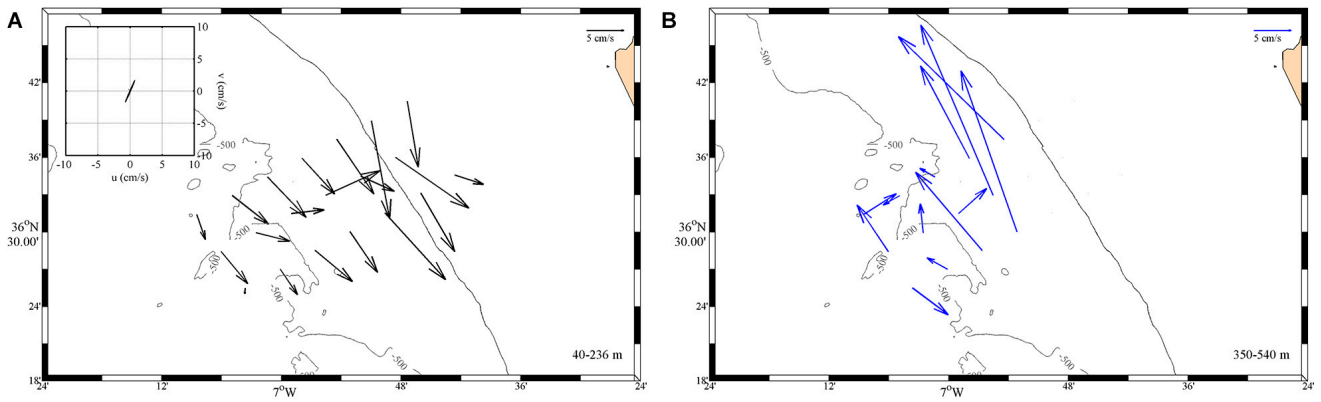


FIGURE 5 | Horizontal distribution of vertically averaged Lowered Acoustic Doppler Current Profilers (LADCP) velocities for the Gazul mud volcano. The figure on the left **(A)** corresponds to the upper layer (40–236 m) and the figure on the right **(B)** to the deep layer (350–540 m). The tidal ellipses in the average location of Gazul are included on the inset in the top left corner of panel **(A)**, with the same scale as the main plot.

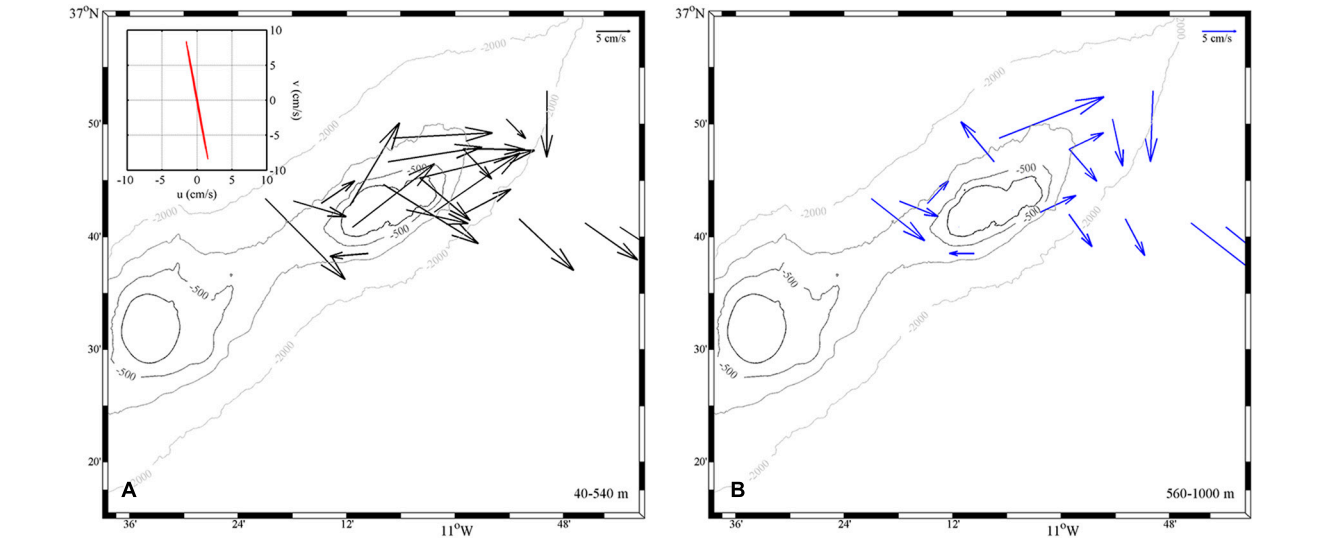


FIGURE 6 | Horizontal distribution of vertically averaged LADCP velocities for the Ormonde seamount. The figure on the left **(A)** corresponds to the upper layer (40–540 m) and the figure on the right **(B)** to the deep layer (560–1000 m). The tidal ellipses in the average location of Ormonde are included on the inset in the top left corner of panel **(A)**, with the same scale as the main plot.

minimum of the Mediterranean waters (**Figure 10D**). Below the MOW there is a rapid decrease of temperature and salinity that indicates the presence of the upper North Atlantic Deep Waters (uNADW).

In the case of Formigas, the first 100 m of the water column (**Figures 11A–C**) are occupied by a mixed layer of about 20–30 m and the seasonal thermocline. Below, the NACW, delimited by the 26.850 kg/m^3 and the 27.200 kg/m^3 isopycnals (150–600 m), shows a decrease of temperature from 14.57 to 11.58°C and of salinity from 35.94 to 35.60. Below the NACW the salinity continues to decrease slightly reaching a minimum value of 35.56 at 675 m. This indicates the presence of Antarctic Intermediate Waters (AAIW), due to the location of the seamount in the surrounding area of the Atlantic Ridge. Under the AAIW, the MOW in Formigas shows an increment of salinity, although less pronounced than in the other two regions, as a result of the dilution that the MOW undergoes during its path from the Strait of Gibraltar. Thus, this diluted MOW, between γ^n of 27.380 and 27.720 kg/m^3, shows a maximum of salinity of 35.81 close to 900 m. The minimum of oxygen concentration (**Figure 11D**) are, in the case of Formigas, practically restricted to the core region, and it does not reach values as low as in Ormonde. The influence of the Mediterranean waters reaches almost the 1,400 m, until the 35.25 isohaline and the 27.820 kg/m^3 isopycnal. The layer close to the bottom is occupied by the uNADW that is characterized by decreasing values of salinity and temperature.

The study of the distribution of water masses shows the characteristic spread of the MOW in the Atlantic. The decrease of salinity from Gazul to Formigas denotes the westward flow of this water mass. The low salinity values present in Formigas are result

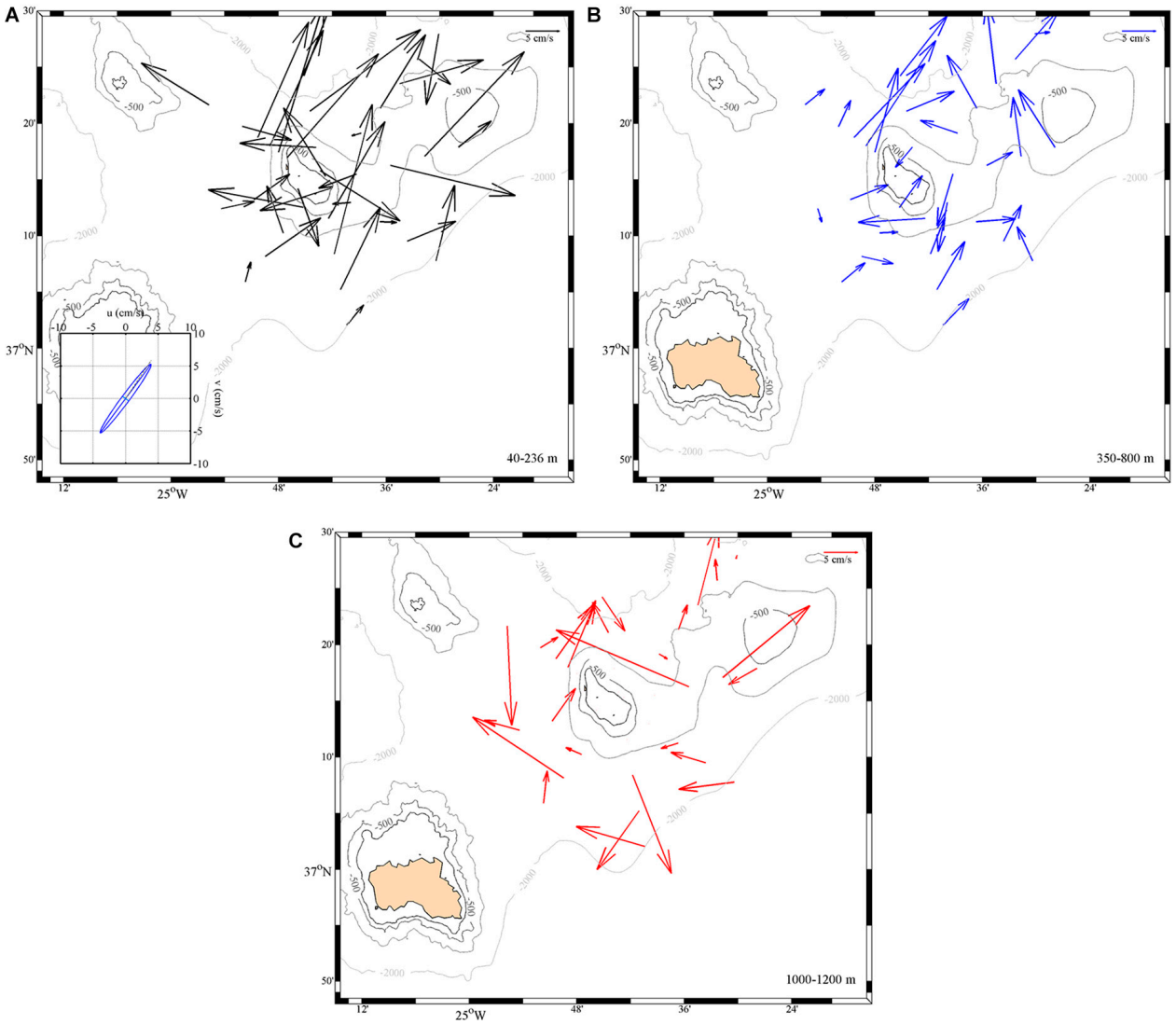


FIGURE 7 | Horizontal distribution of vertically averaged LADCP velocities for the Formigas seamount. The upper figure on the left **(A)** corresponds to the upper layer (40–236 m), the upper figure on the right **(B)** to the intermediate layer (350–800 m) and the bottom figure **(C)** to the upper deep waters (1000–1200 m). The tidal ellipses in the average location of Formigas are included on the inset in the top left corner of panel **(A)**, with the same scale as the main plot.

of the long distance of this seamount with the source. Besides, the depth at which the core is found changes among the regions. In Gazul the MOW occupies the bottom layer, but it gets deeper at Ormonde, where two cores were found. Finally, a more diluted MOW arrives at Formigas. However, in Formigas it can just be described a single not conspicuous core at a depth between the cores in Ormonde.

As a consequence of the presence of the MOW, there are areas below the permanent thermocline, where the Brunt–Väisälä frequency reaches maximum values. In Gazul (**Figure 9E**), two relative maxima are found: the first one, from surface to the upper limit of the NACW, in the area of the seasonal thermocline, and the second one in the boundary between the NACW and the MOW, where an intense halocline occurs. High values are also found near the bottom, close to the core of the MOW. In Ormonde (**Figure 10E**), the maximum Brunt–Väisälä values are in the area of the thermocline. However, relatively high values are also found in the MOW layer, mainly in the limit with the NACW and related with the subsurface salinity maxima. Similarly to what was found in Ormonde, in Formigas (**Figure 11E**) the maximum values of the Brunt–Väisälä frequency occur in the surface, although there is a subsurface maximum in the upper limit of the MOW, related with the relative maximum of salinity.

Thus, these relatively high values of the Brunt–Väisälä frequency, due to the salinity difference produced by the MOW, generate a strong density gradient mainly in the NACW–MOW interface. According to numerical models a mid-water intense stratification layer can boost the internal waves in its particular depth range when interacting with certain slope values

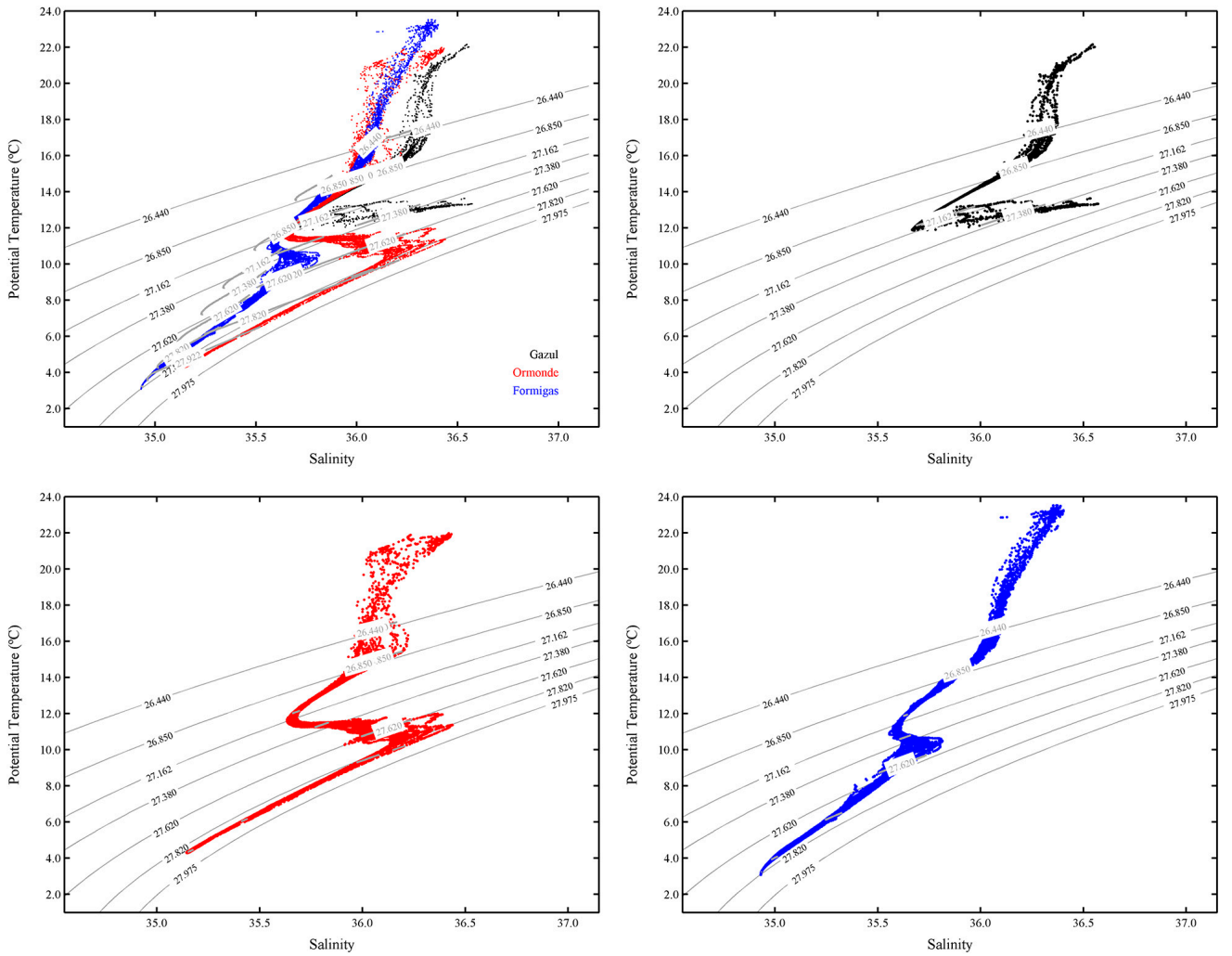


FIGURE 8 | θ/*S* diagrams of all the stations sampled during the MEDWAVES cruise in the Gazul mud volcano (in black), and the Ormonde (in red), and Formigas (in blue) seamounts. The thin gray lines correspond to the density isolines, while the thick gray lines correspond to the neutral density isopycnals.

resulting in local relatively strong currents (Hall et al., 2013). The characteristic slope of these internal waves (c) will be dependent of the Brunt–Väisälä frequency and it is given by:

$$c = \pm\sqrt{\frac{\omega^2 - f^2}{N^2 - \omega^2}}$$

where ω is the wave frequency (in this study the frequency of the semidiurnal tide was used), f is the Coriolis parameter, and N is the Brunt–Väisälä frequency.

The relationship between this angle and the slope of the bottom (γ) will determine the behavior of the internal waves as determined by Cacchione and Wunsch (1974). If $\gamma/c < 1$, the slope is subcritical, and the waves will be transmitted; if $\gamma/c \approx 1$, the slope is critical, and the waves will break; if $\gamma/c > 1$, the slope is supercritical, and the waves will be reflected.

In the Gazul mud volcano (**Figure 12A**) the ratio γ/c goes from subcritical to critical or even supercritical where there is a sudden change in depth, while the steep slope of the Ormonde and Formigas (**Figures 12B,C**) seamounts supports mainly supercritical behaviors, which causes the reflection of internal waves preventing them to break. However, in the areas where the ratio γ/c is critical (**Figure 12**) internal waves will break, producing turbulence.

In addition, at the latitude of the regions of study, poleward 30°N, the local inertial period ($2\pi/f$) is longer that the tide oscillation period and the internal waves can be trapped at the slopes of the seamounts. This trapping may generate a residual current along the slope that can be amplified, with the largest amplification expected at a bottom depth where $N * \sin(\alpha)$ reaches a maximum value being α the inclination of the seabed [i.e., $\alpha = \tan^{-1}(\gamma)$] (Huthnance, 1981).

The depth of the maximum amplification (**Figure 13C**) coincides with the areas of high values of N (**Figure 13B**), modulated by the step topography of those underwater features (**Figure 13A**). In particular, Gazul shows a maximum at the

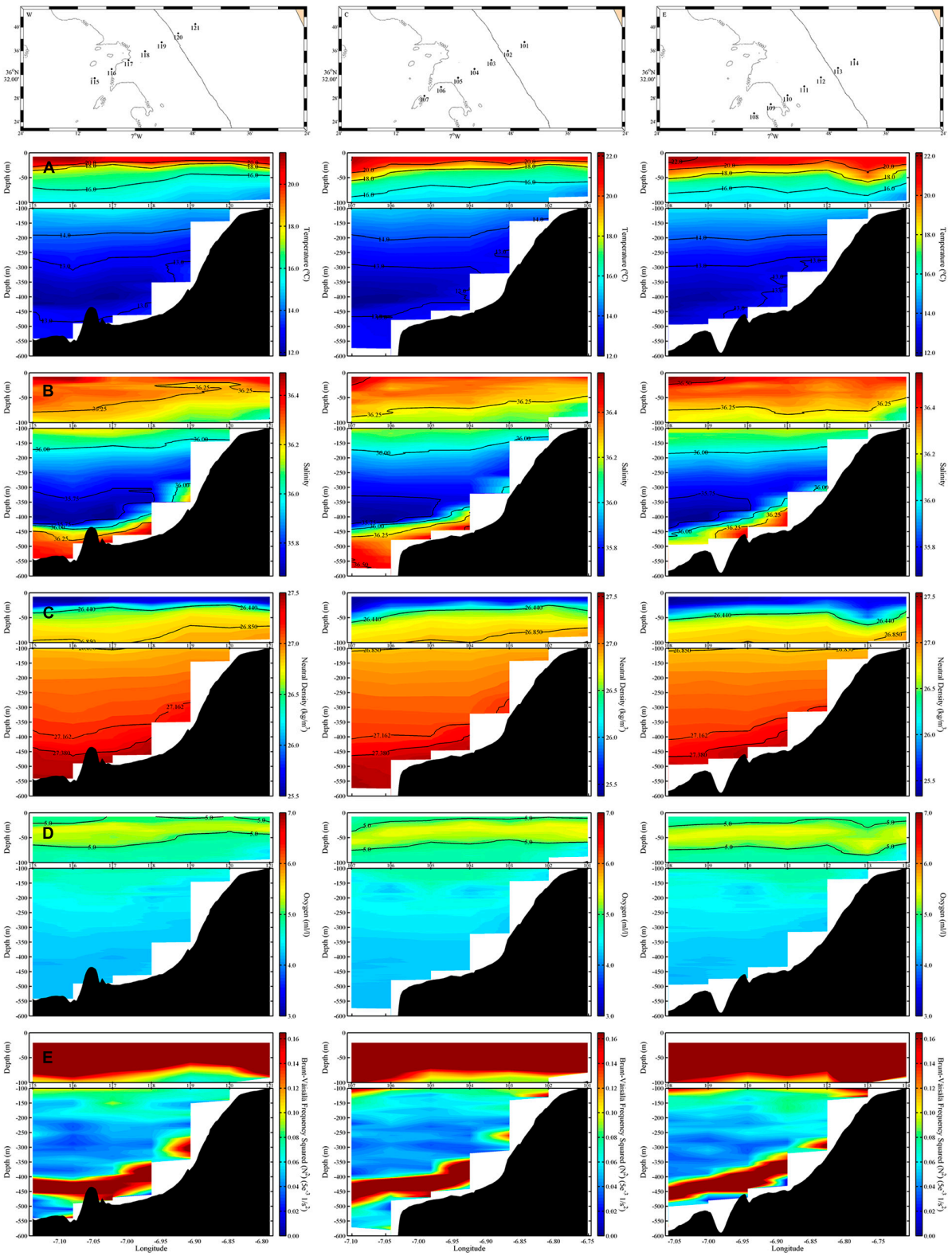


FIGURE 9 | Vertical sections of (from top to bottom) potential temperature (°C) **(A)**, salinity **(B)**, neutral density (kg/m^3) **(C)**, oxygen concentration (ml/l) **(D)**, and Brunt–Väisälä frequency squared (5e^{-3} 1/s^2) **(E)** in the Gazul mud volcano. For each one of the vertical sections, the upper panel corresponds to the top 100 meters, while the lower panel corresponds to the 100–600 meters depth range. The numbers between both panels correspond to the station numbers, which are localized in the corresponding map at the top.

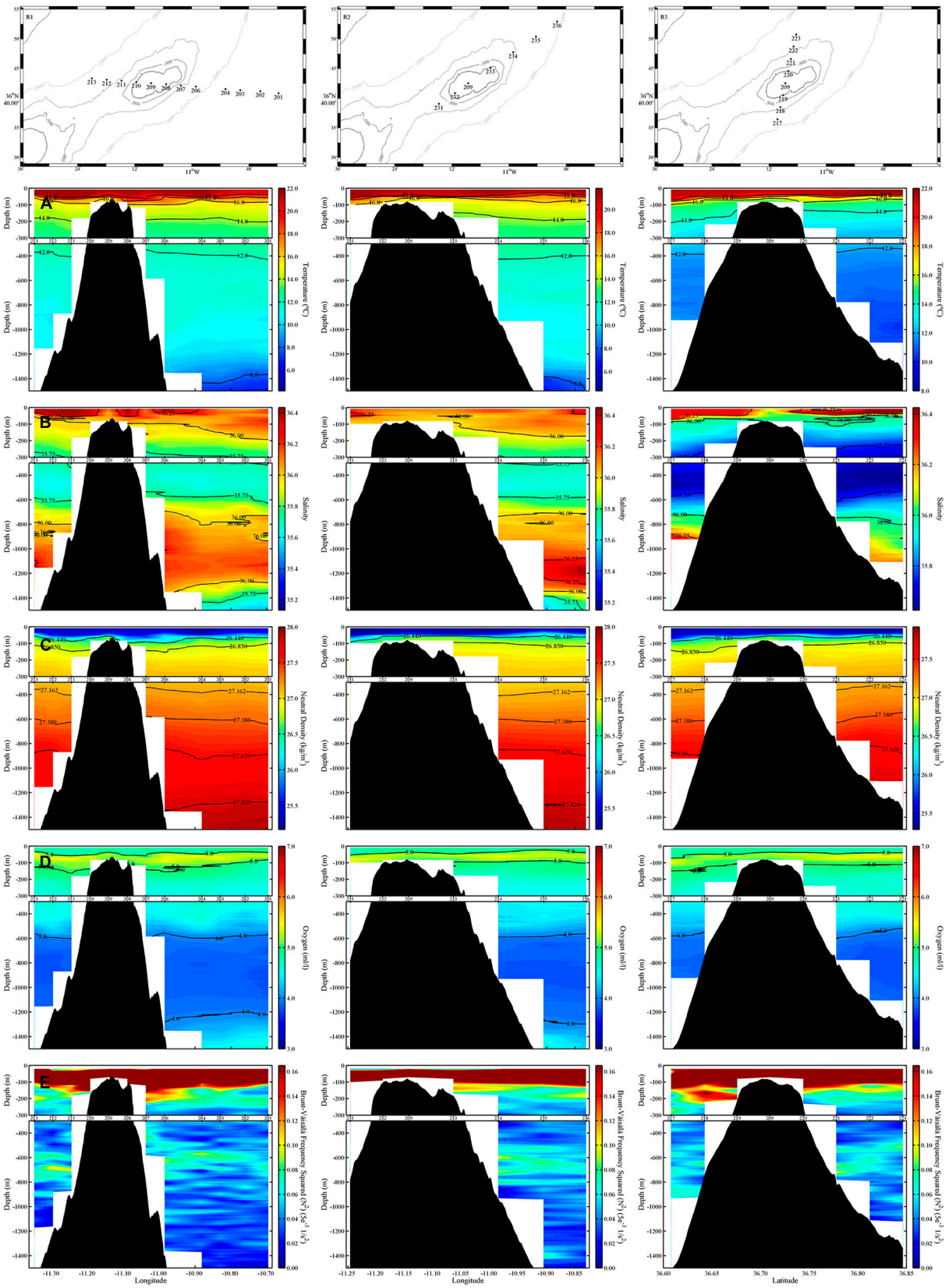


FIGURE 10 | Same as **Figure 9**, but for the Ormonde seamount.

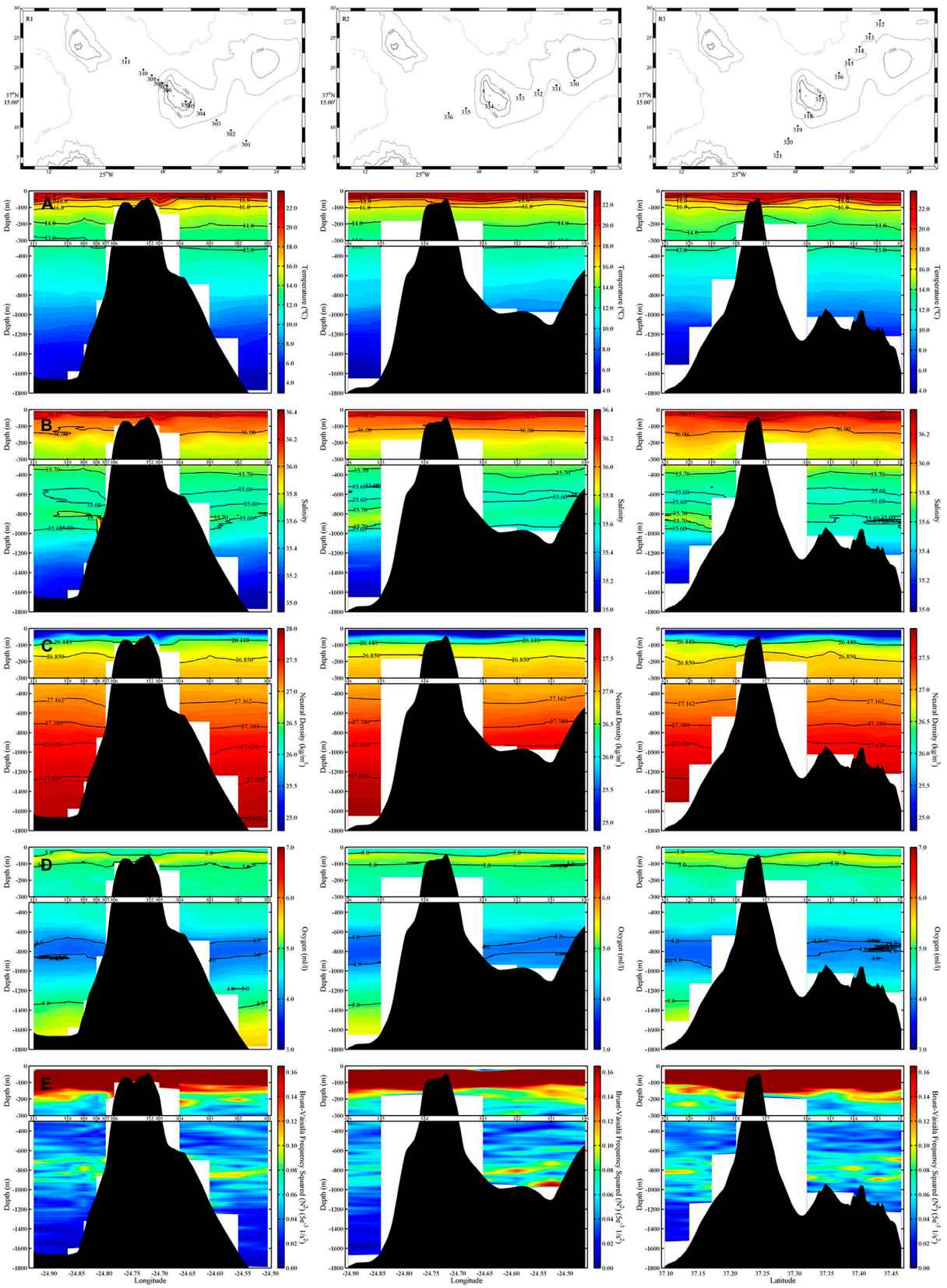


FIGURE 11 | Same as **Figure 9**, but for the Formigas seamount.

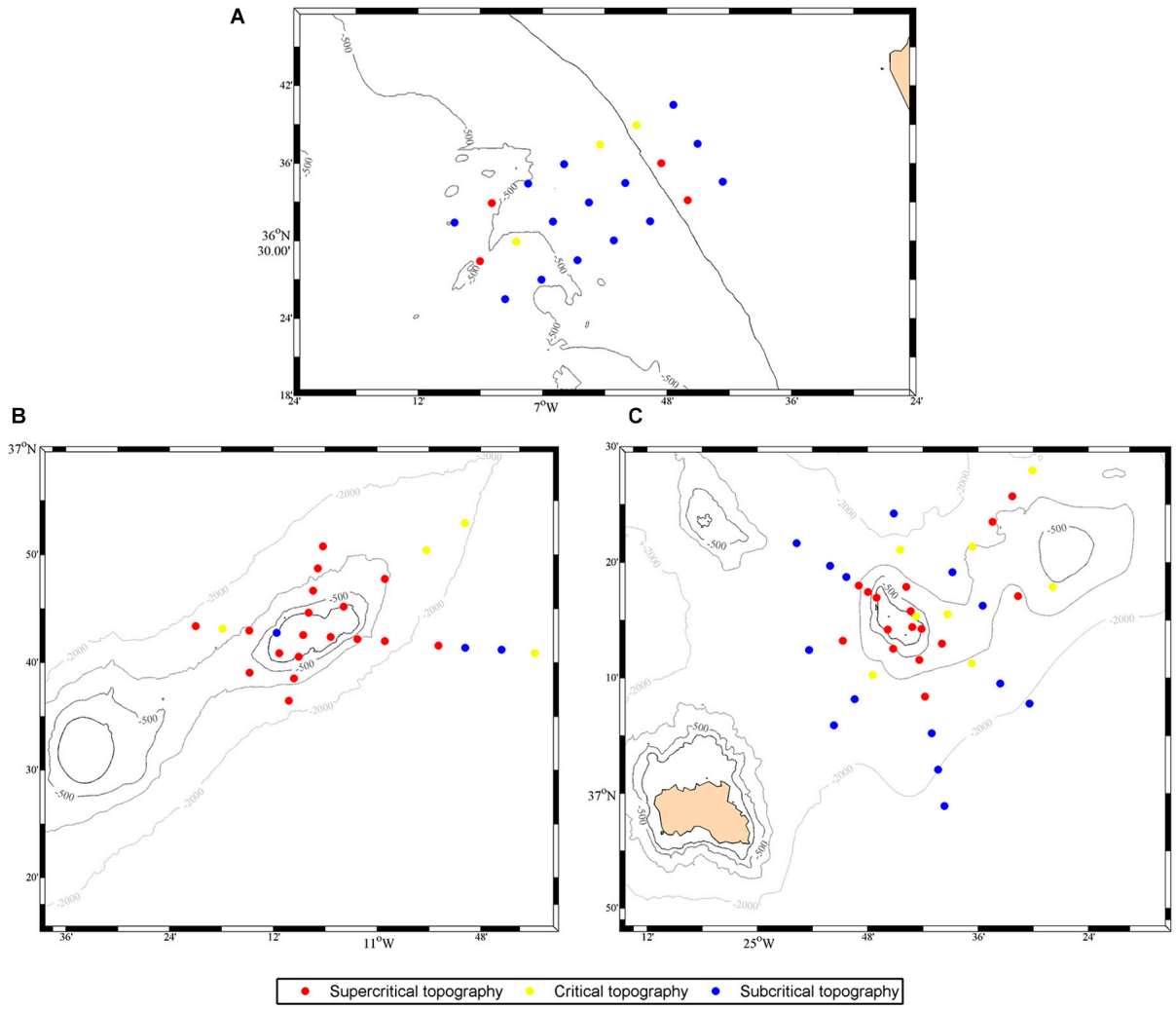


FIGURE 12 | Bottom slope (γ) vs. angle of propagation of internal waves (c) near the bottom for the Gazul mud volcano **(A)**, the Ormonde **(B)**, and Formigas **(C)** seamounts.

NACW–MOW interface. The same maximum can be found in Ormonde, together with a second one at the MOW–NADW interface. The case of Formigas is slightly different, since the presence of a third water mass, the AAIW, between the NACW and the MOW generates a region of maximum amplification from the low boundary of the NACW until the core of the MOW, not showing another significant maximum below the 1,000 m.

Benthic Communities

A total of 9729 megabenthic invertebrates belonging to 5 different phyla (Porifera, Cnidaria, Arthropoda, Echinodermata, and Bryozoa) were identified in the still images, which included 3684 poriferans and 5736 cnidarians (37.87 and 58.96% of the total abundance registered). The average number of organisms of each group was displayed along the depth gradient of the Formigas seamount. The highest number of benthic organisms occurred between 500 and 1,000 m depth, coinciding with the NACW–MOW interface (**Figure 14A**). The same pattern was also observed for porifera and cnidaria (**Figures 14B,C**).

SUMMARY AND DISCUSSION

As indicated by Lavelle and Mohn (2010), the formation of Taylor caps would generate an anticyclonic gyre that isolates the flow on the top of the seamount. However, although the circulation in the three regions of study is disrupted by the presence of the underwater features, the circulation associated with Taylor caps was not observed. Theoretically, the isolation produced by a Taylor cap on the top of a seamount will enhance the productivity in the area. However, the importance of this phenomenon and the likelihood with which it occurs in the field may be uncertain, since flows in the ocean are not usually steady (Lavelle and Mohn, 2010). The dynamical analysis of three features in the path of the MOW does not show any evidence of Taylor caps

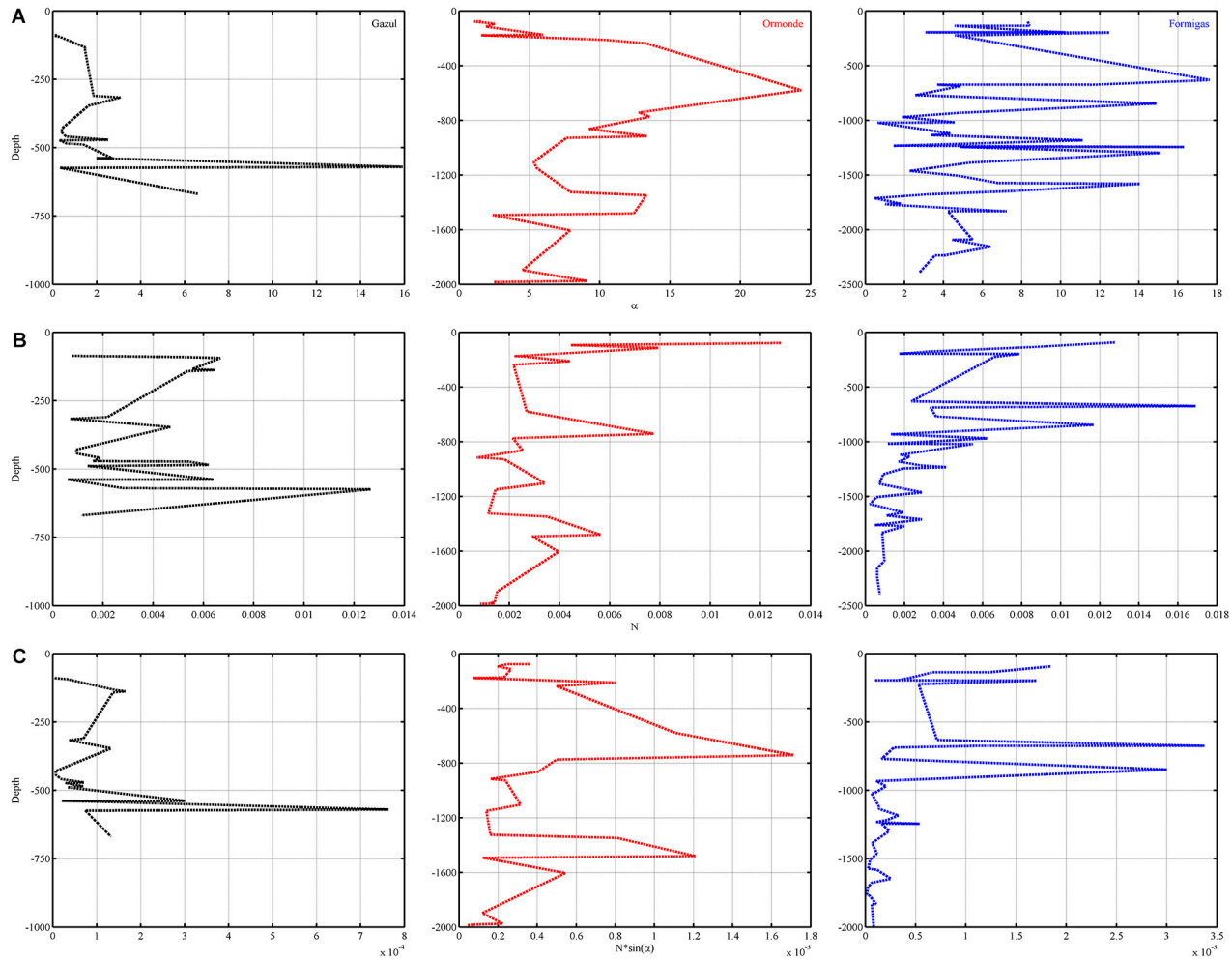


FIGURE 13 | Vertical profiles of (from top to bottom) angle of incline of the seabed **(A)**, Brunt–Väisälä frequency **(B)**, and parameter $N^*\sin(\alpha)$ **(C)** for (from left to right) the Gazul mud volcano (in black), and the Ormonde (in red), and the Formigas (in blue) seamounts.

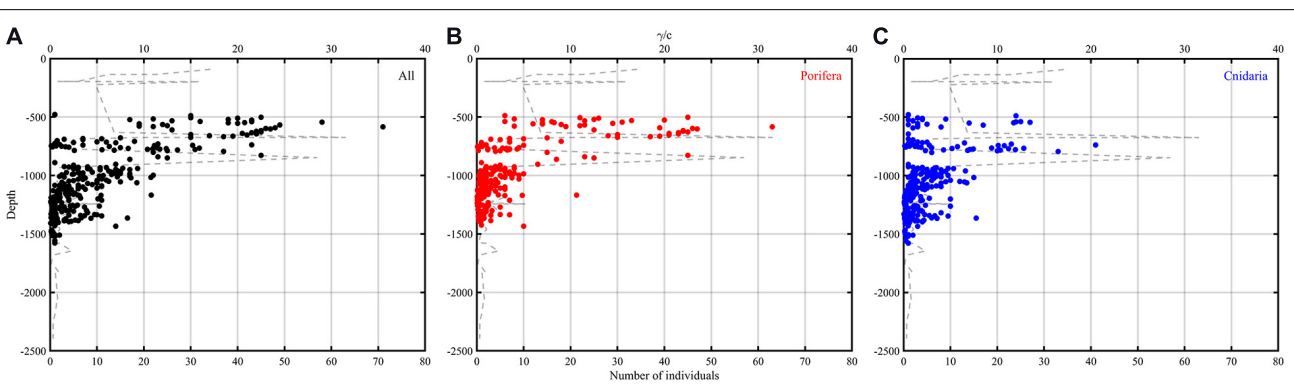


FIGURE 14 | Vertical profiles representing the abundance of benthic invertebrates averaged in 2 m bins for all phyla **(A)**, porifera **(B)**, and cnidaria **(C)** in Formigas seamount. The gray dashed line represents the coefficient between the bottom slope and the angle of propagation of the internal waves (γ/c).

formation during the time when the *in situ* observations were gathered. Furthermore, the seasonality and fluctuation of the flow as indicated by the climatological data (**Figure 3**) lead us to suggest that this particular phenomenon, as well as any other related with a constant flow (i.e., current deflection, turbulence, and persistent upwelling) in case they take place, will not last for

long periods due to the variability of the currents. Moreover, the barotropic tides in the regions of study show values comparable to the ocean currents, particularly in Ormonde, and Formigas, and hence they will override the residual circulation that could be induced by Taylor caps.

The permanent layout of water masses distribution through the water column suggests that the propagation of internal waves could be frequent. The density gradient is a determining factor for the generation and propagation of internal waves (Munk, 1981; Apel, 2004). Therefore, the hydrographical analysis of each one of the studied features allowed us to determine if internal waves might take place and how they would interact with the slope of the seamounts. The vertical distribution of the water masses, and in particular, the presence of the MOW, with its associated salinity gradient, determines the stratification of the water column. The analyses of the vertical distribution of the water masses in each of the three features show an intense stratification at mid-depths in the three regions studied, as it is indicated by the relatively high values of the Brunt–Väisälä frequency. This intense stratification is due to the density difference between the Atlantic and Mediterranean waters, which determines the stability of the water column. The associated high values of the Brunt–Väisälä frequency make the NACW–MOW interface an adequate area for the generation and propagation of internal waves, which after the interaction with the gentle slope of the seamounts, can end up breaking, and therefore enhancing the vertical mixing and producing upwelling (IUCN, 2013; Rivera et al., 2016).

Moreover, at the latitude of the regions of study, poleward 30°N, waves traveling at diurnal periods may be trapped over the slope, generating amplified currents at the depths where N is maximum, i.e., in the interface generated by the presence of the MOW, and as indicated by the barotropic tides, with enough energy for the development of internal waves (White and Dorschel, 2010).

White and Dorschel (2010) proposed that a stable stratification could help the growth of CWC on regions of enhanced energy near the sea bottom. It is in this region of maximum energy, in the interface associated to the presence of the MOW (500–1,000 m), where we have found the higher abundance of benthic suspension feeders in the Formigas seamount (**Figure 14**), particularly invertebrates such as poriferans and cnidarians. Specifically, two relative maxima coincide with critical values of the γ/c relationship, one at the NACW–MOW interface and another at the MOW core; and a third relative maximum is around 1,200 m, due to the MOW–NADW interface. The presence of suspension feeders on the slopes of seamounts has been largely attributed to the activity of internal waves (Frederiksen et al., 1992; Duineveld et al., 2004; De Mol et al., 2005; Mienis et al., 2007; Davies et al., 2009; van Haren et al., 2017). Frederiksen et al. (1992) suggested that corals living on deep waters cannot only be supported by the scarce supply of food coming from the surface layers. Instead, they postulated that the intensification of the mixing at the bottom, due to the interaction of internal waves with a sloping bottom, would produce the mobilization of the organic material deposited on the seabed, enhancing food supply for benthic organisms. The favorable effects caused by internal waves have already been observed in the CWC reefs dominated by the coral *Lophelia pertusa* in areas of the Northeast Atlantic as the Mingulay Reef complex (Davies et al., 2009), Tisler Reef (Wagner et al., 2011), and the Logachev Mounds at Rockall Bank (Duineveld et al., 2007; Soetaert et al., 2016). These processes could favor the settlement and growth of CWC and other benthic taxa on areas of steep topography, such as the slope of the seamounts. The presence of the MOW at mid-depths guarantees a permanent stratification that allows the generation and propagation of internal waves.

We have demonstrated that there is a strong relation between the NACW–MOW interface, associated with the activity of internal waves, and the abundance of benthic suspension feeders. This supports the hypothesis that the biological importance of seamounts in the pathway of the MOW through the eastern Atlantic (WWF, 2004; Oceana, 2005; Rueda et al., 2016) might be associated to internal waves in the NACW–MOW interface, that improves the favorable conditions for benthic suspension feeders to grow on the slope of the seafloor elevations.

AUTHOR CONTRIBUTIONS

PV-B and CO conceived and designed the research. CO, PV-B, JR, SP, VC, and JJ performed the field work. ÁM, PV-B, and SP processed the oceanographic data and elaborated the preliminary results. CD-C and JB-F processed the video transects and provided the video biological data. ÁM, PP, and CO processed the video biological data. ÁM, PV-B, RB, JR, and NF contributed to the further analysis of data. ÁM and PV-B wrote the manuscript. JR, SP, VC, PP, and CO revised the manuscript and contributed to the writing. CD-C, MC-S, and TM contributed to the writing associated with the biological data.

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Significance of Climate Indices to Benthic Conditions Across the Northern North Atlantic and Adjacent Shelf Seas

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The northern North Atlantic Ocean and its adjacent shelf seas, are influenced by several large-scale physical processes which can be described by various climate indices. Although the signal of these indices on the upper ocean has been investigated, the potential effects on vulnerable benthic ecosystems remains unknown. In this study, we examine the relationship between pertinent climate indices and bottom conditions across the northern North Atlantic region for the first time. Changes are assessed using a composite approach over a 50 year period. We use an objectively-analyzed observational dataset to investigate changes in bottom salinity and potential temperature, and output from a high-resolution ocean model to examine changes in bottom kinetic energy. Statistically significant, and spatially coherent, changes in bottom potential temperature and salinity are seen for the North Atlantic Oscillation (NAO), Atlantic Meridional Overturning Circulation (AMOC), Atlantic Multi-decadal Oscillation (AMO), and Subpolar Gyre (SPG); with statistically significant changes in bottom kinetic energy seen in the subpolar boundary currents for the NAO and AMOC. As the climate indices have multi-annual timescales, changes in bottom conditions may persist for several years exposing sessile benthic ecosystems to sustained changes. Variations in baseline conditions will also alter the likelihood of extreme events such as marine heatwaves, and will modify any longer-term trends. A thorough understanding of natural variability and its effect on benthic conditions is thus essential for the evaluation of future scenarios and management frameworks.

Keywords: benthic temperature, benthic salinity, benthic kinetic energy, Atlantic Meridional Overturning Circulation (AMOC), North Atlantic Oscillation (NAO), Atlantic Multi-decadal Oscillation (AMO), Subpolar Gyre Index

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INTRODUCTION

The northern North Atlantic region contains a number of deep-sea ecosystems including cold water corals, sponges, and those in hydrothermal fields, with some being classified as Vulnerable Marine Ecosystems (VMEs). These ecosystems are susceptible to changes in climate (Sweetman et al., 2017; Johnson et al., 2018), however, in order to place future changes in

context and evaluate management measures, it is vital to understand natural climate variability. Whilst the signals of various climate indices on upper ocean conditions have been investigated (e.g., Hátún et al., 2005; Frajka-Williams et al., 2017), potential effects on benthic conditions, and deep-sea VMEs, remain unknown. In this paper, we ask whether climate indices are associated with statistically significant, and spatially coherent, changes in bottom conditions across the northern North Atlantic region. To achieve this, we use an objectively-analyzed observational dataset (EN4) to investigate changes in bottom salinity and potential temperature, and output from a high-resolution ocean model (Viking20) to examine changes in bottom kinetic energy. We provide a first look at the emergent patterns, and examine and describe their spatial coherency and magnitudes. We make some tentative explanations for the physical basis of some of the significant signals, but are careful not to ascribe causality where we investigate only correlation.

CLIMATE INDICES

The northern North Atlantic region, which we here define as that north of 30° N including its adjoining continental shelves and seas (**Figure 1**), has several multi-annual large-scale physical processes that influence upper ocean climate and have the potential to effect deep-sea ecosystems. These processes are often described using a number of basin-scale climate "indices"; the most common being the: North Atlantic Oscillation (NAO), the strength of the Atlantic Meridional Overturning Circulation (AMOC), the Atlantic Multi-decadal Oscillation (AMO), and the strength and extent of the Subpolar Gyre (SPG). Time-series of these indices are shown in **Figure 2**. It should be noted that although we consider each climate index individually, it is likely that they are not fully independent of one another. For example, the SPG may alter ocean heat content and therefore influence the AMO (Häkkinen et al., 2013). Similarly, atmospheric pressure changes related to the NAO may affect the AMO through changes in upper water properties (Yashayaev and Seidov, 2015) and the SPG (Häkkinen et al., 2011). Additionally, model studies suggest a possible link between the AMO and the AMOC on longer time-scales (Zhang, 2008; Buckley and Marshall, 2016), although no relationship has been established in the observational record (Lozier, 2010). Despite these possible inter-dependencies, we follow many previous studies (e.g., Hurrell, 1995; Häkkinen et al., 2011; Tulloch and Marshall, 2012; Yeager, 2015) and consider an index individually. This enables us to interpret our results in the context of other research, and investigate if any indices produce similar patterns of variability.

North Atlantic Oscillation (NAO)

The NAO is an atmospheric pressure index that influences the position and strength of westerly winds (e.g., Hurrell, 1995) and has several effects on the North Atlantic ocean. Sea surface temperatures show a tripole pattern; during a positive NAO: cooler temperatures are seen south of our study area in the tropical Atlantic, warmer temperatures are observed in the Gulf Stream region in the western Atlantic south of ∼45°N, and cooler temperatures are seen in the main subpolar region centered about Greenland (e.g., Marshall et al., 2001). A further area of warmer temperatures, during a positive NAO, is observed on the western European Shelf extending to the oceanic regions immediately west of the UK and Norway (Visbeck et al., 2013). The NAO also effects the intensity of convection in the Labrador and Nordic Seas, which, along with changes in upper waters, determines the properties of intermediate and deep water masses in those basins (Dickson et al., 1996). A positive NAO is associated with cooler and fresher Labrador Sea Water (e.g., Yashayaev, 2007). This signature is spread through the subpolar gyre along the Labrador Sea Water pathways, although transit times to the eastern basins are in the order of 5–10 years (Yashayaev et al., 2007a,b). In contrast, deep waters in the Greenland Sea are warmer and more saline during a high NAO (Dickson et al., 1996; Alekseev et al., 2001). Finally, Iceland Scotland Overflow Water has a lower salinity during a high NAO (Sarafanov, 2009) with less vigorous flow (Boessenkool et al., 2007). No relationship between Denmark Strait Overflow Water salinities and the NAO is observed (Sarafanov, 2009).

Atlantic Meridional Overturning Circulation (AMOC)

The AMOC is a measure of the strength of the overturning circulation in the important North Atlantic region. This circulation involves the conversion of less dense upper waters to denser intermediate and deep waters, and comprises a northward flow in the upper water column balanced by a return flow at depth. The patterns in upper ocean properties have predominantly been investigated in models, with temperatures showing a dipole signal: during a strong AMOC, cooler temperatures are observed in the Gulf Stream region, and warmer temperatures in the subpolar North Atlantic (Zhang, 2008; Tulloch and Marshall, 2012). In observational datasets, warmer sea surface temperatures in the Gulf Stream region, and cooler sea surface temperatures in the subpolar North Atlantic, have been attributed to a weakening AMOC over the past century (e.g., Caesar et al., 2018). This cooling is most pronounced in the Labrador, Irminger and Iceland Basins.

Atlantic Multi-decadal Oscillation (AMO)

The AMO is a measure of mean sea surface temperature over the entire North Atlantic and exhibits low frequency variability with a periodicity in the order of 65–80 years (Kerr, 2000). A positive index is associated with warmer sea surface temperatures over the region, with the greatest warming observed in the western subpolar gyre (Buckley and Marshall, 2016). During negative phases of the AMO, zonally-averaged sea surface temperature anomalies reveal the cooling is also more pronounced north of around 40° N (Frajka-Williams et al., 2017).

Subpolar Gyre (SPG)

The SPG is a measure of both the strength and extent of the subpolar gyre, with the most commonly used index being the first principal component of the sea surface height field (e.g.,

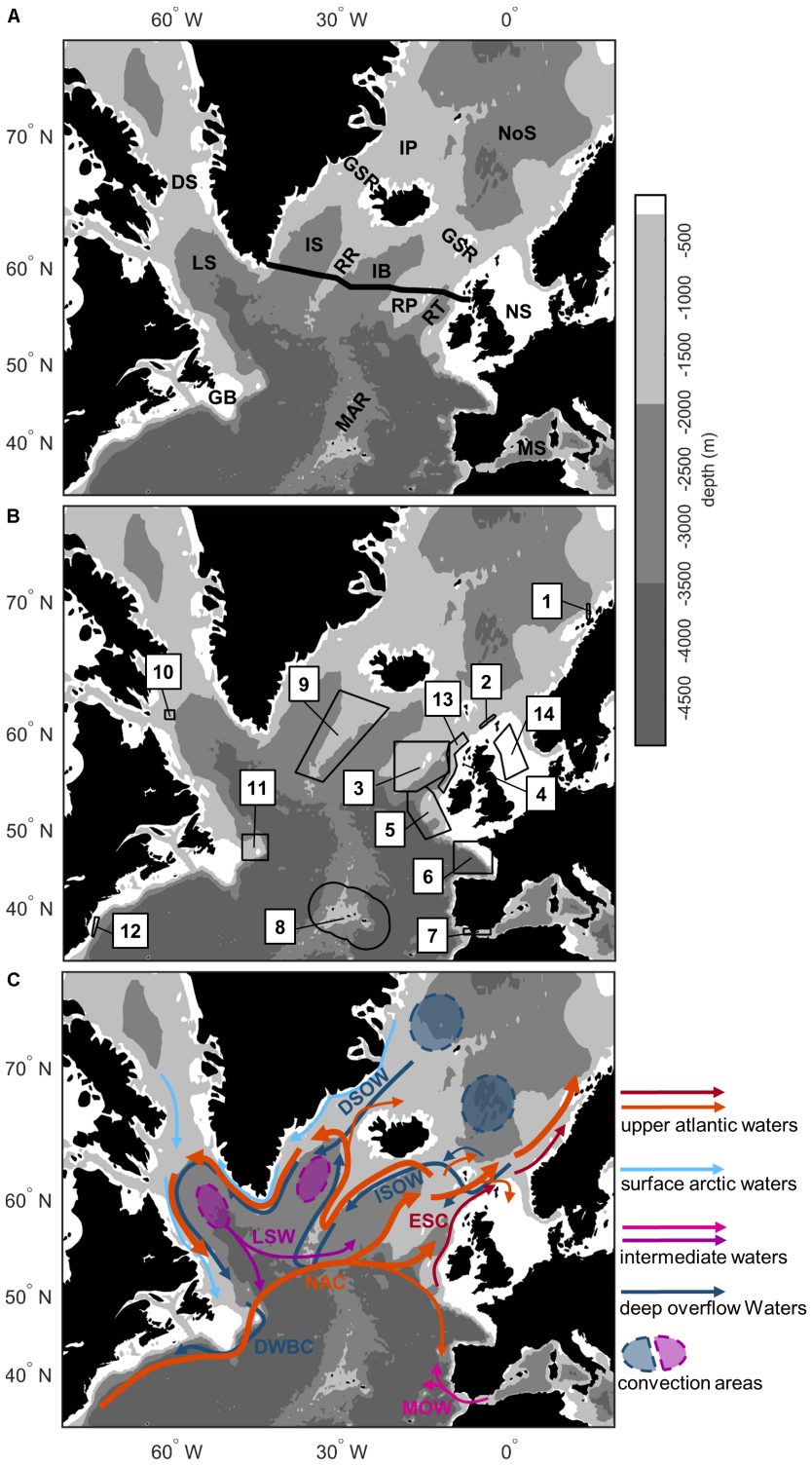


FIGURE 1 | Map of the northern North Atlantic region showing **(A)** bathymetric features referred to in the text, **(B)** the 14 case studies chosen to represent a range of Atlantic Vulnerable Marine Ecosystems and management regimes, and **(C)** a schematic of the circulation. See **Table 1** for case study names. Black line in **(A)** shows the OSNAP-EAST section. Labeled bathymetry: DS, Davis Strait; GB, Grand Banks region; GSR, Greenland-Scotland Ridge; IB, Iceland Basin; IP, Icelandic Plateau; IS, Irminger Sea; LS, Labrador Sea; MAR, Mid-Atlantic Ridge; MS, Mediterranean Sea; NS, North Sea; NoS, Nordic Seas; RR, Reykjanes Ridge; RP, Rockall-Hatton Plateau; RT, Rockall Trough. Contour levels are at 200, 2000, and 3500 m denoting the continental shelves, maximum depth of ARGO floats, and abyssal areas. Labeled currents, DSOW, Denmark Strait Overflow Water; DWBC, Deep Western Boundary Current; ESC, European Slope Current; ISOW, Iceland Scotland Overflow Waters; LSW, Labrador Sea Water; MOW, Mediterranean Overflow Water; NAC, North Atlantic Current.

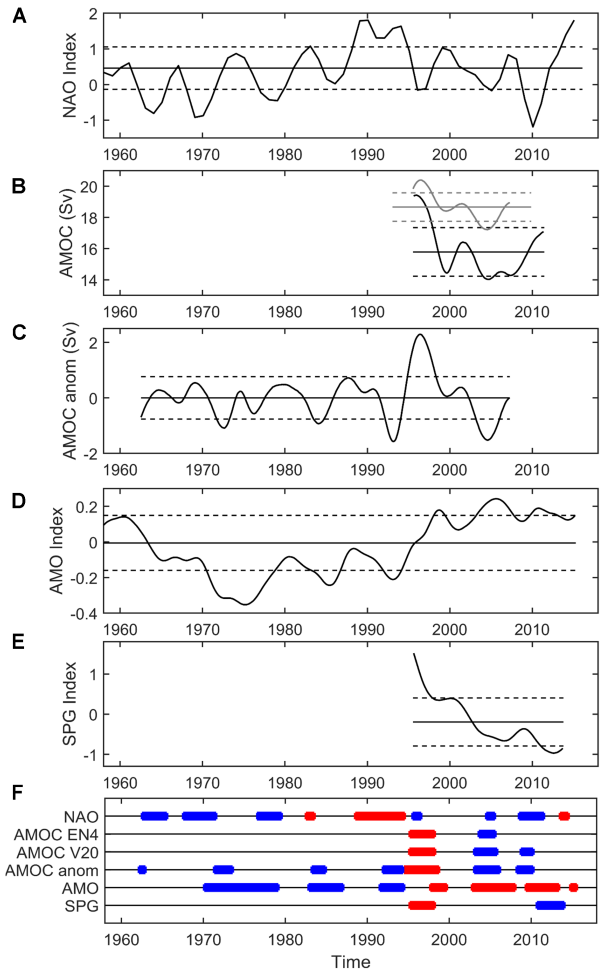


FIGURE 2 | Time-series of climate indices pertinent to the northern North Atlantic region: **(A)** North Atlantic Oscillation (NAO), **(B)** Atlantic Meridional Overturning Circulation (AMOC) (black: EN4 time-series, gray: Viking20 time-series post-1993 only), **(C)** de-trended Atlantic Meridional Overturning Circulation from Viking20, **(D)** Atlantic Multi-decadal Oscillation (AMO), and **(E)** Subpolar Gyre (SPG). All time-series have been smoothed using a 5 years Gaussian filter. Solid line shows the mean, and dashed lines ± standard deviation. **(F)** Shows the high (red) and low (blue) periods for each index that are used in the composite analysis.

Häkkinen and Rhines, 2004; Hátún et al., 2005). During a high SPG, the subpolar gyre is stronger and expands eastward (Thierry et al., 2008). Eastern areas of the subpolar North Atlantic are more strongly influenced by cooler and fresher subpolar water masses, with a reduction in the presence of warmer and saltier subtropical and inter-gyre water masses that enter from the southeast. This change is reflected in upper water properties, with lower temperatures and salinities observed in eastern areas during a high SPG (Holliday, 2003; Johnson et al., 2013). Similarly, at intermediate depths, cooler and fresher conditions are also seen during a high SPG due to the increased influence of Labrador Sea Water and reduced influence of warmer and saltier Mediterranean Water (Lozier and Stewart, 2008).

DATA AND METHODS

In this work, we use an objectively-analyzed observational dataset (EN4) to examine changes in bottom salinity (S_{bot}) and potential temperature (θ_{bot}), and output from a high-resolution, eddy-resolving ocean-only model (Viking20) to investigate changes in bottom kinetic energy (KE_{bot}).

EN4 Data

EN4 is a global, quality-controlled, objectively-analyzed, dataset of observed potential temperature and salinity profiles which has been used extensively (e.g., Prieto et al., 2015; Yang et al., 2016; Zunino et al., 2017; Chafik et al., 2019; Etourneau et al., 2019). It combines data from all types of profiling instruments, including ship-based measurements and ARGO floats, and is available as monthly averages (Good et al., 2013). EN4 has a 1° horizontal resolution meaning that smaller spatial features will not be resolved, and that large property gradients, such as around the boundary of basins, will become smoothed. Although EN4 starts in 1900, we limit our analysis to 1959 onward (to match with Viking20) but extend the analysis until December 2017 to maximize available data.

Bottom potential temperature and salinity were defined as values in the deepest depth bin at any location. The vertical grid in EN4 varies non-linearly with water depth, ranging from 10 m bins in the upper 100 m, to a maximum of ∼300 m below 3000 m. Thus measurements at any location will, at the most, be within 300 m of the sea-bed, with this value reducing as the sea-bed shallows. This vertical resolution is unlikely to greatly impact the representativeness of bottom values when the deep waters are weakly stratified; however, any vertical features smaller than the grid box depth will not be resolved. The EN4 dataset reverts to a 1971–2000 climatology in the absence of any observations (Good et al., 2013). Information for each data point (i.e., for each horizontal grid point, and at each depth level) is given in the weighting variable, which ranges from approximately zero to one. A value of zero indicates the absence of any observations for that data point, during that month, and that climatology is used. Conversely, a weighting of approximately one indicates a high influence of observations. Here we use a cut-off weighting value of 0.1, i.e., we do not use data with a weighting <0.1. This value was chosen to ensure that periods with no observations, where EN4 reverts to a pure climatology, were not included in the analyses, whilst as many observations as possible were incorporated.

Viking20 Data

Viking20 is a 1/20th degree, hindcast-forced, ocean-only model, covering the northern North Atlantic area. It is nested within a global ocean/sea-ice model using the Adaptive Grid Refinement Scheme (Debreu et al., 2008). The model was initiated with climatological temperature and salinity values, and was forced with CORE2 atmospheric data (Large and Yaeger, 2009). More details of the model configuration can be found in Böning et al. (2016). Viking20 has been used in many studies, including those to investigate: the North Atlantic Current (Breckenfelder et al., 2017), convection in the Labrador Sea (Böning et al., 2016),

Denmark Strait Overflow Water (Behrens et al., 2017), the Deep Western Boundary Current (Mertens et al., 2014; Handmann et al., 2018), and seasonal changes in the eastern subpolar North Atlantic (Gary et al., 2018).

We use Viking20 output as 5 days averages from 1959 to 2009 to investigate changes in bottom kinetic energy. Bottom horizontal velocities (u_{bot}, v_{bot}) were extracted from the bottom grid point at a particular location. As for EN4, grid box thickness varies non-linearly with depth; from <10 m in the upper 50 m, to a maximum of ∼250 m in the deepest points of the model domain. The vertical resolution of Viking20 is not dissimilar to that of EN4, and the same limitations apply. For example, real-world smaller-scale frictional effects, such as benthic boundary layers, will not be resolved in the velocity field. As our goal was to study kinetic energy, rather than velocities, u_{bot} and v_{bot} were first linearly interpolated from their respective grids onto the grid containing θ_{bot} and S_{bot}. Bottom mean kinetic energy was then calculated as the sum of the squares of mean u_{bot} and v_{bot}, with the eddy kinetic energy defined as the sum of the variances of u_{bot} and v_{bot}. As our data are 5 days averages, variances represent energy of sub-inertial flows.

Ecosystem Case Studies

As well as considering spatio-temporal patterns at the basin-scale, we examine temporal changes at fourteen case study sites (**Figure 1** and **Table 1**). These sites were chosen to represent a variety of potentially vulnerable deep-sea ecosystems across the northern North Atlantic region as indicated by VME indicator records (Morato et al., 2018). The sites also include a number of existing, or proposed, Marine Protected Areas (MPAs), Ecologically or Biologically Significant Areas (EBSAs), and VME closures (Johnson et al., 2018). Although four sites have maximum depths below 3500 m (**Table 1**), there is no site that truly represents the abyssal plains of the North Atlantic south of 50°N. This reflects the current absence of VME indicator records in these areas (Morato et al., 2018). Time-series were constructed for each case study site. In EN4, data within each case study polygon were simply averaged for each monthly time-step. As case studies 4 and 10 did not contain any EN4 grid points; time-series for these sites were instead extracted from the nearest EN4 grid point. In Viking20, the model grid is curvilinear. Thus, grid points were accordingly area weighted when calculating averages for each 5 days time-step.

TABLE 1 | Description of case study regions chosen to represent a range of Atlantic Vulnerable Marine Ecosystems and management regimes.

Case studies		Area ($\times 10^3$ km^2)	Mean depth (m)	Std depth (m)	Min. depth (m)	Max. depth (m)
1	LoVe Observatory	2.2	746	806	1	2298
2	Western Scottish Slope	5.3	596	133	234	952
3	Rockall Bank	301.4	1470	746	21	3026
4	Mingulay Reef	0.1	196	25	148	230
5	Porcupine Sea Bight	218.2	2187	1517	39	4844
6	Bay of Biscay	238.5	2744	2073	1	5026
7	Gulf of Cadiz/Alboran Sea	43.4	697	434	1	1872
8	Azores	954.2	3064	1104	1	5627
9	Reykjanes Ridge	388.1	1927	453	499	3209
10	Davis Strait	8.2	962	537	518	2319
11	Flemish Cap	124.4	1471	1218	128	4664
12	USA Mid-Atlantic Canyons	16.5	750	717	32	2205
13	European Slope	61.2	1243	807	57	3009
14	North Sea	112.0	99	25	40	179

All statistics exclude areas of land and were calculated using ETOPO2 bathymetry.

Climate Indices

We consider the four most commonly used climate indices for the North Atlantic Ocean: the NAO, AMOC, AMO, and SPG. The NAO index used is defined as the normalized pressure difference between Gibraltar and southwest Iceland (Jones et al., 1997). Data were downloaded from the Climatic Research Unit[1] and the winter (DJFM) mean calculated. As Viking20 is forced with CORE2 atmospheric data, which will include a signature of the NAO, we use the observational NAO time-series to investigate ocean correlations in both the EN4 and Viking20 datasets.

For the AMOC, we use the commonly used definition of the maximum in the overturning stream function in density space (e.g., Mercier et al., 2015; Lozier et al., 2019). As this index is calculated from oceanic rather than atmospheric variables, and changes in the model and observational AMOC may not be contemporaneous, we compute two AMOC time-series: one from EN4 and one from Viking20. For the observational dataset we used the method of Mercier et al. (2015), but using EN4 data along the OSNAP-EAST section (black line, **Figure 1A**). Geostrophic velocities perpendicular to the section were calculated from EN4 temperature and salinity data and referenced to satellite altimetry data. The Viking20 AMOC time-series was calculated using model velocities perpendicular to the OSNAP-EAST section.

We use an AMO index downloaded from the National Oceanic and Atmospheric Administration[2] as monthly averages. This time-series consists of sea surface temperatures, averaged over 0–70°N before de-trending using a 10 year running mean (Enfield et al., 2001). The AMO is also an oceanic index, suggesting that again a model and observational time-series is required. Although the construction of an AMO index from Viking20 was considered, it was discounted for two reasons. Firstly, the AMO index is calculated using sea surface temperatures over the entire North Atlantic; however, the Viking20 nested model domain starts at 32° N (Böning et al., 2016). This makes the calculation of an AMO index from Viking20 more complex. Secondly, Viking20 is an ocean-only model meaning that feedbacks between the ocean and atmosphere are not fully represented. As previous work suggests there is a requirement for fully-coupled models in order to represent important teleconnections

[1] https://crudata.uea.ac.uk/cru/data/nao/

[2] https://www.esrl.noaa.gov/psd/data/timeseries/AMO/

(Ruprich-Robert et al., 2017), we focus on the observational AMO index and therefore do not investigate changes in KE_{bot} using Viking20.

The SPG index used is defined as the first principal component of the sea surface height field between 40 and 65° N and 60° W to 10° E (Berx and Payne, 2017). This was downloaded from https://data.marine.gov.scot/dataset/sub-polar-gyre-index as monthly averages. Again, we considered extracting out a model-based SPG time-series from Viking20 to use in conjunction with the observational index. However, the basin-averaged sea surface height field in Viking20 exhibits a drift after the mid-1990s, which would redistribute power among the principal components used to generate the SPG index. As such, we again focus on the observational SPG and interrogate only the EN4 dataset. Although there may be a large-scale drift in the Viking20 sea surface height field, gradients in sea surface height and the overall circulation patterns in the model output compare well to observations (e.g., Breckenfelder et al., 2017; Gary et al., 2018).

Composite Method

In order to investigate any differences in near-bed conditions associated with each climate index, we use the commonly-used composite method (e.g., Terray et al., 2003; Häkkinen et al., 2011; Tulloch and Marshall, 2012). For each climate index, "high years" were defined as those exceeding one standard deviation above the mean, and "low years" as those less than one standard deviation below the mean. Composites for the high and low climate states were calculated by averaging properties from all high and low years respectively. One of the limitations of the composite approach is that it only considers high and low states, and not transitional processes between the two. As the Viking20 AMOC time-series shows a long-term trend and we are interested in multi-annual changes, we de-trended this index before creating the composites. The time-series was de-trended by assuming a linear long-term trend which may not be entirely appropriate for low-frequency oscillations. However, the record is too short to establish any low-frequency variability more accurately, and de-trending enables us to investigate multi-annual changes over a 50 year period. The number of months averaged to create each composite are shown in **Table 2**.

The statistical significance of observed changes at the 95% confidence level were tested using the method detailed in Terray et al. (2003), which we briefly describe here. At each grid point (X), we assess whether the values observed during the high years, or the low years (class j), are significantly different from a combined group made up of high and low years only. The years within one standard deviation from the mean are not included because the composite analysis only compares two groups: high and low years. The mean of class j ($\overline{x_j}$) is therefore compared to the mean of the combined high and low time-series ($\bar{x}$), with respect to the standard error (Equations 1, 2).

$$U(X) = abs((\overline{x_j} - \bar{x})/s_j) \quad (1)$$

$$s_j = \sqrt{(n - n_j)/(n_j \times (n-1))} \times s \quad (2)$$

where: s is the standard deviation of the combined high and low time-series; and n and n_j the number of data points in the combined time-series and class j respectively.

This procedure tests whether or not the high and low years were allocated randomly from the combined group. If the high years and low years are allocated randomly, $U(X)$ will approach zero. Hence, the larger $U(X)$, the more diverse the high and low years, and the less likely that the high and low years were randomly selected. It should be noted that $U(X)$ calculated with the high years as class j, is identical to $U(X)$ calculated with the low years as class j. We set the critical value as 1.96, with values of $U(X)$ exceeding this indicating that the two means are statistically significantly different at the 95% confidence level.

TABLE 2 | Number of months used to create the high and low composites for each climate index: North Atlantic Oscillation (NAO), Atlantic Meridional Overturning Circulation (AMOC), Atlantic Multi-decadal Oscillation (AMO), and Subpolar Gyre (SPG).

Climate index	Relevant figure	N_{high} (months)	N_{low} (months)
NAO	**Figures 5**, **6A**	32	60
AMOC (EN4)	**Figures 7A,B**	28	16
AMOC (V20)	**Figures 6B**, **7C,D**	43	98
AMO	**Figure 8**	112	169
SPG	**Figure 9**	28	32

*For the AMOC two different time-series are used: (1) the EN4 time-series (black, **Figure 2B**), and (2) the 1959–2009 de-trended Viking20 time-series (**Figure 2C**).*

RESULTS: LONG-TERM MEAN STATE

In order to provide a baseline for interpreting temporal changes, we first present the long-term mean and associated variability as basin-wide maps. Since the variability of shallower waters can be orders of magnitude larger than that of deeper waters, the variability maps are shown on a $\log_{10}$ scale to highlight the changes over the whole domain. We use the objectively-analyzed observational dataset (EN4) to investigate changes in S_{bot} and θ_{bot} (**Figure 3**), and output from a high-resolution model (Viking20) to examine changes in KE_{bot} (**Figure 4**).

The lowest mean S_{bot} values are seen on the North American Shelf (<34.0) and in the Baltic Sea (<10.0), whilst the highest S_{bot} values are seen in the Mediterranean Sea (>37.0) and on the European Shelf west of the UK and Ireland (35.40–35.55) (**Figure 3A**). Relatively high S_{bot} values are also seen over the shallower Rockall-Hatton Plateau (35.0–35.3), over the eastern Greenland-Scotland Ridge (35.0–35.2), and along the Norwegian Coast (35.0–35.2). In contrast, fresher conditions (34.4–34.7) are seen north of the Davis Strait. Bottom salinity in areas deeper than ∼2000 m is fairly uniform (34.85–35.00), although S_{bot} decreases with water depth, and slightly more saline bottom conditions are observed in eastern parts of the subpolar region. There is little difference between S_{bot} values in the northern North Atlantic and Nordic Seas.

Variability in S_{bot} is strongly related to water depth (**Figure 3B**), with the highest variability on the continental shelves (±0.1–0.4), and the lowest variability seen in areas deeper

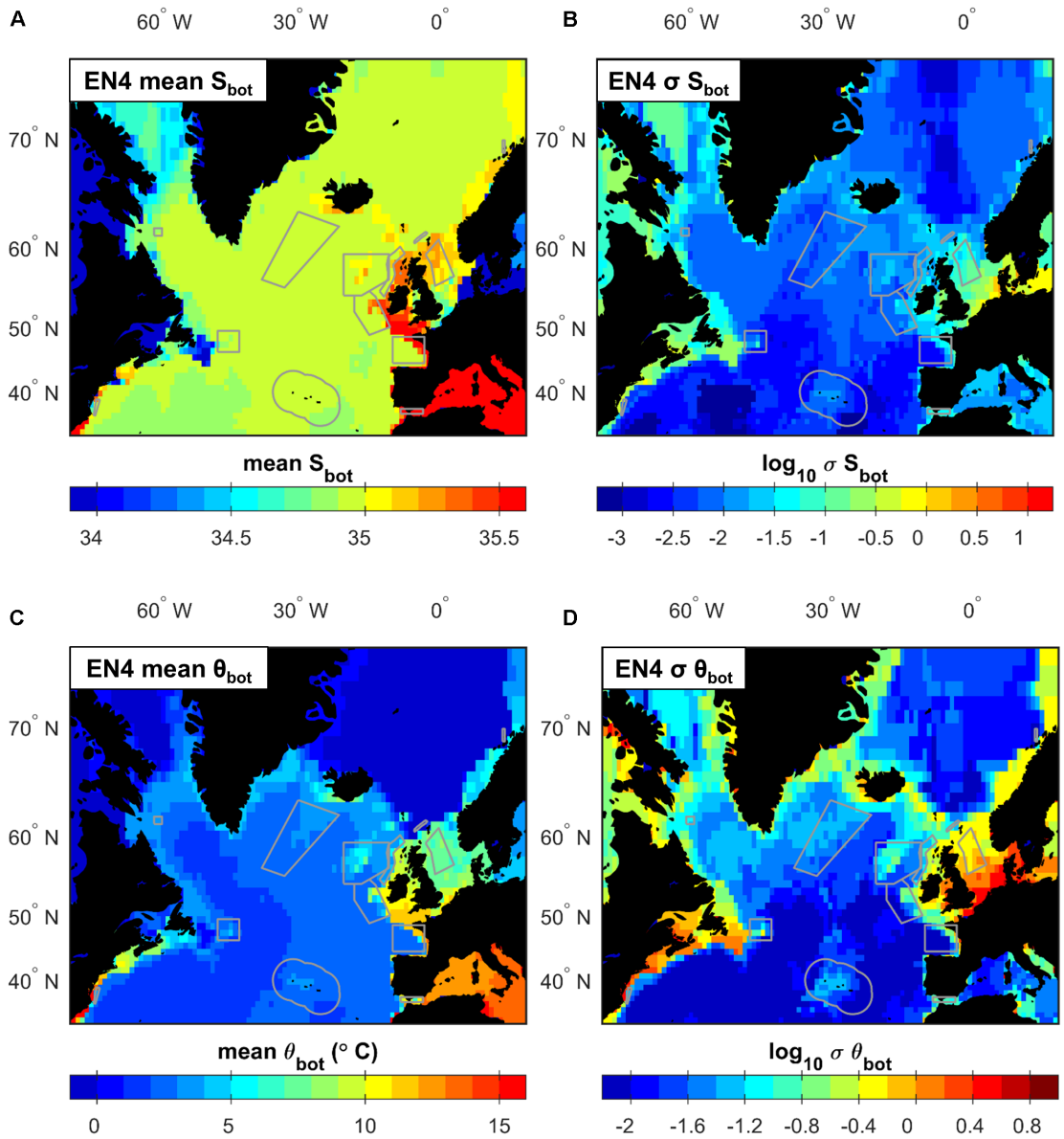


FIGURE 3 | Maps of mean **(A)** bottom salinity and **(C)** potential temperature (°C) between 1959–2017 in EN4, and associated standard deviations **(B,D)**. Gray boxes show case study areas. To fully resolve variability across bathymetric-depths, **(B,D)** are shown on a $\log_{10}$ scale.

than 2000 m (±<0.01). However, there is also spatial variability within these general descriptions. For example, variability is higher in the southern North Sea compared to the northern North Sea and shelf areas west of the UK and Ireland.

The highest θ_{bot} values (>15°C) are seen on the North American Shelf south of around 40°N and in the Mediterranean Sea (>12°C) (**Figure 3C**). Relatively high values are also seen in the southern North Sea and on the European Shelf west of the UK and Ireland (10–12°C). The coldest bottom conditions (<0°C) are seen in the Nordic Seas and north of the Davis Strait. In contrast, θ_{bot} values in the northern North Atlantic range from 1 to 3°C with an east-west split. Warmer θ_{bot} values are seen in areas shallower than approximately 2000 m, such as over the Greenland-Scotland Ridge (3–5°C), around the boundaries of the subpolar basins (3–5°C), and over the Rockall-Hatton Plateau (4–7°C).

Variability in θ_{bot} is again mainly constrained by water depth (**Figure 3D**), with the highest values observed in the southern North Sea (±2.0–4.0°C) and on the North American Shelf (±1.5–3.0°C). In contrast, lower variability is observed in the deep northern North Atlantic and Nordic Seas (±<0.04°C). In the subpolar North Atlantic, higher variability (0.04–0.06°C) is observed in the Labrador Sea and Irminger Sea compared to the more eastern basins.

The highest KE_{bot} ($>10 \times 10^2$ m^2s^{-2}) (**Figure 4A**) is associated with the flow of Denmark Strait Overflow Water in

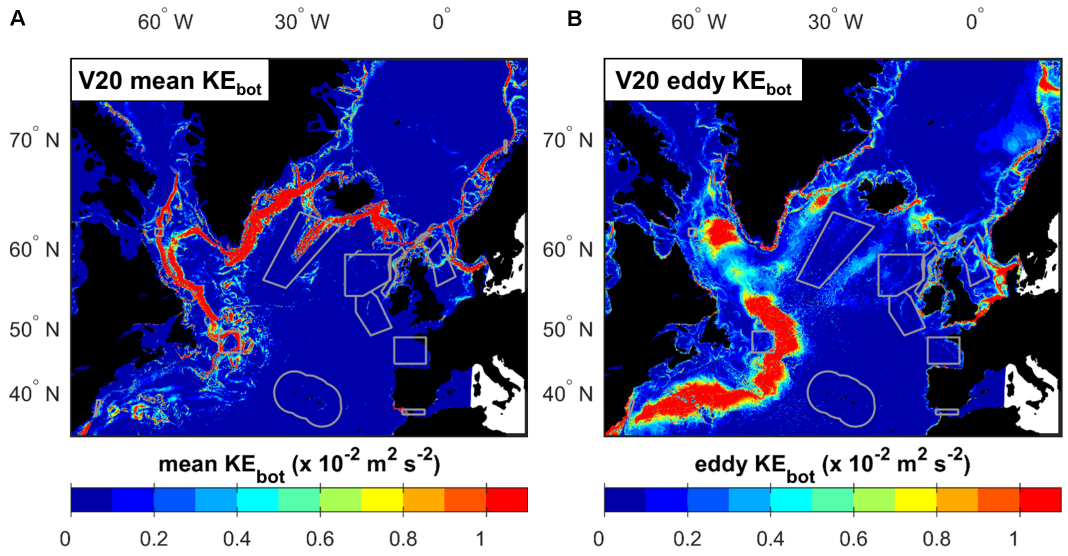


FIGURE 4 | Maps of **(A)** mean bottom kinetic energy and **(B)** associated eddy kinetic energy ($\times 10^{-2}$ m^2s^{-2}) from 1959 to 2009 in Viking20. Gray boxes show case study areas.

the Irminger Sea, and Iceland Scotland Overflow Water in the Iceland Basin. In addition, high KE_{bot} values (1–10 $\times$ 10^{-2} m^2s^{-2}) are observed in the cyclonic boundary currents of the subpolar gyre, including around the boundary of the Labrador Sea and in the Deep Western Boundary Current. Energetic conditions ($>1 \times 10^{-2}$ m^2s^{-2}) are also associated with the European Slope Current along the northern European and Norwegian Shelves. Other areas, such as the deep northern North Atlantic and Nordic Seas, have low KE_{bot} ($<0.1 \times 10^{-2}$ m^2s^{-2}).

The highest values of eddy KE_{bot} (1–2 $\times$ 10^{-2} m^2s^{-2}) (**Figure 4B**) are associated with the Deep Western Boundary Current, although this is over a wider spatial area than the higher KE_{bot} signal. High eddy KE_{bot} values ($\sim 1 \times 10^{-2}$ m^2s^{-2}) are likewise associated with the overflow currents, as well as in the convection areas of the Labrador and Irminger Seas. High eddy KE_{bot} is also seen in the European Slope Current, although this is of lower magnitude than that seen for the deeper currents. Finally, areas of higher eddy KE_{bot} are seen on the continental shelves; including in the southern North Sea, on the North American Shelf south of around 40°N, and on both the East and West Greenland Shelves.

RESULTS: SPATIAL VARIABILITY LINKED TO CLIMATE INDICES

Having described the long-term mean and variability, we now examine changes associated with each climate index in turn using the composite approach detailed in section Composite Method. Again, we use the objectively-analyzed observational EN4 dataset to investigate changes in S_{bot} and θ_{bot}, and output from the Viking20 model to examine changes in KE_{bot}. For EN4, we only describe changes where a cut-off weighting is exceeded for both the high and low composites; this ensures the exclusion of periods with no observations. Plots comparing the spatial footprint of different cut-off weightings, ranging from 0.05 to 0.25, are shown in **Supplementary Figures S1–S4**. For the NAO, the spatial distribution of data for cut-off values ranging from 0.1 to 0.25 is almost identical. For the AMOC, AMO, and SPG there are some small differences; for example: in the eastern Nordic Seas and around the Reykjanes Ridge for the AMOC, in the eastern Nordic Seas and Iceland Basin for the AMO, and in the eastern Nordic Seas for the SPG. However, all cut-off weightings retain data: on the continental shelves, around the boundaries of the basins of the subpolar North Atlantic, over the Reykjanes Ridge, over the Greenland-Scotland Ridge, over the Icelandic Plateau, and around the boundaries of the Nordic Seas. We chose a cut-off weighting of 0.1 to retain as many observations as possible, with only areas where this is exceeded for both the high and low composites included. Although there is a level of subjectivity when choosing the EN4 cut-off weighting, as an additional control we carried out statistical testing (as detailed in section Composite Method). Only changes between the high and low years that are statistically significant at the 95% confidence level are discussed. As pure climatology would have no significant correlations, we can be sure that any statistically significant patterns are due to the presence of data.

North Atlantic Oscillation (NAO)

The largest changes in S_{bot} and θ_{bot} associated with the NAO are observed on the continental shelf areas (**Figure 5**). The European and North American Shelves are anti-correlated: when the NAO is high, warmer and more saline bottom conditions are seen in the North Sea but cooler and fresher values are seen around Grand Banks. Whilst bottom conditions in the Grand Banks area are −0.5 to −1.3°C cooler, and −0.1 to −0.25 fresher, during a high NAO period relative to a low NAO period, the North Sea bottom

values are 1.0–1.3°C warmer and 0.2–1.2 saltier. The area to the west of Norway is also 0.03–0.5°C warmer during high NAO periods compared to low NAO periods, although a corresponding S_{bot} signal is absent.

When investigating signals away from the continental shelves, there is limited observational data, particularly below 2000 m. Nevertheless, some spatially coherent and statistically significant changes can be seen. In the Mediterranean Sea, warmer and saltier bottom conditions (0–0.3°C and 0–0.02) are observed during a high NAO. In contrast, lower S_{bot} and θ_{bot} values (<-0.02 and <-0.2°C respectively) are seen in the subpolar gyre, for example around the boundaries of the Labrador Sea and Irminger Sea, over the Reykjanes Ridge, and over the Rockall-Hatton Plateau. In particular, less saline bottom conditions (-0.02 to -0.04) are observed in eastern areas extending on to the shelf west of Scotland, and over the Greenland-Scotland Ridge along pathways of the North Atlantic Current and European Shelf Current.

Viking20 output can be used to evaluate changes in KE_{bot} (**Figure 6A**). During a high NAO, bottom currents are enhanced along the eastern boundary of the northern North Atlantic with higher KE_{bot} stretching along the European and Norwegian Shelf break, and into the North Sea. This is likely to indicate a stronger European Slope Current during a high NAO. Higher KE_{bot} is also observed along the Denmark Strait Overflow Water pathways around the western boundary of the Irminger Sea, although lower KE_{bot} values are seen around the northern and western boundaries of the Iceland Basin which is influenced by Iceland Scotland Overflow Water. Finally, lower KE_{bot} is seen on shelf areas to the north and west of the Labrador Sea.

Atlantic Meridional Overturning Circulation (AMOC)

To investigate changes associated with the AMOC, we start by using the post-1993 observational AMOC time-series to examine changes in the EN4 dataset (**Figures 7A,B**). The North American, European and Norwegian Shelves all have lower S_{bot} values (-0.1 to -0.5) during high AMOC states. While θ_{bot} values are also lower (-0.4 to -0.8°C) on northern parts of the North American Shelf and around Grand Banks during a high AMOC, south of around 50°N warmer (0.5–2.5°C) bottom conditions are seen. Additionally, on the European Shelf, statistically significant changes in θ_{bot} (-0.4 to -0.8°C) are only observed in the northern areas of the North Sea. The lower θ_{bot} values during a high AMOC on the Norwegian Shelf are also less pronounced than the observed freshening. Hence, on the continental shelves, changes in S_{bot} and θ_{bot} associated with the NAO are not simply correlated.

Moving now to oceanic areas, fresher and in particular cooler conditions are seen in most regions during a high AMOC. The largest changes (up to -0.35°C and -0.05) are seen around the boundaries of the Labrador Sea, Irminger Sea and Iceland Basin, as well as over the Greenland-Scotland Ridge. Although S_{bot} and θ_{bot} are lower during a high AMOC in the majority of areas, warmer and more saline bottom conditions are also seen. For example, the Rockall Trough and eastern Iceland Basin are up to 0.011 more saline during a high AMOC. More saline conditions are also observed in the eastern Nordic Seas. In contrast, areas of warmer bottom conditions during a high AMOC are patchy. Despite the higher S_{bot} values in the Rockall Trough during a high AMOC, fresher (0 to -0.05) conditions are still observed over the shallower Rockall-Hatton Plateau and on the European Shelf west of the UK.

As the timing of changes in strength between the observational and modeled AMOC compare extremely well during the contemporaneous period (**Figures 2B,F**), we now use the de-trended Viking20 AMOC time-series to interrogate the EN4 dataset (**Figures 7C,D**). Applying the Viking20 AMOC time-series to the EN4 data assumes that the relationship between the observed and modeled AMOC persists outside the post-1993 era. However, the advantage is that it increases the amount of observational data used in the construction of the composites (**Table 2**) therefore increasing the spatial extent of the analysis.

Many spatial features observed in the composites created using the observed AMOC time-series (**Figures 7A,B**), are also seen in those created from the de-trended Viking20 AMOC time-series (**Figures 7C,D**). However, the magnitude of changes are often lower in the model AMOC composites. The extended selection period for the ocean observations is particularly noticeable in the relatively data-sparse areas deeper than 2000 m. Changes in bottom conditions are now revealed in the central Labrador and Irminger Seas, and for areas between approximately 40–52°N, which in the observational AMOC composite had a mean EN4 weighting of <0.1 and were therefore grayed out. Bottom conditions in the central Labrador Sea and Irminger Sea are also cooler (<-0.02) and fresher (<-0.2°C) during a high AMOC. While fresher conditions are seen south of approximately 52°N, warmer θ_{bot} values are seen in western areas.

Finally, we use Viking20 and the modeled AMOC time-series to examine changes in KE_{bot}. We present a high minus low map created from the longer de-trended time-series (**Figure 6B**), which is very similar to the composite compiled from the post-1993 time-series in Viking20 (not shown). Stronger bottom currents are seen around the northern and western boundaries of the subpolar gyre as well as around Grand Banks. KE_{bot} in these areas is $0.5–1.5 \times 10^{-2}$ m^2s^{-2} greater during a high AMOC than a low state. Although changes are seen along the European and Norwegian Slopes, these are not statistically significant.

Atlantic Multi-decadal Oscillation (AMO)

As discussed in section Climate Indices, it is not appropriate to apply the AMO time-series to output from Viking20; thus we examine changes using the EN4 dataset only and do not discuss KE_{bot}. High minus low values for the AMO are positive on the North American, Western European, and Greenland Shelves (**Figure 8**), with bottom conditions 0.6–1.0°C warmer and 0.02–0.2 more saline during a high AMO. Warmer and saltier conditions are also seen over the shallower Greenland-Scotland Ridge where S_{bot} and θ_{bot} are up to 0.8°C

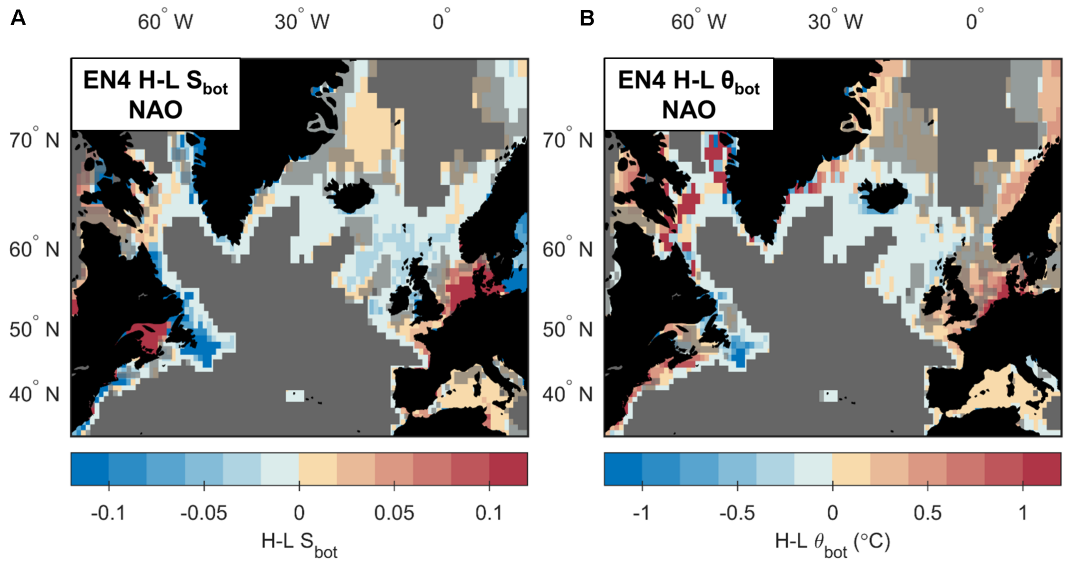


FIGURE 5 | Maps of differences in bottom conditions between high and low states of the North Atlantic Oscillation (NAO) in EN4: **(A)** bottom salinity changes and **(B)** bottom potential temperature changes. Transparent gray shading shows areas where the H minus L is not statistically different at the 95% confidence limit, and solid gray shading areas with an EN4 weighting of <0.1 for either the high or low years.

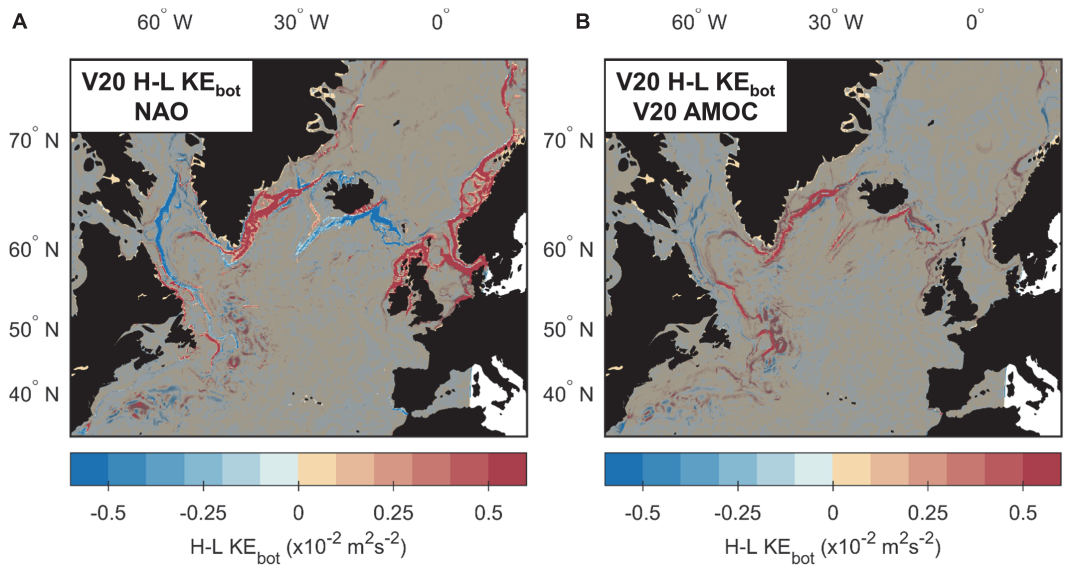


FIGURE 6 | Maps of differences in bottom kinetic energy in Viking20 between the high and low states of the **(A)** North Atlantic Oscillation (NAO) and **(B)** de-trended 1959–2009 Atlantic Meridional Overturning Circulation (AMOC). Transparent gray shading shows areas where the H minus L is not statistically different at the 95% confidence limit.

warmer during a high AMO state relative to a low AMO state, and up to 0.06 more saline. In regions deeper than 2000 m, there is a split between areas north and south of the Greenland-Scotland Ridge. In the deep Nordic Seas, θ_{bot} and S_{bot} are higher during a high AMO. In contrast, cooler and less saline bottom conditions are seen below approximately 2000 m in the northern North Atlantic. The magnitude of the changes in θ_{bot} and S_{bot} in both these regions are ± 0–0.02 and ± 0–0.2°C respectively. There is insufficient data to assess any changes in areas deeper than 2000 m south of around 45–50°N.

Subpolar Gyre (SPG)

For the SPG, we again only examine changes in the EN4 dataset. Bottom conditions are cooler and fresher during a high SPG for the vast majority of the northern North Atlantic region regardless of bathymetric depth (**Figure 9**). On the continental shelves, lower S_{bot} values are seen on the North American (−0.15

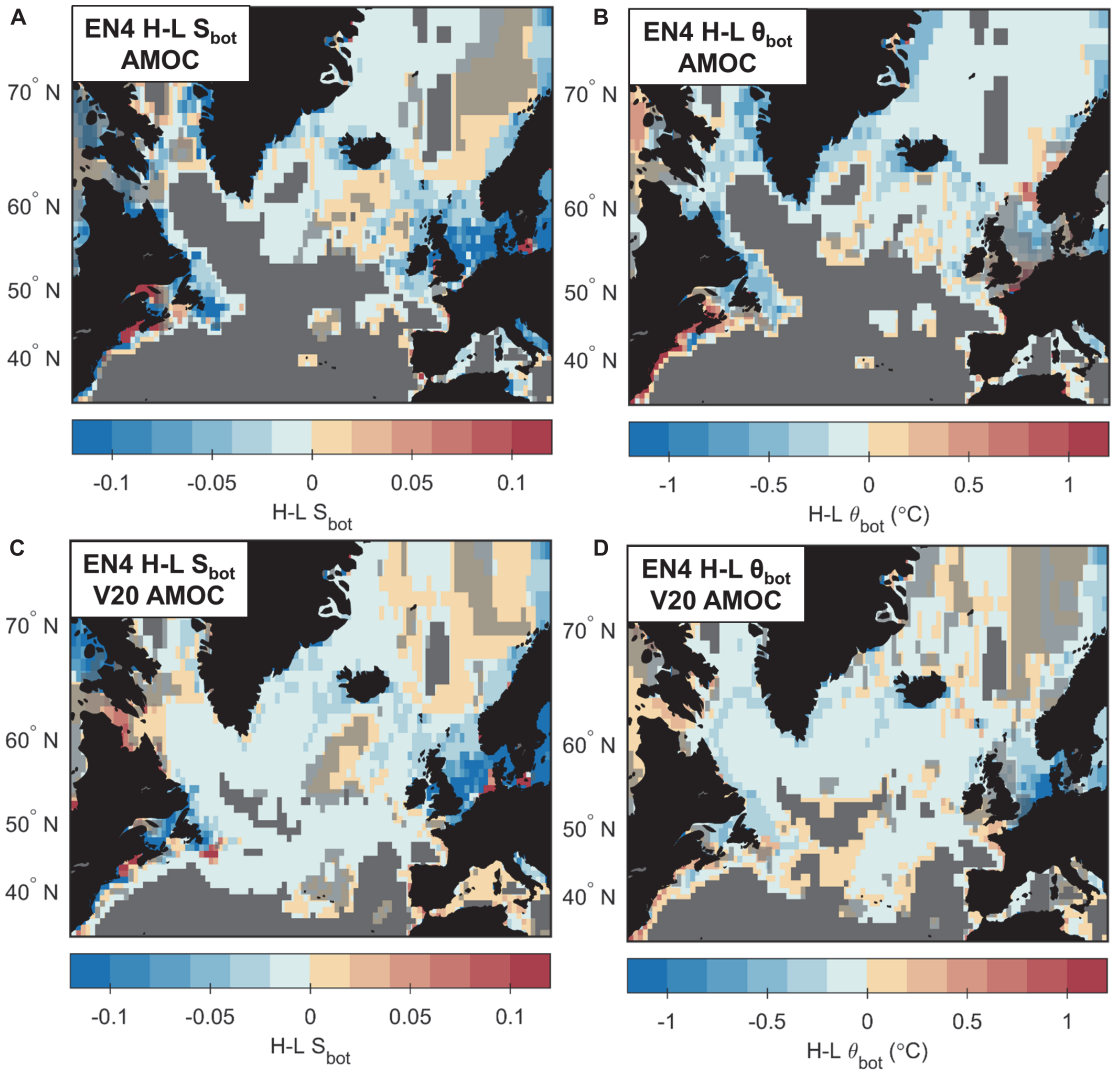


FIGURE 7 | Maps of differences in bottom conditions between high and low states of the Atlantic Meridional Overturning Circulation (AMOC) in EN4: **(A)** bottom salinity changes and **(B)** bottom potential temperature changes constructed using the EN4 AMOC time-series, and **(C)** bottom salinity changes, and **(D)** bottom potential temperature changes constructed using the de-trended 1959–2009 Viking20 AMOC time-series. Transparent gray shading shows areas where the H minus L is not statistically different at the 95% confidence limit, and solid gray shading areas with an EN4 weighting of <0.1 for either the high or low years.

to −0.50), European (−0.04 to −0.25) and Norwegian Shelves (−0.04 to −0.08). However, decreased θ_{bot} values are observed only on the North American shelf (−0.8 to −1.5°C) with the absence of a cooling in the North Sea. On the Norwegian Shelf, cooler bottom waters are only seen north of approximately 70°N, even though the change in S_{bot} is widespread. Hence, whilst S_{bot} and θ_{bot} co-vary on the North American Shelf, this relationship does not exist in the North Sea and Norwegian Shelf. Despite the lack of a statistically robust temperature signal in the North Sea, lower θ_{bot} values (−0.2 to −0.8°C) are still observed on the European Shelf west of Scotland during a high SPG.

Away from the continental shelves, fresher and cooler conditions are observed in the majority of areas during a high SPG. Changes are particularly pronounced around the boundaries of the Labrador and Irminger Seas, and over the Reykjanes and Greenland-Scotland Ridges. In these areas, bottom conditions are −0.02 to −0.06 fresher during a high SPG, relative to a low SPG, and −0.2 to −0.8°C colder. Cooler (0 to −0.1°C) and fresher (0 to −0.01) conditions are also observed in areas of the Labrador and Irminger Seas deeper than 2000 m, although these changes are smaller than those observed at the boundaries. In the eastern subpolar gyre, there are some areas of higher θ_{bot} and S_{bot}. In particular, bottom conditions in the Iceland Basin and Rockall Trough are up to 0.015 more saline during a high SPG than a low SPG. North of the Greenland-Scotland Ridge, the majority of the Nordic Seas show lower θ_{bot} values during a high SPG. However, again there are areas of more saline S_{bot} values, mainly in the eastern portions of the region.

Finally, we note that the pattern of changes in S_{bot} and θ_{bot} seen between the high and low states of the SPG (**Figure 9**),

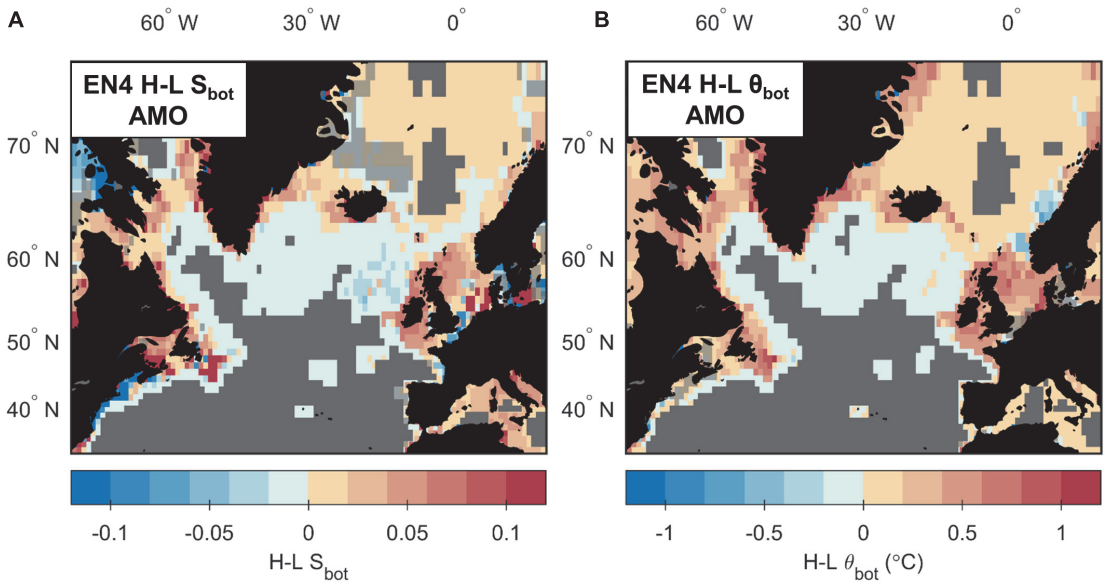


FIGURE 8 | Maps of differences in bottom conditions between high and low states of the Atlantic Multi-decadal Oscillation (AMO) in EN4: **(A)** bottom salinity changes and **(B)** bottom potential temperature changes. Transparent gray shading shows areas where the H minus L is not statistically different at the 95% confidence limit, and solid gray shading areas with an EN4 weighting of <0.1 for either the high or low years.

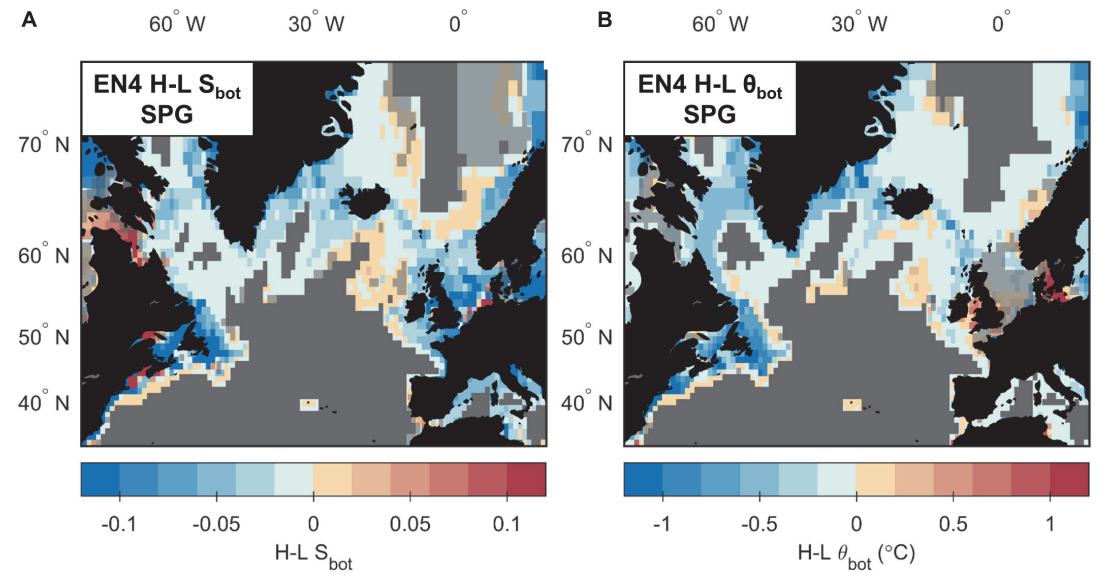


FIGURE 9 | Maps of differences in bottom conditions between high and low states of the Subpolar Gyre (SPG) in EN4: **(A)** bottom salinity changes and **(B)** bottom potential temperature changes. Transparent gray shading shows areas where the H minus L is not statistically different at the 95% confidence limit, and solid gray shading areas with an EN4 weighting of <0.1 for either the high or low years.

are very similar to that seen for the AMOC; particularly when considering the post-1993 AMOC time-series (**Figures 7A,B**). Although this may reflect a link between the two climate indices, the selection periods for the two indices are very similar (**Figure 2F**): the months used to create the high SPG average are almost identical to those used to create the post-1993 high AMOC composite, whilst the input periods for the low composites are sequential to each other. This suggests that a similar signal may be represented for both indices, and thus it is hard to define whether the observed changes are dominated by the SPG, or the AMOC, or indeed whether the two indices act in unison.

Comparison Between Indices

We now examine the spatial dominance of each index by asking a simple question: which climate index is associated with the largest changes at each location? This enables us to examine

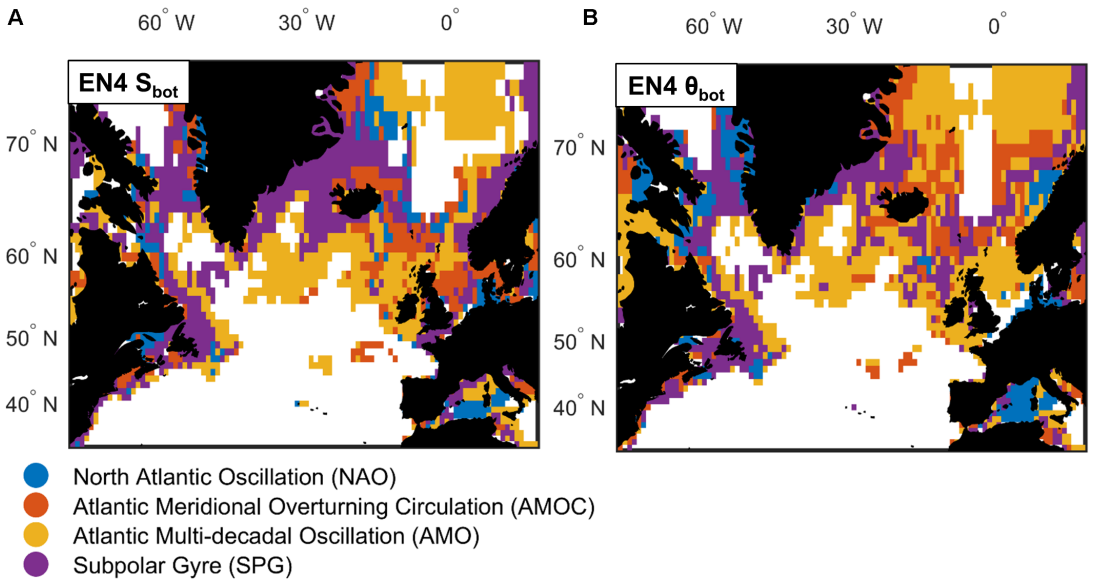


FIGURE 10 | Map summarizing the climate index associated with the largest change in: **(A)** bottom salinity, and **(B)** bottom potential temperature, in EN4. Colors correspond to the dominant climate index, with white areas showing areas where no climate index has significant differences at the 95% confidence level, and EN4 weightings >0.1 for both the high or low years.

whether there are spatially coherent patterns, and how these vary both in the horizontal and vertical. As we have investigated more climate indices in EN4, we focus on the changes in S_{bot} and θ_{bot}. Again, we only consider changes that are statistically significant at the 95% confidence level, and where there is a weighting >0.1 for both the high and low composites. Although the patterns of variability for the AMOC and SPG are very similar, we include both indices separately to see if perhaps there is a spatial difference between the two.

The dominant climate index pattern is reasonably similar for S_{bot} and θ_{bot}, although they are not identical (**Figure 10**). Whilst some areas are patchy, there are also some spatially coherent signals and general observations to be made. For example, where there is sufficient data to assess changes below 2000 m, the AMO is associated with the largest changes. This is true both in the Nordic Seas and northern North Atlantic. In contrast, the SPG dominates changes in areas shallower than 2000 m in the western subpolar North Atlantic, whilst the AMOC becomes more important in eastern areas. In the Mediterranean Sea, the NAO is associated with the largest changes, particularly when considering θ_{bot}. Changes on the North American Shelf are dominated by the SPG, whereas the shelf west of the UK is dominated by the AMO. In the North Sea the AMO also dominates changes in θ_{bot}, whilst the AMOC is more important for changes in S_{bot}.

RESULTS: VARIABILITY AT ECOSYSTEM CASE STUDY SITES

We now move on to discussing changes at fourteen case studies (**Figure 1** and **Table 1**) chosen to represent various VMEs across the northern North Atlantic region. As these sites cover a number of management measures, such as ESBAs, MPAs, and VME closures, and are therefore often considered as a single entity, we show mean conditions averaged across each location. However, we caution that most case studies cover a range of depths (**Table 1**), which may be subject to different processes and signals, as well as lag periods. As such, changes at a particular depth may be different to the mean conditions for the entire case study site. For example, at Case Study 9 on the Reykjanes Ridge (**Figure 1**), the SPG is associated with the largest changes in S_{bot} in areas shallower than approximately 2000 m, whilst the largest changes in deeper areas are linked to the AMO (**Figure 10**). Additionally, if signals at different depths are opposing, changes averaged across the case study as a whole may be muted, despite statistically significant changes in individual depth layers. Similar effects will be produced in spatially heterogeneous areas, for example at case study 14 in the northern North Sea (**Figure 1**). Here, the AMOC is associated with the largest changes in S_{bot} in southern areas, whilst the largest changes in the northern part of the case study region is associated with the AMO (**Figure 10**). However, when the S_{bot} changes are averaged over the entire case study region, only the AMO is associated with statistically significant changes. Finally, as changes are often larger at shallower depths, case study averages are likely to be biased toward processes occurring higher in the water column. As such, we advise the reader to consider the results in this section in conjunction with Section Results: Spatial Variability Linked to Climate Indices and **Figures 5–10**.

We again use the EN4 dataset to examine changes in S_{bot} and θ_{bot}, and output from Viking20 to investigate changes in KE_{bot} although this is only for the NAO and AMOC. Time-series for each case study site are shown in

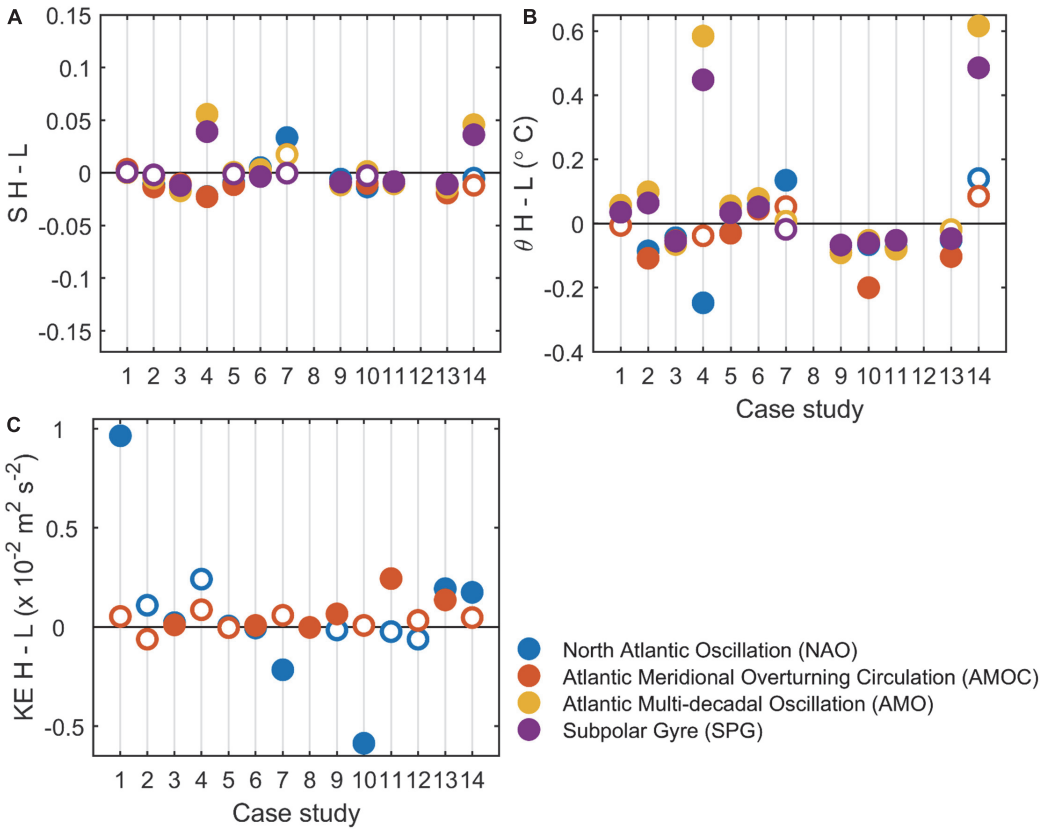


FIGURE 11 | Summary of changes associated with each climate index at the fourteen case study sites: **(A)** EN4 bottom salinity changes, **(B)** EN4 bottom potential temperature changes, and **(C)** Viking20 bottom kinetic energy changes. Filled circles represent changes significant at the 95% level, whilst unfilled circles show non-significant changes. Changes in EN4 where the data weighting is <0.1 for either the high or low composite are not shown. The AMOC in **(A,B)** represents the EN4 time-series, whilst the AMOC in **(C)** represents the post-1993 time-series from Viking20.

Supplementary Figures S5–S18, whilst changes between high and low climate states are summarized in **Figure 11** and **Tables 3**, **4**. Again we consider the AMOC and SPG separately, and only describe changes in EN4 where the mean data weighting over the case study as a whole exceeds 0.1 for both the high and low states.

Case study 1 is situated on the Norwegian Coast. Here, only changes in θ_{bot} associated with the AMO and SPG are statistically significant at the 95% confidence level. Both indices show warmer θ_{bot} during high states, with the AMO having the largest change at 0.06°C. A large positive change in KE_{bot} (0.96×10^{-2} m^2 s^{-2}) is also observed between high and low states of the NAO. At **case study 2**, on the western Scottish Slope, all climate indices are associated with significant changes in θ_{bot}. The NAO and AMOC have cooler θ_{bot} values during the high states, whilst the AMO and SPG show warmer θ_{bot} values. The NAO, AMOC, and AMO all produce similar magnitude changes. With respect to S_{bot}, only the NAO, AMOC, and AMO show statistically significant changes, with all having fresher S_{bot} values during a high state. The largest changes are associated with the AMOC (−0.013) and NAO (−0.011), with the change between high and low states of the AMO half of these values. No statistically significant changes in KE_{bot} are seen.

Case study 3 is at Rockall Bank. Here, changes in both θ_{bot} and S_{bot} are statistically significant for all climate indices. Cooler and fresher θ_{bot} and S_{bot} values are observed during high states. The largest change is associated with the AMO for both θ_{bot} (−0.07°C), and S_{bot} (−0.017). Changes in KE_{bot} though statistically significant are small ($0.01–0.02 \times 10^{-2}$ $m^2 s^{-2}$). **Case study 4**, which has an average depth of 196 m and covers the Mingulay Reef complex to the west of Scotland (Roberts et al., 2009), shows large changes. Statistically significant changes in θ_{bot} are seen for the NAO, AMO, and SPG. The NAO has cooler θ_{bot} during a high state, whilst the AMO and SPG exhibit warmer θ_{bot}. All climate indices show significant changes in S_{bot}. The NAO and AMOC have less saline conditions during high states, and the AMO and SPG more saline S_{bot} values. The largest change in both θ_{bot} and S_{bot} is associated with the AMO (0.58°C and 0.056 respectively). Changes in KE_{bot} between high and low states of the NAO and AMOC are not statistically different at the 95% confidence level.

At **case study 5**, on the Porcupine Sea Bight, θ_{bot} shows statistically significant changes for all climate indices. Warmer θ_{bot} values are seen for high states of the NAO and AMOC, with lower θ_{bot} values seen during high states of the AMO and SPG. The largest change in θ_{bot} (0.06°C) is associated with the

TABLE 3 | Summary statistics from EN4 for the 14 case studies detailed in **Table 1**.

Case study	1959–2017 θ_{bot}			1959–2017 S_{bot}			NAO H-L		AMOC H-L		AMO H-L		SPG H-L	
	Mean (°C)	Min. (°C)	Max. (°C)	Mean	Min.	Max.	θ_{bot} (°C)	S_{bot}	θ_{bot} (°C)	S_{bot}	θ_{bot} (°C)	S_{bot}	θ_{bot} (°C)	S_{bot}
1	−1.01	−1.09	−0.92	34.913	34.876	34.954	–	–	–	–	0.06	–	0.04	–
2	−0.81	−1.07	−0.43	34.913	34.848	34.984	−0.09	−0.011	−0.11	−0.013	0.10	−0.005	0.06	–
3	3.62	3.47	3.79	34.969	34.926	35.019	−0.04	−0.010	−0.05	−0.011	−0.07	−0.017	−0.05	−0.012
4	9.54	8.19	11.05	35.375	35.254	35.460	−0.25	−0.022	–	−0.023	0.58	0.056	0.45	0.039
5	3.62	3.48	3.78	35.007	34.983	35.033	−0.03	−0.009	−0.03	−0.011	0.06	–	0.03	–
6	4.36	4.09	4.56	35.063	35.022	35.098	0.06	0.005	0.04	–	0.08	0.003	0.05	−0.003
7	9.40	8.87	10.08	36.000	35.771	36.203	0.14	0.034	–	–	–	–	–	–
8	2.40	2.36	2.49	34.929	34.911	34.946	–	–	–	–	–	–	–	–
9	2.90	2.69	3.07	34.952	34.915	34.988	−0.07	−0.006	−0.09	−0.012	−0.09	−0.012	−0.07	−0.009
10	3.22	2.95	3.54	34.912	34.877	35.000	−0.07	−0.013	−0.20	−0.010	−0.05	–	−0.06	−0.003
11	2.49	2.24	2.73	34.911	34.877	34.957	−0.07	−0.009	−0.08	−0.010	−0.08	−0.010	−0.05	−0.008
12	2.96	2.77	3.12	34.955	34.906	34.998	–	–	–	–	–	–	–	–
13	3.97	3.74	4.21	34.995	34.921	35.058	−0.05	−0.013	−0.10	−0.019	–	−0.014	−0.05	−0.011
14	7.59	5.89	9.35	35.174	34.838	35.407	–	–	–	–	0.62	0.046	0.49	0.036

Columns two and three contain the mean, minimum and maximum for bottom potential temperature and bottom salinity respectively between 1959 and 2017. All case studies have a mean weighting > 0.1 except case study 8 where the mean weighting is 0.098. Columns four to seven contain the differences in bottom conditions between high and low states of the North Atlantic Oscillation (NAO), Atlantic Meridional Overturning Circulation (AMOC), Atlantic Multi-decadal Oscillation (AMO) and Subpolar Gyre (SPG) respectively. Only differences that are statistically significant at the 95% confidence level, and where data weightings during both the high and low states are>0.1 are shown. AMOC represents the EN4 time-series.

AMOC. Only the NAO and AMOC show statistically significant changes in S_{bot}, with the largest change again being associated with the AMOC (−0.011). Changes in KE_{bot} are not significant at the 95% level for either the NAO or AMOC. **Case study 6** is in the Bay of Biscay. Here, θ_{bot} shows statistically significant changes for all climate indices, with warmer values observed during the high states. The largest change is associated with the AMO (0.08°C). Only the AMOC does not show a statistically significant change in S_{bot} between high and low states. The NAO and AMO have more saline S_{bot} during high states, with the SPG having lower S_{bot} values. The largest change is associated with the NAO although this is still small at 0.005. KE_{bot} changes, whilst significant, are small ($\pm$ 0.01 $\times$ 10^{-2} m^2s^{-2}).

TABLE 4 | Summary statistics from Viking20 for the 14 case studies detailed in **Table 1**.

Case study	1959–2009 KE_{bot} ($\times 10^{-2}$ m^2 s^{-2})			NAO H-L KE_{bot} ($\times 10^{-2}$ m^2 s^{-2})	AMOC H-L KE_{bot} ($\times 10^{-2}$ m^2 s^{-2})
	Mean	Min.	Max.		
1	1.44	0.27	5.90	0.96	–
2	1.08	0.41	2.68	–	–
3	0.11	0.04	0.23	0.02	0.01
4	0.48	0.02	3.00	–	–
5	0.06	0.02	0.15	–	–
6	0.05	0.01	0.24	–	0.01
7	2.66	2.09	3.84	–0.22	–
8	0.02	0.01	0.06	–	0.00
9	0.38	0.21	0.61	–	0.07
10	2.09	0.39	3.98	–0.59	–
11	1.51	0.89	2.93	–	0.24
12	0.50	0.07	1.89	–	–
13	0.40	0.06	1.47	0.19	0.14
14	0.28	0.03	1.03	0.17	–

Column two contains the mean, minimum and maximum for bottom kinetic energy between 1959 and 2009. Columns three and four contain the differences in bottom conditions between high and low states of the North Atlantic Oscillation (NAO), and Atlantic Meridional Overturning Circulation (AMOC) respectively. Only differences that are statistically significant at the 95% confidence level are shown. AMOC represents the Viking20 post-1993 time-series.

Case study 7 is located in the Gulf of Cadiz and has a mean depth of 697 m. Here, only the NAO shows statistically significant changes in θ_{bot} and S_{bot} (0.14°C and 0.034 respectively). In Viking20, the NAO is also associated with weaker KE_{bot} (−0.22 $\times$ 10^{-2} m^2 s^{-2}) during a high state. **Case study 8** is situated around the Azores and is the deepest site with a mean depth of 3064 m. There is insufficient observational data to assess changes here with EN4 weightings <0.1 for all climate indices. Changes in KE_{bot}, as expected for a deep site away from boundary currents, are negligible.

At **case study 9**, which is situated on the Reykjanes Ridge, statistically significant changes are observed for all climate indices with both θ_{bot} and S_{bot}. All changes are negative with cooler and fresher bottom conditions during high states. The largest changes are associated with the AMO and AMOC, with both indices having changes of −0.09°C and −0.012 for θ_{bot} and S_{bot} respectively. Only the AMOC is associated with a small (0.07 $\times$ 10^{-2} m^2s^{-2}), but statistically significant positive change in KE_{bot} between high and low states. **Case study 10** is situated in the Davis Strait. All climate indices show statistically significant changes for θ_{bot}, with cooler conditions during a high state. The largest change is associated with the AMOC (−0.2°C), with this being over 0.1°C greater than changes for the NAO, AMO, and SPG. For S_{bot} the NAO, AMOC, and SPG all show statistically

significant changes in EN4 with fresher conditions during a high state. The changes associated with the NAO and AMOC are three to four times that of changes from the SPG, with the largest change associated with the NAO (−0.013). In Viking20, the NAO is associated with less energetic conditions (-0.59×10^{-2} m^2 s^{-2}) during a high state.

Case study 11, which is situated on the Flemish Cap, shows statistically significant changes with both θ_{bot} and S_{bot} for all climate indices, with cooler and fresher conditions during high states. The largest change in θ_{bot} is associated with the AMOC and AMO, with both indices showing a change of −0.08°C. However, the NAO shows only a slightly smaller change of −0.07°C. All changes in S_{bot} exceed −0.008, with the largest change of −0.010 again associated with the AMOC and AMO. KE_{bot} shows more energetic conditions (0.24×10^{-2} m^2 s^{-2}) during a high AMOC. **Case study 12**, covering the USA mid-Atlantic Canyons, has a lack of observational data with EN4 weightings <0.1 for all climate indices. Additionally, changes in KE_{bot} are not statistically significant.

At **case study 13**, on the European Slope, the NAO, AMOC, and SPG all show statistically significant changes with θ_{bot}, with cooler conditions during high states. The largest change is associated with the AMOC (−0.1°C), with this being twice the size of changes from the NAO and SPG. With respect to S_{bot}, all climate indices show a statistically significant change in EN4 with fresher conditions during a high state. The largest change in S_{bot} is again associated with the AMOC (−0.019). Both the NAO and AMOC are associated with enhanced KE_{bot} ($>0.14 \times 10^{-2}$ m^2 s^{-2}) during high states. **Case study 14** is in the North Sea and is the shallowest site with a mean depth of 99 m. Only the AMO and SPG show statistically significant changes with both θ_{bot} and S_{bot}. Warmer and more saline bottom conditions are seen during high states, with the largest changes for both parameters associated with the AMO (0.62°C and 0.046). In Viking20, a statistically significant change in KE_{bot} (0.17×10^{-2} m^2 s^{-2}) is associated with the NAO.

DISCUSSION

In this paper, we set out to ask whether there are statistically significant changes in bottom conditions across the northern North Atlantic, and its adjacent shelf seas, associated with four major climate indices, and whether these changes are spatially coherent. The answer to both of these questions is "yes," but what of the physical processes responsible for these changes? This is a more nuanced question. Bottom conditions in the northern North Atlantic region span shallow seas to deep oceans; thus in one map we have contrasting dynamical regimes: from highly seasonal shelf seas, and energetic boundary currents, to quiescent abyssal depths. It is likely that different mechanisms are important at different depths, and lag-times between changes in the index and bottom manifestations will also vary. In this discussion section, we touch on some possible physical processes responsible for observed significant correlations, but anticipate that we only scratch the surface leaving deeper analysis for future work.

North Atlantic Oscillation (NAO)

The NAO shows a strong anti-correlation between the eastern and western continental shelves (**Figure 5**): warmer and more saline bottom conditions are seen in the North Sea during a high NAO, with cooler and fresher conditions in the Grand Banks area. The higher θ_{bot} observed in the North Sea during a high NAO, is likely a representation of the higher sea surface temperatures seen in the same region during a positive NAO (Visbeck et al., 2013) due to the tidally well-mixed water column (e.g., Huthnance, 1991). Bottom kinetic energy is higher during a high NAO along the European and Norwegian Shelf break, and along flow pathways into the North Sea (**Figure 6A**). This reduction in the European Slope Current strength in Viking20 during a low NAO, is consistent with evidence of a slowing of the slope current during the 1990's attributed to changes in both the wind-field and the meridional oceanic density gradient (Marsh et al., 2017). Similar changes are observed in the Norwegian Slope Current with enhanced transport during a high NAO (Skagseth et al., 2004).

Away from the continental shelves, lower S_{bot} and θ_{bot} values are observed in the subpolar gyre during a high NAO (**Figure 5**). Convection in the Labrador Sea is enhanced during a high NAO producing cooler and fresher Labrador Sea Water (Yashayaev, 2007). In contrast, convection in the Nordic Seas is reduced during a high NAO resulting in warmer and more saline bottom waters (Dickson et al., 1996; Alekseev et al., 2001). This may explain the cooler and fresher bottom conditions in the Labrador and Irminger Seas. Advection times of Labrador Sea Water to the eastern subpolar regions are in the order of 5–10 years (Yashayaev et al., 2007a,b). This suggests that there may be periods where properties of the Labrador Sea Water in the western subpolar North Atlantic may be out of phase to those in eastern areas. However, the temporal spacing between high and low years in the NAO time-series exceeds this, and we see cooler and fresher conditions during a high NAO right across the subpolar latitudes.

Finally, we see no evidence of the saltier Iceland Scotland Overflow Water during a high NAO observed by Sarafanov (2009), although this is not unexpected for EN4 due to its low horizontal resolution relative to the overflow waters spatial extent. We do, however, see reduced mean KE_{bot} in the Iceland-Scotland Overflow during a high NAO, with coincident increased KE_{bot} in the Denmark Strait Overflow region (**Figure 6A**). Less vigorous flow in Iceland-Scotland Overflow Water during a high NAO is consistent with results from a sediment core on the eastern flank of the Reykjanes Ridge (Boessenkool et al., 2007). Additionally, the anti-correlation between the eastern and western overflow branches is consistent with previous work that shows overflow volume transports are correlated with NAO-type changes in sea level pressure and wind stress curl, and that transports between the eastern and western routes can be out of phase (Biastoch et al., 2003; Bringedal et al., 2018).

Atlantic Meridional Overturning Circulation (AMOC)/Subpolar Gyre (SPG)

As mentioned, the composites produced using the post-1993 AMOC time-series (**Figures 7A,B**), and those produced using

the SPG time-series (**Figure 9**) are very similar; probably reflecting the similar time-periods used in the construction of the composites (**Figure 2F**). As such, it is difficult to tease out whether the AMOC, or the SPG, is the most dominant index, or indeed whether the two indices act in unison. We therefore discuss both indices together here. Cooler and fresher bottom conditions are seen in the western subpolar North Atlantic during a high AMOC/SPG, with pronounced changes around the boundaries of the Labrador Sea, and over the Reykjanes and Greenland-Scotland Ridges (**Figures 7**, **9**). Lower θ_{bot} and S_{bot} values are also seen over the Rockall-Hatton Plateau and on the continental shelf west of the UK during a high AMOC/SPG, although more saline conditions are seen in the Rockall Trough and Iceland Basin.

Upper ocean properties show a dipole pattern for the AMOC. During a high AMOC, cooler conditions are seen in the Gulf Stream region, and warmer conditions in the subpolar North Atlantic (Zhang, 2008; Tulloch and Marshall, 2012; Caesar et al., 2018). As such, we may expect to see similar changes in θ_{bot} in shallower areas which are influenced by the upper waters. However, we see no evidence of this; indeed, shallower areas of the subpolar gyre show cooler (and fresher) conditions (**Figure 7**). This may be because the relationship between upper ocean heat content changes and the AMOC is thought to reflect processes that act on multi-decadal time-scales (Kushnir, 1994; Zhang, 2008), whereas our analysis focusses on multi-annual variability. An alternative possibility is that the SPG dominates upper ocean properties (**Figure 9**). Upper water properties in the eastern and central subpolar North Atlantic are negatively correlated with the SPG (Holliday, 2003; Hátún et al., 2005; Johnson et al., 2013). Whilst at deeper levels, the SPG has also been shown to effect the eastward extent of Labrador Sea Water (Lozier and Stewart, 2008), as well as the northward limit of Mediterranean Overflow Water (Lozier and Stewart, 2008; Bozec et al., 2011).

By definition, a high AMOC indicates a stronger overturning circulation with increased northward flow of upper waters and a similar increase in the return flow of deep waters. Additionally, it specifies enhanced conversion of upper waters to denser waters either in the subpolar gyre and/or Nordic Seas. As expected, KE_{bot} is higher in the northern and western boundaries of the subpolar gyre during a high AMOC (**Figure 6B**), suggesting more energetic flow in the overflow currents and deep western boundary current. These areas also see a lower θ_{bot} and S_{bot} during a high AMOC, which we speculate may be linked to enhanced flow of cooler and fresher dense waters around the subpolar gyre. Although the KE_{bot} composite was created using the AMOC time-series, we also expect this variable to be effected by the SPG as more energetic flows have been observed during a high state (Häkkinen and Rhines, 2004).

Atlantic Multi-decadal Oscillation (AMO)

Spatial changes associated with the AMO are relatively simple (**Figure 8**). Warmer and more saline bottom conditions are observed: around the boundaries of the northern North Atlantic, on the continental shelves, in the Mediterranean Sea, and in the Nordic Seas during a high state. In contrast, cooler and fresher θ_{bot} and S_{bot} are seen in areas deeper than around 2000 m in the northern North Atlantic. The AMO shows a strong positive correlation with ocean heat content changes in the upper 700 m averaged over 45–70°N (Frajka-Williams et al., 2017). As such, it does not seem surprising that areas influenced by upper waters, such as the boundaries of the subpolar gyre and continental shelves, are warmer during a high AMO state. The high AMO years are seen post-1998, whilst the low AMO years are between 1970 and 1994 (**Figure 2D**). Therefore, it is possible that our results represent the global increase in ocean heat content over the past half a century (e.g., Levitus et al., 2012), rather than a signal of the AMO. Although we cannot discount this influence, the fact that bottom temperature and salinity co-vary over the vast majority of the northern North Atlantic region (**Figure 8**), suggests that our composites reflect a process other than just a simple long-term warming. The spatially coherent and statistically significant changes in S_{bot} and θ_{bot} in the deeper northern North Atlantic and Nordic Seas are intriguing. Whilst changes at shallower depth levels and deeper areas are in phase in the Nordic Seas, they appear to be anti-correlated in the northern North Atlantic; that is, during a high AMO the shallower boundaries of the northern North Atlantic are warmer and more saline, whilst the deep interior is cooler and fresher.

CONCLUSION

Our results are the first to examine changes in bottom conditions across the northern North Atlantic Ocean, and its adjacent shelf seas, associated with four major climate indices. We show statistically significant and spatially coherent patterns of change between high and low states of the NAO, AMOC, AMO, and SPG. Although variations in bottom conditions are relatively small, due to the multi-annual nature of the climate indices any associated change may persist for several years. As such, vulnerable deep-sea ecosystems may be exposed to sustained changes in mean conditions, with this deviation in the baseline also altering the likelihood of extreme events such as marine heat waves. Any changes have the potential to effect sessile deep-sea ecosystems to a greater extent than more mobile pelagic species. Additionally, natural changes will be superimposed on any anthropogenic effects, exacerbating or moderating the impact on possibly stressed ecosystems. Thus, a thorough understanding of natural variability is essential for the evaluation of future scenarios and the implementation of management frameworks. Our work provides a first look at the signature of natural variability on benthic conditions in the northern North Atlantic region; we hope that this stimulates further work both on the physical mechanisms and potential effects on deep-sea ecosystems.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

SG extracted the bottom data from Viking20, and MI the bottom data from EN4. CJ carried out the bulk of the analysis and prepared the first draft of the manuscript. All authors contributed to the conception and design of the study, manuscript revision, and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00002/full#supplementary-material

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Science Collaboration for Capacity Building: Advancing Technology Transfer Through a Treaty for Biodiversity Beyond National Jurisdiction

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Marine technology transfer and capacity building are key elements in the development of a historic new agreement for the conservation and sustainable use of marine biodiversity in areas beyond national jurisdiction (BBNJ agreement) under the United Nations Convention on the Law of the Sea (UNCLOS). This vast, deep ocean area remains largely unexplored and poorly understood. Scientific knowledge gaps impede informed decision-making, and most countries lack the capacity to participate in ocean science activities in ABNJ or to benefit from discoveries of new ocean life, habitats, and processes. Consequently, science must play a central role in capacity building aspirations, however, the link between technology transfer and marine scientific research has yet to be examined in depth. Here, we examine the UNCLOS framework for marine technology transfer and highlight linkages with marine scientific research, identifying four capacity building themes: access to data, information and knowledge; equipment; training; and collaboration. We provide examples to illustrate current practices and identify gaps in implementation. We show that marine technology transfer and marine scientific research link in principle and in practice. We propose ways that the BBNJ agreement could strengthen the international framework for the transfer of marine technology in order to boost marine scientific research collaboration, fill knowledge gaps, and strengthen capacity through inclusive international participation.

Keywords: marine scientific research, marine technology transfer, capacity building, high seas, biodiversity beyond national jurisdiction, ocean governance

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INTRODUCTION

Scientific research continues to reveal novel biological diversity from the 64% of the ocean that lies in areas beyond national jurisdiction (ABNJ) that is intricately connected (Danovaro et al., 2017), provides crucial ecosystem services (Ramirez-Llodra et al., 2010; Levin and Le Bris, 2015), and inspires innovation (Snelgrove, 2016) but faces threats from human activities (Merrie et al., 2014). The international community critically depends on science and technology to address such threats because scientific knowledge gaps impede informed decision-making (Rogers et al., 2014). Furthermore, while advancing scientific knowledge brings opportunities for

new discoveries (Danovaro et al., 2014), inequity in scientific and technological capacity (IOC, 2017a) prevents many nations from participating in, and benefitting from, scientific research and potential associated benefits within ABNJ (Salpin et al., 2016). Consequently, the development of a new international legally binding instrument for the conservation and sustainable use of marine biological diversity in areas beyond national jurisdiction (BBNJ agreement) under the United Nations Convention on the Law of the Sea (UNCLOS; UNGA, 2017a) includes technology transfer and capacity building as key objectives.

Technology transfer has long been lamented as one of the most under-implemented areas of UNCLOS (Long, 2007). Many experts believe that the BBNJ agreement offers a historic opportunity to strengthen the international framework, including for capacity building and technology transfer, to better support the conservation and sustainable use of biodiversity (Warner, 2014; Wright et al., 2018). The BBNJ negotiations focus primarily on scientific and technological aspects of capacity building and the technology and cooperation mechanisms required to enable States to fulfill their rights and responsibilities (Long and Rodriguez Chaves, 2015; Wright et al., 2019). For example, "developing marine scientific and technological capacity" and "increasing, disseminating and sharing knowledge," with regard to the conservation and sustainable use of BBNJ, are among the key objectives for capacity building and technology transfer presented in Article 42 of the first draft text of the BBNJ agreement (BBNJ, 2019). The third session of the BBNJ intergovernmental conference appeared to achieve broad consensus that capacity building and technology transfer should take place at all levels and in several forms (IISD, 2019) including: the sharing of data, information and knowledge; infrastructure; and human resources, as per Article 46 of the first draft BBNJ agreement (BBNJ, 2019). However, divergences in views persist on achieving technology transfer and capacity building, including whether measures should be voluntary or mandatory (IISD, 2019). Articles 44, 45, and 46 of the draft text emphasize cooperation as pivotal to achieving capacity building and technology transfer in BBNJ (2019), but the text is otherwise light on implementation mechanisms.

All four elements of the BBNJ agreement critically depend on science: (i) area-based management tools, including marine protected areas; (ii) environmental impact assessments; (iii) marine genetic resources, including sharing of benefits; and (iv) capacity building and marine technology transfer. Scientific expertise and information is particularly vital for environmental impact assessments and the designation, implementation, and monitoring of area-based management tools. Furthermore, access to, and use of, marine genetic resources hinges upon scientific capacity (Broggiato et al., 2014, 2018; Harden-Davies and Gjerde, 2019). Promoting marine scientific research therefore adds a critical priority for the BBNJ agreement that poses a particular challenge given the uneven spread of scientific capacity worldwide (IOC, 2017a). The need for the BBNJ agreement to promote marine scientific research while delivering marine technology transfer punctuates the urgency in understanding the links between these two elements and their relationship to capacity building.

Here, we examine the link between marine scientific research and marine technology transfer, to identify opportunities and challenges facing the BBNJ agreement in relation to capacity building. Noting that capacity building could take different forms, we consider scientific and technological forms of capacity building ranging from global to regional to local scales. First, we examine the UNCLOS framework for marine technology transfer, marine scientific research, and capacity building. We consider definitions of these terms and highlight blurred distinctions. Second, we discuss illustrative examples, identify implementation challenges and consider key scientific gaps to fill. Third, we propose future considerations for the BBNJ agreement and corresponding opportunities to build capacity and advance technology transfer. We intend for this paper to inform ongoing discussion between scientists and policymakers about the role of science and technology in enabling all States to participate in the conservation and sustainable use of BBNJ. We propose that the BBNJ agreement offers a crucial and timely opportunity to strengthen the existing institutional framework for international science cooperation and thus support capacity building.

THE UNCLOS FRAMEWORK

As an implementing agreement under UNCLOS, the BBNJ agreement can and must build on the existing legal framework. This section examines the framework for marine technology transfer, marine scientific research and capacity building in UNCLOS. Gaps, ambiguities, and implementation challenges are identified.

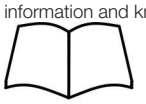
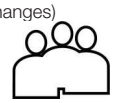
UNCLOS Basis for Marine Technology Transfer, Marine Scientific Research, and Capacity Building

Marine scientific research, capacity building and technology transfer are terms that are used widely and yet lack a common understanding. This section examines the framework for the development and transfer of marine technology established by UNCLOS (Part XIV), and highlights the envisaged role of international science cooperation as the engine for technology transfer. We then discuss the UNCLOS framework for marine scientific research (Part XIII), highlighting that the right to undertake research goes hand-in-hand with the responsibility to share and build capacity. We provide further illustrative examples of the relationship between science and technology transfer in the context of capacity building, highlighting four common themes: data, information and knowledge; training and exchanges; equipment and infrastructure; and cooperation and collaboration (**Table 1**). We illustrate the definitional gaps and blurred distinctions between marine technology transfer (section Marine Technology Transfer; **Table 2**), marine scientific research (section Marine Scientific Research), and capacity building (section Capacity Building).

Marine Technology Transfer

Although UNCLOS does not define the "transfer of marine technology," Part XIV implies a broad meaning and a

TABLE 1 | UNCLOS Part XIV summary.

Theme	Summary of provision for development and transfer of marine technology, UNCLOS Part XIV	UNCLOS article(s)
Data, information and knowledge 	• The acquisition, evaluation, and dissemination of marine technological knowledge and facilitate access to such information and data;	268 (a)
	• Acquisition and processing of marine scientific and technological data and information [via regional marine scientific and technological centers];	277 (e)
	• Prompt dissemination of results of marine scientific and technological research in readily available publications [via regional marine scientific and technological centers];	277 (f)
People (skills, training, exchanges) 	Training	
	• Develop human resources through training and education;	268 (d)
	• Access to skills for scientific and technological centers;	275 (2)
	• Training and educational programs at all levels on various aspects of marine scientific and technological research, particularly marine biology, including conservation and management of living resources, oceanography, hydrography, engineering, geological exploration of the seabed, mining, and desalination technologies; management studies; programmes on protection and preservation of the marine environment and the prevention, reduction and control of pollution.	277 (a, b, c)
	Exchanges	269 (c)
	• Conferences, seminars, symposia on scientific and technological subjects	277 (d)
	• Scientist exchanges	269 (d)
	• Provide technical experts	275 (2)
Equipment (development, access, transfer) 	Development of technology	
	• Develop appropriate marine technology	268 (b)
	• Develop technological infrastructure to facilitate the transfer of marine technology	268 (c)
	Access to technology	275 (2)
	• Provide for necessary equipment to facilitate the establishment and strengthening of national scientific and technological centers	
Cooperation and collaboration 	International cooperation:	268 (e),
	• At all levels, particularly at the regional, subregional and bilateral levels;	270,
	• New programs;	271,
	• Guidelines, criteria, and standards;	272,
	• Coordination of international programs by competent international organizations including regional or global programmes;	273, 274,
	• Cooperation with and between international organizations, including with regional marine scientific and technological centers.	277(i), 278, 276 (2)
	Programs:	270,
	• Facilitate marine scientific research, transfer of marine technology, particularly in new fields, and international funding for ocean research and development;	
	• Technical cooperation [to build marine scientific and technological capacity];	
	• Projects, joint ventures, other forms of bilateral and multilateral cooperation	269 (a, e)
	Establishment of national and regional marine scientific and technological centers:	275,
	• Stimulate and advance the conduct of marine scientific research, enhance national capabilities to utilize, and preserve marine resources; foster the transfer of marine technology;	275, 277
	• Advanced training facilities and equipment, skills, and know-how;	
	Policy:	
	• Create favourable conditions for the conclusion of agreements, contracts and other similar arrangements, under equitable and reasonable conditions;	269 (b)
	• Publicize national policies with regard to the transfer of marine technology and systematic comparative study of those policies.	277 (g)

The provisions of UNCLOS Part XIV (development and transfer of marine technology) can be summarized in four categories: (i) data, information and knowledge; (ii) people, including training and exchanges; (iii) technical and scientific equipment and infrastructure; and (iv) cooperation including through activities, programs, and common criteria, facilitated by new and existing international, regional and national institutions.

close link to marine science. For example Article 266(1) provides that "*States, directly or through competent international organizations, shall cooperate in accordance with their capabilities to promote actively the development and transfer of marine science and marine technology* (…)". UNCLOS provides a strong focus on promoting, and building capacity for marine

TABLE 2 | Examples of technology transfer for the conservation and sustainable use of BBNJ.

Marine technology (IOC, 2005)	**Examples of technology transfer for the conservation and sustainable use of biodiversity beyond national jurisdiction**	
a) Information and data, in a user friendly format, on marine sciences and related marine operations and services;	• Biodiversity data • Oceanographic data • Information on marine scientific research activities • Information and data on scientific capacity	Data and information
b) Manuals, guidelines, criteria, standards, reference materials;	• Open/FAIR data guidelines • Standardized science protocols • Operating instructions • Information on the conduct of technology needs assessment and capacity building strategy development	
c) Sampling and methodology equipment (e.g., for water, geological, biological, chemical samples);	• Access to research vessels and sampling equipment	Equipment and infrastructure
d) Observation facilities and equipment (e.g., remote sensing equipment, buoys, tide gauges, shipboard, and other means of ocean observation;)	• Open and deep ocean observing equipment	
e) Equipment for *in situ* and laboratory observations, analysis, and experimentation;	Laboratory equipment, including for genetic analysis	
f) Computer and computer software, including models and modeling techniques;	Data analysis, including computers, and software	
g) Expertise, knowledge, skills, technical/scientific/legal know-how, and analytical methods related to marine scientific research and observation.	• Training in scientific methods, data analysis, and technical aspects relevant to BBNJ • Long-term mentorship programs • Courses on science-policy	Skills

scientific research; for example, Article 266(2) provides that "*States shall promote the development of the marine scientific and technological capacity of States which may need and request technical assistance in this field* (…)". Indeed, Part XIV established a framework in which the development and transfer of marine technology goes hand-in-hand with marine scientific research (Long, 2007; **Table 1**). The word "transfer" appears only once in UNCLOS Article 268, which instead emphasizes: the *development* of technology including equipment; the sharing of scientific and technological knowledge, data, and information; the training of people; and the establishment of national and regional marine scientific and technological centers.

Consequently, in the context of Part XIV, technology transfer aligns with a multi-directional exchange of data and knowledge, skills, and research opportunities (**Table 1**), rather than a one-way hardware donation. This broad interpretation has been elaborated through the Intergovernmental Oceanographic Commission's Criteria and Guidelines on Transfer of Marine Technology (IOC, 2005), in response to Article 271 of UNCLOS (**Table 2**). These same guidelines have been identified as a cornerstone of the technology transfer regime to be developed under the BBNJ agreement (Long and Rodriguez Chaves, 2015). This framework alludes to four key pillars for technology transfer (**Table 1**):

(i) **Data, information and knowledge**: sharing data, information, and knowledge about marine scientific research activities and outputs, as well as technological development.
(ii) **People**: training in science and technology and exchanging skilled people;
(iii) **Equipment**: access to or transfer of research infrastructure and equipment, including both hardware and software; and
(iv) **Cooperation and collaboration**: for scientific research (including on criteria and standards, programs, funding for ocean science), through activities, programs including international, regional and/or national scientific and technical institutions.

Marine Scientific Research

Given the international marine scientific and technological cooperation envisaged as a key driver of technology transfer

under UNCLOS Part XIV, it is necessary to consider the legal framework for marine scientific research (**Table 3**). UNCLOS identifies the "study, protection and preservation of the marine environment" as a core objective. Marine scientific research, though not defined in UNCLOS, can broadly include "any study or related experimental work designed to increase mankind's knowledge of the marine environment" (see UNCLOS art. 243). Marine scientific research is a freedom of the high seas (art. 87f) and all States have the right to conduct marine scientific research (art. 238) in marine ABNJ (arts. 256, 257). However, far from an absolute freedom, it is conditional on responsibilities including, for example, promoting international cooperation (art. 242) and the publication and dissemination of information and knowledge (art. 244). Furthermore, there are specific provisions for international cooperation in marine scientific research in the Area (art. 143) and transfer of technology (art. 144), including training of people, sharing research results, strengthening research capabilities, and promoting cooperative programmes of scientific research (**Table 3**). Thus, these provisions reinforce the obligations for technology transfer found in Part XIV whereby science provides both an enabler and an objective of marine technology transfer. The BBNJ agreement can build on this existing legal framework.

Capacity Building

Although UNCLOS does not specifically mention or define the term "capacity building," scientific and technological capacity building (technical, human, and institutional) is the centerpiece of Part XIV and provisions can be found in relation to the protection and preservation of the marine environment, the Area and marine scientific research (**Table 3**). For example, Article 266(2) identifies increasing scientific and technological capacity as an aim of technology transfer, with particular reference to the protection and preservation of the marine environment, and marine scientific research. As an illustration of the long-held aspirations regarding scientific and technological capacity, we note that the 1982 "Resolution on Development of National Marine Science, Technology and Ocean Service Infrastructure" emphasized an urgent need to close the scientific and technological gap and strengthen national capabilities in marine science and technology (UN, 1982). However, despite efforts to implement marine technology transfer (IOC, 2017b), concerns persist regarding lack of implementation of Part XIV (Holland and Pugh, 2010). Today, numerous declarations illustrate the persistence of this hurdle by highlighting a need to fill scientific knowledge gaps, transfer marine technology, and build scientific capacity at global, regional, and national scales, such as the United Nations Sustainable Development Goal 14a (UN, 2015), and the roadmap for the UN Decade of Ocean Science for Sustainable Development 2021–2030 (UNGA, 2017b). The inclusion of "capacity building and technology transfer" as one of the four elements of the BBNJ agreement further illustrates the importance of effective capacity building and the perceived link with technology transfer, to enable the conservation and sustainable use of marine biodiversity beyond national jurisdiction. In this paper, we consider forms of scientific and technological capacity building.

Implementation Challenges: Remaining Gaps

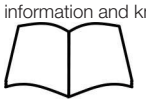
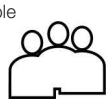
Weak obligations and unclear or absent institutional implementation mechanisms in UNCLOS likely constrain implementation of the transfer of marine technology. Scientists and scientific institutions are tasked with the "heavy-lifting" (**Tables 1**, **3**), however, mechanisms to support the strong emphasis on science cooperation to deliver marine technology transfer are lacking. No coherent mechanism exists to assist States to self-identify and communicate technological need, there is no common mechanism to request technology or capacity building, and no clear practical arrangements exist to deliver marine technology transfer or to monitor and evaluate progress toward capacity building. Even the avenues for implementation identified in the IOC Criteria and Guidelines for the Transfer of Marine Technology rest heavily on existing scientific cooperation, particularly via the IOC (2005). While several areas show progress, such as developing a clearinghouse mechanism to facilitate information sharing, holding events, establishing regional focal points, and assisting the implementation of technology transfer projects (Harden-Davies, 2017; IOC, 2017b); the long-time frames and uncertain funding of several such initiatives also illustrates the perils of ambitious aims that rely on an ambiguous legal framework beset by resource constraints and limited political will. The BBNJ agreement should endeavor to forge workable solutions against this backdrop.

A lack of information presents a further critical challenge to designing, implementing and evaluating capacity building and technology transfer programs, and even marine scientific research programs more broadly. A dearth of information exists on existing science capacity and capacity building needs. Despite some surveys of State practice (IOC, 2008), we still lack a long-term comprehensive reporting mechanism. The inaugural Global Ocean Science Report (IOC, 2017a) marks the beginning of a more comprehensive approach to monitoring ocean science capacity, but given that just 34 IOC Member States responded to the underlying survey that formed the basis of the first report, challenges clearly remain in acquiring baseline information regarding science capacity. Consequently, we lack clarity on possible ongoing capacity building activities that reporting does not capture, opportunities not being seized, and needs not being met. Noting that there are several different actors involved in capacity building (section Discussion: Considerations for the BBNJ Agreement), the following section presents examples of current practice within the international scientific community to advance elements of technology transfer and capacity building.

CURRENT PRACTICE

Following the four key themes identified above (data, information and knowledge; training; equipment; and cooperation and collaboration), this section discusses how marine scientific research creates opportunities for capacity building and marine technology transfer—and vice versa.

TABLE 3 | Summary of provisions relating to scientific and technological capacity building in UNCLOS Parts XI (the Area), XII (protection and preservation of the marine environment), and XIII (marine scientific research).

Theme	Summary of UNCLOS provision broadly referring to scientific and technological capacity building	UNCLOS art(s)
Data, information and knowledge 	Sharing data, information, and knowledge arising from research, e.g.,:	
	• Actively promote the flow of scientific data and information and the transfer of knowledge resulting from marine scientific research, especially to developing States;	244(2)
	• Effectively disseminating the results of research and analysis (from marine scientific research in the Area) when available.	143(3)(c)
	Sharing information about activities:	
	• Provide opportunity to obtain information necessary to prevent and control damage to the health and safety of persons and to the marine environment;	242(2)
	• Make available by publication and dissemination through appropriate channels information on proposed major programmes and their objectives as well as knowledge resulting from marine scientific research.	244(1)
People 	Training:	
	• Programmes of scientific, educational, technical, and other assistance, including training of scientific and technical personnel;	202 (a)(i)
	• Assistance, especially to developing States, concerning the preparation of environmental assessments;	202(c)
	• International cooperation in marine scientific research (in the Area) to train personnel, especially from developing States, in the techniques and applications of research;	143(3)(b)
	• Strengthen autonomous marine scientific research capabilities of developing States through programmes of education and training of technical and scientific personnel;	244(2)
	• Acquire, promote, and encourage transfer to developing States of technology and scientific knowledge, including training in marine science and technology.	144(1)(a), (b), (2)
Equipment 	Development of, access to and transfer of equipment programmes of assistance e.g.,:	
	• Supply necessary equipment and facilities;	202(a) (iii);
	• Enhance capacity to manufacture such equipment;	202(a) (iv);
	• Develop facilities for research, monitoring, educational and other programmes.	202(a) (v)
Cooperative activities 	Studies, research programmes, and exchange of information and data, e.g.,:	
	• Studies, programmes of scientific research, encourage the exchange of information, and data acquired about pollution of marine environment;	200
	• Participate actively in regional and global programmes to acquire knowledge;	200
	• Criteria for regulations, rules standards, practices and procedures;	201,
	• Programmes of scientific, educational, technical, and other assistance to developing States for the protection and preservation of the marine environment;	202 (a)(ii)
	• Facilitating participation in international programmes, including in the Area;	202 (a)(ii), 143(3)(a)
	• International cooperation in marine scientific research for peaceful purposes;	242(1),
	• Develop marine scientific research programs (in the Area) to strengthen research capabilities of developing States;	143(3)(b)(i),
	• Acquire scientific knowledge and technology to promote technology transfer;	144(2)(a)
	• Favorable conditions for the conduct of marine scientific research in the marine environment;	243
	• Integrate the efforts of scientists in studying the essence of phenomena and processes occurring in the marine environment and the interrelations between them.	243

Science for Capacity Building: Four Elements

Data, Information, and Knowledge Sharing

Data, information, and knowledge relevant to BBNJ could include many different elements. For example it may include *information* about marine scientific research activities; raw *data* arising from the research; or aggregated *knowledge* products arising from data analysis. Scientists, funding bodies and managers all widely support open data access facilitated through common approaches such as "FAIR" principles—findable, accessible, interoperable, reusable—(Wilkinson et al., 2016; Levin et al., 2019; Stall et al., 2019). However, the discussion concerning a clearinghouse mechanism for the transfer of marine technology in general, and for the BBNJ instrument in particular, illustrates the perceived need to improve the implementation of FAIR and open sharing of data and information in practice. Currently, available marine biodiversity data straddles multiple databases (some global, some regional, some project specific), with varying degrees of connectedness among key datasets and services (Bingham et al., 2017). Such connectedness crucially requires internationally recognized data portals. The Ocean Biogeographic Information System

(OBIS), for example, connects more than 500 institutions from 56 countries that have provided more than 57 million observations of over 120,000 marine species, including more than 3 million observations from ABNJ, and has a specific deep-sea node. As a collection of coordinated regional and national nodes, OBIS illustrates the role of decentralized network models in facilitating cooperation. However, several nodes rely on "soft" funding and even international coordination faces uncertain futures, for example, the International Oceanographic Data and Information Exchange Committee stressed to the IOC Assembly the need for funding to secure the continuation of OBIS beyond 2019 (Intergovernmental Oceanographic Commission (IOC), 2019). This uncertainty suggests fragility in the international framework that should be considered in the development of a clearinghouse mechanism the BBNJ agreement, guided by the scientific community. Furthermore, notwithstanding a growing trend of open access, not all institutions have access to peer-reviewed literature, the resources to cover fees, the technical capacity to download data, or the hardware and software required to analyse it.

People

Ocean science activities often bring together researchers from different countries providing an opportunity to advance international cooperation, and to identify and pursue common interests (Berkman, 2010), create standardized approaches, and support quantitative and inter-comparable data collection. For example, research cruises provide a platform to share experiences, build collaborations, and train scientists across national borders. However, participation in such initiatives requires opportunity, resources–and research vessels. Technology continues to open up new avenues to involve researchers in cruises–satellite technology and telepresence can enable shore-based researchers to link into research vessels at-sea, enabling online participation in sampling and experimentation. Such technology also enables remote participation in training programs through distance learning, in addition to in-person training courses and workshops.

Ongoing collaborations are important to ensure continued professional development and partnership building, particularly between scientific institutions with differing levels of capacity. Longer-term training through masters and PhD programs can provide an important foundation for such mentoring connections and enduring linkages. Ensuring that capacity building programs train the trainers can promote strengthening of in-country capacity in the long term. But sustaining such efforts depends on people, networks, and resources to support continuing professional development. International ocean observation and monitoring programs, such as the Global Ocean Observing System, offer an important platform to facilitate networking, deliver training, and sustain international science collaboration (Bax et al., 2018; Miloslavich et al., 2018) on which the BBNJ agreement can build.

Equipment

Scientific tools have moved far beyond lowering plumb lines from ships to determine bottom depth and composition, or pulling crude nets and trawls through the water and over seafloor to sample ocean life. Today, new technologies and tools such as next generation sequencing, other omics technologies, novel sensors, autonomous underwater vehicles, imaging, artificial intelligence and machine learning, and *in situ*/shipboard application of these tools (e.g., Scholin et al., 2009) offer promise–for both improving monitoring of ocean health and enabling access and benefit-sharing for marine genetic resources. Although logistically possible with available technology, high costs prohibit many measurements–especially in the deep remote marine areas beyond national jurisdiction (Danovaro et al., 2017), and few nations can afford this technology (IOC, 2017a), further increasing the capacity gap. Maintenance and sustained operation costs add additional challenges, even for comparatively low technology approaches such as net tows or temperature measurement. Technologies that are low-cost to access and maintain are important in improving capacity (Veitayaki and South, 2001), examples include the open access 3D printable microscope (Chagas et al., 2017), the foldscope (Cybulski et al., 2014), USB DNA sequencers (Hsiao, 1991), and image capture using low-cost, off-the-shelf waterproof cameras.

Accelerating technology readiness and affordability in monitoring ocean health requires continued development of new technologies. Tool limitations include, for example, taxonomic capacity for species quantification, availability of genetic and other tools for understanding connectivity across different spatial scales and temporal scales, computational capacity and field verification for ocean predictive models, acquiring sufficient data to determine ecosystem function, and measuring perturbations from individual and cumulative effects. Admittedly, traditional taxonomic expertise based on morphology represents a major bottleneck, but as genetic barcoding libraries expand and help to catalog unknown biodiversity, the technology gap between developed and developing countries will grow. Effective closing of major scientific gaps concerning marine biodiversity of ABNJ critically depends on deploying new technology, as part of sustained and expanded long-term ocean observing infrastructure. For example, ongoing efforts seek to expand ocean observations into the deep ocean (Levin et al., 2019) and offer an important platform to address such knowledge gaps and provide scientific information to inform the implementation of the BBNJ agreement at global and regional scales.

Cooperation and Collaboration

The previous discussion illustrates that science plays a multi-faceted role in capacity building that could take place at global, regional, and national scales. In order to acquire data and knowledge to share, to create opportunities to train people, and to enable opportunities to develop and deploy technology, scientific knowledge gaps must be filled. Large portions of the ocean—perhaps as much as 95%—remain unsampled by science. Even after more than a century of research, <10% of the global seafloor has been mapped to the 100 m resolution already attained for the moon or for Venus (Sandwell et al., 2014). OBIS reports on where

sampling has taken place demonstrate a clear need for greatly accelerated sampling effort in many parts of the world (Webb et al., 2010). Estimates of unknown biological diversity vary from 50% to considerably more than 90% (e.g., Mora et al., 2011), and new habitats were discovered even in the last few decades (Danovaro et al., 2014). Furthermore, many of the questions that inspired early investigators of the deep and open ocean more than a century ago remain at least partially unanswered today. Major knowledge gaps for BBNJ include:

i) **Baseline knowledge of which species live or pass through a given environment**. For most ABNJ we lack even the most basic knowledge of a complete, or even partial, species list (Webb et al., 2010).
ii) **Understanding connectivity between habitats.** Our lack of understanding regarding the connections between populations and habitats (e.g., Baco et al., 2016; Dunn et al., 2019) limits our capacity to assess scales of dispersal, food, and energy flow.
iii) **The role of biodiversity in ecosystem functioning.** Limited evidence suggests that living organisms in the deep sea play a fundamental role in ecosystem processes such as nutrient regeneration (Danovaro et al., 2008), habitat provisioning (Baker et al., 2012), and trophic support (Drazen and Sutton, 2017), but we lack any broad understanding of how species loss or change might affect the delivery of these functions and their role in the Earth system.
iv) **Predicting distributions and patterns from limited sampling.** The vast size of the deep sea and high cost in sampling suggest a need to develop proxies and indicators (e.g., Vierod et al., 2014) that allow extension of limited sampling over broader spatial and temporal scales.
v) **The response of biodiversity to perturbation, or vulnerability.** Although we recognize greater vulnerability of some ecosystems and species to perturbation than others, we lack any comprehensive framework to anticipate how different human activities might cause biodiversity change or loss (Auster et al., 2010).

Collectively, these science questions could inform prediction tools that allows scientists to extend knowledge from limited sampling to a broader range of habitats and taxa, a critical need for policy measures for the conservation and sustainable use of biodiversity beyond national jurisdiction. The questions strongly interlink; neither the questions, nor the knowledge arising, are produced or used in isolation. Addressing these knowledge gaps could support informed decision-making across the BBNJ agreement, including use in environmental impact assessments and area-based management tools (**Table 4**), such as through conducting strategic environmental assessments. Crucially, this type of basic scientific research can also bring opportunities to derive and share benefits from marine genetic resources (Rabone et al., 2019). However, no single nation can address the major scientific knowledge gaps of BBNJ.

The vast area and volume of marine ABNJ, complex and costly logistics, and remote locations of ABNJ collectively require a collaborative approach. Such an approach also aligns with the notion of cooperation and collective good inherent in the UNCLOS provisions for ABNJ. Past programs set a strong precedent for science collaboration of this kind. The Census of Marine Life (2000–2010), for example, embraced international collaboration in engaging more than 2,600 scientists from more than 80 nations to address questions on diversity, distribution, and abundance of life in the global ocean. The program attracted funding of close to US$ 700 million (Snelgrove, 2010) by leveraging philanthropic seed funding to fund and build public and private partnerships and international science networks, some of which live on today (e.g., the International Network for the Investigation of Deep Sea Ecosystems, INDEEP). Lessons from programs such as this can inform future deep-sea scientific investigations to advance knowledge of BBNJ, such as through the UN Decade of Ocean Science for Sustainable Development (2021–2030).

Science advances also offer an opportunity to standardize approaches and methodologies that simultaneously build global capacity and also generate comparable data sets that support meta-analyses and cross-system comparisons. The Census of Marine Life demonstrated the benefits of standardized approaches, as well as the potential for capacity building and technology transfer through targeted workshops and integrated research involvement of research communities varying in focus and capacity. Standards provide a framework for

TABLE 4 | Scientific knowledge needs for the conservation and sustainable use of BBNJ, including relevance to both EIA and ABMTs.

Knowledge gap	Relevance to EIA	Relevance to ABMT
1. Baseline knowledge of species	Attributing changes in species presence or abundance to specific activities requires baseline knowledge on the "*who*" of species presence	ABMTs typically require baseline knowledge on species, including where priority species ("*who*") occur, which are most *vulnerable*
2. Connectivity	Activities that alter potential supplies of recruits, food, or other attributes from one location to another requires knowledge of *connectivity*	Understanding their *connectedness* can inform design of effective MPA networks, fisheries closures, and other strategies to enhance recruitment and sustainability
3. Ecosystem function	EIAs often address impacts of activities on ecological integrity of focus areas, which links to knowledge of *ecosystem functioning*	Evaluating *ecosystem functioning* and species impact on Earth processes can inform strategies to help sustain those functions, such as Marine Protected Area planning
4. Prediction	Sampling limitations may require proxies of status in some cases, requiring good *predictors*	*Predicting* which habitats support the highest biodiversity
5. Measuring response to perturbation	Assessing how different species and ecosystems respond to environmental impacts requires evaluation of response of biodiversity to perturbation, or *vulnerability*	Establishing effective protection and "insurance" against future change requires identifying areas resilient to change and mitigating impacts on those most vulnerable to change

common approaches to measuring ocean variables that enables coordination of scientific research and comparability of the ensuing results. Repeatable protocols and other such guidelines or manuals provide a hierarchy of methodologies appropriate for different levels of scientific capacity, and greater potential for quantitative comparisons among regions and jurisdictions. Several initiatives illustrate the ongoing efforts of the scientific community to streamline and standardize sampling protocols (Konar et al., 2010; Snelgrove, 2010; Woodall et al., 2018), support the acquisition, curation, storage, and sharing of samples and data in the context of genetic resources (Rabone et al., 2019), and international coordination of ocean best practices (Pearlman et al., 2019). In particular, the Global Ocean Observing Systems (GOOS) is developing shared "essential ocean variables" (EOVs) toward a more effective integrated ocean observing system that moves beyond piecemeal efforts, including biological and ecosystem variables (Muller-Karger et al., 2018) to support policy development (Miloslavich et al., 2018), capacity building (Bax et al., 2018), and open data (Bax et al., 2019). These approaches can help to reduce the capacity gap between countries and transfer technology by sharing protocols and co-designing methods that are appropriate and accessible for all. These coordination mechanisms bring cost, but currently rely largely on voluntary and in-kind contributions of individuals and institutions.

Common Challenges and Opportunities

Marine Scientific Research and Marine Technology Transfer Are Mutually Supportive

Scientific advancement goals often catalyze technology development in order to address science objectives. Whether such developments arise as "fit for purpose" or adapt technologies developed for other purposes, they nonetheless create opportunity for innovation and, potentially, inclusivity. Science cooperation offers opportunity for marine technology transfer, through shared approaches to ocean infrastructure and equipment, as well as training. One such initiative, the EAF-Nansen program, provides scientists from developing countries access to a fisheries vessel to manage better their fisheries and protect threatened marine environments. The benefits of international marine scientific research cooperation include standardized approaches supporting inter-comparison among studies, multi-scaler analyses, shared infrastructure platforms (e.g., ships) and instruments, opportunities for training and the exchange of skills and ideas, and tackling far more complex, larger-scale, and interdisciplinary challenges than otherwise possible. In these ways, marine scientific research demonstrably supports the transfer of marine technology, as envisaged in UNCLOS. In turn, technology transfer and capacity building could then generate new data and knowledge and data from previously unknown locations, thus providing positive feedback on scientific advancement. Such efforts should accelerate understanding of biodiversity beyond national jurisdiction and, in doing so, strengthen global capacity to study, protect, and sustain a healthy, functioning marine environment. However, harnessing this potential for capacity building depends on cooperation and collaboration. Learning from the experiences, achievements and challenges of existing capacity building programs, particularly those undertaken by intergovernmental organizations, will be informative in this regard (Cicin-Sain et al., 2018).

Capacity Building and Collaboration: Toward an Enabling Environment

Global, regional, and national networks can play crucial roles in oiling the wheels of international science collaborations–by diversifying funding sources, sustaining support for data storage and platform sharing, amplifying efforts for standardization, and connecting scientists. Several intergovernmental organizations undertake capacity building programs relating to science and technology; examples include the Food and Agriculture Organization, the International Maritime Organization, the International Seabed Authority, and many more (Cicin-Sain et al., 2018). Many scientific networks are voluntary, and future endeavors that might rely on science in this way should therefore consider how to sustain support for such networks, whose finite lifespans rarely extend beyond 5 years. Such preparation in the BBNJ agreement could avoid an over-reliance on unspecified, unsupported, and unpredictable mechanisms for capacity building. Operating a reliable and enduring system collectively requires coordination and support at the global level and strong relationships with regional and national bodies.

Accelerated development and deployment of marine technology could significantly benefit capacity, whether for institutions in small island states or for global scientific community as a whole. For example, the development and deployment of equipment, the adoption of FAIR and open data principles, the strengthening of cooperation mechanisms, or enhancing the scientific knowledge base could promote marine scientific research and boost collective scientific capacity. Such a strategy could focus on advancing knowledge of marine biodiversity itself, by increasing and sharing information from marine science, or of human activities in ABNJ, perhaps using technologies such as vessel tracking (Dunn et al., 2018). It could emphasize training in data analytics, accessing training materials, courses, or information about how to use specialized equipment. Actors in this initiative could include research institutions, private sector members, and philanthropists.

However, tying these threads together in a way meaningful for capacity building requires an enabling environment whereby all elements of technology transfer can be mobilized collectively, in a holistic and integrated manner to meet needs (**Figure 1**). No single form of technology can address science capacity needs alone. For example, equipment requires corresponding skills and resources to maintain and utilize it—a DNA sequencing machine will not be useful in the absence of trained staff to use and maintain it, no access to biological samples to utilize it, no computers and software to analyse data, and no funding for other operating and maintenance costs. Similarly, data access is useful only in tandem with corresponding capacity for interpretation and use; conversely, a trained data scientist cannot reach their full potential without necessary equipment and inputs. Such needs will vary considerably among countries, depending heavily on existing and desired capacity. The following sections address

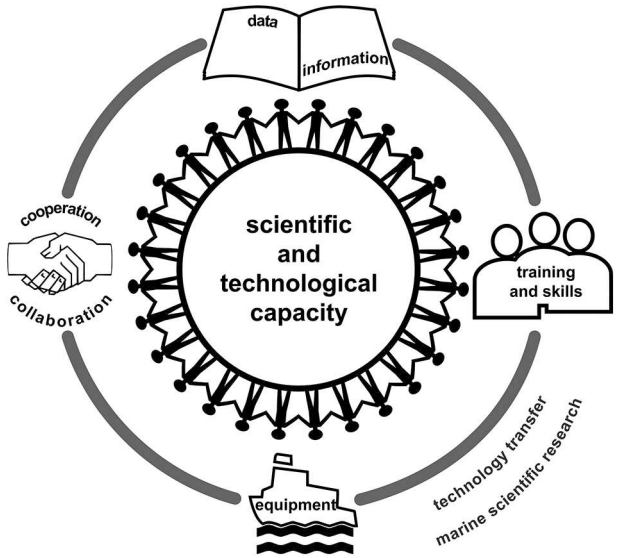


FIGURE 1 | A holistic approach to scientific and technological capacity. Several forms of technology transfer could collectively contribute to capacity building, including data and information; training and skills; equipment and research infrastructure; and cooperation and collaboration. Marine scientific research drives such activities.

ways that the BBNJ agreement could enable States to better identify and meet capacity building needs through marine scientific research and technology transfer.

DISCUSSION: CONSIDERATIONS FOR THE BBNJ AGREEMENT

The examples described above demonstrate the mutually supportive nature of international cooperation in promoting marine scientific research and delivering technology transfer, both in principle and in practice, to the benefit of capacity building. Scientific research presents opportunities to deliver on technology transfer and build capacity at multiple scales–whether for boosting institutional capacity in less-developed States or regions, or for advancing scientific best-practices and cooperation mechanisms for the global marine scientific community as a whole. This opportunity requires a paradigm shift that considers capacity building as more than a training initiative, and technology transfer not merely as bilateral hardware donation, but rather as a strategy to boost science collaboration for the benefit of global science (Bax et al., 2018). Embracing such a shift would position the BBNJ process to follow a broader path that recognizes the crucial role of collaboration in building the body of knowledge crucially needed to address global challenges and the need for mechanisms that support such collaboration (Royal Society, 2011, and Organisation for Economic Cooperation and Development (OECD), 2012). Although a BBNJ agreement cannot solve all ocean science capacity issues, it offers a truly historic opportunity to draw attention to best-practices and areas of weakness, and strengthen the global framework for an enabling environment for science capacity. Seizing these opportunities critically requires leadership, coordination, and support.

In several ways, a BBNJ agreement could strengthen cooperation and coordination of marine scientific research, technology transfer, and capacity building activities.

Coordination

First, the BBNJ instrument could provide institutional clarity and promote institutional support for international cooperation and coordination in scientific research, capacity building, and technology transfer. The closest that the draft text of the BBNJ agreement gets to this specification of institutional responsibility for capacity building and technology transfer is in the management of a clearinghouse mechanism, in Article 51, which suggests potential roles for a secretariat and/or the IOC, in collaboration with relevant organizations such as ISA and IMO. Agreement among states on this issue clearly require further discussions. Whichever institution is tasked with the clearinghouse mechanism could play an important role not only in sharing information about activities, but in coordinating activities more broadly. Such an effort should consider existing coordination mechanisms and bodies.

Identifying and Communicating Capacity Needs

Second, the BBNJ agreement could enable the identification and communication of capacity building needs–which will undoubtedly exceed scientific and technological needs alone. Not all countries have developed national ocean policies or corresponding ocean science and technology strategies or research agendas. Meanwhile information gaps relating to current scientific and technological capacity persist, and we lack a simple mechanism to identify technological need, or to communicate that need. Article 44 of the draft text of the BBNJ agreement notes the importance of ensuring that capacity building activities respond to the needs and priorities of developing States and the potential role of a needs assessment in this regard (BBNJ, 2019).

Technical information and guidelines could support self-identification of technological and scientific capacity building requirements, encouraging States to draw on knowledge contained in national and regional institutions. The process could usefully link to existing assessment processes, such as the IOC Global Ocean Science report. The potential role for the Scientific and Technical Body under the BBNJ agreement to collaborate with existing bodies in undertaking needs assessments, as mentioned in Article 49 of the draft BBNJ text, merits further consideration as a pathway to support coherence across reporting approaches. In addition to national, and potentially regional or subregional initiatives, global assessments of scientific capacity in relation to BBNJ could play a role in shaping future collaborations. A clearinghouse mechanism, as envisaged in Article 51 of the draft BBNJ text, could communicate capacity needs.

Beyond communicating capacity needs, it would be necessary to enable all relevant actors to report on science cooperation, technology transfer and capacity building activities in order

assess their effectiveness and identify gaps to be filled. Article 47 of the draft BBNJ text reflects the need for a process of monitoring and review. Existing networks, as mentioned above, should be invited to play an active role in sharing information. New and existing forums could provide space to exchange experiences and lessons learned between different actors.

Meeting Needs

Third, the BBNJ agreement could include measures that better enable actors, from individual to institutional scales, to access and utilize science and technology in order to participate in the implementation of the agreement. As discussed above, no single form of technology transfer will work–rather, science requires an enabling system in which skilled people can access equipment, information, knowledge, and data for meaningful use. Nevertheless, specific measures for specific categories of technology transfer could be useful, for example:

(i) **Promote access to equipment**: Accelerated development and deployment of new technologies requires additional effort in order to enable accessibility for all nations. The agreement can encourage collaborative research ventures, create mechanisms to request equipment, encourage open-source technology, and task an institution to facilitate such activities.

(ii) **Encourage sustained training of people**: Enhancing cooperation between existing training programs to better identify gaps could offer one pathway to improve the human aspects of technology transfer under the BBNJ agreement. Support for existing and new information sharing mechanisms for human capacity building, including long-term mentoring schemes, remote participation, and collaboration networks, could all play a role.

(iii) **Access to data, information, and knowledge**: The BBNJ agreement could further promote coordination of data standards and support for databases to strengthen the international framework for data sharing. This strategy could include public-private partnerships, support global and regional data nodes, and promote standards and common approaches such as FAIR and open principles. A well-designed and maintained clearinghouse mechanism, developed with strong buy-in from the scientific community, could facilitate information sharing, including on marine scientific research activities and opportunities for capacity building and collaboration. Such sharing of information could also avoid duplication of initiatives and the targeting of capacity building to meet self-determined needs. Furthermore, despite its inherently cooperative activity, marine science currently lacks a central point to share information about activities, pointing to the utility of a portal to share information about marine scientific research activities linked to the clearinghouse mechanism (Rabone et al., 2019).

The clearinghouse mechanism is positioned with a key role in sharing information and delivering technology transfer and capacity building by matching needs with available providers, in Article 51 of the draft BBNJ text (BBNJ, 2019). A human element using existing networks, in addition to a web-based platform, could help to ensure ownership and buy-in to such a system. Developing a usable interface that policymakers, managers, and scientists alike can participate in requires early consultation with potential users.

Implementing the agreement will critically depend on funding, as will enabling all countries to participate in scientific advances. The current text relating to financial resources and funding, in Part VII, Article 52, of the Draft BBNJ text, remains in brackets, suggesting divergent views about the provision of funding. The experiences of scientific networks, intergovernmental organizations, and national management agencies could usefully inform future discussions on the role of funding in delivering scientific and technological capacity building in order to identify potential opportunities to leverage existing initiatives and remaining gaps to fill.

CONCLUSION

UNCLOS established a framework for marine technology transfer that inextricably links marine scientific research and capacity building through: (i) training and exchanging skilled people; (ii) sharing data, information and knowledge; (iii) access or transfer of research infrastructure and equipment; and (iv) cooperation and collaboration. In practice, science cooperation creates opportunities for technology transfer. For example, the Census of Marine Life illustrated the crucial role of well-coordinated international science cooperation in leveraging the funding and capacity needed to undertake ambitious scientific investigations. Such initiatives create opportunities for technology transfer by streamlining standards, opening up access to data, providing opportunities to build long-term global collaboration networks, training, and shared infrastructure access.

Persisting inequity in science capacity worldwide has motivated many States to increase the implementation of UNCLOS Part XIV on the development and transfer of marine technology. At the same time, those nations with such scientific and technological capacity depend upon a fragile mix of public and private funding and fragmented institutional architecture. The absence of a mechanism to enable countries to communicate their capacity building needs to the international community misses an opportunity for strategic and sustained integrated approaches.

Marine scientific and technological capacity represent crucial crosscutting issue for the BBNJ agreement. Designing, monitoring, and managing area-based management tools and conducting environmental impact assessments requires the same types of basic knowledge that motivates discovery-based science. Strengthening capacity at global, regional, and national levels to advance scientific research requires better scientific understanding.

The BBNJ negotiations represent an important opportunity to strengthen the international framework for marine technology transfer, marine scientific research and capacity building. The BBNJ agreement can strengthen the existing framework for marine technology transfer and promote marine scientific research through enhanced coordination; promoting support for data, sharing information about training mechanisms and access to infrastructure; and critically, encouraging and enabling States to self-identify needs for capacity building, technology and science. Fleshing out critical details, including for the clearinghouse mechanism, requires discussion within the scientific community. Ultimately, capacity building requires a long-term strategy adaptable to changing needs including, but not limited to, science and technology. The UN Decade of Ocean Science for Sustainable Development 2021–2030 offers a unique chance to put such an approach into practice.

AUTHOR CONTRIBUTIONS

HH-D and PS conceived the research, conducted the analysis, and developed the recommendations.

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Public Perceptions of Deep-Sea Environment: Evidence From Scotland and Norway

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Knowledge of people's understanding of environmental problems is vital for the effective implementation of the ecosystem approach to marine management. This is especially relevant when conservation goals are aimed at ecosystems in the deep-sea that are remote to the consciousness of most people. This study explores public perceptions of the deep-sea environment among the Scottish and Norwegian public. It further analyses the relationships between respondents' pro-environmental concerns toward the marine environment and personal characteristics using a multiple indicators multiple causes model. The results show that public knowledge of the deep-sea environment is low for Scottish and moderate for Norwegians. Awareness of cold-water corals was high for the Lofoten case study area amongst the Norwegian public and low for the Mingulay reef complex in the Scottish case. These differences might arise because Norway is known to host the world's largest cold-water corals in the Lofoten area; a fact that has been well-publicized. We find that most people think changes in the deep-sea have at least some effect on them. On average, the public perceive the deep-sea condition to be at most "fairly good" but are dissatisfied with the management of it with approximately only one third or less thinking it is well-managed. Generally, the public perception from both countries show ecocentric attitudes toward the marine environment implying that they recognize the value of ecosystem services, the current ecological crisis and the need for sustainable management.

Keywords: perception, deep-sea, marine environment, cold-water coral, Norway, Scotland

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INTRODUCTION

Oceans provide vital ecosystem services that benefit humans (Armstrong et al., 2012). These include regulating services related to carbon sequestration, provisioning services such as food and energy as well a plethora of highly varied cultural services that provide value to mankind. Many of these services are threatened by pressures emanating from human activities (Barbier et al., 2014; Mengerink et al., 2014), questioning our understanding of the interaction between oceans and humans. It has been noted that the public's understanding of such interactions is limited, with ocean literacy substantially lagging behind more broad environmental literacy (Uyarra and Borja, 2016). Most ocean literacy studies are broad in scope (Fletcher et al., 2009) or mostly coastal in nature (Steel et al., 2005; Hynes et al., 2014), while deep-sea literacy is even less well-known (Rogers et al., 2014). In this work we therefore focus on deep-sea environments, more specifically cold-water corals, in order to ascertain the public's knowledge and perceptions regarding threats, potential, and

management, in Norway and Scotland. Public knowledge and perceptions are important in order to ensure conservation measures which demand political decision-making. This is potentially extra demanding in relation to the deep-sea which is spatially and temporally distant to most people. With this in mind, this paper examines the public's knowledge and perceptions of the deep-sea in two maritime nations. Norway presents an interesting case study as it hosts the world's largest cold-water corals in the Lofoten area with continual pressure to open it for petroleum exploration. Scotland on the other hand, hosts the Mingulay Reef Complex (MRC), the only known inshore coral reef in UK waters. The reef supports high level of biodiversity.

Since the expansion in the exploration of deep-water environments using new technologies in the mid-1980s, new insights have been revealed about the largest biome on earth which has challenged conventional wisdom of the deep-sea (Mengerink et al., 2014). Cold-water corals were now found in dark, cold, nutrient rich-waters which lacked the symbiotic light-dependent algae that was a characteristic of the known tropical corals (Freiwald et al., 2004). They can live at depths of 40 to 2,000 m, in temperatures as low as 4°C. *Lophelia pertusa* is the most common habitat-forming, reef-building cold-water coral which has been the focus of deep-sea research since the recognition of their vast, world-wide extent two decades ago (Arnaud-Haond et al., 2017). *L. pertusa* have been shown to provide habitat, concentrate biomass and act as feeding and nursery grounds for many species, including those targeted by commercial fisheries (Arnaud-Haond et al., 2017). In the Scottish cold-water coral Mingulay reef complex for example, *L. pertusa* provides a complex three-dimensional habitat for many species including communities of suspension invertebrates such as sponges and other corals (Henry and Roberts, 2007; Henry et al., 2013; Douarin et al., 2014). According to Blanchard et al. (2014), the Lofoten area cold-water coral reefs in Norway have been characterized as having high ecological value and are considered a vulnerable marine ecosystem. The area constitutes spawning ground for Northeast Arctic cod and haddock and is a nursery for cod, herring, saithe, and haddock larvae.

Anthropogenic activities coupled with climatic changes pose a threat to the deep-sea and marine wildlife, including cold-water corals (Ramirez-Llodra et al., 2011). Climate change and mineral exploitation are of concern in terms of maintaining marine biodiversity (Armstrong et al., 2019). However, in the case of deep-sea cold-water corals, the greatest threat is destructive fishing practices, particularly bottom trawling (Puig et al., 2012; Pusceddu et al., 2014), given that corals are fragile and slow growing (Hall–Spencer et al., 2002). Moreover, pollution from marine litter presents one of the growing challenges (Newman et al., 2015). Recent discoveries have shown that despite the deep-sea and its resources being remote to the daily lives of most people, the adverse anthropogenic pollution effects are approaching sufficient severity to cause impacts in the deep-sea areas (Ryland, 2000; Cole et al., 2011; La Beur et al., 2019). Social media images of the deep sea, including the litter found there, are increasing public awareness of these impacts[1]. According to Pham et al. (2014), plastic is the most prevalent litter on the seafloor and litter from fishing activities (derelict lines and nets) is particularly common on sea mounts, banks, mounds, and ocean ridges.

With such pressures, the attention given to the deep-sea and its cold-water coral species from researchers and conservation activists has increased with a call for nations to protect deep-sea coral ecosystems (Barbier et al., 2014; Mengerink et al., 2014). One vital conservation strategy for deep-sea reefs is the designation of marine protected areas (MPAs) (Huvenne et al., 2016). Protection of deep-sea vulnerable marine ecosystems like cold-water coral reefs was initially a problem in the EU, as the EU Habitats and Birds Directives, the main legal tool for nature conservation in the EU, allowed Member States to set up two types of protected areas, namely the Special Areas of Conservation (SACs) for wildlife habitats and species and Special Protection Areas (SPAs) for birds, but only for terrestrial areas and territorial waters. By being only applicable to territorial waters of up to 12 miles from the coast, the directive thereby excluded further offshore cold-water coral reefs. A court ruling in 1999 permitted applying the directive to waters out to the 200 nm Exclusive Economic Zones (De Santo, 2013).

Consequently, deep-water MPAs, MPA networks, and SACs have been established around many cold-water corals (e.g., off Norway and Ireland, around the Azores, and many more places) to ban extraction of living and non-living resources that can invoke activities harmful to the corals (Armstrong and van den Hove, 2008; Armstrong et al., 2014; Huvenne et al., 2016). In Scotland, the MRC has been designated as a MPA (La Beur et al., 2019). In Norway, the Lofoten area was closed to fossil fuel extraction after intense political deliberation. However, there is continual pressure from lobby groups to open the area for petroleum exploration due to expected fossil fuel richness[2]. Marine conservation policies may therefore be essential to protect deep-sea resources in the area. However, as knowledge of deep-sea ecosystems is limited, success of protective measures could be marginal. Without significant understanding of the public awareness of the importance and vulnerability of these ecosystems, what additional information should be provided to the public in regard to marine conservation will be unknown, and potentially beneficial policies may not be implemented due to insufficient public support.

The implementation of protective measures such as MPAs naturally involves reallocation of resources and property rights (Hattam et al., 2014) which prohibits or reduces access to marine resource use. This invariably impacts communities which reside nearby and utilize those resources. As such, MPAs are often met with resistance from stakeholders who fear loss of their livelihoods and recreational opportunities and for whom little is known of their understanding of the marine ecosystems. Given this complex relationship between people and their environments, it is crucial to deal with conservation problems

[1]https://news.nationalgeographic.com/2018/05/plastic-bag-mariana-trench-pollution-science-spd/

[2]https://www.ft.com/content/c2dad93c-7192-11e7-aca6-c6bd07df1a3c

together with the beliefs, customs, attitudes, and practices of the relevant society (Gray et al., 2010; Hynes et al., 2018). Hence, the EU Marine Strategy Framework Directive (MSFD), which aims to achieve good environmental status for EU marine waters, proposes an ecosystem-based approach to marine management with humans at the center. Since society is made up of ordinary persons, the public perceptions and opinions on the use of marine resources and support for sustainable management is as important as the positions of organized stakeholder groups whose opinions are often captured through policy consultations in marine policy programs. This is because communities are made up of heterogeneous individuals (hereafter referred to as the public) whose collective choices related to the marine resource they use, the areas they visit or reside in, is what drives the many key pressures on the marine environment (Norton and Hynes, 2018).

PUBLIC PERCEPTIONS OF THE MARINE ENVIRONMENT IN THE LITERATURE

Public perception research aimed at understanding stakeholder and resource users have come to matter in marine science given that societal behavior change has the potential to reduce pressures on marine systems (Jefferson et al., 2015) through production and consumption choices. Moreover, public engagement and acceptability as well as participatory governance drives conservation programs to restore and protect marine resources (McKinley and Fletcher, 2012; Voyer et al., 2012). As a result, knowledge of people's understanding of environmental issues is required for attaining conservation goals. In the context of this study, "perception" is used as an umbrella term following Jefferson et al. (2015) to include components such as knowledge, interest, social values, attitudes, or behaviors. Studies examining these components are extensive and either assess general marine environmental conditions or specific marine ecosystems, resources, or user groups using qualitative and quantitative approaches (see Trenouth et al., 2012; Hamilton and Safford, 2015; Daigle et al., 2016).

Empirical evidence shows that public perceptions are defined in varying contexts. The evidence also shows that there is considerable heterogeneity in perceptions which is influenced by socio-demographic profiles, behavioral attitudes, and beliefs. They further vary by the scope of marine components or activity and between nations. For instance, a review of various reports across European countries point toward considerable support for marine planning initiatives (Potts et al., 2016); a matching of public perception with scientific consensus regarding climate change impact on seas, but low awareness of certain climate change components such as ocean acidification. Marked differences were observed between countries. Generally, females and older people were found to be more concerned about the issues raised, while distance to the sea shaped perceptions toward the marine environment (Buckley et al., 2011).

In a recent questionnaire-based study by Lotze et al. (2018), 21 countries involving 32,000 respondents were compared from around the world to examine marine threats and protection. The authors showed that more than two-thirds believed the marine environment was under threat from human activities and the most severe threats were pollution, fishing, habitat alteration, and climate change. There was a general consensus toward major perceived threats and willingness to support conservation goals. Within national borders, Hynes et al. (2014) show that Irish people demonstrate reasonable knowledge of threats facing marine environments and of the market and non-market importance of marine ecosystem services. Skepticism does exist, however, among the public concerning the government and private industry ability to manage the marine economy, while there is more trust in scientists. In repeat surveys conducted in 2005, 2010, and 2015 by Hawkins et al. (2016) to evaluate awareness and attitudes toward marine protection in the United Kingdom, respondents showed pessimism, perceiving sea health, and management to be poor to fair and largely in decline, with about two-thirds of the respondents agreeing that more than 40% of UK seas should be protected from fishing and other damaging activities.

Rose et al. (2008) show that much of the marine environment and conservation research relates to coastal areas, except those studies concerned with a relatively small number of specific creatures such as whales or focused on fishing and pollution issues. The authors then show in a survey of about 3,000 respondents in the UK that <1% of the population could name a topographic or living element of a real deep-sea landscape. About 44% thought the deep-sea was generally, utterly or mostly barren in their region and often talked about the coast when asked about the sea.

Jefferson et al. (2014) assess public perceptions toward UK subtidal species and marine health to determine positive connections between society and the sea. Many respondents showed interest in traditionally charismatic species but lacked knowledge of their existence in UK seas. Pollution from marine litter was considered the greatest indicator of marine health but lacked consensus that the presence of megafauna was an indicator. In exploring sources of heterogeneity in perceptions, the authors identified gender and experience as key influencers on public perceptions of species. Perceptions of marine health was on the other hand found to be influenced by social values.

Against the backdrop of the emerging importance of public perceptions research of the deep-sea (Jefferson et al., 2015) and the sparse literature of what people know and feel about the deep-sea, the current study contributes with public perception of the deep-sea environment in Norway and Scotland. It further disentangles influencing factors using a multiple indicators multiple causes model, to aid public engagement and policy formulation toward the achievement of good environmental status of Europe's marine environment.

METHODS

Participants

The survey was conducted to collect data on the people of Scotland (hereafter Mingulay, indicating the deep-sea areas of the MRC) and Norway (hereafter LoVe, indicating the Lofoten-Vesterålen coral reefs) and is used to analyze their perceptions of the marine environment and deep-sea areas. Following a pilot

test of the survey questions, the questionnaire was implemented online through market research companies who drew from recruited and registered online panels of respondents. The recruitment of respondents was in accordance with EU standards in terms of research code of conduct and data protection bylaws. Participants had the option to decide whether to take part in the survey or not. The Mingulay survey started in January 2019 and spanned over a period of 4 weeks while the LoVe survey started in March 2019 and lasted over a period of 3 weeks. A total of 1,025 and 1,024 respondents participated in the Mingulay and LoVe surveys, respectively, and the demographic profiles are presented in **Table 1**. In both surveys, young adults were the least represented. The age group 55+ years were the most represented (44%) in the LoVe survey while the 36–55 years group were the most represented (49%) in the Mingulay survey. Males constituted 44 and 57% of respondents for Mingulay and LoVe, respectively. Gender is slightly skewed from the respective national population ratios of ∼50%. While about half of the Mingulay respondents had tertiary education, ∼86% of LoVe respondents were in the same category.

Survey Design

Participants were asked questions about their knowledge, perceptions and attitudes toward the Scottish and Norwegian seas and wildlife, as well as the Lofoten-Vesterålen cold-water coral reef in Norway and the Mingulay reef complex in Scotland[3]. The locations of these deep-sea ecosystems of MRC and LoVe are shown in **Figures 1A,B**, respectively, below.

Prior to answering the questions, participants were informed about the background to the survey. Information provided included the impact of changing environmental conditions and anthropogenic activities on the seas and wildlife, how the government was responsible for managing it and the potential cost of management on households. The MRC and LoVe were then introduced in each survey as a unique ecosystem in Scotland and Norway, respectively, and the ecosystem services they provide, current management measures in place, potential economic benefits and threats were presented.

The first part of the questionnaire assessed respondents' prior knowledge of the information provided in the introduction of the questionnaire on the deep-seas and wildlife in the respective countries using a scale of 1 to 5 where 1 indicates "I knew none of it" and 5 indicates "I knew everything." Prior awareness of the MRC and LoVe were assessed through a Yes/No response. Respondents' perception of the condition of the deep-sea areas were rated on a scale of 1 (indicating very poor) to 5 (indicating very good), personal effect of the deep-sea and wildlife was rated as "no effect on me," "some effect on me," and "major effect on me" while perceived management of the deep-sea areas rating was scored as "well," "neither," and "poorly." "Don't know" was given as an option in all scores.

The second part of the survey captured information including any visits to marine areas, participation in marine related activities, and exposure to the BBC's Blue Planet II documentary. Respondents pro-environmental concerns and beliefs in relation to the marine environment were also evaluated on an 11-item 5-point Likert scale ranging from "strongly disagree" to "strongly agree," with a don't know option. The 11 items covered areas including ecological crisis, pressures, conservation, and ecosystem services. The items were an adaptation of 2 sentences (first two) from the New Ecological Paradigm (NEP) scale (Dunlap et al., 2000) and 9 author self-constructed sentences from the European Union Marine Strategy Framework Directive (MSFD) qualitative descriptors for good environmental status (GES) and other literature sources. It therefore reveals the convergence between public perception and the EU Directive on what good environmental status for the marine environment should be. For subsequent analysis, the scores of item 10 (Economic growth is more important than protecting the marine environment) are reversed to match the other indicators so that higher overall scores reflect ecocentrism (nature-centered values of the environment) while lower values indicate anthropocentrism (human-centered values of the environment).

TABLE 1 | Indicators of pro-environmental concerns toward the marine environment.

Items	Item Short Phrase	Source
The balance of marine biodiversity is very delicate and easily upset	Delicate marine biodiversity	NEP
Human activities are severely abusing marine ecosystems such as marine organism abundance and diversity, and biological integrity of the sea-floor	Human abuse	NEP
The key pressures on marine biodiversity are fisheries	Fisheries pressure	MFSD GES (D1)
The key pressures on marine biodiversity are physical damage to the sea floor	Sea floor damage	MFSD GES (D1)
All commercial fish stocks should be sustainably exploited in order to secure high long-term yield and healthy stocks	Sustainable exploitation	MFSD GES (D3)
Marine litter is one of the key challenges to the marine environment and biodiversity	Marine litter challenge	MFSD GES (D10)
Healthy seas are central to our well-being	Central to our well-being	author
Healthy seas are central to economic security	Central to economic security	author
Establishment of marine protected areas is one important measure for protecting valuable, vulnerable or threatened organisms	MPA is important	author
Economic growth is more important than protecting the marine environment	Economic growth	author
As humans we are responsible to protect natural resources to benefit future generations	Environmental citizenship	author

Author indicates author phrased statements sourced from marine literature.

Analytical Approach

The data were analyzed using basic statistical summaries, charts and cross tabulations. Where necessary, the Pearson Chi-square test was used to test for statistical independence across samples and variables. Basic regression models including logistic and

[3] A sample questionnaire for Scotland can be accessed by clicking here.

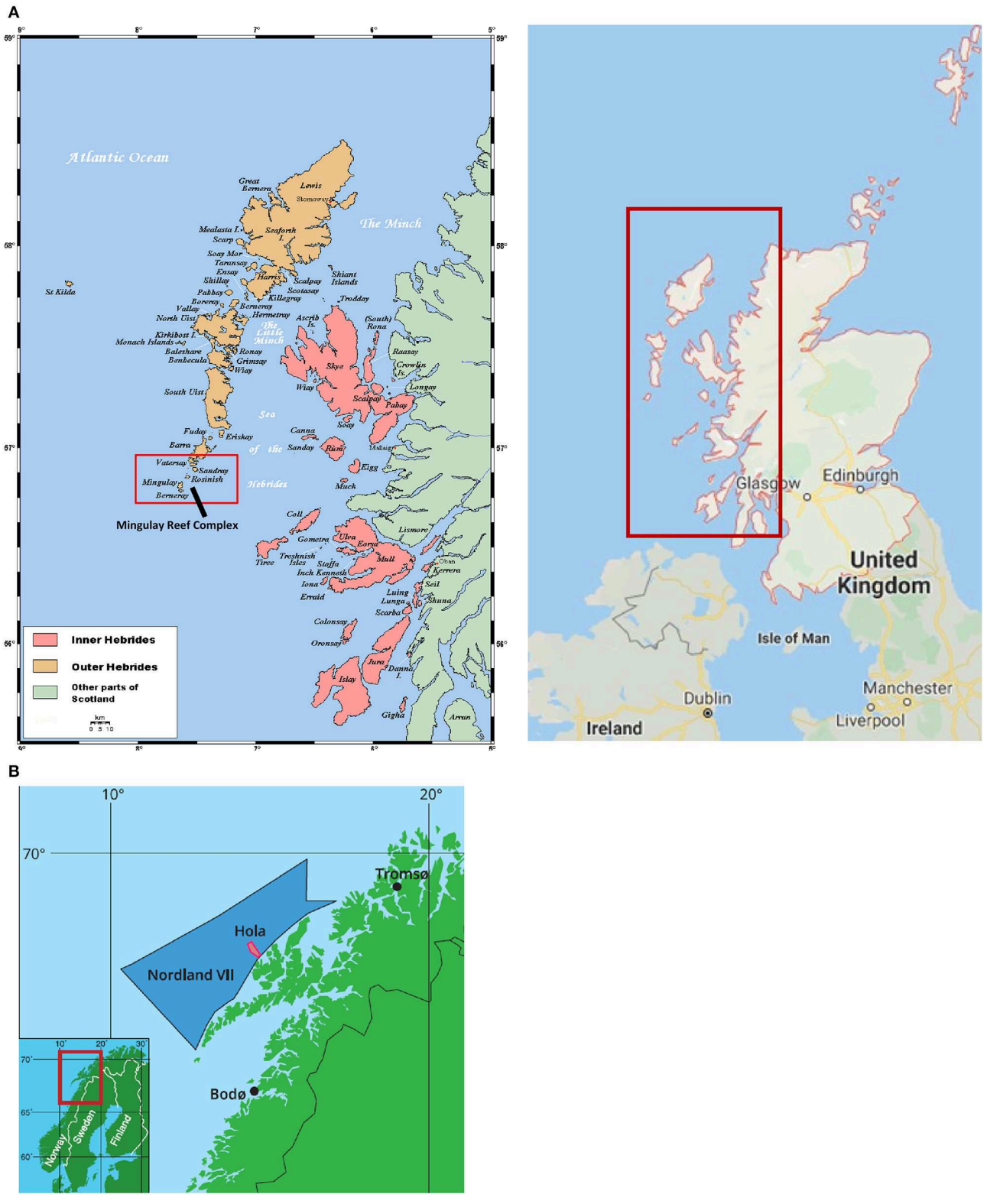


FIGURE 1 | (A) The Mingulay reef complex. **(B)** The Lofoten-Vesterålen.

ordinal logistic regressions were employed to evaluate the relationship between respondent characteristics and outcome variables of interest due to the ordinal and binary nature of the outcome variables.

Regarding the analysis of relationships between respondents' pro-environmental concerns toward the marine environment and personal characteristics, generalized structural equation modeling (GSEM) is employed. The GSEM can accommodate large numbers of endogenous and exogenous variables and build models that include latent variables as well as response variables that are not continuous measures. In this study, the Multiple Indicators Multiple Causes (MIMIC) model is used based on a generalized structural equation model founded on the following conceptual model (**Figure 2**).

In the MIMIC model, it is assumed that the observed indicators (y) are manifestations of a latent concept (unobserved pro-environmental concern, η) and that there are other exogenous variables $\boldsymbol{x}$ (with covariates 1 to S) that influence the latent factor (Jöreskog and Goldberger, 1975; Rabe-Hesketh et al., 2004). In the dataset, we captured the pro-environmental concern items as discrete indicators which are generalized responses of a categorical (ordinal) nature. Therefore, the generalized structural equation model (GSEM) is employed as opposed to structural equation models which assume continuous indicator responses. The GSEM formulation of MIMIC consists of the simultaneous estimation of two equations. The measurement model for pro-environmental concern can be written in terms of the underlying continuous responses

$$\mathbf{y}^{*}=\wedge_{y}\boldsymbol{\eta}+\mathbf{e}$$

and the structural equation is written as

$$\boldsymbol{\eta}=\boldsymbol{\beta}\mathbf{x}+\mathbf{v}$$

with the reduced form

$$\mathbf{y}^{*}=\pi\mathbf{x}+\mathbf{u}$$

where $\mathbf{y}^{*}$ is the latent component for $\mathbf{y}$, $\boldsymbol{\beta}$, and $\wedge_{y}$ are the corresponding structural parameters relating the latent dependent variable to the covariates, and factor loading matrix, respectively. $\boldsymbol{\pi}=\boldsymbol{\beta}\wedge_{y}{}'$ are vector of parameters to be estimated. $\mathbf{v}$ is a vector of respondent disturbance, $\mathbf{u}$ is a random error term assumed to be standard logistic, and $\mathbf{u}$ is the reduced form error composed of $\mathbf{u}=\wedge_{y}\mathbf{v}+\mathbf{e}$. To achieve model identification, typically the first factor loading is restricted to unity.

With respect to the measurement equation, $j(j=1,2,\ldots,J)$ and τ_j denote agreement levels and thresholds associated with these agreement levels, respectively. These unknown thresholds are assumed to partition the propensity into $J-1$ intervals. The unobservable latent variable $\mathbf{y}^{*}$ is related to the observed ordinal variable $\mathbf{y}$ by the τ with a response mechanism of the form:

$$\boldsymbol{y_i=j,\ if\ \tau_{j-1}<y_i^{*}<\tau_j,\ for\ j=1,2,\ldots,J}$$

To ensure well-defined intervals and natural ordering of observed agreement levels, the thresholds are assumed to be ascending in order, such that $\tau_0<\tau_1<\ldots<\tau_J$ where $\tau_0=-\infty$ and $\tau_J=+\infty$.

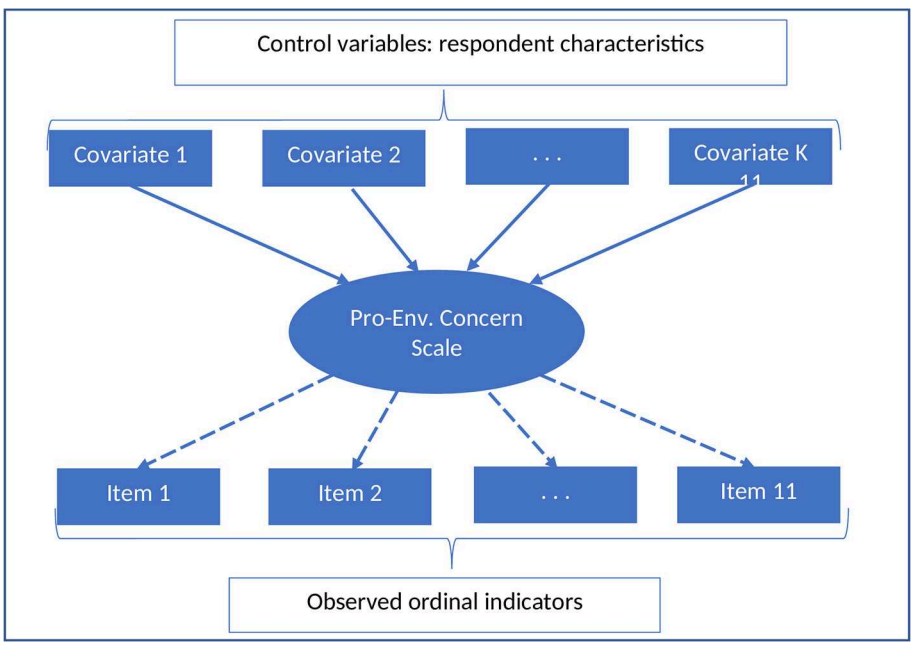


FIGURE 2 | A MIMIC Model of single latent variable: pro-environmental concern.

TABLE 2 | Summary statistics.

	Mingulay		LoVe	
Variable	**Mean**	**Std. Dev.**	**Mean**	**Std. Dev.**
Age 18–35	0.101	0.302	0.168	0.374
Age 36–55	0.493	0.500	0.394	0.489
Age 56 and above	0.406	0.491	0.438	0.496
Male	0.440	0.497	0.572	0.495
Tertiary education	0.518	0.500	0.864	0.343
Full time employed	0.380	0.486	0.592	0.492
Part time employed	0.133	0.339	0.092	0.289
Student	0.064	0.246	0.052	0.222
Unemployed	0.044	0.205	0.021	0.145
Resident of highlands and islands	0.063	0.244	–	–
Marine Sports	0.384	0.487	0.466	0.499
Visit to sea areas	0.276	0.447	0.639	0.481
Have visited island of Mingulay [or LoVe]	0.023	0.151	0.639	0.481
Have visited island of barra	0.119	0.324	–	–
Have visited elsewhere in the outer hebrides	0.238	0.426	–	–
Have seen blue planet II	0.549	0.498	0.429	0.495
Member of environmental organization	–	–	0.108	0.311

"–" indicates information was not applicable or captured in the particular survey.

RESULTS

A summary statistic of the survey respondents' attitudes is presented together with the socio-economic profiles in **Table 2**. As shown, only 6% of the Scottish respondents are residents of the Highlands and Islands. A significantly higher fraction of Norwegian respondents was engaged in marine sports (47%) as compared to the Scottish respondents (38%). In terms of visits to the sea areas, only about 2% of Scottish respondents have specifically visited the MRC, and 28% have visited the sea areas around Scotland including the island of Barra and elsewhere in the Outer Hebrides. Comparatively, 64% of the respondents in the Norwegian sample had visited Lofoten-Vesterålen.

Knowledge and Awareness of Deep-Sea Areas

Figure 3A below presents the distribution of prior knowledge levels of the information presented in the introduction section of both the Mingulay and LoVe surveys. The LoVe responses appear symmetric while Mingulay is positively skewed with respective mean (standard deviation) scores of 3.13 (0.88) and 1.75 (0.78) and a median score of 3 and 2. This reflects that on average, the majority of the Norwegian respondents perceived themselves more knowledgeable of the deep-seas and wildlife within their marine environment than did the Scots. However, the average perceived prior knowledge levels were low with Scottish respondents lying close to "I knew little of it" while Norwegians were close to "I knew some of it." A Pearson Chi-square test of independence of distribution of responses between the two samples was $x^2\,(4) = 883$ ($pvalue = 0.00$). This indicates that independence is rejected and hence confirms that Norwegians had higher prior perceived knowledge than their Scottish counterparts. The standard deviation estimates relative to the mean also shows higher variation in perceived knowledge levels for the Norwegian respondents (Coefficient of Variation, CoV = 50%) than the Scottish (CoV = 25%).

In terms of awareness represented in **Figure 3B** below, the Mingulay survey shows only 16% of Scottish respondents were aware of the MRC while a significantly higher share (59%) of the Norwegian respondents were aware of the cold-water coral reefs at Lofoten-Vesterålen. In general, we conclude that knowledge levels related to the deep-sea environment is low among the Scottish and moderate among Norwegians, but the latter with high variance.

Given the ordinal and binary nature of responses to prior knowledge and awareness, we use ordered and binary logistic regressions to evaluate how responses differ across respondents. The results are shown in **Table 3** below. On prior knowledge, we do not identify any significant differences between gender and age in the Mingulay survey. However, the senior-aged group in the LoVe survey appear to have more perceived prior knowledge of their seas and wildlife. Variables including tertiary education, having watched the Blue Planet II deep-sea documentary, association with a sea related industry, engagement in marine sports and those who had visited the sea areas were more likely to have high perceived prior knowledge given the statistical significance at the 1% level. Moreover, living in the region of the Highland and Islands (in the case of Scottish respondents) and being a member of an environmental organization (in the case of Norwegians) have significant positive effect on perceived prior knowledge.

In regard to awareness, no significant differences exist for gender and having a tertiary education in either country. However, the age cohorts 36–55 and 56 and above were more likely to be aware of the MRC while age had no significant effect on the awareness of the Lofoten-Vesterålen cold-water coral reefs. Having watched Blue Planet II, being associated with a sea industry or having visited the sea areas previously all have significantly positive effect on awareness. Marine sport participation has a significantly positive impact on awareness of the Lofoten-Vesterålen cold-water coral reef as does being a member of an environmental organization. No significant differences existed among those living in the region of the Highlands and Islands.

Public Perceptions of the Deep-Sea Condition, Management, and Personal Effect

Respondents' rating of the deep-sea condition, management and whether they perceive changes in the deep-sea to have an effect on them were assessed with the distribution of responses presented in **Figures 4–6**. Perceptions of the deep-sea condition shows a similar distribution for both Mingulay and LoVe surveys where most respondents rated it to be "fairly good" with respective fractions of 46 and 50%. The mean (standard deviation) rating

TABLE 3 | Influencers of prior knowledge and awareness.

	Mingulay				LoVe			
	Prior know (Ologit)		Awareness (Logit)		Prior know (Ologit)		Awareness (Logit)	
Variables	**Coef**	**S. E**	**Coef**	**S. E**	**Coef**	**S. E**	**Coef**	**S. E**
Male	0.134	0.122	0.089	0.184	−0.113	0.124	0.224	0.138
Age 36–55	0.066	0.211	0.911**	0.459	0.223	0.180	0.174	0.196
Age 56 and above	0.289	0.216	1.571***	0.456	0.414**	0.181	0.285	0.200
Tertiary education	0.322***	0.123	−0.198	0.186	0.575***	0.179	0.275	0.196
Blue planet II	0.495***	0.124	0.473**	0.191	0.543***	0.125	0.870***	0.141
Highlands and islands	0.677**	0.248	0.349	0.311				
Sea industry	1.088***	0.216	0.902***	0.276	0.612***	0.171	0.572***	0.195
Marine Sport	0.488***	0.125	0.252	0.186	0.614***	0.125	0.481***	0.139
Visit to sea areas	0.874***	0.137	1.209***	0.188	0.451***	0.132	0.547***	0.144
Member of environmental organization				0.480	0.551***	0.198	0.624**	0.239
Constant			−3.761***				−1.255***	0.258
Observations	1,025		1,025		1,024		1,024	
Wald Chi2	133.71***		89.14***		100.59***		104.84***	
Pseudo R2	0.061		0.113		0.049		0.087	

*Robust standard errors (S.E) reported. ***, **, and * indicate 1, 5, and 10% significance level, respectively.*

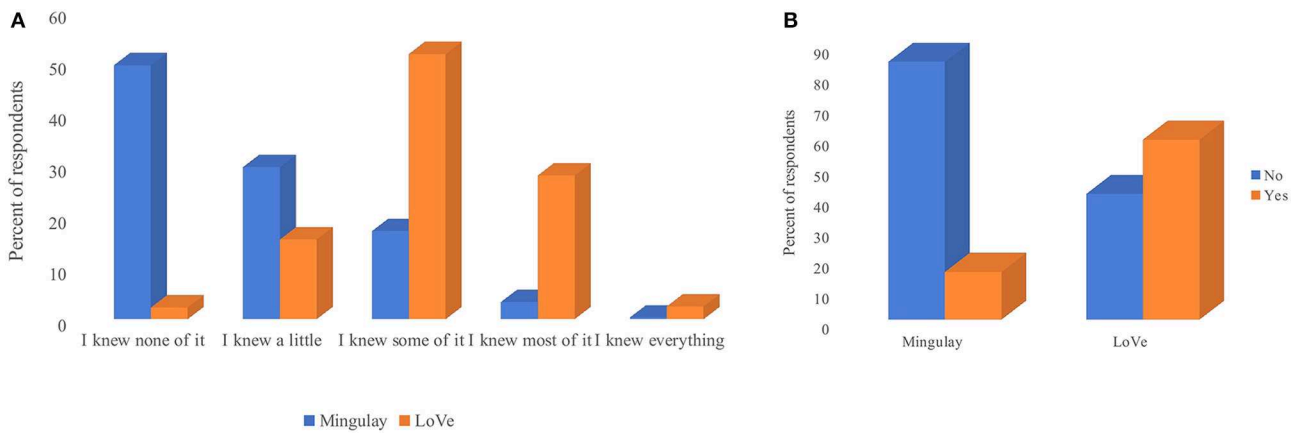


FIGURE 3 | (A) Prior knowledge of the deep-sea and wildlife information. **(B)** Awareness of cold-water coral reefs.

for LoVe was 3.5 (0.81) and Mingulay was 3.6 (0.81) which are relatively similar. A Pearson Chi-square test of independence rejects the null: x^2 (5) = 145 (*pvalue* = 0.00) and shows that the odds (odds ratio = 1.3, excluding the "don't know" group) of Scottish respondents rating the deep-sea to be in good condition is higher than for the Norwegian respondents.

With the ordinal nature of the deep-sea condition responses, an ordinal logistic regression shows that males were more likely to rate the deep-sea condition higher in the LoVe survey, whereas no significant differences existed for Mingulay. For both surveys, the age group >35 years perceived the deep-sea condition to be good as opposed to the age cohort 18–35 years. However, slightly higher odds were observed for age 56 and above in Scotland and age 35–55 in Norway. Moreover, the Blue Planet II effect was significant and positively impacted the Mingulay perceived rating of deep-sea condition, though not for LoVe. On the other hand, association with a sea-industry and visits to the sea-shore had a significant effect on the LoVe perceived deep-sea condition rating.

With the perceived rating of deep-sea management outcomes shown in **Figure 5**, we observed 34 and 22% of respondents rating the deep-sea as being well-managed for Mingulay and LoVe respondents, respectively, while 12 and 76% rated it poorly. Moreover, **Figure 5** shows zero observed frequencies for the "neither" and "don't care" responses in the LoVe and Mingulay surveys, respectively. For ease of comparison, we evaluated the differences in responses to be binary (1/0) outcomes where 1 indicates "well-managed" and 0 otherwise.

A logistic regression of perceived deep-sea management (shown in **Table 4**) indicates significant variations occurred

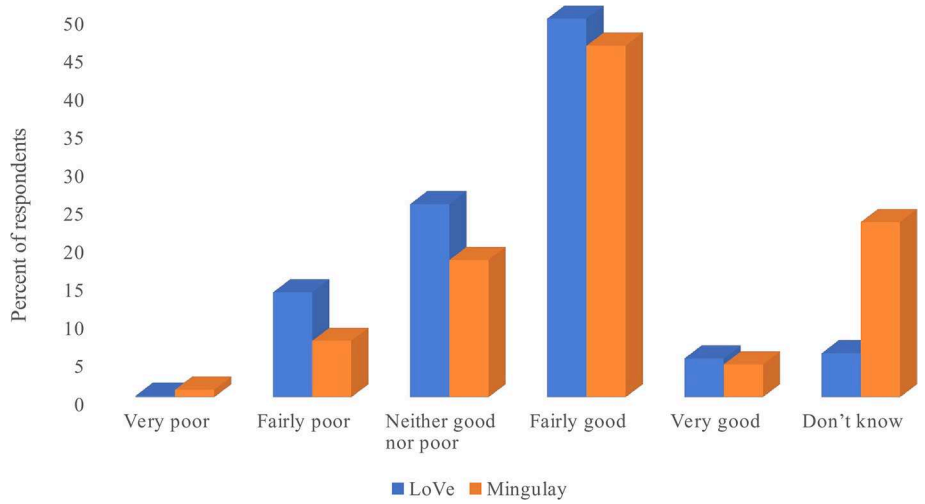


FIGURE 4 | Rating of deep-sea environmental condition.

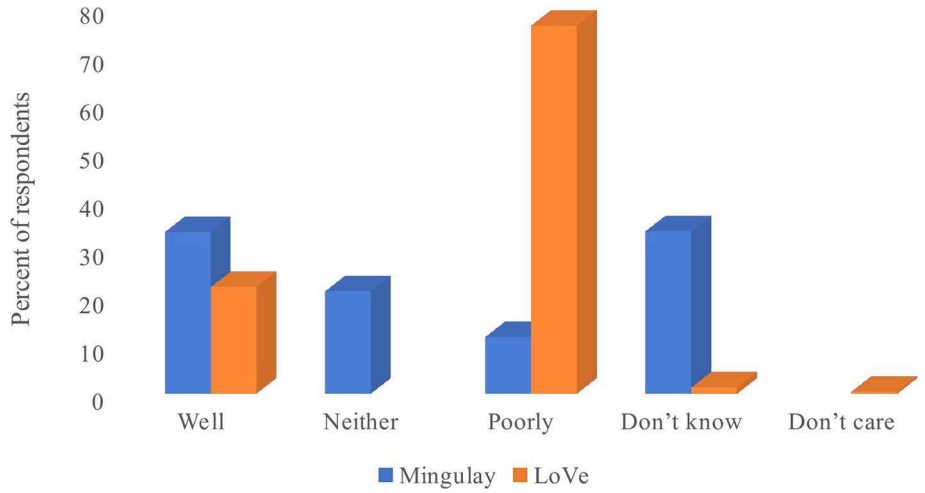


FIGURE 5 | Rating of deep-sea management.

between those who had watched the Blue Planet II documentary and those who visited the sea-areas in the Mingulay survey. These relationships were significantly positive. Regarding the LoVe survey, perceived better management of the deep-sea was significantly positive at the 1% significance level for males, as was association with a sea-industry, participation in a marine sport, a visit to the sea areas and being a member of an environmental organization.

Regarding respondents' perception of whether changes in the deep-sea has "personal effect on them," **Figure 6** shows that for both Mingulay and LoVe surveys, most respondents perceive it has "some effect" on them, with shares of 61 and 62%, respectively. A Pearson Chi-square statistic of: $x^2\,(3) = 147$ ($pvalue = 0.00$) reveals that the test of independence is rejected and an odds ratio of 0.40 for Mingulay shows that Norwegian respondents perceive changes in the deep-sea to have a larger effect on them than their Scottish counterparts. This is reflected in the mean (standard deviation) rating scores of 1.82 (0.60) for Mingulay and 2.09 (0.59) for LoVe. The Mingulay regression analysis shows that only those with tertiary education, an association with a sea-industry or those whom have visited the sea areas, significantly influence "effect on me" positively at the 1% significance level. For the LoVe survey, respondents experiencing personal effects were more likely to be females, were 36–55 years, watched the Blue-Planet II documentary, engaged in marine sports and were members of an environmental organization.

Pro-environmental Concerns Toward the Marine Environment

The public's concern in relation to the marine environment was captured by 11 item indicators and reflect statements

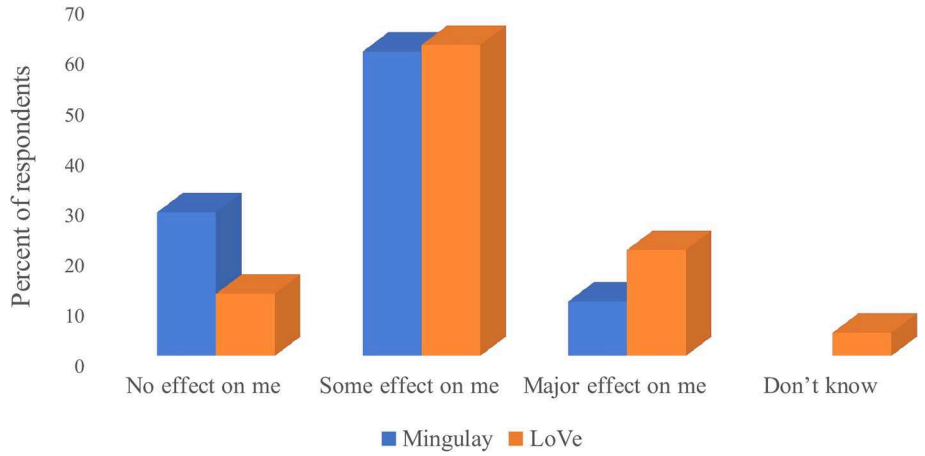


FIGURE 6 | Perception of deep-sea effect on respondent.

TABLE 4 | Influencers of perceived deep-sea condition, management, and personal effect.

	Condition (Ologit)				Management (Logit)				Effect on me (Ologit)			
	Mingulay		LoVe		Mingulay		LoVe		Mingulay		LoVe	
Variables	**Coef**	**S. E.**	**Coef**	**S. E.**	**Coef**	**S. E.**	**Coef**	**S. E.**	**Coef**	**S. E.**	**Coef**	**S. E.**
Male	0.029	0.143	0.593***	0.126	0.042	0.136	0.735***	0.176	−0.104	0.129	−0.777***	0.143
Age 36–55	0.463**	0.228	0.440**	0.190	0.230	0.245	0.268	0.253	0.213	0.207	0.400**	0.190
Age 56 and above	0.629***	0.238	0.385**	0.193	0.300	0.247	0.304	0.253	−0.223	0.212	0.127	0.191
Tertiary education	0.202	0.142	0.122	0.188	−0.156	0.135	−0.338	0.234	0.324**	0.129	0.124	0.213
Blue planet II	0.401***	0.144	0.009	0.129	0.353**	0.136	0.274*	0.165	0.140	0.127	0.572***	0.139
Highland and islands	0.309	0.267			−0.302	0.292			0.117	0.262		
Sea industry	−0.416	0.256	0.50***	0.186	−0.320	0.250	1.104***	0.202	0.528**	0.251	0.157	0.188
Marine sport	0.074	0.147	−0.068	0.130	0.106**	0.137	0.795***	0.168	0.044	0.130	0.768***	0.142
Visit to sea areas	0.273*	0.164	0.285**	0.137	0.322***	0.150	0.700***	0.186	0.610***	0.147	0.274*	0.141
Member of environmental organization			−0.274	0.196			0.671***	0.244			0.982***	0.204
Constant					−1.149	0.253	−3.006	0.346				
Observations	789		965		1,025		1,024		1,025		977	
Wald Chi2	31.54***		47.92***		17.18**		105.97***		41.58***		105.28***	
Pseudo R2	0.016		0.023		0.014		0.11		0.03		0.072	

*Robust standard errors (S. E.) reported. ***, **, and * indicate 1, 5, and 10% significance level, respectively.*

toward ecological crisis, pressures on the marine environment, ecosystem service benefits and the need to protect it through sustainable management. The concerns were captured on a 5-point Likert scale where higher overall scores designate ecocentrism and lower scores indicate anthropocentrism. The distribution of responses is shown in **Table 5**. The mean itemized score ranges from 3.59 to 4.62 with an overall mean of 4.17 for the Mingulay survey. The range for LoVe is 3.23–4.52 with an overall mean of 4.09. This reflects that on average the public tend to agree with the statements indicating a direction toward ecocentrism.

For the Mingulay survey, the highest mean score is linked to agreement with the statement that humans are responsible for protecting natural resources to benefit future generations. The highest fraction, 91% either tend to, or strongly, agree with this statement. The same statement scores highest in the LoVe survey with 93% agreeing. The statement "marine litter is one of the key challenges to marine environment and biodiversity" has the second highest mean score for Mingulay and fourth in the LoVe survey. For both surveys, the least agreed upon is the statement that the "key pressures on marine biodiversity are fisheries," with the share of respondents agreeing with this statement being less than half of the sample.

In order to determine the relationships between respondents' personal characteristics and their pro-environmental concerns toward the marine environment, we assume that the 11-item indicators form a unidimensional latent construct underlying their perceptions. This latent indicator is therefore explained by the respondents' characteristics. To validate this assumption,

TABLE 5 | Distribution of pro-environmental concern INDICATORS.

Item code	Mingulay				LoVe			
	Obs.	Mean	*SD*	AGREE % (Tend to + Strongly)	Obs.	Mean	*SD*	AGREE % (Tend to + Strongly)
Delicate marine biodiversity	942	4.31	0.71	80.88	1,024	4.09	0.77	82.52
Human abuse	964	4.31	0.77	81.18	1,024	4.30	0.72	89.26
Fisheries pressure	812	3.59	0.87	44.19	1,024	3.23	0.79	33.1
Sea floor damage	806	3.87	0.82	53.27	1,024	3.49	0.79	49.03
Sustainable exploitation	937	3.97	1.04	67.03	1,024	4.34	0.77	88.87
Marine litter challenge	969	4.47	0.70	86.93	1,024	4.15	0.78	82.52
Central to our well-being	988	4.38	0.74	85.07	1,024	4.52	0.72	92.48
Central to economic security	948	4.14	0.80	75.22	1,024	4.19	0.80	83.01
MPA is important	973	4.36	0.72	83.8	1,024	4.12	0.87	80.47
Economic growth	979	3.86	1.06	65.85	1,024	4.04	0.93	75.49
Environmental citizenship	1,002	4.62	0.62	91.22	1,024	4.54	0.75	92.48
Mean		4.17	0.31			4.09	0.40	

Mean of items in Mingulay survey computed without the "don't know" responses.

we first conduct a single latent exploratory factor analysis to determine whether the items are sufficiently correlated and reliable to qualify as a unidimensional latent construct. The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy of the correlations resulted in an estimate of 0.903 (item range of 0.78–0.94) for the Mingulay survey and 0.892 (item range of 0.86–0.93) for the LoVe survey. These estimates compared to the Kaiser (1974) thresholds[4] show values indicate sufficient correlation between items. The Cronbach Alpha coefficient for Mingulay was 0.827 (item range of 0.80–0.84) and LoVe was 0.849 (item range of 0.82–0.86). This coefficient by Cronbach (1951) is used to determine the internal consistency and acts as a measure of reliability. A value of 0.6 is considered acceptable and according to Hair et al. (2011), a value of 0.8 or higher is regarded as satisfactory.

Given the adequacy and reliability of using the statements as a unidimensional latent factor, we proceed to estimate the factor loadings and the latent-covariate relationships in a MIMIC generalized structural equation model. The results are presented in **Table 6**. The measurement model provides the factor loadings where all items are significantly loaded on to the latent variable at the 1% significance level. The first item had the factor loading coefficient constrained to unity.

For both surveys, we observed significant and positive association between pro-environmental concerns and those respondents who had watched Blue Planet II, those who believe that changes in the deep-sea had personal effect on them and those who at least had some *a priori* knowledge of their seas and wildlife surrounding them. Being associated with the sea-industry however showed a significantly negative effect on pro-environmental concerns. In the LoVe survey, females were more likely to be pro-environmental (ecocentric) than males, while no significant difference was observed in the Mingulay survey. While there was no age effect in the LoVe survey, the 56 and above age group appeared to be more pro-environmental in the Mingulay survey than the age cohorts below 56 years. Education was only weakly significant in the LoVe sample (at the 10% significance level) but had no effect in Mingulay. Also, being a member of an environmental organization showed a positive and significant effect on pro-environmental concern in the LoVe sample.

[4]Kaiser (1974) threshold values of 0.8–0.89 and >0.90 indicate "meritorious" and "marvelous" correlations, respectively.

DISCUSSION AND CONCLUSION

The study of public perceptions; including knowledge level, opinions of how the public feel about the marine environment and pro-environmental attitudes is a critical socio-economic assessment tool for the success of any marine management program (Jefferson et al., 2015; Potts et al., 2016). While public perception studies toward the marine environment are evolving and measured in various facets, the public knowledge and understanding of the deep-sea areas has not featured prominently in the literature. This study contributes to this gap by assessing how the Scottish and Norwegian general public perceive the deep-sea areas and their marine environment. Variations in perception by the public's demographic profile and experiences of the sea are then characterized.

The results suggest that the perceived public knowledge level of the deep-sea areas and wildlife for the Scottish public can be classified as low (a rating of 2 on an ascending scale of 1–5) while that of the Norwegian public can be classified as moderate (a rating of 3). A significant share of Norwegians (59% of the respondents) were aware of the LoVe deep-sea cold-water coral reef while comparatively only 16% of Scottish respondents were aware of the cold-water coral reef complex at Mingulay. The difference in knowledge level between the two countries is not surprising because the Røst Reef off the Lofoten Islands is one of the world's best known *Lophelia* reefs. Except for the awareness of cold-water coral reefs by the Norwegian public,

TABLE 6 | MIMIC GSEM: Influencers of pro-marine environmental concerns.

	LoVe		Mingulay	
Structural	**Coeff**	**S. E.**	**Coeff**	**S. E.**
Male	−0.64***	0.14	−0.01	0.13
Age 36–55	0.17	0.20	0.28	0.23
Age 56 and above	0.14	0.20	0.54**	0.24
Tertiary education	0.39*	0.22	0.20	0.14
Blue Planet II	0.69***	0.14	0.73***	0.14
Member of environmental organization	1.13***	0.23		
Highland and Islands			0.28	0.28
Sea industry	−0.82***	0.19	−0.54**	0.24
Marine sport	0.10	0.14	−0.05	0.14
Visit to sea areas	0.06	0.14	0.30*	0.16
Deep-sea changes effect on me	0.71***	0.12	1.38***	0.14
At least some prior knowledge	0.38***	0.18	0.38**	0.18
Measurement* **				
Delicate marine biodiversity	1.00		1.00	
Human abuse	1.16	0.08	0.87	0.08
Fisheries pressure	0.20	0.04	0.38	0.04
Sea floor damage	0.45	0.05	0.58	0.05
Sustainable exploitation	0.65	0.06	0.78	0.07
Marine litter challenge	1.35	0.15	1.17	0.10
Central to our well-being	0.70	0.07	0.81	0.07
Central to economic security	1.02	0.08	1.40	0.12
MPA is important	0.77	0.08	0.44	0.04
Economic growth	1.48	0.16	1.53	0.15
Environmental citizenship	0.60	0.07	0.32	0.04
Obs	1,024		1,005	
Loglik	−10,479		−11,311	
BIC	21,415		19,679	

*Robust standard errors (S. E.) reported. ***, **, and * indicate 1, 5, and 10% significance level, respectively.*

it would appear that both the Norwegian and Scottish public display limited knowledge about the deep-sea. This might be due to its remoteness, and by it being out of sight and mind. The low knowledge level confirms Rose et al. (2008), Jefferson et al. (2014), and Spence et al. (2018) who provide evidence across various knowledge dimensions toward the marine environment. It is also evident that direct and indirect exposure to the sea has the potential to increase marine life knowledge level as identified by the difference between Scottish and Norwegian public.

Despite the low levels of perceived knowledge and awareness among the public, the ratings of deep-sea conditions were similar across countries and rated higher at the "fairly good" level. The deep-sea condition rating however did not appear to correlate positively with the perceptions of deep-sea management which may reflect pessimism with regard to management authorities. In the case of Norway, this might be due to the contentious ongoing pressure to open LoVe for petroleum exploration. This finding may suggest that management authorities need to do a better job of explaining to the public what they are doing in terms of protecting the marine environment, and that they are doing so in a manner that is efficient and competent. If the relevant management institutions do not exhibit these characteristics or keep the public informed of their ongoing conservation and management activities, then even individuals who believe that marine environmental conservation is an important public goal may still oppose increasing public spending on additional policy measures that protect the deep-sea environment.

The results also demonstrate that the public in both countries perceive that changes in the deep-sea have at least some effect on them personally. The personal effect due to changes in the deep-sea contributes to the gap in literature that has been raised in Jefferson et al. (2015) that, assessing values of "*how people feel about the deep-sea*" is essential to contributing to marine conservation efforts. Though Jefferson et al. (2015) argue about the emotional connection, the realization of how changes in the deep-sea affect people personally is the starting point to connect emotions to a resource that is remote to the majority. The recognition of deep-sea changes having personal effects appears to be reflected in the public's ecocentric attitude toward the marine environment via recognition of the current ecological crisis associated with key pressures such as marine litter, and the need to be "environmental citizens" by supporting the protection and sustainable management of marine ecosystems.

Furthermore, the public associate with these concepts because of the recognition of marine ecosystem benefits; i.e., healthy seas being central to economic security and well-being. The consensus toward ecological crisis and healthy seas benefits agree with the literature regarding the marine environment. For instance, Lotze et al. (2018) provide a baseline comparison where the authors identify more than 70% of respondents in a 21 cross-country survey who believed the marine environment is under threat and had support for marine protected areas in their region. Lotze et al. (2018) provide support for respondents' rating of marine litter where a consensus was reached that pollution from marine litter was the top threat to the environment. Potts et al. (2016) also found that ecosystem services are recognized to be important by the public in terms of economic security and by being central to our well-being. The ecocentric perceptions showed by the Norwegian and Scottish public were also present in the Irish population where Hynes et al. (2014) found that the public have reasonable knowledge of the main threats facing the marine environment and the importance of ecosystem services.

Since some of the pro-environmental concern indicators were derived from the EU Marine Strategy Framework Directive's descriptors for GES, the evidence shown in this study suggests that the Norwegian and Scottish public share similar views and might support policies that target the achievement of GES of the European marine environment despite Norwegians (and soon the British) being outside of the EU. In spite of Brexit, indications are that the UK will remain committed to the Marine Habitats Directive. Socio-demographic characteristics and experience with the sea through different mediums seems to influence people's perceptions with some variations across the two countries. Age, gender, and education have varying associations with awareness of deep-sea changes on human

well-being, perceptions of deep-sea condition and management as well as general pro-environmental attitudes and values. Hence, formal education can be used as a medium for increasing public knowledge of the deep-sea and its interaction with humans. Similarly, direct and indirect sea experiences such as living in the Highlands and Islands region, association with a sea-industry, marine sports, visits to sea areas or viewing documentaries like Blue Planet II influence the public's perception. Therefore, policies aimed at exposing the public to the sea, either physically or virtually could increase awareness and support marine conservation. Nevertheless, caution should be taken in that the relationships captured reflect correlations rather than causation.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Norwegian Centre for Research Data (for the Norwegian survey) and the Research Ethics and Integrity, University of Edinburgh (for Scottish data collection). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

IA-Y, BX, SH, and CA contributed conception and design of the study. IA-Y, SH, and BX organized the database. IA-Y performed the statistical analysis and wrote the first draft of the manuscript. CA wrote introductory section of the manuscript. All authors contributed critically to manuscript revision, read, and approved the submitted version.

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frontiers in Marine Science

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The Meso- and Bathypelagic Fishes in a Large Submarine Canyon: Assemblage Structure of the Principal Species in the Gully Marine Protected Area

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Midwater trawl surveys were conducted during 2007–10 at meso- and bathypelagic depths in and near The Gully, a large submarine canyon off Nova Scotia that is also a Marine Protected Area. The fish assemblage in the canyon was highly diverse but 20 species together comprised more than 90% of the catch by number and 80% by weight. The most numerous was the gonostomatid *Cyclothone microdon* while the myctophid *Benthosema glaciale* was next in number and first in weight. Most of those principal species would be expected in catches taken in oceanic waters beyond the shelf break. Only the bottom-spawning *Melanostigma atlanticum* was, within the surveyed area, distinctively a species of the canyon. Multivariate analyses showed that the primary variations in the assemblage were aligned with drivers that act in open ocean: depth, water mass and both diel and seasonal cycles. However, the effect of the canyon was evident in an up-canyon decline in the catches of most species. We hypothesize that the oceanic species are passively carried into The Gully by the known inflow and are there exposed to intense predation, depleting their numbers. We estimate that biomass flux as sufficient to support the Marine Protected Area's signature species: northern bottlenose whales (*Hyperoodon ampullatus*).

Keywords: submarine canyon, mesopelagic, bathypelagic, fish, The Gully, Marine Protected Area

INTRODUCTION

The pelagic realm of the oceans comprises the great majority of the habitable volume on our planet (Herring, 2002). The fishes of subsurface waters, in the meso- and bathypelagic zones (200–4,000 m depth), fill important roles in transport of carbon and energy downwards from the surface, as well as in their recycling and utilization (e.g., Davison et al., 2013; Hudson et al., 2014; Trueman et al., 2014). Those fishes have most often been studied over abyssal depths, though sometimes over continental slopes and rises while, in recent decades, there has been increased attention to the deep pelagic ichthyofaunas over seamounts and mid-ocean ridges (e.g., Moore et al., 2003b, 2004; Sutton et al., 2008, 2013; Cook et al., 2013). In contrast, surveys of meso- or bathypelagic fishes

in submarine canyons have been limited. Apart from studies using visual observations or gears better suited to demersal species (e.g., Baker et al., 2012; Ross et al., 2015), there have been a few continental-slope surveys that have sampled waters overlying minor canyons (e.g., Feagans-Bartow and Sutton, 2014) but none that have fished within a canyon, below its rim depth, using midwater trawls larger than macroplankton nets. In consequence, the similarities and differences between the pelagic fish assemblages within canyons and those outside their mouths are essentially unknown.

The Gully, a canyon incised into the continental margin immediately east of Nova Scotia's Sable Island (**Figures 1**, **2**), is one of the few large enough for deployment of trawls within its depths. The thalweg meanders ≈50 km from the canyon head to the shelf break, where it is ≈2,000 m below the surface, and can be traced from there down the continental slope (for a detailed description, see Kenchington et al., 2014b). Certain components of The Gully's biota are notably enriched, including the cold-water corals, euphausiids, cetaceans, and some exploited fishes (Breeze, 2002; Sameoto et al., 2002; Cogswell et al., 2009; Whitehead, 2013). Early studies sought an explanation for that enrichment through local enhancement and retention of primary production (e.g., Kepkay et al., 2002; Mann, 2002). However, Greenan et al. (2013, 2014) have shown that phytoplankton production over the canyon is unaffected by the presence of deep water beneath, while any local enhancement would be swiftly advected over adjacent banks. Thus, the enrichment must depend on allochthonous energy. Various routes for its input have been suggested (e.g., Harding, 1998; Hooker et al., 2002a; Moors-Murphy, 2014) but no attempts have yet been made to quantify any of the biomass fluxes.

In 2004, much of The Gully was declared a Marine Protected Area ("MPA:" Department of Fisheries Oceans, 2008), with objectives that include both preservation of the diverse biota and conservation of an endangered population of northern bottlenose whales (*Hyperoodon ampullatus*). Dozens of those whales feed in the canyon at any one time, primarily in the central canyon and southwards to the mouth, especially along the eastern side. They probably consume mostly armhook squid (*Gonatus fabricii* and *G. steenstrupi*) and certainly eat quantities far larger than could be supported by local primary production (Hooker et al., 2001, 2002a,b; O'Brien and Whitehead, 2013). Thus, the MPA's management requires, *inter alia*, both documentation of the species found within its boundaries and an understanding of their trophic structures, especially the energy sources that support the whales.

Themelis and Halliday (2012) surveyed the oceanic mesopelagic fishes occurring south of the shelf break off Nova Scotia, and there have been similar surveys elsewhere in the northwest Atlantic (e.g., McKelvie, 1985; Moore et al., 2003b, 2004). However, fieldwork over the adjacent continental slopes has been limited (Baker et al., 2012; Feagans-Bartow and Sutton, 2014). Meanwhile, although there have been extensive studies of The Gully's ecosystems, before the research reported here knowledge of the subsurface nekton and micronekton was confined to the results of limited sampling with macroplankton nets, which suggested enriched abundances (Sameoto et al., 2002).

Four midwater-trawl surveys of The Gully were therefore undertaken during the summers of 2007–09 and in March 2010, as both a first investigation of the pelagic fauna of a canyon and a contribution toward the knowledge requirements of the MPA's management (Kenchington et al., 2009, 2014a). Identification of specimens is on-going but the surveys took at least 255 species of fish, in addition to crustaceans, cephalopods, and other invertebrates (Kenchington et al., 2014b; MacIsaac et al., 2014). Almost all specimens of the most abundant fish species in the catches, *Cyclothone microdon*, were badly damaged in the trawls and could be neither counted nor measured. However, Thompson and Kenchington (2017) have examined that species' distribution in the canyon, based on catch weights. Kenchington et al. (2018) explored the distributions and length frequencies of each of the other 19 abundance- and biomass-dominant fish species individually, comparing information from The Gully to prior knowledge of their biology. Eleven of the 20 species had distributions centred outside the canyon mouth, with abundances and biomass densities decreasing up-canyon. A further six were at least as abundant in the central canyon as immediately outside its mouth but declined toward the canyon head. Moreover, 11 of the 19 species for which length data are available showed an up-canyon increase in the average sizes of the individuals taken, resulting from more-pronounced declines in the abundance of smaller size-classes than those of large ones (Kenchington et al., 2018). However, neither of those studies attempted statistical tests of the observed trends.

We here present multispecies analyses of the assemblage structure of the 19 species examined by Kenchington et al. (2018), with particular attention to the effects of the canyon on that structure, and we test departures from spatial and temporal equality of catches across the survey design. Building on our results, and drawing on the body of multi-disciplinary research that has been conducted in the canyon, we argue that passive horizontal drift of mesopelagic fish biomass, into The Gully from outside the MPA, is of sufficient magnitude to be the principal energy source supporting the northern bottlenose whales.

OCEANOGRAPHY OF THE GULLY

The observed distributions of the fishes can only be understood within the context of the water masses and movements both inside the canyon and outside its mouth. Both the general patterns and the specific conditions at the times of the midwater-trawl surveys have been drawn together by Kenchington et al. (2009, 2014b), as a foundation for interpretation of the catch data. Key points are summarized here.

In most respects other than size, The Gully (**Figure 2**) is broadly typical of submarine canyons. The surrounding banks give it a rim depth of 200 m or less, though the steep canyon walls begin at 400 m. Unusually, the canyon's head

Abbreviations: CIL, Cold Intermediate Layer; IYGPT, International Young Gadoid Pelagic Trawl; LSW, Labrador Sea Water; MDS, non-metric Multi-Dimensional Scaling; MPA, Marine Protected Area; WSW, Warm Slope Water.

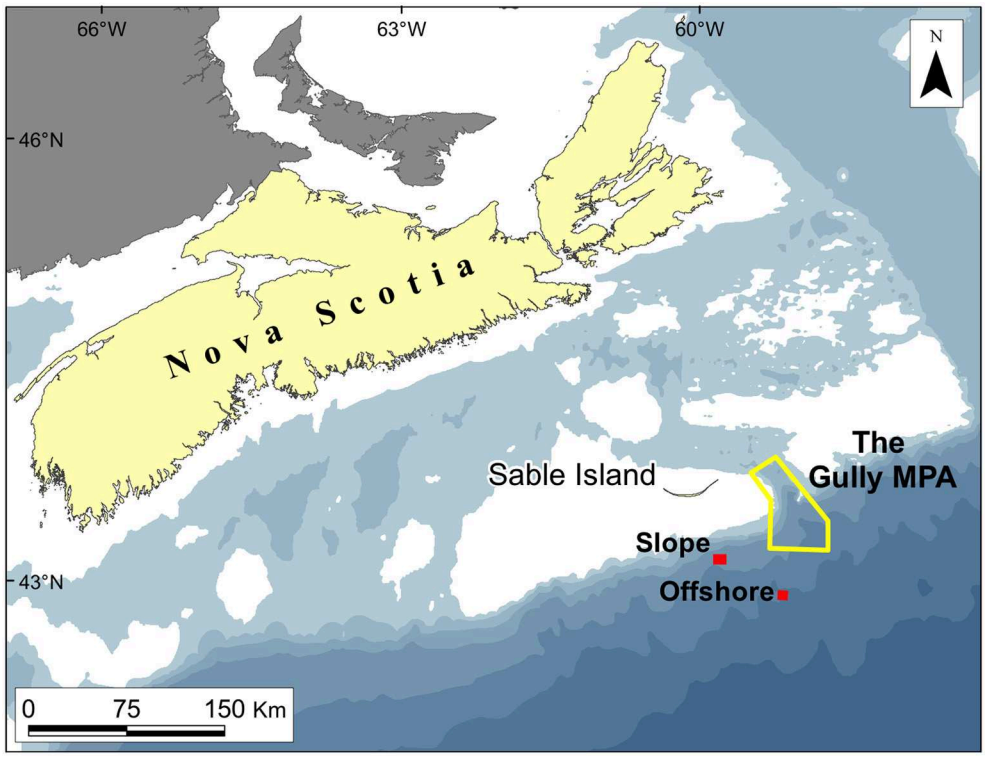


FIGURE 1 | Location of The Gully and The Trough, showing the Offshore and Slope trawling stations: White areas are shallower than 100 m, while those shaded in the lightest blue are 100–200 m deep.

communicates, via continental-shelf valleys, with a large, mid-shelf basin, "The Trough" (**Figure 1**), providing an outlet for water flowing up-canyon.

The water masses in and over The Gully are complex and variable. At the surface, most of the canyon is covered by the three layers typical of the Scotian Shelf, which include a Cold Intermediate Layer ("CIL") at ≈50–100 m depth, with a typical summer core temperature of ≈5°C. The surface temperature varies from 0°C in winter to >20°C in summer. A southwest-going shelf-break current carries those waters across the mouth of The Gully. Weaker anticyclonic gyres circle the surrounding banks, while exchange between the gyres produces a south-westward flow over much of the canyon (taking about 3 days to cross the deep water) and a slower north-eastward drift across its head. The surface waters show no apparent response to the presence of the deep hole in the seabed beneath them (Greenan et al., 2013, 2014; Kenchington et al., 2014b).

The Scotian Shelf waters extend to a shelf/slope boundary which usually lies well south of the shelf break, though its location is exceptionally variable, on temporal scales from seasons to days. South of that boundary, the surface layer is composed of Warm Slope Water ("WSW"), formed on the fringe of the Gulf Stream near Cape Hatteras. Although a surface water, WSW reaches depths of 300 or 400 m, its temperature off Nova Scotia typically being 10–13°C, though WSW exceeds 20°C at the surface in summer. It sometimes extends under the CIL, where it contributes to the Scotian Shelf's subsurface temperature maximum. The main body of the WSW flows eastward, far south of The Gully. However, its complex northern fringe moves irregularly south-westwards over the continental slope (Kenchington et al., 2014b).

In 2007, there was exceptional development of the CIL across the Scotian Shelf (Petrie et al., 2008), with core temperatures over the Gully at the time of the survey as low as 0°C. The shelf/slope boundary was pushed southwards, beyond the trawling stations. That year, the spring blooms of phytoplankton and copepods were exceptionally rich. Although long over by the time of the survey, the effects of the enhanced production may have lingered higher in the trophic system. In contrast, the 2008 survey encountered conditions approximating to long-term summer norms. At regional and seasonal scales, 2009 was even closer to those norms but the survey that year coincided with the presence of a tongue of WSW moving across the canyon's mouth, which pushed the shelf/slope boundary to the shelf break (Kenchington et al., 2009, 2014b).

Beneath the Scotian Shelf waters and the WSW, there are two alternative water masses: Labrador Sea Water ("LSW") and North Atlantic Central Water, the former being slightly colder and less saline at any given depth. Each water mass is cooler at greater depths, reaching ≈4°C by 1,000 m. Most of the subsurface waters within the canyon and outside its mouth during the 2007, 2009, and 2010 surveys resembled North Atlantic Central Water,

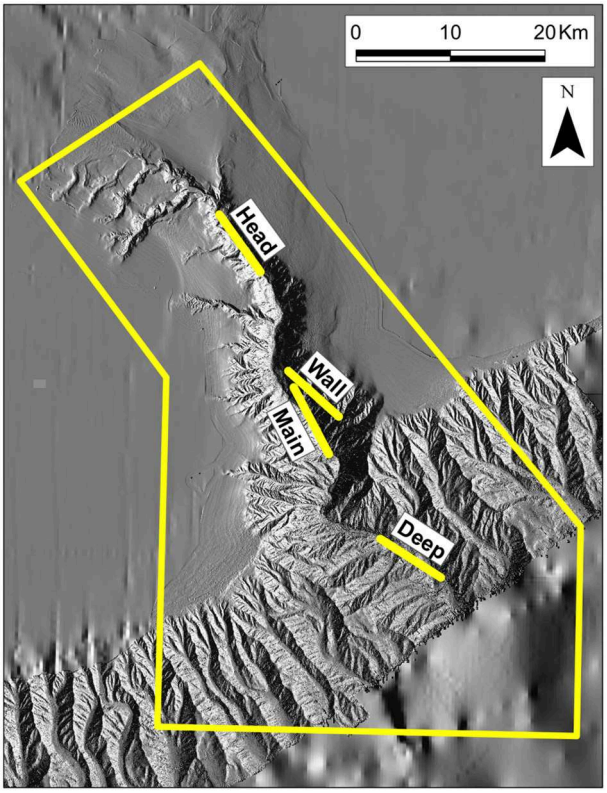


FIGURE 2 | Bathymetry of The Gully, showing the locations of four trawling stations: The boundary of the MPA is in yellow.

though the canyon head was flooded with water that had the characteristics of LSW. Data from the 2008 survey are deficient but suggest that the canyon may then have contained LSW throughout, beneath the surface layers (Kenchington et al., 2009, 2014b).

In The Gully, north of the shelf break and below 500 m depth, cross-canyon flows are minimal but there is a net inflow, estimated at a mean rate through the central canyon and below 200 m depth of 35,500 m^3s^{-1}–sufficient to carry a water particle from the canyon's mouth to its head in 30 days. That inflow, while slow (generally <0.02 ms^{-1}), implies upwelling in the upper canyon, with a vertical velocity of 14 m per day, which carries the water over the canyon rim or else into the shelf valleys and thence to The Trough. In the central canyon, the inflow is displaced toward the eastern side, while (particularly in summer) there is a reverse flow to the west, at depths of about 300–600 m, which may form part of a weak gyre (Greenan et al., 2013, 2014; Shan et al., 2014a,b).

MATERIALS AND METHODS

Field Methods

The field methods of the surveys have been presented in full by Kenchington et al. (2009, 2014a) and are only summarized here. There were three surveys in late summer (August/September of 2007–09) and one in early spring (March 2010). The primary gear, and the only one that contributed data to the present analyses, was the International Young Gadoid Pelagic Trawl ("IYGPT"), a midwater otter trawl with a mouth area of approximately 60 m^2, which was fitted with a rigid, "aquarium" codend. That gear was fished on six fixed stations (**Figures 1**, **2**). Three (named "Head," "Main," and "Deep") were arrayed along The Gully's thalweg, respectively, near the canyon head, in the central canyon and outside its mouth. One was placed over the canyon wall ("Wall Station"). The other two were, respectively, south of the canyon at a location previously sampled by Themelis and Halliday (2012; "Offshore Station") and over the continental slope, away from the canyon's influence but where seabed depth matched that on the Main Station ("Slope Station"). The Offshore and Wall stations were only worked as time permitted. The Slope Station was added to the design in 2009 and sampling there was limited.

Like all other pelagic sampling gears, the IYGPT is selective and samples only a portion of the species and sizes present. The detailed work needed for inter-calibration of alternative gears (e.g., Potter et al., 1990) has never proven practical at mesopelagic depths, hence the selective properties of particular nets can only be inferred from the catches taken. Thus, the assemblage examined here is one conditioned on the characteristics of the IYGPT and, indeed, of the IYGPT when fished according to the design of the Gully surveys.

The water column was divided into four depth strata (0–250, 250–750, 750–1,250, and 1,250–1,750 m—the latter not fully sampled until the final survey), though seabed depths prevented fishing in the deeper strata on some stations. By intent, two replicate sets were deployed to each available stratum, at each station, in each of daylight and night (avoiding periods within 1 h of sunrise and sunset) during each survey, though typically only one set per survey was made above 250 m in daylight at each station. On the Main Station in 2007, a third replicate was attempted in each stratum and diel phase. Constraints on available ship time and other factors (primarily weather) prevented completion of that survey design, but six additional, non-standard sets were made, most reaching below the deepest available or defined stratum on the respective station. The numbers of replicates yielding data suitable for the multivariate analyses reported here are given in **Table 1**.

The IYGPT is an open net and each set necessarily fished from the surface to its maximum depth and back. Sets that fished below 250 m followed double-oblique ("V") profiles throughout. Most fished for 30 min above 250 m and 60 min in each deeper stratum. However, the protocol followed in 2007 produced slightly faster shooting and hauling when above the set's nominal stratum, while the extra-deep, non-standard sets made on the Deep Station (**Table 1**) each fished for more than 60 min below 1,250 m (Kenchington et al., 2009, 2014a). At those depths and in summer, catches of the species analysed here were limited (Kenchington et al., 2018), hence the prolonged fishing had little effect on the analysed data. Sets which fished no deeper than 250 m were towed for 60 min, most following a "W" profile, and so their catches were not directly comparable with those from deeper sets.

TABLE 1 | Number of IYGPT sets in each cell of the survey design that were utilized in the multivariate analyses (numbers of sets made in each of the 2007, 2008, 2009, and 2010 surveys shown in sequence).

Station	Head		Wall		Main		Deep		Offshore		Slope	
Nominal stratum	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**
0–250	1,1,1,1	3,2,2,2	1,0,0,0	2,0,1,0	3,1,1,1	3,2,2,2	1,1,1,0	2,2,1,3	1,0,0,0	1,0,0,0	—	—
250–750	3,2,2,2	2,1,1,2	3,0,1,0	2,0,2,0	3,2,2,2	3,2,2,2	2,2,0,1	2,3,2,2	1,0,0,0	1,0,0,0	0,0,1,1	—
750–1,250					3,2,1,1	3,2,2,2	1,2,2,0	2,2,2,2	1,0,0,0	1,0,0,0	—	—
1,250–1,750							0,0,0,2	0,1,2,2	—	—		
Non-standard	—	1,0,0,0			1,0,0,0	—	0,0,2,1*		—	1,0,0,0	—	—
Max. depth fished (m)		905			1,503		2,379			1,647		
Seabed depth (m)	700–1,200		1,200–1,300		1,300–2,000		2,600–2,700		2,800–3,000		1,400–1,600	

—Sampling not attempted in cell; blank cells indicate insufficient depth for sampling the stratum.

**Two of the three sets made on the Deep Station below 1,750 m depth spanned sunset.*

Seabed depths given are those at each end of the station, not the minimum and maximum along its line. The Wall Station lay across ridges shallower than 750 m.

The nets were towed at a speed through the water averaging $\approx$1.5 m.s^{-1} (Kenchington et al., 2014a). With 60 m^2 nominal mouth area, they therefore filtered $\approx 5 \times 10^5$ m^3 during each set made to 750 m depth, $\approx 8 \times 10^5$ m^3 during each 1,250 m set and $\approx 11 \times 10^5$ m^3 during each 1,750 m set. The wingspread and headline height of the IYGPT, the speed of the net through the water and the time spent in passing through each depth range were, necessarily, variable, both from set to set and within individual sets. However, excluding sets rejected as non-standard, deviations from the standard overall volumes filtered were minimal (Kenchington et al., 2009, 2014a) and no *post-hoc* standardization of catches was necessary. There were larger within-set variations in the volumes filtered at particular depths, resulting from changeable net geometry and irregularities in tow profiles, but corrections for those could not be applied as the precise depths of capture of the various species cannot be known.

The survey design was developed with the intent of estimating the catches taken from each stratum by subtracting, from the catch of each set which fished to the stratum's lower boundary, the average amount caught by sets deployed to the depth of its upper limit (at the same station, on the same survey and in the same diel phase)—an approach used successfully with data on the crustaceans caught (MacIsaac et al., 2014). However, while variation amongst the fish catches of replicate sets within the same cell of the survey design was low, by the standards of spatially extensive surveys, that variation was nevertheless high enough to confound estimation by subtraction. Thus, we here confine our analyses to the full catch taken by each set, as the net fished between the surface and its maximum depth, and interpret our results accordingly.

Following each set, the catch was retrieved from the net, the codend washed down and the rest of the net picked through for specimens caught in the meshes. In general, the fishes were sorted, identified, the weight and count of each taxon recorded, and each individual measured (standard length). Specimens that could not be identified at sea were preserved for examination ashore, following counting, weighing and measurement. The dominant myctophid in the catches, *Benthosema glaciale*, was sometimes too abundant for comprehensive length measurements. When necessary, a weighed subsample was counted and measured, the total number caught being estimated subsequently by expansion. Finally, although very large numbers of *Cyclothone* spp. were taken, most were retrieved from the nets as broken fragments. At sea, they were identified only to genus and neither counted nor measured, though each catch was weighed and samples were returned to shore (cf. Thompson and Kenchington, 2017). In the absence of count data, *Cyclothone* spp. were excluded from the analyses reported here.

Data Preparation

The surveys were followed by an extensive process of specimen identification and data verification, leading to generation of a catch database, from which data were extracted and prepared for analysis. Highly variable data on the many rarities were excluded by retaining only those species which comprised more than 1% of the total IYGPT fish catch, by either number or weight, or else more than 2% of the catch from any one of the three principal stations (Head, Main, or Deep)—the latter criterion chosen so that species locally important in parts of the canyon would be included. After exclusion of *Cyclothone* spp., 19 species met at least one criterion (**Table 2**). Small numbers of specimens that might have been members of a selected species could only be identified to genus or family, usually because of damage in the net. Such specimens were either added into or excluded from the analysed data after review of the time and location of their capture, relative to the distribution across the survey design of the species to which they might be assigned (see Kenchington et al., 2018 for details).

Some sets made during the surveys were deemed non-valid because of irregularities in the work at sea (Kenchington et al., 2009, 2014a) or subsequently when deficiencies in data recording were discovered. Inevitably, the at-sea data collection only recorded positive catches, rendering missing data indistinguishable from zero catches. After review of the data and the distributions of the 19 species across the survey design (Kenchington et al., 2018), there was residual uncertainty over possible missing data for one or more species for five sets. Those five and all non-valid sets were dropped from further consideration, leaving 148 available for analysis.

TABLE 2 | Species included in the analyses.

Order	Family	Species	Catch included in analysed data	
			Number	Weight (kg)
Anguilliformes	Nemichthyidae	*Nemichthys scolopaceus*	1,517	23.7
	Serrivomeridae	*Serrivomer beanii**	2,811	45.7
Saccopharyngiformes	Eurypharyngidae	*Eurypharynx pelecanoides*	304	6.0
Osmeriformes	Bathylagidae	*Bathylagus euryops*	1,177	11.1
Stomiiformes	Stomiidae	*Chauliodus sloani*	1,933	28.6
		Malacosteus niger	311	6.6
		Stomias boa	2,277	32.7
Aulopiformes	Paralepididae	*Arctozenus risso*	1,827	5.0
Myctophiformes	Myctophidae	*Benthosema glaciale*	49,125	61.5
		Ceratoscopelus maderensis	1,196	2.7
		Hygophum hygomii	1,799	3.2
		Lampanyctus macdonaldi	276	2.3
		Lobianchia dofleini	1,633	0.8
		Myctophum punctatum	1,196	3.4
		Notoscopelus kroyeri	1,336	1.6
		Notoscopelus resplendens	1,516	1.8
Stephanoberyciformes	Melamphaidae	*Scopelogadus beanii**	1,580	36.1
Beryciformes	Anoplogastridae	*Anoplogaster cornuta*	55	3.7
Perciformes	Zoarcidae	*Melanostigma atlanticum*	176	1.0

**To avoid confusion between* Serrivomer beanii *and* Scopelogadus beanii*, their generic names are spelt out throughout the text.*

For some species and sets, a count of specimens caught was available but not a corresponding weight or else the reverse. For each of those, the missing data were reconstructed using the average per-individual weight of the species in question from the catches of other sets. The numbers of specimens affected was usually small. However, at-sea recording of data on *B. glaciale* was sometimes confused when subsampling and catch counts totalling over 8,200 individuals were reconstructed from weight data (see Kenchington et al., 2018 for details).

The final outcome of those processes was a pair of data matrices (presented by Kenchington et al., 2018 and as **Supplementary Data Sheet**), containing the catches of the 19 principal species taken by the 148 sets, by weight and number, respectively.

Assemblage Analyses

All multivariate analyses were performed using PRIMER 6 version 6.1.6 (Clarke and Gorley, 2006). The catch data were ln (X+1) transformed, to stabilize variances. Four Bray-Curtis similarity matrices were prepared, respectively, for each of sets and species, based on transformed weights and numbers. Assemblage composition was first examined through non-metric Multi-Dimensional Scaling ("MDS") of the Bray-Curtis matrices. Each MDS had 100 restarts, a minimum stress of 0.01 and followed Kruskal fit scheme 1. Unweighted Pair Group Method with Arithmetic Mean ("UPGMA") clusters of sets and species, by both weights and numbers, were prepared from the Bray-Curtis matrices using the SIMPROF routine. Each mean profile was estimated from 1,000 permutations and 999 were used for simulation. Significant clusters were identified at the 5% level.

Catch compositions were compared through a series of one-way ANOSIM analyses of the transformed data, following each dimension of the survey design (survey, station, depth, and diel phase), and separately performed for transformed weights and numbers caught. Additionally, the 2007–09 data were merged into a "summer" group, contrasted with the "spring" data from March 2010. With the very large number of hypotheses that might have been tested, application of the Bonferroni adjustment would require that statistical inferences be drawn against some $\alpha < 0.0001$. The consequent reduction in statistical power would prevent meaningful biological differences from being detected as "significant." Thus, statistical significance was judged against an arbitrary standard of estimated $P \leq 0.001$, accepting the inflated risk of Type I errors among the multiple tests. ANOSIM analyses were initially run with up to 999 permutations. Those which returned $P \leq 0.1$ were re-run with up to 9,999 permutations, to better estimate probabilities—without changing any interpretations of significance.

The survey design was necessarily incomplete, because bottom depth precluded deep fishing on some stations, while realization of the design was unbalanced (**Table 1**). The results of each one-way analysis were therefore confounded by the effects of dimensions other than the one of immediate interest. Interpretation of the data was further complicated by reliance on an open net and by the contrasting tow profiles used above and

below 250 m depth. The latter limitations were circumvented, and the confounding narrowed, through further analyses, each of which only utilized data from sets that reached the same maximum depth. For that purpose, the sets were arrayed in three depth groups: those which only fished to 250 m, those which reached 750 m and those which fished to 1,250 m or deeper—the initial MDS and clustering having shown little depth-linked distinction between the catches of 1,250, 1,750 m and deeper sets. (The sole set that fished below 750 m on the Head Station was excluded, since its maximum depth did not accord with any of the three groups.) The MDS, clustering and one-way ANOSIMs were repeated for each of the three depth groups. Because the catches taken by sets which fished only to 250 m showed a marked difference between diel phases, the ANOSIMs were further repeated using only sets made in that depth stratum at night—too few replicate shallow sets being made in daylight for meaningful results to be obtained by a parallel analysis restricted to those. Although the full suite of ANOSIM analyses described here was performed, results are only reported below for those which returned significant outcomes and those for which the absence of significance can illuminate assemblage structure.

Where pairwise ANOSIM found a significant difference when analysing depth-specific data, SIMPER was used to examine the contributions that each of the 19 species made to that difference and to the similarity amongst the catches of sets in each group of the pair. To avoid a confusion of results, we present here SIMPER outputs for comparisons between seasons but not for those between individual surveys. Likewise, we present SIMPER outputs for comparisons between adjacent stations along the canyon thalweg (i.e., Head to Main and Main to Deep) but not for those between non-adjacent pairs. For the sets which fished only to 250 m depth, we do not present SIMPER outputs for comparisons that used night-only data. As the critical probability used in determining significance was arbitrarily chosen, we also present abbreviated SIMPER results for four comparisons for which ANOSIM returned marginally non-significant results—two being cases where there were marked differences in individual species, though not in the entire assemblage, and two where the high variability in the catches of the shallow sets eroded the power of ANOSIM to detect the effects of factors that had significant effects on the composition of catches taken by deeper sets.

RESULTS

Overview

Across the four surveys, the IYGPT sets took more than 80,000 fishes (aside from *Cyclothone* spp.), with a combined weight of about 350 kg. Data on 72,045 individuals of the 19 principal species, together weighing 275.687 kg, were included in the analysed matrices. Within those, the sets deployed to 750 m on the Head Station, hence across most of the water column there, caught an average of <1 kg, whereas those deployed to 1,750 m on the Deep Station took nearly 5 kg in summer and 4 kg in spring. Average biomass densities, without correction for the species' catchabilities in IYGPT gear, varied from $<0.001\,g.m^{-3}$ on the Head Station in spring to $0.005\,g.m^{-3}$ on the Deep Station in summer (**Table 3**).

The assemblage of IYGPT-vulnerable fish was dominated in number (*Cyclothone* spp. aside), and to a lesser degree in weight, by the myctophid *B. glaciale*. The remaining 18 principal species comprised seven other myctophids, three species of the Stomiidae (each in a different subfamily), and single members of eight other families (**Table 2**).

Spatio-Temporal Structure of the Assemblage

Whole Data Set

MDS, whether based on number or weight data (2D stress 0.14 and 0.15, respectively), showed a large group of closely-similar sets, centred on those that fished to 1,250 m or deeper but including many that did not go below 750 m (**Figures 3**, **4**). That close grouping contrasted with a wide scatter of the 250 m sets. The latter showed some divergence by diel phase, season, station (sets on the Head Station being particularly scattered) and perhaps among the three summer surveys.

Resolving structure amongst the sets which fished below 250 m depth required cluster analysis. Clustering based on abundance data found 13 significant clusters and three additional singletons (**Figure 5**). However, most sets fell into one of seven major groups. At the core of the dataset was a group of sets ("C" in **Figure 5**) made in summer (mostly in 2007) on the Main or Deep stations to either 750 or 1,250 m, which group was significantly subdivided into daylight and night sets. To that were joined two other clusters, a group ("B") of sets made to 750 m on the Main and Wall stations in summer, most of them in daylight, and another ("D") of sets that reached 750 m or deeper, most made on the Deep Station in March 2010. Group "E" comprised sets made in summer to depths of 750 m or deeper, most on the Deep Station, while group "F" was largely composed of 250 m sets made on the Main or Deep stations, all of them during summer nights. Group "G" contained almost entirely 250 m sets made at night on the Wall, Main or Deep stations. There was a significant subdivision between summer sets and those made during March 2010. The last major group ("A") contained 750 m sets made on the Head Station in summer. Three such sets, all made in 2007, were significantly separated from the rest. The remaining sets, outside of those major groups, were mostly ones made to 250 m depth. They formed three loose clusters, plus two singletons, with little pattern except for a tendency for sets made in 2007 (and to a lesser extent those made in 2010) to cluster together and apart from sets made during other surveys.

Clustering the sets by biomass data generated a broadly similar tree (**Figure 6**), though with ten major groups. The core ("VI") comprised mostly sets made on the Main or Deep Stations to depths of at least 1,250 m, with a significant subdivision between summer and spring. To that were joined in turn a group ("V") of sets made in summer, most on the Deep Station to depths of 750 m or more, a group ("IV") of sets made in spring on the Main or Deep stations, again to depths of 750 m or more, a group ("III") of sets made in summer on the Main or Wall stations to 750 m depth and a group ("II") of sets made on summer nights, mostly

TABLE 3 | Average water-column fish catches and IYGPT-catchable biomass densities (by volume and sea-surface area) of the 19 principal species at the three principal stations, by season.

Station	Depth range fished (m)	Average fish catch (kg)		Density (g.m^{-3})		Density (g.m^{-2})	
		Summer	Spring	Summer	Spring	Summer	Spring
Head	0–750	0.89	0.45	0.0018	0.0009	1.350	0.675
Main	0–1,250	3.31	1.96	0.0041	0.0024	5.125	3.000
Deep	0–1,250	4.30	2.04	0.0053	0.0025	6.625	3.125
	0–1,750	4.71	3.96	0.0042	0.0035	7.350	6.125

Densities calculated using the nominal mouth area of the IYGPT, the average towing speed and the designed durations of the sets.

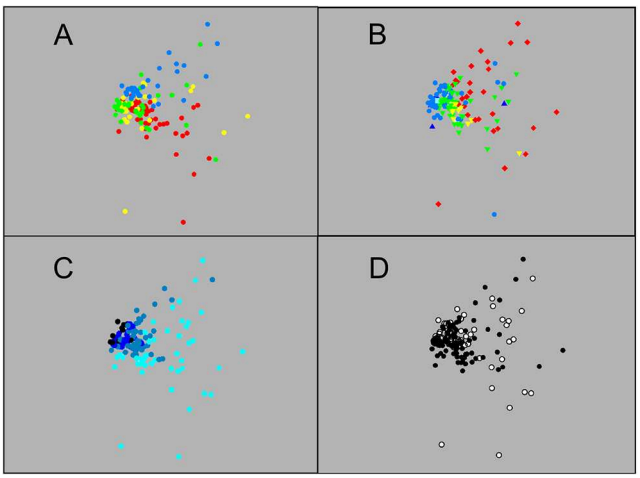


FIGURE 3 | Ordination of the 148 sets based on catch data in numbers: **(A)** Sets identified by survey—red: 2007, yellow: 2008, green: 2009, blue: 2010; **(B)** Sets identified by station—red: Head, yellow: Wall, green: Main, light blue: Slope, medium blue: Deep, dark blue: Offshore; **(C)** Sets identified by maximum depth reached—light blue: 250 m, medium blue: 750 m, dark blue: >750 and ≤1,250 m, black: >1,250 m; **(D)** Sets identified by diel phase—open circle: daylight, filled circle: night (MDS 2D stress 0.14).

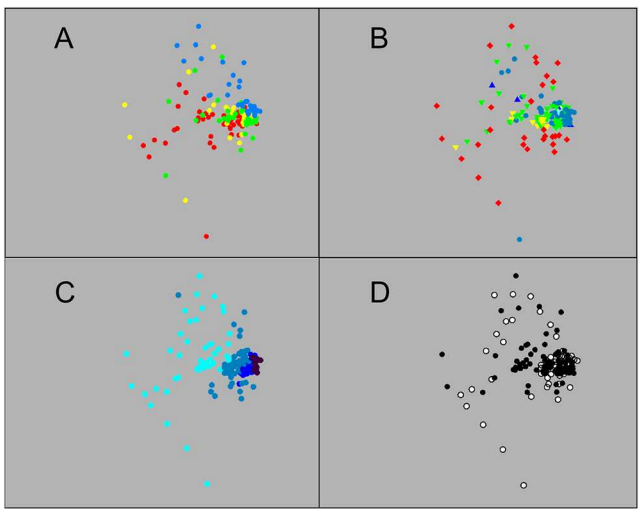


FIGURE 4 | Ordination of the 148 sets based on catch weight: Sets identified by **(A)** survey, **(B)** station, **(C)** maximum depth reached, and **(D)** diel phase, using same colour coding as in **Figure 3** (MDS 2D stress 0.15).

on the Deep Station and to depths of 250 or 750 m. More loosely associated were a group ("VII") of 750 m sets made on the Head Station in summer, a group ("VIII") of 250 m night sets made on the Head, Wall or Main stations, with significant subdivision of spring and of summer 2007 sets from a larger subgroup of sets from a mixture of the three summer surveys. The 250 m sets largely fell into one of three groups: "I," containing those made on the Head Station in spring, "X," containing mostly those made on the Head Station in summer, and "IX," which included sets made on all surveys and most stations but primarily in daylight.

Hence, there was some differentiation of 750 m sets from deeper ones but little apparent difference between the catches of those which fished to 1,250 m and the few which went even deeper. In effect, species that were either abundant enough or of sufficient individual weight to be selected for the present analyses had depth distributions centred in the comparatively productive waters above 1,250 m depth. Deploying the open IYGPT to greater depths did not materially affect catches of such fish. There was some tendency for sets that reached at least 750 m depth to cluster by season and by station. For the latter, only the sets made on the Head Station were markedly distinct, though those on the Main and Wall stations often clustered together, while the few Offshore and Slope station sets clustered amongst the greater number made on the Deep Station. Inter-annual differences among the three summer surveys were not marked, through the 2007 sets stood out somewhat. Unlike the 250 m sets, those which fished deeper showed only weak grouping by diel phase, presumably because the open net could catch migrant fishes whether they were at the shallow or the deep end of their circuits.

ANOSIM of the entire data matrices, whether using weights or numbers, found significant differences between the catches of 250 m sets and those which reached either 750 or 1,250 m (though not between the latter two groups). There were also significant differences between the catches taken by each of the summer surveys and that in March 2010, but not among any of the summer surveys (**Table 4**). Catches on each of the Head, Main and Deep stations were significantly different

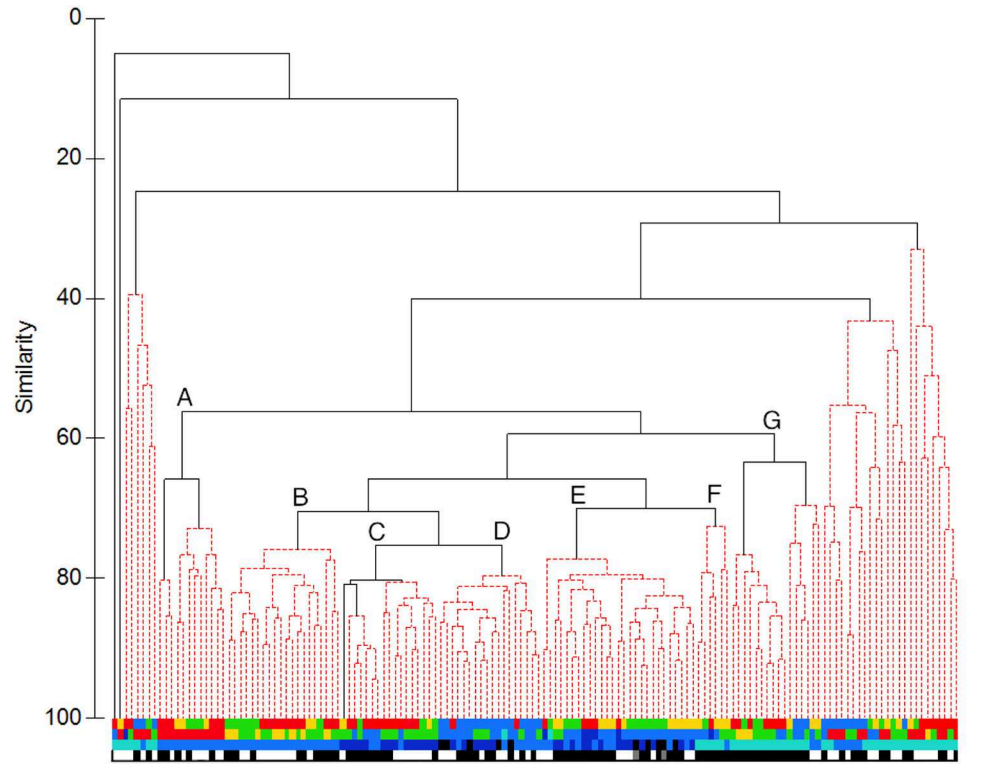


FIGURE 5 | UPGMA cluster of sets based on catch data in numbers: Clusters significant at $P = 0.05$ are highlighted in red. Letters identify the major clusters described in the text. The sets are identified by four bands of colour coding: Top band: survey, second band: station, third band: maximum depth reached, bottom band: diel phase (colour coding as in **Figure 3**, except for bottom band, where: white: daylight, black: night, grey: sets that spanned sunset).

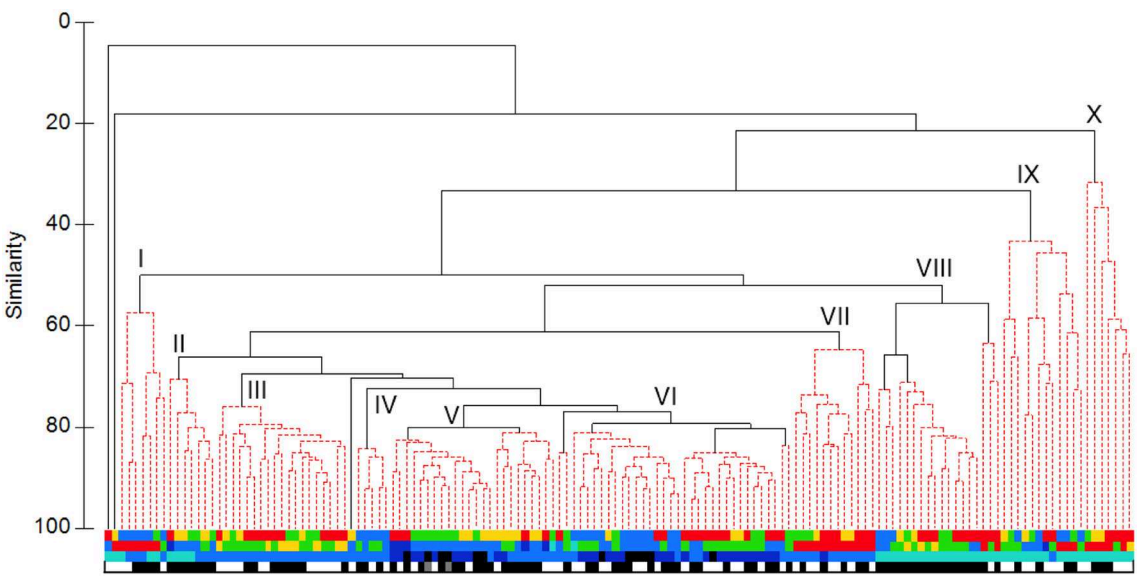


FIGURE 6 | UPGMA cluster of sets based on catch weight: Colour coding as in **Figure 5**. Roman numerals identify the major clusters described in the text.

from those on either of the others. Those taken on the Wall Station differed from the Deep and Offshore catches. However, some of those differences will have partly been because of the absence of deep sets on the Head and Wall stations. The effects of diel phase on the catches did not quite reach significance.

TABLE 4 | Results of pair-wise ANOSIM tests on the whole data matrices that returned $P \leq 0.01$ and of selected tests which did not.

Comparison	Permutations	Numbers		Weights	
		R	*P*	R	*P*
Between diel phases	9,999	0.066	0.002	0.045	0.001
By max. depth, 250 vs. 750 m	9,999	0.358	≤0.001	0.445	≤0.001
By max. depth, 250 vs. 1,250 m	9,999	0.324	≤0.001	0.406	≤0.001
By max. depth, 250 vs. 1,750 m	999	0.164	ns	0.249	ns
By max. depth, 750 vs. 1,250 m	999	0.026	ns	0.074	ns
By max. depth, 1,250 vs. 1,750 m	999	0.092	ns	0.055	ns
Between surveys, 2007 vs. 2010	9,999	0.249	≤0.001	0.212	≤0.001
Between surveys, 2008 vs. 2010	9,999	0.227	≤0.001	0.187	≤0.001
Between surveys, 2009 vs. 2010	9,999	0.216	≤0.001	0.179	≤0.001
Between stations, Head vs. Main	9,999	0.390	≤0.001	0.312	≤0.001
Between stations, Head vs. Wall	999	−0.038	ns	−0.116	ns
Between stations, Head vs. Deep	9,999	0.531	≤0.001	0.471	≤0.001
Between stations, Main vs. Wall	999	−0.016	ns	−0.048	ns
Between stations, Main vs. Deep	9,999	0.137	≤0.001	0.108	≤0.001
Between stations, Wall vs. Deep	9,999	0.376	≤0.001	0.356	0.001
Between stations, Wall vs. Offshore	9,999	0.618	≤0.001	0.493	≤0.001
Between stations, Deep vs. Offshore	999	0.065	ns	0.097	ns
Between stations, Deep vs. Slope	999	−0.110	ns	−0.147	ns

ns: P > 0.01.

Deep Sets

MDS of the catches of sets which sampled the water column to at least 1,250 m depth (ordinations not presented here) suggested a seasonal distinction, some inter-annual variability in summer and a weak clinal variation extending from the Main Station, through the Deep to the Offshore, but no diel differences. The sets formed three significant clusters which primarily contained those from (1) the March 2010 survey, (2) the Offshore Station in 2007 plus the Deep Station in 2008 and 2009 and (3) the Main Station in summer plus the Deep Station in 2007 (tree not presented here). In the clustering based on numbers data, only two sets fell outside that pattern, but there were more aberrant sets when weight data were used.

The difference between the summer and March 2010 catches was significant, by ANOSIM, while inter-annual variation in summer fell short of significance, though narrowly so between 2007 and 2009 (**Table 5**). The spring catches were generally lower than those taken in summer (**Supplementary Table 1**). Myctophids other than *B. glaciale* were especially depressed and the warm-water (Moore et al., 2003a; Themelis and Halliday, 2012; Kenchington et al., 2018) *Hygophum hygomii*, *Lobianchia dofleini*, and *Notoscopelus resplendens* were absent entirely—an absence that accounted for 26% of the seasonal difference in number terms. The lower catches in spring included those of *Stomias boa* and *Arctozenus risso*, which dropped to one third of their summer amounts. Together, declines in nine species accounted for 66% of the seasonal dissimilarity in number terms and 59% in weight. In contrast, catches of *Chauliodus sloani*, *Malacosteus niger*, *Nemichthys scolopaceus*, and *Serrivomer beanii* were higher in spring, when larger numbers but lower weights of *Scopelogadus beanii* were taken. *Anoplogaster cornuta*, *Bathylagus euryops*, and *Melanostigma atlanticum* were equally numerous in the catches in both seasons but increased in weight terms in the spring—the large individual size of *A. cornuta* making it the leading contributor to the seasonal dissimilarity in catches, in weight terms.

Most of the species were both more abundant and taken in greater weights in the catches from the 2009 survey, when the surface water at the mouth of The Gully was WSW, than in 2007, when the canyon was overlain by an exceptionally cold and extensive CIL. That trend was particularly prominent in the warm-water myctophids *H. hygomii*, *L. dofleini*, and *N. resplendens*, the first two of which increased by about an order-of-magnitude between those years (**Supplementary Table 2**). Higher catches in 2007 were seen only in *Myctophum punctatum*, known to be a northern species (Moore et al., 2003a; Møller et al., 2010; Themelis and Halliday, 2012; Dolgov, 2015; Kenchington et al., 2018), *M. niger* and *M. atlanticum*.

The catches on the Main Station were significantly different from those taken outside the canyon mouth but no difference was found between catches on the Deep Station and the few taken on the Offshore (**Table 5**). For most species, catches on the Main Station were smaller than those on the Deep Station, with the three warm-water myctophids showing triple the abundance on the latter. Together, they accounted for 26% of the dissimilarity between the catches on the two stations in number terms (**Supplementary Table 3**). *M. punctatum* showed the reverse trend. Otherwise, only *M. niger*, *S. boa* and the bottom-associated *M. atlanticum* were more abundant in catches

TABLE 5 | Results of pair-wise ANOSIM tests on sets made to 1,250 m or deeper that returned $P \leq 0.01$ and of selected tests which did not.

Comparison	Permutations	Numbers		Weights	
		R	*P*	R	*P*
Between diel phases	999	0.039	ns	−0.003	ns
Between surveys, 2007 vs. 2010	9,999	0.478	≤0.001	0.462	≤0.001
Between surveys, 2008 vs. 2010	9,999	0.921	≤0.001	0.833	≤0.001
Between surveys, 2009 vs. 2010	9,999	0.853	≤0.001	0.849	≤0.001
Between surveys, 2007 vs. 2008	9,999	0.265	0.009	0.145	ns
Between surveys, 2007 vs. 2009	9,999	0.391	0.001	0.361	0.002
Between surveys, 2008 vs. 2009	9,999	0.231	ns	0.199	ns
Between stations, Main vs. Deep	9,999	0.267	≤0.001	0.243	≤0.001
Between stations, Main vs. Offshore	1,140	0.739	≤0.001	0.713	≤0.001
Between stations, Deep vs. Offshore	999	0.172	ns	0.174	ns

ns: P > 0.01.

taken on the Main Station than the Deep, while greater weights of *A. cornuta*, *M. punctatum*, and *Lampanyctus macdonaldi* were taken there—those three together accounting for 25% of the dissimilarity between the stations in weights caught, compared to 19% for the three warm-water myctophids. That the weight caught increased up-canyon, while numbers had the opposite trend, shows that average individual weights were higher on the Main Station. Ten species showed more than 10% greater average individual weights on the Main Station than on the Deep (with a maximum of 2.3 times greater in *M. punctatum*), while only three species showed the reverse.

Although the catches on the Deep and Offshore stations were not significantly different when considered as assemblages, there were marked differences in the amounts taken of myctophids other than *B. glaciale* (**Supplementary Table 4**). Catches of *N. resplendens* were an order-of-magnitude higher on the Offshore Station than the Deep, and those of *H. hygomii* were six times higher in number and eight times in weight, while *L. dofleini* saw a lesser increase in the same direction. Since the Offshore Station was only sampled in 2007, there was potential for spatial differences to be confounded with inter-annual variation. However, inspection of the data from that 1 year showed the differences between the catches on the two stations to be at least as well-marked as in the formal, all-years analysis.

Above 750 m

MDS of sets which fished to 750 m depth (ordinations not presented here) showed no diel variation but a difference between summer and spring that was especially marked at the Head Station. Little evidence of inter-annual variation amongst the summer catches was apparent. There was a limited along-canyon trend, in which the Head Station stood out, while the Wall Station was closely similar to the Main and the Slope Station resembled the Deep, rather than the Main. Those trends were visible in both weights and numbers, a parallelism that continued through most ANOSIM results (**Table 6**). There were significant differences between the catches on the Head, Main and Deep stations. The Wall Station was most similar, in catch composition, to the Main and significantly different from the Deep.

SIMPER showed that the average similarities within each season were much lower, and the dissimilarities between them much higher, than was seen with the catches of the deeper sets (**Supplementary Tables 1**, **5**). The March 2010 catches taken by sets that reached 750 m depth were distinguished from those taken in summer by lower weights and numbers of almost all species, especially much lower catches of myctophids, four species of which were absent from the spring catches, when a fifth, *L. dofleini*, was represented by a single individual taken on the Slope Station. Even the catches of *B. glaciale*, which tended to be relatively stable across most comparisons, fell to one fifth of their summer average in numbers and to below one sixth in weight. The spring survey saw at least as much *C. sloani*, *N. scolopaceus*, *Eurypharynx pelecanoides*, and (in numbers but not in weights) *Serrivomer beanii* as did the summer surveys.

The Head Station (which had low average similarity amongst sets) was distinguished from the Main by much lower abundances and weights of almost all species, leading to high dissimilarity between the stations. *B. glaciale* was more than an order-of-magnitude less abundant on the Head Station than the Main, though that species remained the most abundant fish in the catches on the Head (exclusive of *Cyclothone* spp.) and second only to *Serrivomer beanii* in weight terms (**Supplementary Table 6**). Catches of *S. boa* were also an order-of-magnitude smaller on the Head Station in number terms and 45 times lower in weight. The three warm-water myctophids, *H. hygomii*, *L. dofleini*, and *N. resplendens*, were scarce on the Main Station but entirely absent from the catches on the Head. The principal exception to that up-canyon decline in numbers and weights was bottom-associated *M. atlanticum*. The deep-living (Themelis and Halliday, 2012; Kenchington et al., 2018) myctophid *L. macdonaldi* was also more common on the Head Station, due to up-canyon elevation of its depth range raising individuals above 750 m (Kenchington et al., 2018). *E. pelecanoides* and *M. niger* had higher numbers, and especially higher weights, on the Head Station, than the Main, though neither was common in the 750 m catches. *A. risso* was taken in lesser numbers but greater weight on the Head Station than the Main.

TABLE 6 | Results of pair-wise ANOSIM tests on sets made to 750 m that returned $P \leq 0.01$ and of selected tests which did not.

Comparison	Permutations	Numbers		Weights	
		R	*P*	R	*P*
Between diel phases	999	0.060	ns	0.029	ns
Between surveys, 2007 vs. 2010	9,999	0.464	≤0.001	0.461	≤0.001
Between surveys, 2008 vs. 2010	9,999	0.276	≤0.001	0.281	≤0.001
Between surveys, 2009 vs. 2010	9,999	0.272	≤0.001	0.250	≤0.001
Between surveys, 2007 vs. 2008	9,999	0.257	0.001	0.171	ns
Between stations, Head vs. Main	9,999	0.526	≤0.001	0.466	≤0.001
Between stations, Head vs. Wall	999	0.212	ns	0.117	ns
Between stations, Head vs. Deep	9,999	0.553	≤0.001	0.500	≤0.001
Between stations, Main vs. Wall	999	−0.037	ns	−0.085	ns
Between stations, Main vs. Deep	9,999	0.302	≤0.001	0.300	≤0.001
Between stations, Wall vs. Deep	9,999	0.573	≤0.001	0.588	≤0.001
Between stations, Deep vs. Offshore	120	−0.011	ns	0.053	ns
Between stations, Main vs. Slope	190	0.449	ns	0.273	ns
Between stations, Deep vs. Slope	120	−0.070	ns	−0.175	ns
Between stations, Offshore vs. Slope	3	0.000	ns	−0.250	ns

ns: P > 0.01.

The Main Station was likewise distinguished from the Deep by lower abundances of most species, especially the warm-water myctophids *H. hygomii* and *N. resplendens*, plus *Scopelogadus beanii* and *C. sloani* (**Supplementary Table 7**). The average catch of each of those, in both weight and number terms, was at least three times higher on the Deep Station than the Main. Conversely, the northern (Moore et al., 2003a; Møller et al., 2010; Themelis and Halliday, 2012; Dolgov, 2015; Kenchington et al., 2018) myctophids *M. punctatum* and *N. kroyeri* were twice as abundant, and the former three times the weight, on the Main Station. *Ceratoscopelus maderensis* and *M. atlanticum* were also more abundant on the Main Station than the Deep, the latter with double the weight. In all, the species replacement amongst myctophids, other than *B. glaciale*, contributed one half of the dissimilarity between the catches on the two stations in both numbers and weights. Otherwise, *A. risso*, *E. pelecanoides*, *N. scolopaceus*, and *S. boa* were caught in smaller numbers but greater weight on the Main Station, while *Serrivomer beanii* was taken in about equal amounts in weight terms but smaller numbers than on the Deep Station, all of those indicating larger average individual sizes inside the canyon mouth.

There was very little fishing to 750 m depth on each of the other three stations—a limitation which both reduced statistical power and increased the potential for confounding the effects of different dimensions of the survey design. Nevertheless, the Main and Wall stations clearly produced similar catches, average dissimilarity being 25.07 by numbers and 23.09 by weights. Catches on the Slope and Offshore stations were equally similar to one another (average dissimilarity by numbers: 24.61) and to those taken on the Deep Station (dissimilarities 25.72 and 26.10, respectively).

Above 250 m

Unlike the deeper sets, the sets which only fished to 250 m depth showed significant differences between daylight and night catches (in both weight and number terms) by ANOSIM (**Table 7**). However, variability was so high that most other trends were non-significant, whether tested using data from all of the shallow sets or only those made at night. Only the difference between the 2007 and 2010 catches was significant and only in weight terms.

The diel difference comprised much lower catches in daylight for almost every species taken by the shallow sets—about 20 times lower in *B. glaciale*, which alone accounted for 21% of the dissimilarity in numbers and 14% in weight, while the migratory myctophids as a whole accounted for 55 and 40%, respectively (**Supplementary Table 8**). Only *M. niger*, which was rarely taken so near the surface, chanced to be caught in a greater amount in daylight (4 individuals, vs. 2 at night).

When considered as assemblages, the catches taken above 250 m did not differ significantly between the seasons. However, most of the myctophids were entirely absent in spring, while catches of *C. maderensis* and *N. kroyeri* were much reduced (**Supplementary Table 9**). In contrast, *B. glaciale* and the deep-living *L. macdonaldi* were taken in approximately equal quantities in both seasons—the latter perhaps because its reduced numbers in the water column (**Supplementary Tables 1**, **5**) were balanced by sufficient shift in vertical distribution to lift a few individuals above 250 m depth. Of the non-myctophids, *C. sloani*, *E pelecanoides*, *M. atlanticum*, *N. scolopaceus*, *Scopelogadus beanii*, and *Serrivomer beanii* were all more abundant in shallow catches in spring but *B. euryops* and *M. niger* were absent then, while *A. risso* and *S. boa* were much reduced (*A. cornuta* was never taken by a 250 m set).

The shallow catches taken on the Head Station were not significantly different from those taken on the Main but, on average, those on the Head contained lower abundances of almost all species—more than 20 times lower in the case of *B. glaciale*, which was responsible for 24% of the large dissimilarity between those stations in numbers (**Supplementary Table 10**). Only *C. sloani*, *E. pelecanoides*,

TABLE 7 | Results of pair-wise ANOSIM tests on sets made to 250 m that returned $P \leq 0.01$ and of selected tests which did not.

Comparison	Permutations	Numbers		Weights	
		R	*P*	R	*P*
Daylight and night sets					
Between diel phases	9,999	0.253	≤0.001	0.253	≤0.001
Between surveys, 2007 vs. 2010	9,999	0.296	0.004	0.361	≤0.001
Between surveys, 2008 vs. 2010	9,999	0.144	ns	0.175	0.009
Between surveys, 2009 vs. 2010	999	0.128	ns	0.144	ns
Between stations, Head vs. Wall	999	−0.127	ns	−0.246	ns
Between stations, Head vs. Main	9,999	0.207	0.005	0.167	0.003
Between stations, Head vs. Deep	999	0.135	ns	0.097	ns
Between stations, Main vs. Deep	999	0.083	ns	0.081	ns
Night sets only					
Between surveys, 2007 vs. 2010	9,999	0.357	0.002	0.416	≤0.001
Between surveys, 2008 vs. 2010	1,716	0.171	ns	0.247	0.008
Between surveys, 2009 vs. 2010	999	0.112	ns	0.180	ns
Between stations, Head vs. Wall	220	0.007	ns	−0.202	ns
Between stations, Head vs. Main	9,999	0.359	0.006	0.224	0.005
Between stations, Head vs. Deep	9,999	0.331	0.001	0.204	ns
Between stations, Main vs. Deep	999	0.095	ns	0.116	ns

ns: P > 0.01.

and *M. atlanticum* showed the reverse trend in both weights and numbers, while *L. macdonaldi* and *Serrivomer beanii* were equally scarce in the shallow catches taken on both stations. Most of those differences paralleled patterns seen in the catches of 750 m sets. The trends in *C. sloani* and *Serrivomer beanii* likely resulted from elevation of depth distributions toward the canyon head. *B. euryops* were taken in smaller numbers but greater weights on the Head Station, indicating a larger average individual size amongst the few caught.

Species Distributions

Cluster analyses of the 19 species found no significant groupings by either abundance or weight (**Supplementary Figures 1**, **2**). *Serrivomer beanii* and *C. sloani* did cluster closely (though non-significantly) by both measures, which also agreed on a rather looser grouping of the warm-water myctophids *H. hygomii*, *L. dofleini*, and *N. resplendens*. Otherwise, each of the 19 species had its own unique distribution in space, depth and time, necessitating species-by-species examination (see Kenchington et al., 2018).

DISCUSSION

Overview of Fish Assemblage

The surveys showed that, in numbers, the IYGPT-vulnerable meso- and bathypelagic fish assemblage of The Gully is dominated by *C. microdon*, the characteristic *Cyclothone* of the northern North Atlantic. Although not effectively sampled by the IYGPTs, extrapolating from the weights of samples (Thompson and Kenchington, 2017) suggests that the 16 kg of *Cyclothone* spp. recorded by the surveys included some 60,000 individuals. Next in abundance, and dominating the biomass, was *B. glaciale*, the principal myctophid of waters north of the Gulf Steam and North Atlantic Current (Kenchington et al., 2018). Those two, with the seven other myctophids, three stomiids and eight other species analysed here, comprised over 90% of the individuals and 80% of the biomass of fish caught by the IYGPT. The residue included members of at least 235 other fish species. Such an assemblage composition is consistent with the results of other North Atlantic mesopelagic survey programs (e.g., McKelvie, 1985; Moore et al., 2003b, 2004; Sutton et al., 2008, 2013; Themelis and Halliday, 2012).

The 19 species included in the present analyses were mostly the ones expected to be abundant in open ocean immediately south of the canyon's mouth, though the proportions of the various myctophids change at the shelf/slope boundary (Themelis and Halliday, 2012) and hence not far from the shelf break. The sole exception to that similarity between the assemblages of canyon and ocean was *M. atlanticum*, a species of continental slopes and shelf valleys (e.g., Chouinard and Dutil, 2011; Ross et al., 2015) which spawns in seabed burrows (Markle and Wenner, 1979; Silverberg et al., 1987; Silverberg and Bossé, 1994). It was seen in The Gully primarily on the Head and Wall stations, though also on the Main Station. While each of the 19 species analysed had its own unique distribution, the dominant *B. glaciale* and the non-myctophids other than *M. atlanticum* were broadly distributed across the stations, years, and seasons (but not depths) of the survey design, whereas the seven sub-dominant myctophids had more restricted distributions, suggesting responses to particular environmental drivers.

The Gully is noted for its rich biota but there is no apparent enrichment of mesopelagic fish biomass. Fully quantitative

comparisons with biomasses in other areas are prevented by the dissimilar survey protocols of various programs, even when comparable nets are used. However, the (IYGPT-catchable) water-column biomass density on the Deep Station in summer averaged $\approx$7 g.m^{-2} and was lower further up the canyon, especially on the Head Station, where it was $<$1 g.m^{-2} in spring (**Table 3**). In contrast, mesopelagic fish biomass densities two orders of magnitude higher have been suggested for the Arabian Sea (Gjøsaeter and Kawaguchi, 1980) and for one study site in the Tasman Sea (May and Blaber, 1989). While there are many uncertainties in the estimates, it is sure that no large standing biomass of meso- and bathypelagic fishes, sufficient to support enough squid predation to sustain the consumption of the northern bottlenose whales, exists in The Gully.

Principal Drivers of Assemblage Composition

ANOSIM tests for differences among the catches of groups of sets, such as those taken by sampling to different maximum depths. The method cannot test for the effects of depth, nor those of other drivers of catch composition, let alone for underlying causes, such as behavioural responses to light levels. Nevertheless, where a significant difference between catches is found, it is often possible to infer some major correlate of the causative factors, such as depth or the proximity of a particular water mass, though the controlling mechanisms must remain unknown until targeted experiments become possible.

As in all marine systems and despite the use of an open net, depth proved to be one correlate of meso- and bathypelagic fish assemblage composition in the Gully, though the only significant difference was between the catches of the shallowest sets and those which fished to at least 750 m (**Table 4**), while amounts of the 19 principal species were little affected by sending the net below 1,250 m (**Figures 5**, **6**). There were also differences between daylight catches and those taken at night, though those differences were only statistically significant amongst the 250 m sets (**Table 7**). As expected, almost all of the analysed species were much less abundant by day at such depths (**Supplementary Table 8**). While not significant by ANOSIM, some diel differences at greater depths were indicated by clustering (**Figures 5**, **6**), despite the nets fishing through the depth ranges of the 19 species. Examination of the catches of individual species found that many more *C. maderensis*, *H. hygomi*, *N. kroyeri*, and *N. resplendens* were taken at night than in daylight (Kenchington et al., 2018), presumably because of a difference in catchability.

Despite there having only been one spring survey in the series, the seasonal cycle expected in northwest Atlantic ecosystems was observed, both in the whole dataset and in two of the depth bands examined (**Tables 4**–**6**). Catches of most species, especially the sub-dominant myctophids, were lower in March 2010 than during the summer surveys, three species being almost or entirely absent in spring (**Supplementary Tables 1**, **5**). Even in warmer waters far south of the continental slope, Themelis and Halliday (2012) found *H. hygomi* and *L. dofleini* scarce in survey catches during February and April. However, those authors saw a large increase in *C. maderensis* in April, which was not reflected in the spring catches in The Gully. It may also be noted that the few sets which sampled to 1,750 m in March 2010 took nearly twice as much as those which only fished to 1,250 m, in contrast to the much smaller difference seen in summer (**Table 3**), suggesting that some of the fish biomass had withdrawn to depth for the winter.

Variation in catches was much less marked among the summer surveys but there was some tendency for the deeper sets to cluster with others from the same survey. Likewise, ANOSIM found a significant difference between the catches of sets which fished below 750 m in 2007, when the CIL was unusually well-developed (Petrie et al., 2008; Kenchington et al., 2009), and those in 2009, when the WSW lay across the mouth of The Gully (Kenchington et al., 2014a). Most species, but especially the warm-water myctophids *H. hygomii*, *L. dofleini*, and *N. resplendens*, were taken in greater abundance during the latter survey. The exaggerated development of the CIL in 2007 was a season-long event, as the lingering effects of the exceptional spring bloom that year may have been, but the presence of WSW in 2009 only lasted for days and so the observed variation among surveys cannot be said to be inter-annual. That variation was, in part, a much shorter-term phenomenon.

The catches of deep sets made on the Deep Station in 2008 and 2009 clustered with those on the Offshore Station (not the Deep) in 2007 (**Figures 5**, **6**). The common factor appears to be that the stations lay close to the location of the shelf/slope boundary at the time of the respective survey. In contrast, *M. punctatum*, primarily a northern species, was abundant on the Deep Station in 2007 but much scarcer there during the subsequent summer surveys (Kenchington et al., 2018). Thus, the observed spatio-temporal distinction was consistent with the expected influence of water-mass characteristics on the abundances and biomasses of mesopelagic fishes, especially myctophids (e.g., Themelis and Halliday, 2012).

In summary, the multivariate analyses presented here have shown that much of the variability in the meso- and bathypelagic fish assemblage in the wider study area, including the stations outside the canyon, is aligned in space and time with the principal drivers that operate on equivalent assemblages away from the continental margin: depth, distribution of water masses, diel and seasonal cycles, plus temporal variability. The results of the SIMPER analyses of those patterns were broadly in accord with prior examination of the distributions of each of the 19 species individually (Kenchington et al., 2018), despite the very different approaches. While the multivariate analyses provide more rigor, the single-species approach incorporated information on the lengths of individuals caught, as well as considering prior knowledge of each species' biology. It found that the distributions generally followed expectations derived from published literature, which (with the exception of bottom-associated *M. atlanticum*) meant expectations largely based on oceanic and continental-slope studies—hence consistency with the drivers active in open ocean.

Canyon Effects

The primary interest in the Gully surveys, however, lies in the effects of the canyon on the fish assemblage, as deviations from oceanic norms. Those have been addressed by Thompson and Kenchington (2017) and by Kenchington et al. (2018) in terms of trends along the thalweg, from the Deep Station via the Main to the Head, in the number and weight of each species caught (**Table 8**). Changes within depth strata were confounded by elevation of the depth distributions of deeper-living species, where the seabed rose into proximity with the fish, though some species showed only truncation of the lower portion of their distributions, not elevation of their upper bounds. ANOSIM and SIMPER nevertheless found differences in catch composition along the thalweg, though those in the 0–250 m catches were non-significant.

The Head Station was particularly distinctive, with much lower catches of most species (**Table 6**, **Supplementary Table 6**). Only *M. atlanticum* was more abundant on that station than on the Main, though a greater weight (but lesser numbers) of *A. risso* was taken on the Head Station. Although abundant in open ocean, that species is especially frequent on continental slopes and in deep shelf valleys (e.g., Gartner et al., 2008; Chouinard and Dutil, 2011; Feagans-Bartow and Sutton, 2014; Ross et al., 2015). The depth distributions of four species that are primarily bathypelagic in open ocean, *E. pelecanoides*, *C. microdon*, *M. niger*, and *L. macdonaldi*, were strongly elevated toward the canyon head. The catches of them taken above 750 m depth on the Head Station, though not their water-column totals, were as large or larger than those on other stations (Thompson and Kenchington, 2017; Kenchington et al., 2018).

The differences between the catch compositions on the Main and Deep stations were more complex (**Tables 5**, **6**, **Supplementary Tables 3**, **6**). The former saw lower abundances of most species, though some of those were the warm-water myctophids that were only common near the shelf/slope boundary and hence on the Deep Station during the 2009 survey. Apart from *M. atlanticum*, the species with larger numbers on the Main Station were mostly migratory myctophids with colder-water associations, though *B. euryops* (in 0–750 m sets), *M. niger* and *S. boa* (in deeper sets) were also more abundant there than on the Deep Station. Additionally, larger average individual sizes led to greater catch weights of *N. scolopaceus* and *A. risso* on the Main Station, despite lower numbers than were taken on the Deep. As *A. risso* is common on continental slopes and in shelf valleys, so *N. scolopaceus* is a species of the "oceanic rim," more than of mid-ocean environments (Feagans-Bartow and Sutton, 2014).

In contrast, there was no significant cross-canyon trend, above 750 m depth, between the Main and Wall stations. However, a number of species were taken in smaller amounts over the canyon wall than over the thalweg, most notably *Scopelogadus beanii*, while *M. atlanticum* showed the reverse trend, as did some deeper-living species that had elevated depth distributions in proximity to the seabed (Kenchington et al., 2018).

While few data are available, the similarity of Slope-Station catches to those taken on the Deep Station suggests that the continental-slope assemblage is continuous across the mouth of The Gully and is little affected by the presence of the canyon. Where catches on the Main and Deep stations differed, the Slope Station followed the Deep, despite having been chosen for seabed depths similar to the Main—suggesting that the observed up-canyon trends in the assemblage result from more complex causes than bathymetry alone.

Since the Gully surveys were the first to deploy midwater trawls in a canyon, there are no other observations to which those trends can be compared. Nor is it yet possible to suggest whether the results reported here can be extrapolated to other canyons. The Gully's unusual connection to the Trough, and the major up-canyon water flow at depth which that link permits, may have unique ecological consequences.

Canyon Processes

The complex structuring of the IYGPT-vulnerable assemblage of meso- and bathypelagic fishes in The Gully could have multiple contributory causes. Notably, the marked difference between the catches on the Head Station and those taken elsewhere might be linked to the apparent predominance of LSW on that one station during three of the surveys. However, we here offer a single explanatory model (**Figure 7**), which explains the observed distributions of the fish by linking the oceanography of the canyon with fish behaviour and trophic ecology, as a hypothesis for future testing.

N. scolopaceus, *A. risso*, and *M. atlanticum* are especially frequent along continental slopes. Hence, they may be supposed to have evolved behaviours which allow them to maintain position over suitable seabed depths. In contrast, the other species of present concern are essentially oceanic and, on the scale of ocean basins, planktonic. As a first approximation, we therefore suggest that those species can be supposed to drift passively in horizontal flows and that, having evolved away from the seabed, they lack effective behavioural responses to being swept into a canyon. Directed, diel horizontal migrations of mesopelagic fishes have been observed (e.g., Benoit-Bird et al., 2001; Benoit-Bird and Au, 2006; McManus et al., 2008) but only in an island-associated, boundary community—hence in populations analogous to the three continental-slope species found in The Gully, not the oceanic ones. Given our postulate of passive drift, the known inflow into The Gully (Greenan et al., 2014) must carry a flux of midwater fish biomass into the canyon.

In contrast to their supposed horizontal passivity, each of the 20 dominant fish species has well-developed vertical behaviour, which shapes its depth distribution and, for some species, includes pronounced diel migrations. As passive horizontal drift carries individuals into a canyon with slowly upwelling water, such as The Gully, they will seek to maintain their preferred depths, through active downward movement relative to the rising water. They will thus filter themselves out of the flow, which should lead to their retention in the canyon head, as the water escapes over the top of the walls. That process should operate despite the decreasing seabed depths compelling some individuals upward, to an extent dependent on the vertical behaviour of the particular species (**Table 8**), while demersal predators take those individuals which swim too close to the bottom.

TABLE 8 | Up-Canyon trends in the distributions and sizes of the 19 analysed species (after Kenchington et al., 2018) and for *Cyclothone microdon* (after Thompson and Kenchington, 2017).

Species	Up-canyon trend in depths	Center of horizontal distribution	Occurrence on Head Station	Up-canyon trend in lengths
Nemichthys scolopaceus	Truncation	Main and Wall Stations	Scarce	Decline of small fish
Serrivomer beanii	Truncation, except large fish elevated	Outside canyon mouth	Reduced numbers, relative to other stations	Decline of small fish
Eurypharynx pelecanoides	Elevation	Outside canyon mouth	Low but higher than 750 m sets elsewhere	None?
Bathylagus euryops	Truncation, except elevation near-bottom	Deep Station	Reduced numbers, relative to other stations	Decline in average size
Cyclothone microdon	Elevation	Outside canyon mouth	Biomass equal to Main Station	No data
Chauliodus sloani	Elevation	Outside canyon mouth	Scarce	Decline of small fish
Malacosteus niger	Elevation	Outside canyon mouth	Reduced numbers but higher than 750 m sets elsewhere	Decline of small fish and increase in large
Stomias boa	Elevation	Evenly distributed in numbers, except Head Station	Scarce	Decline of small fish and increase in large
Arctozenus risso	Unaffected	Numbers declined but weights increased up-canyon	Reduced numbers but increased weight	Decline of small fish
Benthosema glaciale	Unaffected	Evenly distributed, except Head Station	Much reduced numbers, relative to other stations	Weak decline of small fish in summer
Ceratoscopelus maderensis	Unaffected	Evenly distributed, except Head Station	Scarce	Decline of small fish
Hygophum hygomii	Unaffected	Near Warm Slope Water	None	–
Lampanyctus macdonaldi	Elevation	Outside canyon mouth	Higher than 750 m sets elsewhere	None?
Lobianchia dofleini	Unaffected	Near Warm Slope Water	None	–
Myctophum punctatum	Unaffected	Main and Wall Stations	Reduced numbers, relative to other stations	Decline of small fish
Notoscopelus kroyeri	Unaffected	Main and Wall Stations	Scarce	Decline of small fish to Head Station
Notoscopelus resplendens	Unsure	Outside canyon mouth	None	–
Scopelogadus beanii	Truncation	Outside canyon mouth	Reduced numbers, relative to other stations	Unsure
Anoplogaster cornuta	Unsure	Unsure	Scarce	Unsure
Melanostigma atlanticum	Unaffected	Main, Wall and Head Stations	Abundant	Unsure

"Elevation:" Depth distribution elevated up-canyon; "Truncation:" Lower portion of depth distribution truncated by presence of seabed but upper limit not elevated; –: Species too rarely caught in canyon for trend to be observed.

The combination of passive horizontal drift with active control of depth would, however, result in a concentration of fishes in the canyon head—the reverse of what was seen. We suggest that those mechanisms do operate but that very high loss rates during the month-long drift from the canyon's mouth to its head (Greenan et al., 2014) result in the observed up-canyon decline in numbers and biomass of most species. There are two obvious mechanisms for that loss. Firstly, where diel migration is combined with current shear between water layers in open ocean, migrants will be dispersed but not necessarily transported outside their preferred habitats. In contrast, in The Gully a migrant individual caught by the deep indraught in daylight would be transported to places from which near-surface nocturnal drifts would carry it across the canyon and ultimately over an adjacent bank, where the fish's thwarted attempt at downward migration at dawn would leave it vulnerable to epipelagic and demersal predators. With short summer nights and the estimated three-day crossing time, for surface water passing over much of the canyon (Greenan et al., 2014), diel migrants entering The Gully in the main inflow on the eastern side should average about a week before being swept over the shallows of Sable Island Bank. While those individuals that encounter the sloping flank of the bank at dawn likely have some ability to return to deep water through active down-slope swimming, the potential for large-scale losses is clear.

The observed up-canyon decline in numbers and biomass was not, however, confined to diel migrants but was also seen in

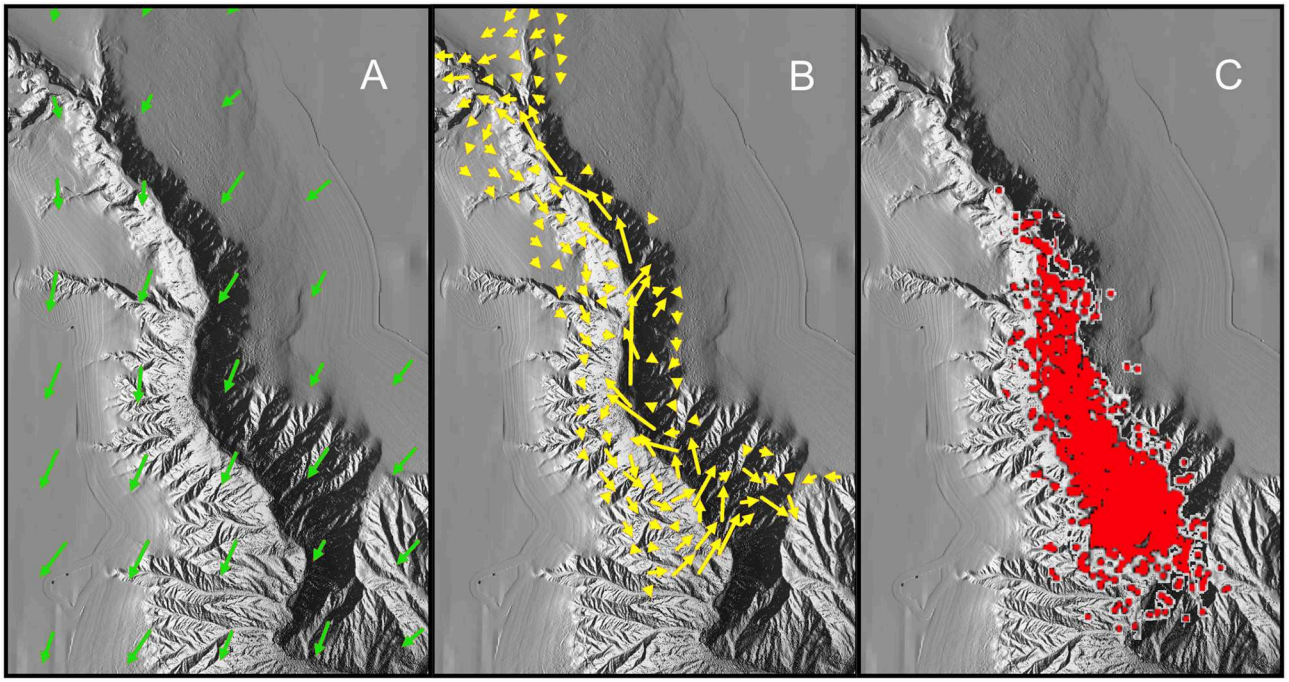


FIGURE 7 | Illustration of hypothesis explaining the observed distribution of the fish assemblage: **(A)** Modelled surface current over The Gully in August—length of arrows proportional to volume of flow (simplified from Shan et al., 2014b); **(B)** Modelled volume transport of water below 200 m depth in August (simplified from Shan et al., 2014b); **(C)** Locations of surface observations of northern bottlenose whales (mapped by Hooker et al., 2002b), here supposed indicative of the distribution of concentrations of *Gonatus* spp. at depth. The modelled current and volume transports differ in detail from the empirical observations summarized in section Oceanography of The Gully.

the non-migratory species, which are not subject to the cross-canyon surface flows. For most species, that decline was also more pronounced in the smaller individuals, the only confirmed exceptions being *E. pelecanoides* and *L. macdonaldi*, the catches of which were particularly confounded by vertical elevation (Kenchington et al., 2018: see **Table 8**). In the pelagic realm, where predation rates generally fall with increasing body size, that size-differential suggests that the abundance declines were consequences of intense predation on the fish, as they drift up the canyon.

The nature of the predators cannot be a certain. However, elsewhere in the North Atlantic, the northern bottlenose whale is a specialist predator of armhook squid. Available evidence suggests that those are also their principal prey in The Gully, where the whales are known to feed close to the canyon walls at depths of 500–1,500 m, and the presence of actively feeding *H. ampullatus* indicates a high biomass of *Gonatus* spp. deep in the canyon (Hooker and Baird, 1999; Hooker et al., 2001, 2002a), though they cannot be observed directly. [Aside from brooding females, subadult and adult *Gonatus* spp. are very active (Arkhipkin and Bjørke, 1999) and successfully evade midwater trawls. Only juveniles and spent females were taken during the 2007–10 surveys.] Adult *G. fabricii* are known to eat macroplanktonic crustaceans, fishes (including myctophids), and cephalopods. Stable-isotope analyses of beaks (bulk tissue) have shown an ontogenetic increase in trophic level with individual size, reaching an estimated >5 in the largest (Hooker et al., 2001; Cherel et al., 2009; Jereb et al., 2015; Golikov et al., 2018). Thus, mesopelagic fish are likely an important component of the diet of *Gonatus* spp. in The Gully and hence of the food chain leading to the whales.

Although northern bottlenose whales are continuously present in The Gully, at least in summer, most individuals divide their time between that canyon and other, smaller ones to the eastward (Wimmer and Whitehead, 2004). Their abundance has been estimated, based on field data from the two summers following the midwater trawl surveys, at 143 individuals in the entire Scotian Shelf population, of which 116 spent time in The Gully (O'Brien and Whitehead, 2013). Gowans et al. (2000) estimated that one third of the Gully individuals are in the canyon at any one time during summer but O'Brien and Whitehead (2013) concluded that more than half of the Scotian Shelf population is present there. Thus, The Gully supports the entire summer feeding of the equivalent of 40–80 whales. Hooker et al. (2001) examined the energy requirements of *H. ampullatus*, concluding that an average individual eats ≈59 kg of *Gonatus* spp. daily, implying a population consumption of 2.4–4.8 $t.d^{-1}$ in The Gully during summer. No estimates of the ecological efficiencies of deep-living squids are available but, if *Gonatus* spp. approximated to a conventional 10% ecological efficiency, the whales' consumption would indicate that the squid eat between 20 and 50 $t.d^{-1}$.

The average density of IYGPT-catchable fish biomass on the Deep Station, during the summer surveys and averaged across the water column was ≈0.005 g.m^{-3} (**Table 3**). The mean flow through the central canyon below 200 m depth (net of the outflow on the western side) has been estimated as 35,500 m^3.s^{-1} (Greenan et al., 2014) and the inflow through the canyon mouth cannot be less. Thus, the biomass flux through the mouth in late summer would be ≈15 t.d^{-1}–assuming only passive horizontal drift, ignoring net efficiency, and the biomass of other species not included in the present analyses, while setting aside vertical and cross-canyon structuring of both water flow and fish distributions (including diel migrations to the surface layer above the inflow). Under the assumption of passive drift, there is no escape for those fishes and no pool of accumulated biomass where survivors could live for more than a few weeks.

That calculation offers, at best, an order-of-magnitude estimate of the flux of mesopelagic biomass to the canyon's ecosystems through passive drift. It excludes macroplanktonic crustaceans, which are also potential prey of *Gonatus* spp. (Jereb et al., 2015; Golikov et al., 2018). In the IYGPT catches on the Main Station in summer (MacIsaac et al., 2014), those crustaceans showed a similar water-column biomass density to that estimated here for the fishes. Conversely, some portion of the biomass flux through the canyon's mouth will be lost to Gully ecosystems when vertically migrant fishes are swept over the adjacent banks. Another, and potentially larger error in the 15 t.d^{-1} estimate arises from net efficiency. There have been recent suggestions that the catchability of mesopelagic fishes in midwater trawls is very low, including one estimate that the density of *B. glaciale* ahead of a Harstad trawl is two orders of magnitude greater than indicated by the catch of per unit volume of water filtered (Kaartvedt et al., 2012). Those suggestions rely on an untested assumption that observed acoustic backscatter comes from the same organisms as are vulnerable to net capture, while (from differences in net geometry and mesh sizes) an IYGPT would be expected to have higher efficiency for small fish than does a Harstad trawl. Nevertheless, while other uncertainties in the estimated biomass flux into The Gully might outweigh the effects of net efficiency and the exclusion of crustaceans, the true flux is likely considerably larger than is estimated here. Even 15 t.d^{-1} of fish supply would be of the right order to support the estimated consumption of *Gonatus* spp.

We therefore suggest that passive drift of meso- and bathypelagic fishes into The Gully, from beyond the shelf break, provides a substantial part of the trophic support of the northern bottlenose whales in the canyon. If that conclusion has merit, it serves to explain the distribution of the whales in terms of canyon bathymetry, its shaping of water flow and hence the availability of prey across two trophic levels. The principal weakness in this explanation of our observations is that it depends on an inference that fish species evolved for life in open ocean lack any means, within their behavioural repertoires, for active avoidance of the inflow into the canyon. While a reasonable first approximation, that supposed inability to escape from The Gully cannot be supported by data.

Elaborations of the model may explain other features of fish distributions in the canyon. A weak gyre appears to form at canyon-rim depth, in summer and in the vicinity of the Main Station (Greenan et al., 2014; Shan et al., 2014a). That alone should serve to retain fishes in the central canyon but it was primarily five species of diel-migrant myctophids that showed higher abundance on the Main Station than the Deep. For them, the combination of current sheer and migration creates, in effect, a stronger, behaviourally mediated gyre–up-canyon on the east side at depth, cross-canyon in the surface flow and down-canyon in the outflow along the western wall—concentrating such species in the central canyon.

The seasonal variation in the fish assemblage may also be partly explained by water movements. Modelling suggests a stronger up-canyon flow at depth in winter, with less of a counter flow to the west (Shan et al., 2014a). Thus, those species which do not withdraw to bathypelagic depths, thereby avoiding much of the inflow, will experience The Gully in early spring with a unidirectional current, rather than the retention effect of the summer's partial gyre.

Implications for MPA Management

Well-designed MPAs, with enforced conservation measures, can sometimes protect the biota within their boundaries from the effects of local deleterious anthropogenic activities. Most cannot, however, protect against the consequences of distant activities, if those consequences are transported across MPA boundaries. For The Gully, Hooker et al. (2002a) noted that conservation of the northern bottlenose whales requires measures to protect an area much larger than the existing MPA, encompassing the sources of the allochthonous energy which supports that signature species. However, those authors could only speculate as to the pathways through which the energy enters the canyon. The present work has shown that passive drift of meso- and bathypelagic fishes is one plausible mechanism for an energy flux large enough to be a principal pathway supporting the whales. We therefore suggest that long-term achievement of the MPA's goals requires effective protection of the sources from which those mesopelagic fishes are drawn, initially as a precautionary measure. Fortunately, the Gully management regulations prohibit anthropogenic activities outside the MPA's boundaries that have deleterious effects on the biota within (Department of Fisheries Oceans, 2008). That authority should be used to protect the whales' supply of prey—though the extent of the area from which the fishes are drawn remains to be determined.

DATA AVAILABILITY STATEMENT

All datasets analysed for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

Marine fish surveys conducted at sea present special circumstances regarding euthanasia of the animals caught. Guidelines developed by the American Fisheries Society exempt fish caught by such surveys from standard euthanasia practices because of the numbers of specimens collected at one time (https://fisheries.org/policy-media/science-guidelines/

guidelines-for-the-use-of-fishes-in-research/#8.1). As expected during deep sampling, most of the fish caught during the Gully surveys died in the trawls and the remainder expired soon after being brought aboard, while being sorted. The study was carried out under the auspices of Fisheries and Oceans, Canada and the Animal Care Committee of Fisheries and Oceans, Canada, Maritimes Region, approved that approach to euthanization.

The trawling was conducted under authorizations, from the Regional Director, Science Branch, Maritimes Region, of Fisheries and Oceans, Canada, to engage in fishing and related activities on the Atlantic coast of Canada, subject to the provisions of the Fisheries Act and Regulations thereunder. Four of the stations lay within The Gully Marine Protected Area. Trawling and other operations there were conducted under Ministerial Approval (by the Minister of Fisheries and Oceans, Canada) to engage in research activities under Section 6(1) of the Gully MPA Regulations, subject to the provisions of the Fisheries Act and following review of the survey's plans. No protected species were captured by the trawls.

AUTHOR CONTRIBUTIONS

TK led all scientific aspects of the research program and the survey cruises, supervising the fishing at sea. He coordinated the post-survey work, edited the catch database, interpreted the analytical results, and drafted the paper. DT and SD had primary responsibility for fish identifications, both at sea and ashore. EK secured funding and ship time for the surveys, provided technical staff, and oversaw administration of the program. She also performed the multivariate analyses. All authors contributed to development of the final paper from initial drafts.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00181/full#supplementary-material

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REVIEW
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Influence of Water Masses on the Biodiversity and Biogeography of Deep-Sea Benthic Ecosystems in the North Atlantic

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Circulation patterns in the North Atlantic Ocean have changed and re-organized multiple times over millions of years, influencing the biodiversity, distribution, and connectivity patterns of deep-sea species and ecosystems. In this study, we review the effects of the water mass properties (temperature, salinity, food supply, carbonate chemistry, and oxygen) on deep-sea benthic megafauna (from species to community level) and discussed in future scenarios of climate change. We focus on the key oceanic controls on deep-sea megafauna biodiversity and biogeography patterns. We place particular attention on cold-water corals and sponges, as these are ecosystem-engineering organisms that constitute vulnerable marine ecosystems (VME) with high associated biodiversity. Besides documenting the current state of the knowledge on this topic, a future scenario for water mass properties in the deep North Atlantic basin was predicted. The pace and severity of climate change in the deep-sea will vary across regions. However, predicted water mass properties showed that all regions in the North Atlantic will be exposed to multiple stressors by 2100, experiencing at least one critical change in water temperature (+2°C), organic carbon fluxes (reduced up to 50%), ocean acidification (pH reduced up to 0.3), aragonite saturation horizon (shoaling above 1000 m) and/or reduction in dissolved oxygen (>5%). The northernmost regions of the North Atlantic will suffer the greatest impacts. Warmer and more acidic oceans will drastically reduce the suitable habitat for ecosystem-engineers, with severe consequences such as declines in population densities, even compromising their long-term survival, loss of biodiversity and reduced biogeographic distribution that might compromise connectivity at large scales. These effects can be aggravated by reductions in carbon fluxes, particularly in areas where food availability is already limited. Declines in benthic biomass and biodiversity will diminish ecosystem services such as habitat provision, nutrient

cycling, etc. This study shows that the deep-sea VME affected by contemporary anthropogenic impacts and with the ongoing climate change impacts are unlikely to withstand additional pressures from more intrusive human activities. This study serves also as a warning to protect these ecosystems through regulations and by tempering the ongoing socio-political drivers for increasing exploitation of marine resources.

Keywords: North Atlantic, deep-sea, biodiversity, biogeography, water masses, vulnerable marine ecosystems

INTRODUCTION

Deep-sea ecosystems (i.e., >200 m water depth; Levin et al., 2019) have been traditionally considered vast habitats characterized by a stable and homogeneous environment (i.e., darkness and constant low temperatures). Such conditions were thought to indicate a lack of barriers for dispersal, resulting in large biogeographic areas with broad distributions of deep-sea species (Smith et al., 2006; McClain and Hardy, 2010). In the last few decades, new technologies have enabled sampling of some remote ecosystems, revealing new descriptions of species, and ecological paradigms (Danovaro et al., 2014; Cunha et al., 2017). These include the discovery of various geomorphological features and the diversity of their associated ecosystems, such as those in submarine canyons (Fernandez-Arcaya et al., 2017), seamounts (Morato et al., 2013), hydrothermal vents (Ramirez-Llodra et al., 2007b), cold-water coral reefs (Roberts et al., 2006) or sponge grounds (Hogg et al., 2010). Biodiversity has been also proved to be enhanced by numerous factors, including high habitat complexity (Buhl-Mortensen et al., 2010; Henry et al., 2010; Beazley et al., 2013), carbon cycling (Duineveld et al., 2012; White et al., 2012; Cathalot et al., 2015; Rix et al., 2016; Soetaert et al., 2016), recently discovered ecological interactions (Buhl-Mortensen and Mortensen, 2004; Carreiro-Silva et al., 2017; Henry and Roberts, 2017), or chemosynthetic production in the deep-sea (Ramirez-Llodra et al., 2007a; Rodrigues et al., 2013; Levin et al., 2016). Thus, the old view of low diversity, food-poor, and low metabolic activity has been reconsidered in many deep-sea areas (Ramirez-Llodra et al., 2010; Danovaro et al., 2014; McIntyre et al., 2016; Cunha et al., 2017).

Besides seafloor topography and sedimentary features (Levin and Sibuet, 2012; Tong et al., 2012; Collart et al., 2018), many other factors can drive biodiversity and biogeography in the deep-sea (Henry et al., 2014; Radice et al., 2016). Most of them are inherent to, or related to, the water mass characteristics, including temperature (Yasuhara and Danovaro, 2014), flow regime (Mienis et al., 2007; van Haren et al., 2014), oxygen concentration (Levin, 2003; Woulds and Cowie, 2007), organic matter supply (White et al., 2012; Cathalot et al., 2015), and circulation patterns (Henry et al., 2014; Somoza et al., 2014) among others. In the North Atlantic Ocean, the Atlantic Meridional Overturning Circulation (AMOC) re-distributes warm, saline water masses of the upper water column northwards, compensated by a returning flow of cooler fresher waters at depth. In addition, the properties and spatial extent of water masses in the North Atlantic vary on inter-annual to decadal timescales creating a fluctuating environment at local, regional and basin scales. To preserve deep-sea biodiversity and ensure sustainable socio-economic development in the North Atlantic Ocean, ecosystem-based management is needed on the same spatial and temporal scales as the key ocean circulation features and atmospheric drivers (Johnson et al., 2018; Armstrong et al., 2019). Re-organizations in the North Atlantic water mass structure have been occurring since the Atlantic's genesis 200 mya, influencing the biodiversity, distribution and connectivity of deep-sea communities and species. For instance, the re-organizations in water mass structure related to AMOC and Sub-Polar Gyre dynamics during the early Holocene triggered an unprecedented post-glacial re-expansion of the cold-water coral (CWC) *Lophelia pertusa* over 7,500 km in ∼400 years (Frank et al., 2011; Henry et al., 2014; Wienberg and Witschack, 2017; Hebbeln et al., 2019). Thus, changes in the North Atlantic deep-water circulation are of particular interest in order to understand deep-sea species distribution, community composition, ecosystem functioning and dynamics. Moreover, this can shed light on future climate changes and how they affect deep-sea organisms.

This review does not intend to provide an exhaustive summary of all previous studies on oceanographic factors influencing deep-sea megafauna, but instead focuses on studies that clearly discuss the implications of water mass properties on biodiversity and biogeography. Thus, we address the importance of the North Atlantic circulation, from 20° to 70° N, and the role of the key water masses and their properties to derive a basin-scale synoptic view of key ocean controls on the deep-sea biodiversity and biogeography patterns. We particularly focus on sessile megafaunal species, such as CWCs and sponges, compiling results obtained from experimental work, field observations and modeling on these organisms from physiological to community level. These organisms form Vulnerable Marine Ecosystems (VME), which occur from the continental shelves to the bathyal regions of the deep-sea, connected in many cases across the entire North Atlantic through the basin-scale circulation. The vulnerability of these ecosystems is defined as the likelihood to experience substantial alteration from short-term or chronic disturbance, and the likelihood to recover in a given time frame (FAO, 2009). This, in turn, is related to the ecosystem characteristics such as rarity, fragility, structural and functional significance, longevity, slow growth rates or similar traits that limit the probability of recovery (FAO, 2009). Cold-water corals and sponges present many of these life-history traits and are also ecosystem-engineering organisms (Jones et al., 1994) which are able to form complex three-dimensional habitats such as CWC reefs, coral gardens or sponge grounds that promote life and enhance biodiversity in the deep-sea.

The North Atlantic circulation patterns, as well as the physical and chemical properties of the deep ocean, are already

experiencing changes due to climate change (Purkey and Johnson, 2010; Helm et al., 2011; Levin and Le Bris, 2015; Perez et al., 2018). A clear understanding of the patterns and drivers of deep-sea benthic biodiversity is needed to inform and develop future projections under climate change conditions. In this sense, different projections for future water mass properties in the deep North Atlantic basin have been simulated and are presented in this work. The possible consequences for deep-sea benthic communities in these future scenarios are discussed considering the effects of the current and future water mass properties. This review aims to facilitate the integration of current knowledge on biodiversity related to water masses properties as well as the likelihood of future changes and consequences on the ecological and evolutionary trajectories of deep-sea ecosystems. Such information is needed to identify the assessment, management and regulation actions to support proper management and preservation of the deep-sea VMEs.

NORTH ATLANTIC CIRCULATION AND KEY WATER MASSES

Atlantic Meridional Overturning Circulation

The North Atlantic is globally important due to the conversion of upper waters to denser intermediate and deep waters. In this review, we mainly considered and discussed the circulation patterns and water masses in the North Atlantic ranging from 20° to 70° N latitude and 78° W to 10° E longitude, but occasionally address some aspects of the tropical and more northern regions when necessary. The AMOC consists of a northward flowing upper limb balanced by a southward flow at depth. The warm and salty waters transported northwards within the Gulf Stream, both recirculate within the subtropical gyre and flow, via the North Atlantic Current (NAC), into more northern areas (**Figure 1**). Around 40% of the water entering subpolar latitudes continues northward over the Greenland-Scotland Ridge into the Nordic Seas (Sarafanov et al., 2012) where it is subject to further heat loss and mixing. The resulting, denser intermediate and bottom waters are trapped to the north of the Greenland-Scotland Ridge; however, some overflows into the North Atlantic (Hansen and Østerhus, 2000). The remaining 60% of the water transported northwards in the NAC recirculates cyclonically within the subpolar gyre (Sarafanov et al., 2012). As the waters circulate, they become cooler and fresher, and are subject to winter storms, particularly in the Labrador and Irminger Seas (Yashayaev, 2007; Jong and Steur, 2016). The resulting intermediate water mass flows southward, along with the overflow waters, in the Deep Western Boundary Current forming the return limb of the AMOC (**Figure 1**). Recent work suggests that the AMOC is dominated by dynamics to the east of Greenland, rather than convection in the Labrador Sea (Lozier et al., 2019).

AMOC strength has varied through time. During the last glacial maximum, 19–21 kya, a moderate to strong AMOC probably persisted in the intermediate layers (Lynch-Stieglitz et al., 2007; Lippold et al., 2009; Ritz et al., 2013). This was followed by a slowdown of the AMOC between 12 and 19 kya, coinciding with the abrupt Younger Dryas event (Hughen et al., 1998). Fossil records indicate that the currently wide-spread CWC *Lophelia pertusa* remained in a few refugia during the last glacial maximum and Younger Dryas (Henry et al., 2014). The rapid spin-up of the AMOC after the Younger Dryas (Rogerson et al., 2006; Xie et al., 2012) coincided with a rapid and wide-spread return of *L. pertusa* to northern Europe after a hiatus of over 65 kyr (Frank et al., 2011). Today, the AMOC is still a crucial part of the Earth's climate system. However, models indicate that it is likely to weaken by 2100 (Gregory et al., 2005), whilst recent studies suggest that the AMOC may have weakened in the past 100–200 years (Caesar et al., 2018; Thornalley et al., 2018).

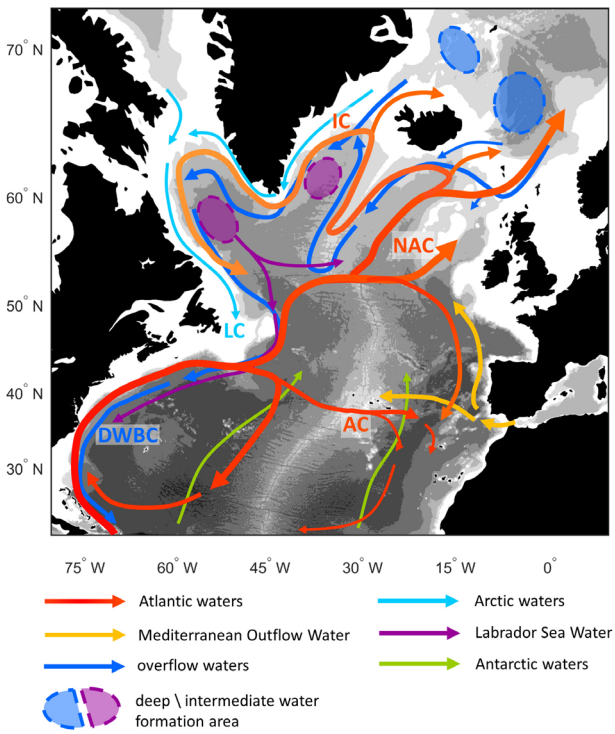


FIGURE 1 | Schematic of the main circulation in the North Atlantic Ocean color coded by water mass type. Main currents are labeled as: the North Atlantic Current (NAC), Azores Current (AC), Irminger Current (IC), Labrador Current (LC), and Deep Western Boundary Current (DWBC).

Key Water Masses

As the properties and depth distribution of water masses varies spatially across the North Atlantic (Liu and Tanhua, 2019), we describe the key water masses in general terms in four depth bands: upper bathyal (200–1000 m), intermediate bathyal (1000–2000 m), lower bathyal (2000–3000 m) and abyssal (>3000 m). Mean properties and associated variability ranges for each depth band are shown in **Table 1**.

In the upper bathyal depth range (200–1000 m), the predominant upper water mass is North Atlantic Central Water (NACW), which is found in the topmost 500–800 m. However, several denominations of this water mass exist. For example,

TABLE 1 | Present-day (year 2000) and predicted future (year 2100) average values [range] of the main water mass properties, temperature (T), particulate organica carbon (POC), pH, aragonite and calcite saturation states (Ω) and dissolved oxygen (DO), influencing deep-sea biodiversity in the North Atlantic in the upper (200–1000 m), intermediate (1000–2000 m), lower (2000–3000 m) bathyal, and abyssal (>3000 m) regions.

Depth	Period	T (°C)	POC (mg C·m^{-2}·day^{-1})	pH	Aragonite (Ω)	Calcite (Ω)	DO (ml·l^{-1})
200–1000	2000	5.19·[−0.36, 17.17]	16.43·[0.82, 55.39]	8.08·[7.76, 8.16]	1.73·[0.66, 2.92]	2.8·[1.14, 4.53]	0.26·[0.11, 0.33]
	2100	7.01·[0.94, 19.73]	12.05·[0.45, 48.79]	7.81·[7.46, 8.02]	1.07·[0.64, 2.08]	1.73·[1.09, 3.16]	0.25·[0.1, 0.32]
	Δ	1.82·[−0.5, 4.29]	−4.38·[−25.36, 2.7]	−0.26·[−0.44, −0.02]	−0.66·[−1.36, −0.02]	−1.07·[−2.15, −0.04]	−0.02·[−0.03, 0.01]
1000–2000	2000	4.97·[−0.15, 14.94]	7.6·[0.78, 32.87]	8.08·[7.96, 8.14]	1.52·[0.65, 2.73]	2.46·[1.11, 4.07]	0.27·[0.13, 0.32]
	2100	5.56·[0.85, 17.13]	5.49·[0.43, 30.98]	7.9·[7.72, 8.03]	1.05·[0.63, 2.12]	1.71·[1.07, 3.18]	0.25·[0.12, 0.3]
	Δ	0.59·[−0.65, 2.8]	−2.12·[−18.62, 2.39]	−0.18·[−0.36, −0.01]	−0.46·[−1.05, −0.02]	−0.76·[−1.65, −0.03]	−0.02·[−0.03, 0]
2000–3000	2000	4.84·[0.63, 12.77]	4.38·[0.75, 25.31]	8.06·[7.93, 8.13]	1.28·[0.57, 2.49]	2.08·[0.97, 3.7]	0.27·[0.11, 0.32]
	2100	4.92·[0.8, 14.36]	3.24·[0.41, 17.97]	7.94·[7.82, 8.03]	1·[0.56, 2.09]	1.62·[0.95, 3.17]	0.25·[0.11, 0.29]
	Δ	0.08·[−0.93, 2.06]	−1.14·[−15.39, 1.54]	−0.12·[−0.28, −0.01]	−0.28·[−0.68, 0]	−0.46·[−1.1, −0.01]	−0.02·[−0.04, 0.01]
>3000	2000	2.88·[0.63, 12.56]	2.2·[0.31, 16.97]	7.98·[7.93, 8.1]	0.78·[0.55, 1.86]	1.3·[0.93, 2.9]	0.25·[0.11, 0.31]
	2100	2.86·[0.69, 12.56]	1.53·[0.23, 11.07]	7.94·[7.87, 8.02]	0.7·[0.52, 1.75]	1.17·[0.9, 2.66]	0.24·[0.11, 0.29]
	Δ	−0.02·[−0.78, 1.68]	−0.67·[−10.61, 0.98]	−0.04·[−0.21, 0]	−0.08·[−0.4, 0]	−0.13·[−0.66, 0.01]	−0.01·[−0.04, 0]

Δ indicates change between present-day and predicted future conditions. Adapted from Mora et al. (2013); Sweetman et al. (2017) and Morato et al. (2020).

"subtropical" NACW (found south of around 42°N) is warmer and more saline, whilst "subpolar" NACW found to the north is cooler and fresher (Ríos et al., 1992). NACW properties also vary zonally (Ríos et al., 1992; Pollard et al., 2004). In eastern areas, the NACW (termed eastern NACW, ENACW) is warmer and more saline, whilst western NACW (WNACW) is cooler and fresher. However, the freshest, coldest and densest water mass found in the upper 800 m is seen in the western subpolar basins and is termed SubArctic Intermediate Water (SAIW; García-Ibáñez et al., 2015). This water mass is also found further east and south, but in these areas, it is found below the NACW layer at around 500 m (Pollard et al., 1996; Wade et al., 1997). The final key upper bathyal water mass is Antarctic Intermediate Water (AAIW) which is again found below the NACW layer. AAIW, which has been observed as far north as 60°N (Tsuchiya, 1989), has a slightly elevated salinity but is most easily identified by a mid-depth silicate maximum (Read, 2000).

At intermediate bathyal depths (1000–2000 m), two main water masses are observed: Mediterranean Outflow Water (MOW) and Labrador Sea Water (LSW). The MOW overflows the Straits of Gibraltar and spreads out at around 1200 m in the Atlantic (García-Ibáñez et al., 2015). It is characterized by a mid-depth salinity maximum with low dissolved oxygen (DO) concentrations and has been traced to at least 60° W and 52° N (Needler and Heath, 1975; Bower et al., 2002). The LSW is a denser water mass characterized by a broad salinity minimum and high DO concentrations (Read, 2000). It is centered upon approximately 1500 m, although its exact density varies inter-annually with changes in convection depth in the Labrador Sea (Yashayaev, 2007).

In the lower bathyal range (2000–3000 m), the main water masses are those that have overflowed the Greenland-Scotland Ridge. The main locations for dense overflow are south of the Faroes and between Greenland and Iceland (Hansen et al., 2016; Jochumsen et al., 2017). These overflow waters are cool, dense and well oxygenated, and together with the less dense LSW exit the subpolar gyre as North Atlantic Deep Water (NADW).

The densest water mass in the North Atlantic, found at abyssal depths (>3000 m), is Antarctic Bottom water (AABW). This water mass is easily identified by its high silicate concentration (McCartney, 1992). Whilst it is more prevalent in southern areas, a diluted form is also seen in the eastern subpolar basins (Van Aken and De Boer, 1995; New and Smythe-Wright, 2001).

WATER MASS PROPERTIES AS DRIVERS OF DEEP-SEA BIODIVERSITY AND BIOGEOGRAPHY

Marine biodiversity at the global-scale, shows decreasing biodiversity with both increasing depth (Rex et al., 2006; Roberts et al., 2009b; Costello and Chaudhary, 2017) and increasing latitude (Rex et al., 1993; Lambshead et al., 2000; Gage, 2004). These patterns have been usually related to the decreasing organic carbon flux to the seafloor (Willig et al., 2003; Rex et al., 2005) and to decreasing water temperature at depth (Lambshead et al., 2000). These different trends in biodiversity and distribution

are commonly driven by the physical, chemical, and biological properties of the water masses (e.g., Levin et al., 2001; Mohn et al., 2014; Yasuhara and Danovaro, 2014; Buhl-Mortensen et al., 2015; Eigaard et al., 2016). However, the strong collinearity among water mass properties and depth, make it very difficult to discern the roles of hydrostatic pressure and other depth-correlated parameters (Mortensen et al., 2001; Lundsten et al., 2010). For instance, *L. pertusa* reefs off Norway occur in waters as shallow as 50 m; with it being impossible to determine whether temperature (up to 10°C) or salinity (down to 32) limit the upper bathymetrical distribution (Mortensen et al., 2001). Therefore, assertions on the potential controls of deep-sea species distributions should be taken with caution (Huff et al., 2013). In addition, the relative importance of these factors varies between taxa and regions, but also with the spatial and temporal window of observation (Buhl-Mortensen et al., 2015; Radice et al., 2016). Temperature is usually one of the leading factors at the global scale and over longer time scales (Watling et al., 2013; Yasuhara and Danovaro, 2014; Buhl-Mortensen et al., 2015), whereas at medium spatial scales (10 s of km), the presence of large geomorphological features and biological structures is significant (Henry and Roberts, 2007; Buhl-Mortensen et al., 2010). Substrate typology and food supply appear more important at finer spatial scales (m to km; Vetter and Dayton, 1998; McClain and Barry, 2010; Collart et al., 2018) and over shorter time scales (Yasuhara and Danovaro, 2014).

In fact, observations of deep-sea biodiversity actually showed a wide variability of trends with depth or latitude, from increases (e.g., polychetes, bivalves, and foraminifera; Sanders, 1968; Allen and Sanders, 1996; Olabarria et al., 2005), decreases or irregular trends (e.g., gastropods Stuart and Rex, 2009), to no relationship with depth or latitude (e.g., asteroids, Price et al., 1999) depending on the taxa considered (Gage, 2004; Stuart and Rex, 2009; Costello and Chaudhary, 2017). These trends can also result from other factors, such as large-scale environmental heterogeneity imposed by topography, bottom currents, and strong variations in nutrient input (Willig et al., 2003; Kendall and Haedrich, 2006), or oxygen minimum zone impingement (Levin and Gage, 1998; Rogers, 2000).

This variability in controls of deep-sea species distribution illustrates the complexity of large-scale patterns in deep-sea biodiversity and the difficulty of interpreting them as the product of a single mechanism (Lambshead et al., 2000; Danovaro et al., 2009; Costello and Chaudhary, 2017). Chronic under-sampling of the deep-sea (Ramirez-Llodra et al., 2010) frustrate efforts to obtain a comprehensive broad scale snapshot of the spatial distribution of biodiversity and prevents the full characterization of species distributional ranges. This renders the extraction of biogeographic patterns difficult (Costello and Chaudhary, 2017), where species richness, isolation and endemicity are also likely to play important roles (McClain and Hardy, 2010; Moalic et al., 2012; Watling et al., 2013; Costello and Chaudhary, 2017). For instance, broad faunal distributions across ocean-basin scales have been described for some soft-bottom taxa inhabiting the vast abyssal plains (Smith et al., 2006). However, large scale distributions (Van Dover et al., 2002; McClain, 2007; Clark et al., 2010) and genetic homogeneity (McClain and Hardy, 2010; Teixeira et al., 2013) have also been observed for several endemic species from highly patchy and specialized environments, such as hydrothermal vents and seamounts. In addition, the published information on the effect of water mass properties in the deep-sea megabenthic communities heavily relies on the responses of the most studied organism, the reef-forming CWC *L. pertusa.* Due to the imbalance level of information available among the different taxa, caution should be exercise since the responses of *L. pertusa* might not be necessarily representative of other less- or unstudied taxa.

Sea Temperature

The relative spatio-temporal stability of water temperature below ∼1000 m depth, has historically led to this factor receiving less attention as a possible control of deep-sea biodiversity (Yasuhara and Danovaro, 2014). However, it is likely that stability makes deep-sea organisms highly sensitive to small temperature changes, as evidenced by significant temperature–diversity relationships detected in several studies (Danovaro et al., 2004; O'Hara and Tittensor, 2010; Yasuhara and Danovaro, 2014). Temperature might be the most important factor shaping recent large-scale biodiversity patterns (at least at the alpha diversity level) due to different physiological tolerances of deep-sea taxa (Tittensor et al., 2010; Yasuhara and Danovaro, 2014). Over a broad range of temperatures, the response of deep-sea diversity is unimodal with a peak at around 5–10°C (Yasuhara and Danovaro, 2014). Nevertheless, the responses to temperature at species level are widely variable and usually related to the life-history traits. For instance, the response might be size dependent as observed for the mussel *Bathymodiolus azoricus.* The thermal niche in this species is broader for intermediate sizes than for small or large mussels (Husson et al., 2017). Overall, small species with very short generation times from days to months, such as nematodes (Danovaro et al., 2004), react strongly and rapidly to temperature changes but also may adapt to such changes through generations. In contrast, large taxa with longer generation times of years, such as mollusks, corals or echinoderms (Rowe et al., 1992), might in general be more resilient to the effects of rapid changes, but then may be unable to adapt over short time scales (Yasuhara and Danovaro, 2014).

Thermal boundaries and optimal temperature seem to be mainly species-specific in deep-sea taxa. The distribution of the reef-forming CWCs *L. pertusa* and *Madrepora oculata,* 4–12°C (Freiwald, 2002; Davies and Guinotte, 2011; Naumann et al., 2014), match the temperature range of cold intermediate North Atlantic waters below the summer thermocline. These conditions are generally found in relatively shallow waters (50–1000 m) at high latitudes, and at great depths (up to 4000 m) at low latitudes (Roberts et al., 2006, 2009b). Some deep-sea octocorals, like *Radicipes gracilis*, *Acanella arbuscula* and *Acanthogorgia armata*, can be found at lower temperatures, 1.5–6.1°C (Buhl-Mortensen et al., 2015). However, thermal ranges also vary intra-specifically between populations inhabiting different geographic regions. For example, *L. pertusa* is commonly found between 12.5 and 14°C in the Mediterranean Sea (Tursi et al., 2004; Freiwald et al., 2009). Likewise, *M. oculata* can temporarily tolerate temperatures up to 20°C in the Indian Ocean (Keller and Os'kina, 2008).

Species-specific tolerance, together with the magnitude and time of exposure to increased temperatures, are determinant for the response of the deep-sea organisms as observed in their natural environment (Guihen et al., 2012; Mienis et al., 2014), as well as in experimental conditions (Dodds et al., 2007; Naumann et al., 2014). For instance, a natural increase of 4°C in 24 h (up to 12°C) was observed at Tisler reef (Norway) followed by a mass mortality event of the sponge *Geodia baretti*, although it did not affect the *L. pertusa* reef despite exceeding its typical physiological temperature limit (Guihen et al., 2012). However, a subsequent *ex situ* experiment exposing the same sponge to acute thermal conditions (up to 5°C above ambient temperature for 14 days) did not induce any mortality (Strand et al., 2017). These results suggest that other processes (e.g., low oxygen concentrations, elevated nutrients levels, reduced salinity and disease) in combination with the heat wave could be responsible for the mortality event in those sponges. The upper temperature limit for *L. pertusa* is around 15°C but, it can survive short term (24 h) temperature spikes up to 20°C as demonstrated in aquaria experiments (Brooke et al., 2013). Temperature changes have a strong effect on CWC metabolism, with a specific acclimation among taxa. Experimental research proved that *L. pertusa* has a greater capacity to change its respiratory metabolism and acclimatize to decreased temperature (from 12 to 6°C) than *M. oculata* (Naumann et al., 2014). The different thermal tolerances have been also used to explain the dominance of *M. oculata* in warmer Mediterranean waters and *L. pertusa* in colder regions of the NE Atlantic. However, *L. pertusa* also forms important reefs off SE USA and the Gulf of Mexico (Reed et al., 2006; Brooke and Schroeder, 2007; Mienis et al., 2012a; Georgian et al., 2014), highlighting also the importance of different geographic populations (Brooke and Schroeder, 2007; Georgian et al., 2014; Brooke et al., 2017). The scleractinian CWC *Dendrophyllia cornigera* also reduced respiration and calcification rates when temperature was experimentally lowered to 8°C (Gori et al., 2014). The physiological performance of this species increased when elevating temperatures from 12 to 17.5°C, while that temperature change negatively impacted other CWC species such as *Desmophyllum dianthus* (Naumann et al., 2013). Indeed, *D. cornigera* seems to be absent from most of the NE Atlantic, where temperatures range from 5 to 10°C (Purser et al., 2013; Dullo et al., 2008; Roberts et al., 2009a).

In addition, temperature might trigger more important effects on deep-sea biota in combination with other factors or stressors (synergies), such as ocean acidification, low food availability, or reduced oxygen (e.g., Lunden et al., 2014; Gori et al., 2016; Büscher et al., 2017).

Salinity and Density

Overall, salinity only varies up to one unit worldwide at deep depths, but some biogeographic areas of distinct salinity can be identified in the main basins (Watling et al., 2013). In the North Atlantic, the most saline waters are those carried in the upper column, the Gulf Stream, and in the MOW northward spreading into the eastern Atlantic (**Figure 1**). In contrast, salinity becomes more uniform in the deepest waters below 3500 m, with some influence of upper water layers down to 2000 m depth (Watling et al., 2013). Salinities up to 800 m depth in the northernmost areas of the NW Atlantic show much lower values due to the influence of ice cover (Watling et al., 2013). For instance, glacial meltwater has had a large impact on freshwater inputs to the NW Atlantic, where increasingly large seasonal fluxes have been observed (Belkin, 2004).

The occurrence of CWCs in the NE Atlantic has been correlated in some areas with water density, a parameter defined by salinity and temperature (Dullo et al., 2008; Davies et al., 2010). Living *L. pertusa* reefs were firstly delimited to a narrow water density envelope (potential density; σ_θ = 27.35–27.65 kg m^{-3}), which further studies in other North Atlantic regions proved to be larger than initially suggested (σ_θ = 27.1–27.84 kg m^{-3}; Davies et al., 2010; Huvenne et al., 2011; Kenchington et al., 2017). This highlights the importance of physical conditions for CWCs growth and distribution, and the role of intermediate water masses limiting these boundaries (Mortensen et al., 2001; Bryan and Metaxas, 2006). Another example is the presence of a peak in the number of deep-sea taxa in the depth range (800–1300 m) where MOW is often found (Schönfeld and Zahn, 2000), with variations in near-bottom MOW current strength linked to abundance variability (Zenk and Armi, 1990).

Salinity changes during larval stages of benthic organisms are likely to significantly affect their survival rates (Pechenik, 1999). Although this topic is scarcely investigated, experimental work conducted with *L. pertusa* demonstrated that larvae can survive at salinities as low as 25 for long periods of time (up to 10 months) and cope with changes in salinity of up to five units (Strömberg and Larsson, 2017). Vertical migration of *Lophelia* larvae were also observed in aquaria (Strömberg and Larsson, 2017), suggesting that in nature, *Lophelia* larvae may migrate to the surface, where they would likely be exposed to a wide range of salinities and water densities and may cross water mass boundaries (Strömberg and Larsson, 2017). In contrast, other experiments with shallow water invertebrates (e.g., mussels, starfish, and sea urchins) revealed that the presence of haloclines inhibit larvae vertical migration (Sameoto and Metaxas, 2008). Thus, this high plasticity to salinity gradients and the great longevity of *L. pertusa* larvae could facilitate the wide geographical dispersal range and distribution for this species. Whether this versatility is shared by other deep-sea species due to selective pressure for broad scale dispersal remains to be investigated and could shed light on the role of currents and water masses on connectivity patterns.

Currents and Food Supply

Food availability is one of the main drivers related to the occurrence, distribution abundance and diversity of deep-sea taxa (Tittensor et al., 2011; Pape et al., 2013; Pusceddu et al., 2016). The vertical flux of organic matter from surface waters to the sea floor (∼1–10 g *C* org·m^{-2}·yr^{-1}; Glover and Smith, 2003; Watling et al., 2013) is the principal food source for most of the deep-sea organisms below 200 m (Davies et al., 2009; Wagner et al., 2011). For instance, the carbon of CWCs skeletons is mainly derived from this surface organic carbon (Griffin and Druffel, 1989; Sherwood et al., 2005; Roark et al., 2009).

Food particles are also transported laterally by advective fluxes, facilitating the expansion in the distribution of deep-sea taxa to areas not located beneath regions with high primary production (Davies et al., 2009; Mienis et al., 2009; Hebbeln and Wienberg, 2016). Thus, the occurrence of deep-sea benthic suspension feeders, such as CWCs and sponges, is frequently associated with highly hydrodynamic environments (Mohn et al., 2014). These areas are characterized by strong current velocities, with ∼15 $cm{\cdot}s^{-1}$ on average (Duineveld et al., 2007; Davies et al., 2009; Mienis et al., 2012b; Khripounoff et al., 2014) but peaking up to 80 $cm{\cdot}s^{-1}$ (Davies et al., 2009), that enhance particle suspension (Mienis et al., 2007; Roberts et al., 2009a; White and Dorschel, 2010; Khripounoff et al., 2014; van Haren et al., 2014) and prevent burial by sediments (White et al., 2005; Roberts et al., 2006; Mienis et al., 2007). Cold-water corals in particular seem to prefer areas with periodically varying flow speeds (Ruggeberg et al., 2007; Davies et al., 2009; Mienis et al., 2012a; van Haren et al., 2014), which allow high food supply during the peak current period and high capture rates under low flow (Purser et al., 2010; Orejas et al., 2016). To maximize encounter rates with food particles, CWCs can adjust their colony morphologies to face into the prevailing bottom current (Mortensen and Buhl-Mortensen, 2004; Roberts et al., 2009a). Intensified hydrodynamics are also associated with unique current patterns, such as recirculation gyres, or topographically steered currents like water cascading in submarine canyons (Canals et al., 2006; Palanques et al., 2006; Mulder et al., 2012; Khripounoff et al., 2014), and collision of water masses against seamounts (Genin and Dower, 2007; White et al., 2007a; Lavelle and Mohn, 2010). These areas are usually hot-spots for CWCs and sponges (Thiem et al., 2006; Rowden et al., 2010; Huvenne et al., 2011; Wagner et al., 2011; Howell et al., 2016; Serrano et al., 2017a).

The boundaries between water masses can also help to redistribute and pump the suspended food particles to deeper ecosystems (White et al., 2005, 2007b). Internal waves can occur at the interface of two water masses with different densities as well as along the pycnocline (Dorschel et al., 2007; Mienis et al., 2007; Wienberg et al., 2009; Pomar et al., 2012). For example, coral mounds in the Campeche Bank (Gulf of Mexico) were formed only during interglacial periods when an interface between the AAIW and the Tropical Atlantic Central Water existed; since during glacial ones this boundary was replaced by a vertically homogeneous water column (Matos et al., 2017). Similarly, fossil records of coral mounds at the Porcupine Seabight (NE Atlantic) indicate that mound aggradation was active when the boundary between MOW and ENACW was at a similar depth level as the mounds (Raddatz et al., 2014). While current coral mounds are located in the permanent thermocline between these two water masses (De Mol et al., 2005; White and Dorschel, 2010). Occurrence of conspicuous concentrations of deep-sea sponge grounds (Rice et al., 1990; Klitgaard et al., 1997) and *L. pertusa* reefs (Frederiksen et al., 1992) have been found on the upper slope all around NW Europe, where the combination of a steep slope with the hydrographic conditions cause internal waves that accelerate local currents (Mienis et al., 2007).

Recent studies showed reciprocal feedback between the occurrence of suspension feeders and the enhancement of food supply in their inhabiting areas. It has been suggested that cold-water sponges transform dissolved organic matter to particulate forms, making it available to higher trophic levels (De Goeij et al., 2013; Cathalot et al., 2015; McIntyre et al., 2016; Rix et al., 2016). In addition, CWC framework and mounds areas have more suspended particles than the surrounding coral rubble or no-reefs areas (Guihen et al., 2013; Cathalot et al., 2015; Soetaert et al., 2016; Van Oevelen et al., 2018).

Carbonate Chemistry

Carbonate chemistry influences marine organisms through its critical role in mediating physiological reactions and determining the availability of carbonate ions required for biocalcification (Pörtner and Farrell, 2008; Doney et al., 2012). Deep waters are characterized by low pH, resulting from microbial degradation of organic matter, and low concentrations of carbonate ions (Wenzhöfer et al., 2001; Perez et al., 2018). Therefore, deep-sea calcifying organisms, such as, corals, mollusks, echinoderms and bryozoans, may be particularly sensitive to changes in carbonate chemistry (Guinotte et al., 2006; Doney, 2009; Wicks and Roberts, 2012). Calcium carbonate minerals in the oceans occur mainly in the form of aragonite and calcite. Aragonite presents a more resistant structure for high energy environments and it is formed by scleractinian corals, some mollusks and bryozoans. In contrast, calcite is less prone to dissolution and forms the shells and skeletons of foraminifera, echinoderms, crustaceans, calcareous sponges and most gorgonian corals (Ries et al., 2009; Ries, 2010). However, both minerals dissolve at low carbonate ion concentrations. Thus, the distributions of deep-sea ecosystem-engineering organisms with carbonate skeletons, are largely restricted to waters above the carbonate saturation horizon (SH; Guinotte et al., 2006; Davies and Guinotte, 2011; Yesson et al., 2012), i.e., those oversaturated for calcium carbonate minerals. Other calcifying taxa, such as echinoderms, are found throughout the world's oceans, but are far less abundant or even absent in undersaturated waters (Lebrato et al., 2010). The carbonate SH in the North Atlantic is very deep, >2000 m (Guinotte et al., 2006), but still constrains the distribution of multiple deep-sea calcifying organisms.

Ocean absorption of anthropogenic CO_2 has already reduced natural pH values (∼0.12) since the preindustrial time (Hennige et al., 2014) and the calcium carbonate saturation state (Ω; Orr et al., 2005; Perez et al., 2018); affecting particularly the intermediate and deep waters masses (Sweetman et al., 2017). Therefore, multiple studies have already focused on the impacts of ocean acidification (OA) in deep-sea organisms in the last decade.

Experimental OA studies on corals, mollusks and echinoderms, have predominantly showed reduced growth/calcification in response to reduced pH in adults and juveniles (Wicks and Roberts, 2012; Gazeau et al., 2013; Wall et al., 2015). However, responses can be species-specific or even region specific for a given taxa (Ries et al., 2009; Gazeau et al., 2013; Maier et al., 2019). For instance, low pH values (∼7.9–7.7) caused the deformation of skeletons

in the CWC *L. pertusa* (Hennige et al., 2015; Wall et al., 2015). Nevertheless, experimental studies using the CWCs *L. pertusa* and *M. oculata* from the NE Atlantic and the Mediterranean Sea showed that the two species were able to calcify and grow in acidic and undersaturated conditions (Form and Riebesell, 2012; Maier et al., 2013, 2019; Hennige et al., 2014; Büscher et al., 2017). Also, Norwegian populations of *L. pertusa* could maintain growth at low pH with elevating feeding rates (Georgian et al., 2016). In contrast, *L. pertusa* inhabiting low carbonate or undersaturated conditions in the Gulf of Mexico and California showed great reductions in calcification rates and increased skeletal dissolution (Lunden et al., 2014; Georgian et al., 2016; Kurman et al., 2017; Gómez et al., 2018). Thus, resilience to OA effects might be related to adaptation in CWC, either genetic or due to acclimation in early stages (Kurman et al., 2017). The capacity of CWCs to cope with OA has been related to their ability to increase internal pH at the site of calcification (McCulloch et al., 2012a; Raybaud et al., 2017). However, it remains unclear whether calcification can be sustained indefinitely, as this is an energy demanding process (20–30% of CWC energy budget; Cohen and Holcomb, 2009) and OA also affects the coral metabolism (Hennige et al., 2014) and, the loss of the tissue surrounding and connecting polyps (Gammon et al., 2018).

Another important reported consequence of OA is the dissolution of shells and skeletons exposed to corrosive low pH seawater (Rodolfo-Metalpa et al., 2011; Doney et al., 2012). The dissolution effect is more pronounced in dead carbonate skeletons which lack the organic protective tissue, as observed in different mollusk gastropods, CWCs (Tunnicliffe et al., 2009; Rodolfo-Metalpa et al., 2011) and tissue-free portions of skeletons of *L. pertusa* (Hennige et al., 2015; Wall et al., 2015). Therefore, one of the most important predicted consequences of OA is the dissolution and weakening of the reef framework that may result in their structural collapse (Hennige et al., 2015; Büscher et al., 2019).

The impact of OA on other ecosystem-engineering organisms, such as octocorals or sponges, is still poorly known. Experimental studies showed a reduction in calcification and growth in *Corallium rubrum* (Cerrano et al., 2013), suggesting that gorgonians may also be negatively affected by OA. However, a study from the Southern Ocean found that, despite some evidences of dissolution in gorgonians, many species thrive in undersaturated conditions to at least −30% without major impacts in skeletal structure or growth rates (Thresher et al., 2011). The long-term acclimation to these conditions and unlimiting food supply are thought to facilitate tolerance of low-carbonate environments (Thresher et al., 2011). Calcareous sponges are expected to suffer similar impacts than other calcifying organisms under acidified conditions. However, most sponges have siliceous spicules and therefore, are generally more tolerant of OA and might even benefit from future acidified conditions (Bell et al., 2018). The silica cycle in the deep ocean is still not well understood (Ragueneau et al., 2000) but the silica flux from surface to deep waters could be strongly affected by OA (Petrou et al., 2019). However, the dissolved silica from the spicule mats formed by the sponges might be enough to build their new skeletal material (Chu et al., 2011; Maldonado et al., 2017, 2019). The very few studies on the impacts of OA in calcareous sponges, mainly included shallow water species and short-term responses (Goodwin et al., 2014; Morrow et al., 2015; Bates and Bell, 2018; Bell et al., 2018). Despite the high tolerance to OA reported (Goodwin et al., 2014; Morrow et al., 2015), species- specific differences were found (Bell et al., 2018) resulting in negative impacts on some sponges such as, mortality, tissue degradation (Bates and Bell, 2018) or changes in the associated microbial community (Bell et al., 2018). Bioeroding sponges have been the major focus of the OA studies in this group since they are potentially becoming more efficient under acidified conditions, thereby, accelerating the weakening of CWC reef frameworks (Wisshak et al., 2012, 2014). In addition to its important role in biomineralization/dissolution processes, OA might also lead to mortality, compromised reproduction (Verkaik et al., 2017) and/or the development of early life stages of benthic organisms (Kurihara, 2008; Dupont and Thorndyke, 2009; Byrne, 2011). Although synergic effects of OA and other factors have been seldom studied for deep-sea taxa, the few published studies suggest a great susceptibility of CWCs species to OA in combination with warming and/or deoxygenation, with decreased metabolic and calcification rates, increased skeletal dissolution, and induced mortality (Lunden et al., 2014; Georgian et al., 2016; Gori et al., 2016).

Oxygen Concentration

Most of the global ocean has DO values near saturation, ranging from 2.5 $ml{\cdot}l^{-1}$ off SW Africa to 6 $ml{\cdot}l^{-1}$ in the NW Atlantic (Watling et al., 2013). The highest DO values are generally associated with the colder, deeper, and more recently formed waters since DO solubility decreases with increasing temperatures and is consumed during degradation of organic matter. For instance, a drastic drop in DO, from 6.85 to 5.40 $ml{\cdot}l^{-1}$was observed in the Galicia Bank at MOW depths between 800 and 1200 m, which is warmer than the surrounding ENACW and NADW (Wienberg et al., 2009; Serrano et al., 2017a). Indeed, the *L. pertusa* reefs in this area inhabit the MOW-ENACW boundary (Somoza et al., 2014; Serrano et al., 2017a,b). The majority of *L. pertusa* colonies found in the North Atlantic coincide with a range of relatively low to moderate DO values (∼1.5–5 $ml{\cdot}l^{-1}$), which occurs between 300 and 1600 m water depth (Davies et al., 2010; Somoza et al., 2014; Brooke et al., 2017).

Most organisms are not very sensitive to variations in DO until it drops below a certain threshold, when they suffer from a variety of stresses related to reduced metabolic rates, leading ultimately to death, if the low oxygen concentrations remain for too long (Keeling et al., 2010). Thresholds for hypoxia vary greatly between marine taxa (Vaquer-Sunyer and Duarte, 2008), but when concentrations are above 1 $ml{\cdot}l^{-1}$, effects on mega- and macrobenthic diversity are probably minor (Levin and Gage, 1998).

Hypoxic and anoxic conditions are common in all oceans (Kamykowski and Zentara, 1990), varying from permanent zones to gradients over geologic time (Reichart et al., 1998; Ramirez-Llodra et al., 2010), seasonally varying areas (Guihen et al., 2018) or episodic events (Rogers, 2000; Levin, 2018). These different temporal scales drive different adaptations and tolerance levels in benthic taxa. Extensive permanent hypoxic zones, where oxygen is limiting for living organisms (Levin et al., 2001; Stramma et al., 2010), occur at midwater regions (100–1200 m depth), being present in the Atlantic only in the south basin, off Namibia and Angola (Hebbeln et al., 2017; Hanz et al., 2019). These oxygen minimum zones (OMZs; 0.2–0.5 ml·l^{-1}) are formed by microbial degradation of organic matter beneath highly productive waters (Levin et al., 2001). For the bathyal fauna in the Atlantic, hypoxia might have more influence on species richness, while organic matter regulates species distribution and community evenness (Levin and Gage, 1998). Thus, within OMZs the mega- and macrofauna exhibit low species richness and very high dominance, but dense aggregations at the edges, where high organic matter fluxes and still suitable DO levels may occur (Levin, 2003). While annelid species are prevalent in the OMZ cores (Rogers, 2000; Soltwedel, 2000; Levin et al., 2001; Ramirez-Llodra et al., 2010), taxa with calcified shells or exoskeletons, such as echinoderms, crustaceans and mollusks, tend to be absent (Rogers, 2000). Benthic organisms inhabiting OMZs maximize the oxygen uptake through morphological and physiological adaptations, such as: raised ventilation rates, increased respiratory surfaces, reduced diffusion distances, development of respiratory pigments, vertical migrations, or enzymatic adaptation to anaerobic metabolism (Levin, 2003). OMZs may also present a barrier, disrupting species distribution or isolating populations across the inhospitable waters (Rogers, 2000). Thus, oxygen exerts tremendous control on marine biodiversity mostly through thresholds effects on evolution, physiology, reproduction, behavior, and species interactions (Levin and Le Bris, 2015).

However, living colonies of calcified organisms such as the CWCs *L. pertusa* and *M. oculata* have been found in South Atlantic OMZs at DO levels of 0.6 and 1.1 ml·l^{-1}, respectively (Hebbeln et al., 2017; Hanz et al., 2019), drastically reducing the previous limiting DO levels obtained by modeling and experimentation (2.37 ml·l^{-1}; Dodds et al., 2007; Davies et al., 2008). The effect of hypoxia on the occurrence of *L. pertusa* when food supply is high enough is difficult to be determined (Levin and Gage, 1998; Freiwald, 2002; White et al., 2005; Roberts et al., 2006). Nevertheless, recent studies in these OMZs suggest that CWCs and the associated fauna may compensate unfavorable conditions induced by low DO and high temperatures with an enhanced food availability (Hanz et al., 2019). Experimental research revealed that *L. pertusa* maintains constant rates of oxygen consumption over a range of DO concentrations, and colonies are able to survive short-time periods of anoxia (1 h) and hypoxia (up to 96 h; Dodds et al., 2007). However, both oxygen consumption and survivorship are sensitive to temperatures (6.5–9°C; Dodds et al., 2007). Indeed, oxygen consumption of *L. pertusa* at 11°C was 50% higher than that recorded at 9°C (Dodds et al., 2007). Complete mortality of *L. pertusa* nubbins has been observed at DO levels of 1.5 ml·l^{-1}and 14°C (Lunden et al., 2014).

DEEP-SEA BENTHIC ECOSYSTEMS SHAPED BY THE NORTH ATLANTIC WATER MASSES

The biodiversity of VMEs and the biogeographical affinities in deep-sea benthic communities can vary over space and time due to regional and basin-scale changes in the oceanographic conditions. On one hand, this section discusses local scale effects through examples of how key water masses and oceanographic processes affect VMEs at particular locations of the North Atlantic. On the other hand, we also provide a larger scale overview of the distribution of the main VMEs at a basin-scale and the critical roles of water masses in the species distribution, connectivity, endemicity and biodiversity patterns. We mainly focused on ecosystem-engineering organisms such as CWC and sponges, but more information on VME records across the North Atlantic can be found in the open access databases of multiple international organizations related to scientific, management and conservation purposes (e.g., ICES, NOAA).

Cold-Water Coral Reefs and Gardens

Cold-water corals have a global distribution (Tittensor et al., 2009; Yesson et al., 2012), being particularly well described throughout the North Atlantic in both eastern (e.g, Roberts et al., 2009a; Foubert et al., 2011; Buhl-Mortensen and Buhl-Mortensen, 2014; Serrano et al., 2017b) and western basins (e.g., Reed et al., 2006; Brooke and Schroeder, 2007; Buhl-Mortensen et al., 2015; Hourigan et al., 2017). Aggregations of CWCs have previously been described as either "reefs" or "coral gardens" (OSPAR, 2008). Coral gardens can consist of very different species and groups of corals inhabiting the seafloor in close spatial proximity (Rossi et al., 2017), and are very often found to be dominated by gorgonians, bamboo corals (Octocoral, Alcyonacea) and/or black corals (Hexacorallia, Antipatharia; ICES, 2007; OSPAR, 2008). Their flexible skeletons and the arborescent vertical development of many of these species give them the appearance of "animal forests" (Rossi et al., 2017). In contrast, Scleractinians (also known as stony corals) often occur at relative high densities or develop reefs with multigenerational growth that might produce sizable calcium carbonate structures over time (Rossi et al., 2017). There are few scleractinian CWCs that build reefs and *L. pertusa*, being one of the main reef-building organisms in the deep-sea (**Figure 2**), is the most ubiquitous and studied species in the North Atlantic. Overall, the distribution of CWCs have been mainly correlated with water temperature and highly hydrodynamic areas (e.g., Frederiksen et al., 1992; Davies et al., 2009; Buhl-Mortensen et al., 2015). In particular, *L. pertusa* reefs are present in waters with salinities higher than 34 and temperatures between 4 and 12°C, corresponding to depths as shallow as 100 m at high latitudes (Mortensen et al., 2001; Dullo et al., 2008; Buhl-Mortensen et al., 2015) but down to 1200 m in other continental margins

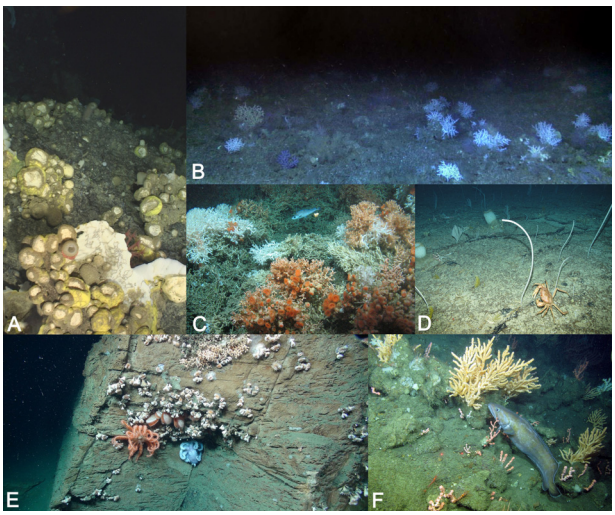


FIGURE 2 | Images showing the diversity of Vulnerable Marine Ecosystems, including cold-water coral reefs, coral gardens and sponge grounds, at different locations across the North Atlantic Ocean. **(A)** Astrophorid sponge ground typical of the Davis Strait area (2500 m), credit: Department of Fisheries and Oceans, Canada. **(B)** Cold-water coral reef dominated by *Madrepora oculata*, with scarce colonies of *Lophelia pertusa* and black corals (*Antipathes dichotoma*) at Gazul mud volcano (380 m, northern Gulf of Cadiz), credit: Instituto Español de Oceanografía, INDEMARES project. **(C)** *Lophelia pertusa* reef from Logachev Mounds (600 m, Rockall Bank), credit: J.M. Roberts, University of Edinburgh (Changing Oceans Expedition 2012, RRS James Cook cruise 073). **(D)** Coral garden formed mainly by *Narella versluysi* and *N. bellisima* with some Hexactinellid sponges (1000 m) in the Formigas seamount (Azores), credit: MEDWAVES, ATLAS project. **(E)** Cup corals (*Desmophyllum dianthus*), *Solenosmilia variabilis*, bivalves (*Acesta cryptadelphe*), a brisingid seastar (*Novodinia* sp.), and an octopod in a consolidated mud wall (1300 m) at Norfolk Canyon, credit: Steve Ross. **(F)** Coral garden of white and red *Paragorgia arborea* in Baltimore Canyon (430 m), credit: Steve Ross.

(De Mol et al., 2002) and canyons (De Mol et al., 2011; Hourigan et al., 2017; van den Beld et al., 2017).

The MOW seems to represent one of the main water masses driving the distribution of CWCs across the NE Atlantic (Dullo et al., 2008; Somoza et al., 2014), promoting connectivity by the natural export of Mediterranean species and populations (Henry et al., 2014; Arnaud-Haond et al., 2017; Boavida et al., 2019). Several studies noted the presence of deep-sea suspension feeding species previously known only from the Mediterranean (e.g., the sponges *Geodia anceps*, *Coelosphaera cryosi,* and *Petrosia raphida*) at NE Atlantic locations, such as the Gulf of Cadiz (Spain; Palomino et al., 2016; Sitjá et al., 2018). This area is dominated by aggregations of scleractinians and gardens of large gorgonians and black corals (e.g., *M. oculata, Acanthogorgia* spp., *Antipathes dichotoma, Leiopathes glaberrima;* **Figure 2**) with particular locations, such as Gazul mud volcano, representing a biodiversity hotspot with more than 400 associated species (Rueda et al., 2016; Ramalho et al., 2018; Sitjá et al., 2018). The current distribution of living *L. pertusa* and *M. oculata* in the canyons of the Bay of Biscay coincides with the lower limit of the boundary between the ENACW and the MOW (De Mol et al., 2011), as does the distribution of carbonate mounds and CWC reefs in the Porcupine Seabight (De Mol et al., 2002, 2005; White and Dorschel, 2010) and other contourite systems in the NE Atlantic (Van Rooij et al., 2007a,b; Hernández-Molina et al., 2009). Indeed, the intensification of currents and the increased flow of MOW into the NE Atlantic after the last glacial period, mentioned in the previous section, is thought to have allowed Mediterranean CWCs to recolonize the Porcupine Seabight (De Mol et al., 2005; Henry and Roberts, 2008; Henry et al., 2014). This hypothesis was also supported by genetic data for *L. pertusa* (Henry et al., 2014; Boavida et al., 2019). It may also hold true for *M. oculata*, although this species shows a more complex pattern of genetic differentiation. This suggests multiple refugia at the origin of the post-glacial recolonization of the NE Atlantic, as well as stronger present day barriers to connectivity (Boavida et al., 2019).

Biogeographic regions or affinities are also related to water mass properties (McClain and Hardy, 2010; Watling et al., 2013). Faunistic communities in the Galicia Bank (NW Spain) encompass Macaronesian, Mediterranean, NE and NW Atlantic species, due to the confluence of different intermediate and deep water masses in the area (Ruiz-Villarreal et al., 2006; Cartes et al., 2013). The afore mentioned turbulent ENACW-MOW boundary might allow the transport of coral larvae along the NE Atlantic margins (Somoza et al., 2014). At the Mid Atlantic Ridge, the Azores region hosts an exceptional biodiversity of CWCs (**Figure 2**), mostly gorgonians (75% of the octocoral species of European waters), with a greater affinity to the Lusitanian-Mediterranean biogeographic region (71% shared species) and to a lesser extent to the NW Atlantic (Braga-Henriques et al., 2013; Sampaio et al., 2019). The presence of multiple intermediate and deep water masses (NACW, subpolar origin waters, MOW, AAIW, NADW; Johnson and Stevens, 2000; Amorim et al., 2017) along the slopes of many seamounts are hypothesized to shape composition and bathymetrical distribution of coral gardens in the Azores (Braga-Henriques et al., 2013). Braga-Henriques et al., 2013 reported maximum Antipatharian diversity at 400–500 m coinciding with the cold and less dense NACW; whilst the maximum diversity of Alcyonacea (e.g., *Viminella flagellum*, *D. meteor*, *Callogorgia verticillata,* and *A. armata*) occurs at 500–600 m coinciding with the less saline subpolar-origin waters. The maximum diversity of Scleractinians (e.g., *Caryophyllia cyathus*, *M. oculata,* and *L. pertusa*) occurs at 500–800 m and for Stylasteridae (e.g., *Errina dabneyi*) at 800–1000 m, which appear to be more diverse and abundant where the saltier and warmer MOW waters occur. It should be noticed, however, that this pattern was based mostly on corals collected as bycatch from longline fishing.

In the NW Atlantic, a *L. pertusa* reef was recently discovered in the Davis Strait area (Kenchington et al., 2017) on a steep slope with relatively stable bottom temperature, the highest salinities at intermediate depths (800–900 m) and exceptional persistently high currents of >15 cm s^{-1} at 1000 m. Signals of consistent vertical and horizontal transport over the reef area likely arose through a combination of local convection from the surface and advection of cooled and freshened waters at depth from the Irminger Sea to the east (Kenchington et al., 2017). Further

to the south, in the Flemish Cap, biodiversity patterns of trawl caught invertebrates, including CWCs, were associated with the intensity of long-term trawling effort (NAFO, 2018). But also, the presence of the warmer NAC supports higher diversity in Flemish Cap areas under the influence of this water mass (NAFO, 2018). Whether the NAC supports higher diversity only by warming the bottom water or also through the northward transport of larvae from richer biogeographic regions in the south remains unclear.

Finally, the Gulf Stream mainly influences the oceanography of much of the southern part of the NW Atlantic, delimiting a biogeographic latitudinal boundary between warm-temperate and cool-temperate regions, particularly in the vicinity of Cape Hatteras (offshore North Carolina, United States). This is a transition region for many faunal groups, particularly fish and corals, which reach their southern and northern limits in this area (Ross and Quattrini, 2007; Obelcz et al., 2014; Csa Ocean Sciences et al., 2017). Off Nova Scotia (Canada) and the Mid-Atlantic Bight (United States), CWCs occur (Buhl-Mortensen et al., 2015; Csa Ocean Sciences et al., 2017) mainly in areas influenced by warm southwestward meanders of the Gulf Stream (Mienis et al., 2014). Similarly to the NE Atlantic, *L. pertusa* re-established at ∼7 kya in the NW Atlantic, in the Cape Lookout area (offshore North Carolina, United States), after a glacial period (Hebbeln et al., 2019). Ocean surface productivity and deep-sea temperatures reached interglacial levels several thousand years earlier, but did not facilitate *L. pertusa* to return to this area. Only the dramatic increase of the hydrodynamics ∼7 kya was likely to have enabled the return of this CWC (Matos et al., 2015). The intrusion of the Gulf Stream into the upper slope and the consequent increase of food supply is assumed to have promoted the re-establishment of *L. pertusa* (Matos et al., 2015; Hebbeln et al., 2019).

Deep-Sea Sponge Grounds

An intriguing feature of invertebrate communities in the deep-sea of the North Atlantic is the occurrences of large-sized (massive) sponges which form distinct habitats referred to as sponge grounds. One of the first reports of these habitats was by Rice et al. (1990), who observed dense aggregations (density values ∼1.5 ind·m^{-2}) of the hexactinellid *Pheronema carpenteri* (**Figure 2**) in the Porcupine Seabight (NE Atlantic). Subsequently, records of sponge grounds came both from the eastern (e.g., Klitgaard and Tendal, 2004; Howell et al., 2016; Roberts et al., 2018; Kazanidis et al., 2019) and western deep North Atlantic (e.g., Murillo et al., 2012, 2016a, 2018; Knudby et al., 2013; Kenchington et al., 2014; Beazley et al., 2018). These included records not only of hexactinellids, but also of demosponges and especially those from the family Geodidae (Order Astrophorida, commonly known as *ostur*; **Figure 2**). Specifically, extensive studies in the NE Atlantic by Klitgaard and Tendal (2004) revealed two types of *ostur*: firstly, a boreal *ostur* dominated by *G. barretti*, *G. macandrewi*, *G. atlantica*, *Isopsphle graei*, *Stryphnus ponderosus,* and *Stelletta normani* found at the Faroe Islands, Norway, Sweden, Barents Sea, and Iceland. Secondly, a cold water *ostur* characterized by the same genera but represented by different species, i.e., *G. mesotriaena*, *I. graei pyriformis,* and *S. rhaphidiophora* found north of Iceland, Denmark Strait, East Greenland, and north of Spitzbergen. Cárdenas et al. (2013) supported the observations of boreal and arctic species of geodids put forward by Klitgaard and Tendal (2004) and extended the description to the full North Atlantic.

The species composition of deep-sea sponge grounds in the NW Atlantic, from Davis Strait to Flemish Cap (Murillo et al., 2012, 2016b, 2018), is similar to the boreal sponge grounds described by Klitgaard and Tendal (2004) for the NE Atlantic, while arctic astrophorids are found in southern Baffin Bay (Murillo et al., 2018). Dense aggregations of a globally unique population of the glass sponge *Vazella pourtalesii* is found on the Scotian Shelf over large spatial scales (Beazley et al., 2018). Glass sponges are also common on the walls of submarine canyons in the Mid-Atlantic Bight (Csa Ocean Sciences et al., 2017). In contrast, glass sponge grounds formed by *P. carpenteri* form extensive aggregations in the NE Atlantic. Further south in the NE Atlantic, the Gorringe Bank (SW off Portugal coast) is a hotspot for demosponge fauna (Xavier and Van Soest, 2007). The influence of the Azores current and the MOW in this area and the presence of several seamounts, allows the presence of demosponge assemblages with a wide Atlanto – Mediterranean distribution (61%) together with highly endemic (28%) species (Xavier and Van Soest, 2007).

Hydrography plays an important role in shaping the distribution of these dense sponge grounds, and several authors have noted the association of sponges with particular water masses due to their temperature and salinity characteristics or the hydrodynamic conditions, such as tides and internal waves, which enhance the food supply (Bett, 2001; Klitgaard and Tendal, 2004; Murillo et al., 2012; Beazley et al., 2015, 2018; Roberts et al., 2018; Davison et al., 2019; Kazanidis et al., 2019). For example, in the continental margin offshore of Newfoundland (eastern Canada), there is evidence for a relationship between dense sponge aggregations with a warm (∼3.0–3.5^{o}C), and salty (∼34.85–34.90), water mass that occurs between ∼1300 and 1723 m depth and is thought to be a remnant of the Irminger Current (Beazley et al., 2015). Modeling work to predict the presence of deep-sea sponge grounds concluded that depth and bottom minimum salinity were major predictors of the distribution of sponge grounds in these areas (Knudby et al., 2013). As in the Flemish Cap area, boreal geodiid species in Davis Strait and Baffin Bay (NW Atlantic) were associated with the presence of water transported in the Irminger Current (**Figure 1**), while the Arctic geodiids were associated with Baffin Bay Deep Water between 1200 and 1800 m depth, and Baffin Bay Bottom Water > 1800 m. This association of boreal sponge grounds with Irminger Water in the areas mentioned above, points to it being a major determinant of distribution, with the NAC and its branch, the Irminger Current, providing a connectivity pathway between the NE and NW Atlantic (Bersch et al., 1999), potentially explaining the basin-scale distribution of some of these species. As the NAC and Irminger Currents (**Figure 1**) are integral to the AMOC (Cuny et al., 2002), any changes in this circulation may impact the distribution of deep-water sponges. Interestingly, geodiid sponge grounds off the Flemish Cap and Grand Banks have persisted for the last 130 kya (Murillo et al., 2016a), despite large shifts in water mass structure alternating between the warmer Atlantic waters and the cooler Labrador

Current. Murillo et al., 2018 further noted that the structure-forming *Geodia* species were found in areas with high primary production and fast currents that would provide the high food supply needed to reach their large biomasses. The importance of current regime and interactions between water masses has also been shown for the Faroe-Shetland Channel deep-sea sponge aggregations (Kazanidis et al., 2019), the Arctic sponge ground on the Schultz Seamount (Arctic Mid-Ocean Ridge; Roberts et al., 2018) and deep-sea aggregations of hexactinellids in the NE Atlantic (Rice et al., 1990; Barthel et al., 1996).

FUTURE WATER MASS PROPERTIES IN THE NORTH ATLANTIC

The occurrence of CWCs reefs and gardens (Mortensen et al., 2001) and sponge grounds (Murillo et al., 2012; Beazley et al., 2015; Howell et al., 2016) have been tightly related to water mass properties and circulation (e.g., Davies et al., 2009; Mohn et al., 2014; Kenchington et al., 2017; Lacharité and Metaxas, 2018) as well as the forcing of climate conditions such as glacial periods, the presence and strength of fronts, etc. (e.g., Frank et al., 2011; Montero-Serrano et al., 2011; Hebbeln et al., 2019). However, climate models forecast that anthropogenic climate change will modify circulation patterns and fluxes, energy flow and water mass properties of the Atlantic Ocean by 2100 (Mora et al., 2013; Rahmstorf et al., 2015; Sweetman et al., 2017; Osman et al., 2019). A 25% weakening of the AMOC is predicted, and although a collapse of the AMOC is thought unlikely, it has not been excluded (Schmittner, 2005; Liu et al., 2018; Thornalley et al., 2018). The deep ocean is already experiencing changes in physical and chemical properties due to warming, OA or deoxygenation, which are predicted to impact deep-sea ecosystems (Levin and Le Bris, 2015; Johnson et al., 2018).

Based on the projections of Mora et al. (2013); Sweetman et al. (2017), and Morato et al. (2020), which used all available data generated by Earth System Models (Earth System Grid Federation, 2019), we reviewed the forecasted changes in the water mass properties at the seafloor in the deep North Atlantic (20°–70° N and 78° W–10° E). Namely, we evaluated how potential temperature at the seafloor (°C), particulate organic carbon (POC) flux at 100 m depth (mg $C{\cdot}m^{-2}{\cdot}d^{-1}$), DO concentration at the seafloor ($ml{\cdot}l^{-1}$) and pH at the seafloor, and were forecasted to change from 1951 to 2000 (historical simulation) to 2081–2100 (RCP8.5 or business-as-usual scenario). The POC flux at the seafloor was calculated was calculated based on CIMP5 ocean biogeochemical nutrient–phytoplankton–zooplankton– detritus models (Fu et al., 2016) and the Martin curve (Martin et al., 1987) with an export depth set to 100 m. Forecasted changes in aragonite and calcite **Ω** at the seafloor, as described in Morato et al. (2020), were also evaluated here. The multimodel averages of the projections of water mass properties based on all available Earth System Models ensure the highest possible precision and accuracy of the predictions (Mora et al., 2013). Further details of projections and model performance can be found in Mora et al. (2013). It is important to note that the business-as-usual scenario is the IPCC worst-case scenario where greenhouse gas emissions, world population growth and technology development (Riahi et al., 2011) continuously increase. Consequently, the projected future water mass properties are the most extreme forecasts and present greater uncertainty than other intermediate scenarios. Nevertheless, these forecasts and their possible consequences for VMEs in the North Atlantic are critical for decision-makers for the development of long-term sustainable management plans (Rheuban et al., 2018).

Global warming due to the influx of CO_2 to the atmosphere increased ocean temperatures both in surface and deep waters (Purkey and Johnson, 2010; Levitus et al., 2012). The average global temperature of the upper ocean (0–2000 m) has already warmed by ∼0.09°C between 1955 and 2010 (Levitus et al., 2012). Recent climate models forecast an average 0.76°C temperature increase at bathyal depths but with no major changes in the abyss by 2100 (**Table 1**). However, some northern areas of the North Atlantic will experience an increase in temperature >1°C or >2°C (**Figure 3**), with the largest increases in temperature in the upper and intermediate bathyal layers (**Table 1**). In contrast, a large bathyal area between the Azores and Iceland has been forecasted to experience a decrease in seafloor temperatures of ∼0.7°C (**Figure 3**). This is one of the few areas in the world's oceans where seafloor temperatures are predicted to decrease instead of increase.

Enhanced warming of the upper ocean, stratification and OA is expected to reduce the export flux and quality of POC that reaches the seafloor (Smith et al., 2008; Jones et al., 2014; Sweetman et al., 2017). On average, most of North Atlantic bathyal seafloor is not currently food limited (POC flux > 10 mg $C{\cdot}m^{-2}{\cdot}day^{-1}$; **Table 1** and **Figure 3**). However, the POC flux is predicted to decrease by 2100 up to 40% in the continental margins and critically to reduce by >50% in the central-eastern Atlantic (**Figure 3**).

The deep North Atlantic is the most alkaline of the world oceans (Sweetman et al., 2017) with present-day pH values ranging on average from 7.91 to 8.14 (**Figure 4** and **Table 1**). Model predictions indicate that pH at the seafloor will further decrease by ∼0.2 in the bathyal zone, with smaller changes in the abyss (**Figure 4** and **Table 1**). The greatest reduction in pH (>0.3) is expected at higher latitudes (**Figure 4**) in waters shallower than 1000 m, as a result of the subduction of high-CO_2 waters via the AMOC (Gehlen et al., 2014; Sweetman et al., 2017; Perez et al., 2018).

Large decreases in the carbonate **Ω** have been predicted worldwide (Orr et al., 2005), with severe changes in the North Atlantic (Perez et al., 2018). Present-day aragonite **Ω** in the North Atlantic varies greatly with depth (**Figure 4**). In general, bathyal depths are supersaturated, while abyssal areas are undersaturated (**Table 1**). However, aragonite **Ω** is expected to decrease by ∼32% above 3000 m depth and by ∼8% at the bathyal seafloor (**Table 1**). Thus, most of the deep North Atlantic will become undersaturated in aragonite by 2100 (**Figure 4**). On average, the aragonite SH will shoal by ∼800 m to depths of around 3000 m in the western North Atlantic, and by ∼1500 m to depths of 2000 m in the central and eastern North Atlantic (**Figure 4**). Shoaling will be greater

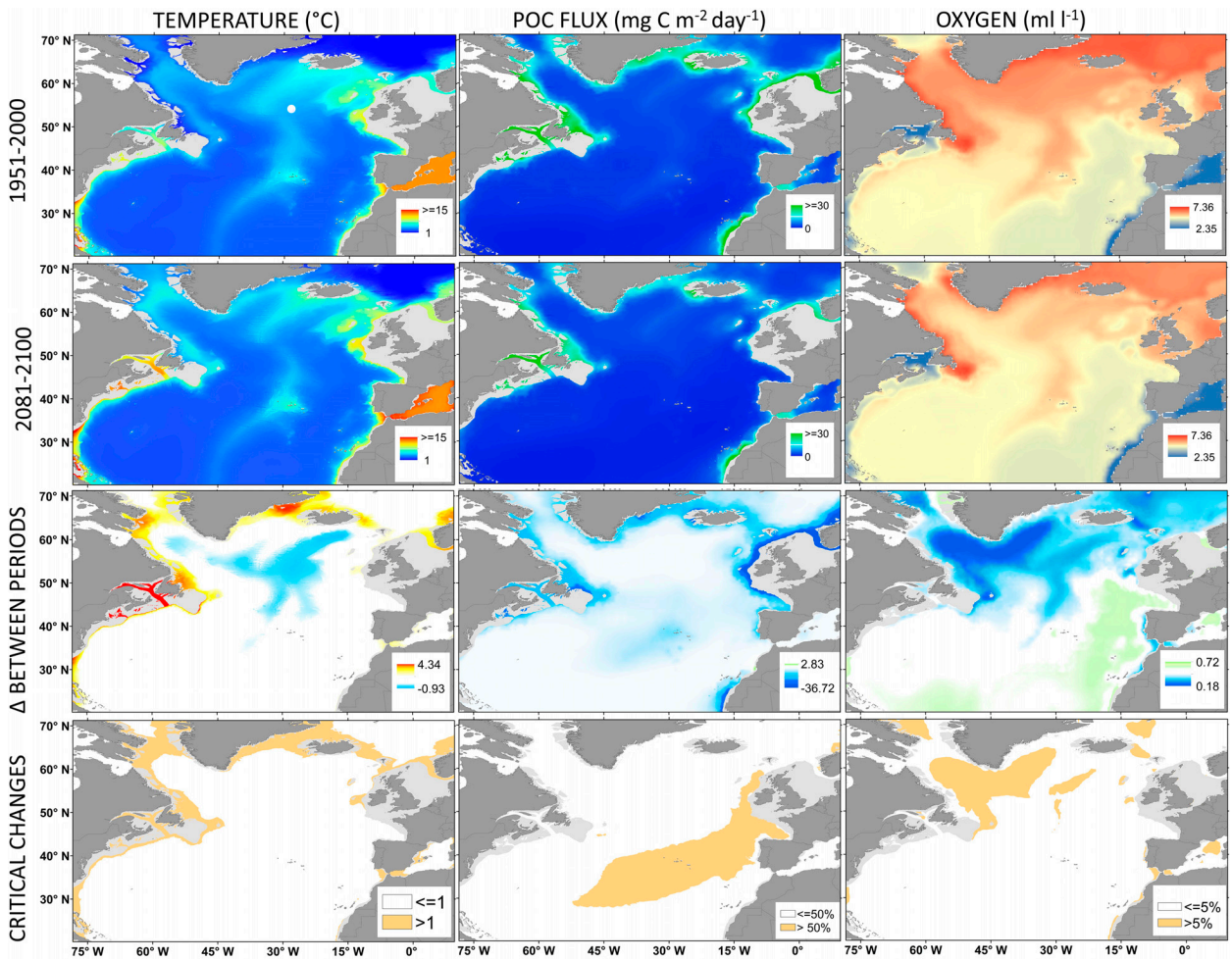


FIGURE 3 | Present and future scenarios predicted for temperature, particulate organic carbon (POC) flux and dissolved oxygen at the seafloor in the North Atlantic Ocean. Changes, as increment (Δ) between periods, were measured as the difference between present-day and the modeled conditions by 2100. Areas with critical changes in the values of a given water mass property are highlighted.

in the northernmost areas moving aragonite SH to depths as shallow as 200 m. Areas deeper than 3000 m will experience smaller changes (**Figure 4**). Most of the North Atlantic seafloor is also currently supersaturated in calcite, except for areas below 5000 m (**Table 1** and **Figure 4**). Similar reductions are expected for calcite **Ω** in the bathyal and abyssal areas, but with most of the seafloor remaining supersaturated. The calcite SH will shoal to 4500 m in the southernmost parts of the North Atlantic (**Figure 4**).

Ocean warming also causes the loss of DO in ocean waters, through reduced solubility, intensified biological respiration, and increased stratification of water masses (Keeling et al., 2010; Levin, 2018). The open ocean has already lost on average 2% of DO since the preindustrial era, particularly in intermediate waters between 100 and 1000 m depth (Stramma et al., 2010; Bopp et al., 2013; Levin, 2018). Model simulations forecast that most of the seafloor below 200 m is currently well oxygenated (>5 ml·l^{-1}; **Figure 3** and **Table 1**). A slight decrease of ∼5% in both abyssal and bathyal zones is expected by 2100 (**Figure 3** and **Table 1**). A maximum decrease of 10% in DO will occur in northernmost areas (**Figure 3**), but no moderately (∼1.5 ml·l^{-1}) or severely (< 0.5 ml·l^{-1}) hypoxic conditions are expected in the North Atlantic in the future.

RISKS AND IMPACTS OF FUTURE ENVIRONMENTAL SCENARIOS IN DEEP-SEA BENTHIC ECOSYSTEMS

The assessment of ecologically critical climate conditions requires an understanding of how climate (i.e., environmental conditions) drives biological responses (see section Water Mass Properties as Drivers of Deep-Sea Biodiversity and Biogeography), forecasts of how climate will change (see section Future Water Mass Properties in the North Atlantic), and an identification of where those critical climate changes will occur (Diffenbaugh and Field, 2013). To contribute to this discussion, we built maps

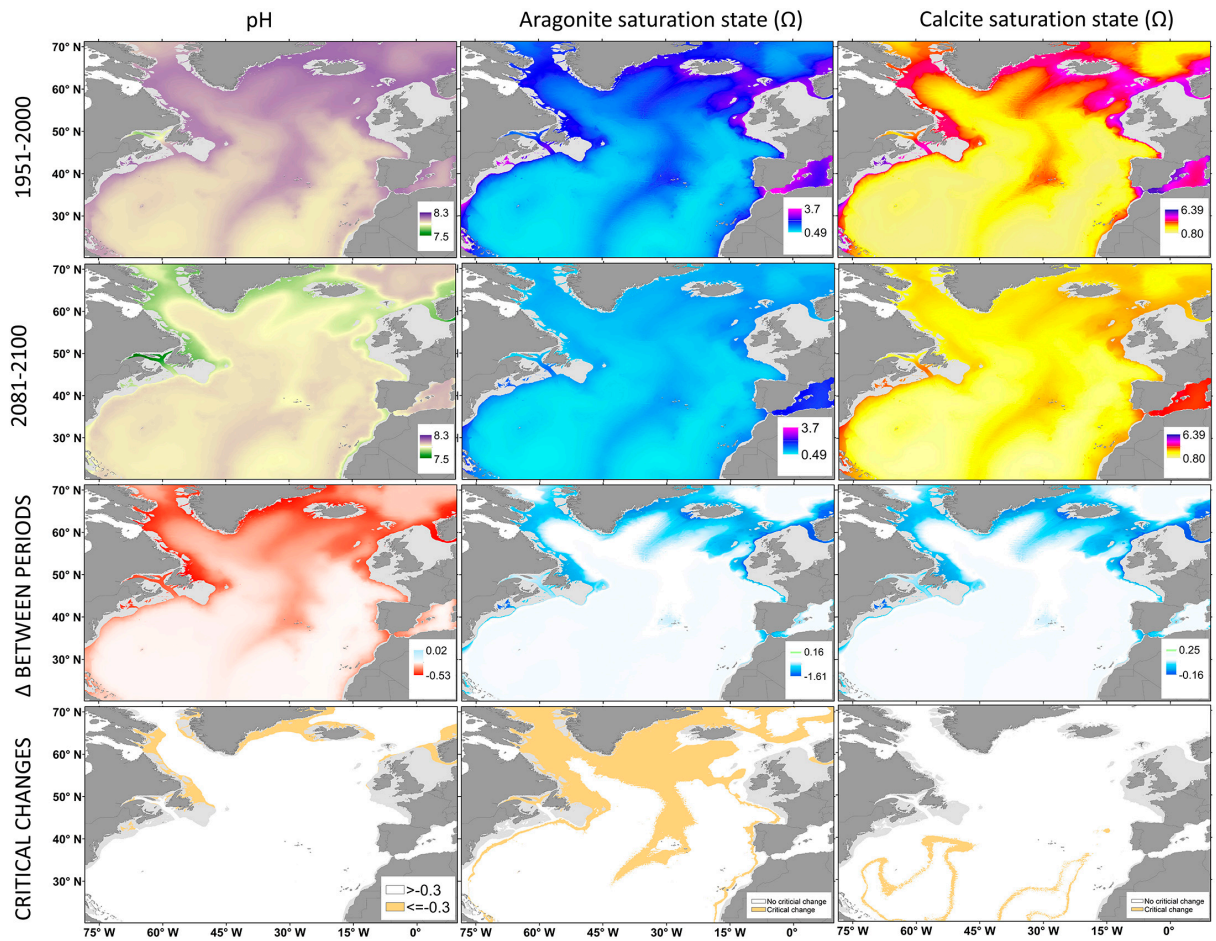


FIGURE 4 | Present and future scenarios predicted for pH and aragonite and calcite saturation states at the seafloor in the North Atlantic Ocean. Changes, as increment (Δ) between periods, were measured as the difference between present-day and the modeled conditions by 2100. Areas with critical changes in the values of a given water mass property are highlighted.

of cumulative critical changes. Cumulative critical changes were assumed to be (1) temperature increases >1°C (**Figure 5A**) or >2°C (**Figure 5B**; IPCC, 2014), (2) POC flux reductions >40% (**Figure 5A**) or >50% (**Figure 5B**; Mora et al., 2013; Sweetman et al., 2017), (4) pH reductions >0.3 (IPCC, 2013), and (4) new areas where aragonite and (5) calcite saturation was reduced to levels <1 (Caldeira and Wickett, 2003; Orr et al., 2005). Two values of critical changes were adopted for temperature and POC flux reduction because of the uncertainty about the degree of change that is critical for the survival of deep-sea benthic communities. Maps of cumulative critical changes were produced by identifying how many of the five water mass properties will change to the afore mentioned critical water mass properties at a certain cell. Most abyssal areas of the North Atlantic are forecasted to experience critical environmental changes affecting deep-sea benthic biodiversity (**Figure 5**). Northern areas, such as the Labrador Sea, Davis Strait and Western Greenland, will experience critical changes of pH, aragonite saturation and temperature (**Figure 5**). The NE Atlantic region close to the Bay of Biscay will experience changes in aragonite, pH, and POC flux. Several regions will also experience critical changes of at least two parameters. A large area of the Azores is expected to present critical changes in aragonite saturation and POC flux, while the NW Atlantic will face critical changes in aragonite saturation or temperature (**Figure 5**).

Climate models forecast that the deep seafloor at high latitudes of the North Atlantic is likely to experience warming of 2°C. Despite many CWC reefs occurring in these regions, temperature is not expected to exceed the range (4–12°C) where *L. pertusa* is generally found in the North Atlantic (Gass and Roberts, 2006; Roberts et al., 2009b), nor exceed the mortality temperatures reported, >14°C (Brooke et al., 2013; Lunden et al., 2014). Warming is more likely to impact CWCs living close to their upper temperature limit of physiological tolerance (e.g., Gulf of Mexico; Brooke et al., 2013; Lunden et al., 2014, and the Mediterranean Sea; Gori et al., 2016). In addition to increased average temperatures, marine heat waves are already becoming more frequent under climate change conditions (Frölicher et al., 2018), causing devastating impacts on marine ecosystems and/or even mass mortality

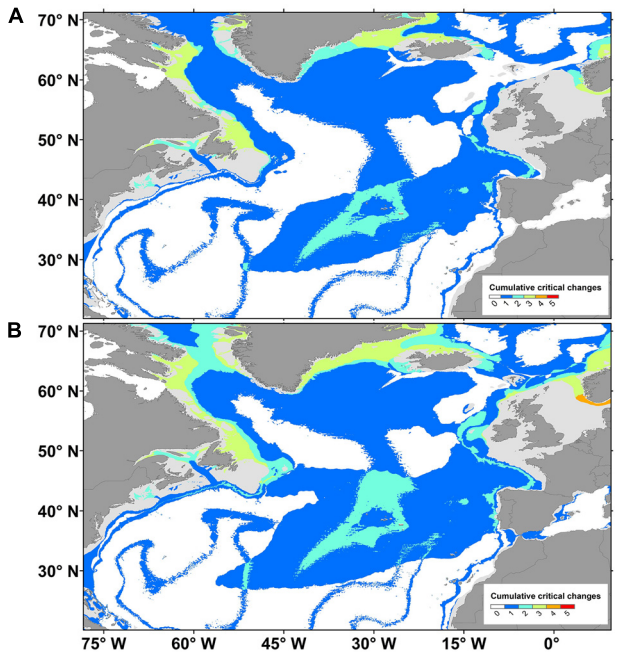


FIGURE 5 | Predicted cumulative critical changes in seafloor conditions in the North Atlantic Ocean by 2100. Critical conditions include temperature increase of **(A)** >1°C or **(B)** >2°; particulate organic carbon (POC) flux reduction of **(A)** >40% or **(B)** >50%; pH reduction >0.3 and aragonite and calcite saturation levels <1. Dissolved oxygen will not likely achieve hypoxic conditions values <1.5 ml·l^{-1} in 2100 so it was not included.

events (Guihen et al., 2012; Cavole et al., 2016; Frölicher and Laufkötter, 2018). Despite the tendency of marine heatwaves to mainly propagate in surface waters, they might impact deep-sea ecosystems as well, particularly in the northernmost areas of the North Atlantic, where CWCs and sponges inhabit shallower waters due to the colder conditions.

Some scleractinian CWC species are able to calcify and grow under warmer conditions (Δ 3–4°C), even when combined with acidified waters (Hennige et al., 2014; Büscher et al., 2017; Maier et al., 2019). However, the energetic cost of these process in such conditions may diminish other biological and physiological processes, or prevent sustained growth over long-term periods (Dodds et al., 2007; Hennige et al., 2015). This is particularly true when combined with aragonite undersaturation and low food conditions. Thus, the resilience of CWCs to warming and acidification may be reduced in areas with limited food (McCulloch et al., 2012b), compromising coral metabolism and even the survival of corals (Maier et al., 2016).

The predicted shoaling of the aragonite SH is expected to lead to a loss of suitable habitat for slow-growing reef-forming CWC species (Davies and Guinotte, 2011; Perez et al., 2018), which are commonly found at aragonite SH depth at present-day (Guinotte et al., 2006; Davies and Guinotte, 2011). According to model simulations, during the pre-industrial period, 87% of CWC reefs were surrounded by aragonite oversaturated waters, while projections for 2100 suggest that around 73% of these reefs will suffer from undersaturated waters (Guinotte et al., 2006; Zheng and Cao, 2014). Scleractinian CWCs in the NE Atlantic are predicted to be particularly vulnerable to OA since they are mainly formed by aragonite, with 75% of CWCs below 1000 m being exposed to aragonite undersaturated waters by 2060 under the "business as usual" RCP 8.5 scenario (Perez et al., 2018). According to climate models forecasts, northern areas within the Reykjanes Ridge below 1000 m and Davis Strait and western Greenland as shallow as 200 m may be exposed to corrosive (i.e., aragonite understaturated) waters in the future. Despite the apparent physiological resilience of CWCs to OA, how OA or the high energetic cost for adaptation will affect other important physiological processes, such as reproduction, is still unknown. The long-term survival of reefs may be impaired by the chemical dissolution and biological erosion of the unprotected tissue of the reef framework exposed to corrosive waters (Hennige et al., 2015; Schönberg et al., 2017; see also section Water Mass Properties as Drivers of Deep-Sea Biodiversity and Biogeography). The balance between construction and erosion processes ultimately determines if the reef will grow or recede (Schönberg et al., 2017). Shifts toward net negative balances may lead to loss of reef growth potential, reef structural collapse, and diminished ecosystem service provisioning such as nutrient cycling, carbon storage and habitat provision, with severe consequences such as the loss of biodiversity associated with these ecosystems (Rossi et al., 2019).

This shoaling of aragonite undersaturated waters and the resultant reduction of habitat suitability for *L. pertusa* in the NW Atlantic due to OA can also have important consequences on the connectivity pathway between the NW and NE Atlantic populations (Kenchington et al., 2014). However, most of the large living CWCs reefs and banks on the Atlantic coast of USA occur in waters shallower than 1000 m depth and some in the NE Atlantic above 200 m (e.g., Mingulay reef complex, Rockall Bank on the UK continental shelf, CWC reefs on the Norwegian shelf), which will not be subjected to corrosive waters. Thus, those might provide a refuge for important habitat-building species such as *L. pertusa* in the North Atlantic. The conservation of these VMEs within Marine Protected Areas (Johnson and Kenchington, 2019) where for example trawling is banned, provides additional support to ensure the long-term survival of these habitats under regional predictions of 85% CWC loss due to aragonite SH shoaling for this area of the NE Atlantic (Jackson et al., 2014). Deep-sea ecosystems in more southerly locations of the North Atlantic (e.g., Cape Cod, the Azores or the Bay of Biscay) are located above the aragonite SH shoaling depths predicted for 2100 and will thus be protected from corrosive waters. However, as suggested from several experimental studies, reduction of pH even continuing within supersaturated water, might also negatively impact CWCs and gorgonians growth (Maier et al., 2009; Bramanti et al., 2013; Gómez et al., 2018).

The model forecasting suggests large reductions in POC fluxes in areas where shoaling of the aragonite SH and warming is also expected, including Iceland, Greenland and Eastern Canada, where the northernmost populations of *L. pertusa* are found. This will likely reduce the biogeographic distribution of this reef-forming species. The reductions in POC can have extreme effects in areas such as the Azores, where food availability is already

limited (Jones et al., 2014). In particular, seamount features, such as the many seamounts in the northern Mid-Atlantic Ridge, are projected to experience large declines in POC fluxes and benthic biomass (Jones et al., 2014). Global projections of changes in POC export associated with other climate change effects suggest CWC ecosystems will suffer the greatest declines in benthic biomass and biodiversity and as a consequence, in ecological functioning and services provided (Jones et al., 2014; Armstrong et al., 2019).

REMARKS FOR THE FUTURE

With the potentially significant future changes in ocean water masses and circulation, deep-sea VMEs, such as the CWC reefs, gardens and sponge grounds found in the North Atlantic, are very likely to experience a dramatic loss of species diversity and population densities. However, many knowledge gaps remain in the biological processes and oceanographic dynamics in the deep-sea. Critical information for predicting tipping points, adaptation or resilience are still unknown for most of the deep-sea benthic organisms at species, population, and community-level processes (Hebbeln et al., 2019). An improved understanding of these drivers would help enable us to more clearly identify and describe the various impacts of climate change. It will also help us to understand the risks and how to mitigate them better, e.g., where we need to be more precautionary in terms of economic development of marine resources, where we may need to step up investment in monitoring and management, or how to establish efficient conservation strategies to preserve these fragile and precious deep-sea ecosystems.

The loss in biodiversity will potentially reduce severely the ecosystem resilience to both climate change adaptation and mitigation. Despite of the socio-political pressures for increasing the exploitation of marine resources, the deep-sea VMEs which are more likely to be impacted by multiple stressors are unlikely to withstand these additional pressures from human activities. Multiple interactive stressors imposed by global climate change and anthropogenic activities will impair the biological impacts and responses beyond the influence of any single variable (Hofmann et al., 2010; Büscher et al., 2017). Therefore, the backdrop of climate change will narrow the margins for safe ecological and thus operational limits of existing and emerging ocean industries over the next century. Further, most of the areas currently closed to protect VMEs in the North Atlantic will be impacted by climate change (Johnson et al., 2018) and will require monitoring and reconsideration of boundaries in future. Beyond marine spatial planning, regulatory frameworks and conservation actions, the blue economy should adopt precautionary approaches so as not to further push living marine resources beyond their tipping points and to ensure sustainable development.

AUTHOR CONTRIBUTIONS

PP, CO, L-AH, and MC-S designed the structure of the manuscript. PP coordinated, supervised, and wrote the manuscript. C-LW developed the projections of future environmental conditions for the deep North Atlantic. TM, JG-I, and MC-S downscaled future projections and designed critical changes. All authors were substantially involved in the literature search and writing of the different sections of the manuscript, contributed to the final product in significant ways, and provided approval for publication.

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Physical Connectivity Between the NE Atlantic Seamounts

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Within the Portuguese Exclusive Economic Zone, the Great Meteor and Madeira-Tore complexes are highly productive areas, which are likely to be classified as marine protected areas (MPAs) due to their ecological vulnerability. This was the main focus of the BIOMETORE project and, framed on it, the aim of the present study was to investigate the physical connectivity between both seamount complexes. Using the HYbrid Coordinate Ocean Model coupled with the Connectivity Modeling System (CMS) (a Lagrangian tool), a series of experiments was conducted in order to determine the influence of the main oceanographic phenomena governing the area in: (i) the origin of the particles that reach each complex, (ii) their capacity to capture and retain incoming particles, and (iii) the physical connectivity between them as well as the intra-connectivity within each seamount system. Due to the geographical location of both groups of seamounts, the Azores Current (AzC) and its associated eddies were identified as the main transport pathways, its influence being stronger at intermediate waters and decreasing with depth. Notwithstanding, the Great Meteor and the Madeira-Tore were mainly affected by the AzC southward and eastward branches, respectively, resulting in a non-significant connectivity between the two groups. Meanwhile, the inter-connectivity between seamounts slightly varied with depth at the Great Meteor complex while increasing at Madeira-Tore. In addition, the Plateau, Irving, and Cruiser (PIC) seamounts from the Great Meteor complex and Gorringe and Coral from the Madeira-Tore complex proved to incorporate the regional connectivity routes. Although containing the three smallest seamounts, Madeira-Tore showed the higher capturing capacity per square kilometer, highlighting the influence of the "sticky water effect." In the Great Meteor complex, the "seamount effect" seems to be the main phenomenon responsible for the greater retention and self-recruitment abilities of these seamounts. The presented results provide valuable information for the design of a MPA to preserve these vulnerable habitats.

Keywords: Lagrangian transport, drifting particles, physical connectivity, seamounts, northeast Atlantic Ocean

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INTRODUCTION

Seamounts are wide and prominent underwater features of volcanic or tectonic origin that occur mainly around mid-ocean ridges, island-arc areas, and above mantle plumes (Etnoyer et al., 2010; Staudigel and Clague, 2010; Wessel et al., 2010). The size of the seamount is an important factor to consider and is usually defined by their height or relief (Kitchingman et al., 2007). According

to Pitcher et al. (2007), elevations higher than 1,000 m are defined as large seamounts, whereas small seamounts are within the range of 100–1,000 m. Recent studies have estimated that the total number of large seamounts (>1,000 m) worldwide varies between 25,000 and 140,000, whereas small ones (100–1,000 m) are more abundant, approximately between 125,000 and 25 million (Wessel et al., 2010; Yesson et al., 2011). Nevertheless, seamount abundances can vary considerably, depending on the methodology applied and the definition of a seamount (Wessel et al., 2010). Despite this uncertainty, most authors highlight seamounts as one of the world's major (underwater) biomes (Etnoyer et al., 2010).

Seamounts are characterized by high productivity and food availability, being considered hotspots for several benthic and pelagic communities, although this is not true for all seamounts as their distinct morphological and oceanographic features may alter biodiversity and productivity patterns (Morato et al., 2016). The productivity of seamounts is closely related to their shallowness since the interaction between the topographical and the physical features (e.g., internal tides) enhances the vertical movement (upwelling) of nutrients toward the euphotic zone (Tuerena et al., 2019). If the local biomass production is sustained long enough, it will allow the transfer of energy to higher trophic levels. Otherwise, seamounts must rely on outer inputs of organic material to support resident populations (Rogers, 1994; White et al., 2008). Their communities are dominated by suspension feeders, dense aggregations of demersal and benthopelagic fishes, and elevated abundances of zooplankton and micronekton (Clark et al., 2010). Moreover, seamounts are important habitats for species with commercial value since they can create large aggregates that spawn or feed in the vicinity, thus reducing the fishing effort (Clark et al., 2016). However, previous studies showed that seamount-aggregating fishes have higher intrinsic vulnerability to fishing due to their life history attributes, such as slow development, longer lifetime, later sexual maturation, and lower natural mortality (Morato et al., 2006).

Due to the ecological vulnerability of these habitats, the Portuguese government plans to classify the Great Meteor and the Madeira-Tore complexes as marine protected areas (MPAs) under the European Marine Strategy Framework Directive (Jorge et al., 2016). The status of fisheries at Great Meteor seamounts is still unclear, even though evidences of exploratory fishing were found. The fish species most commonly caught in this area are *Macroramphosus scolopax*, *Capros aper*, *Trachurus picturatus*, and *Anthias anthias* (Fock et al., 2002). At the Madeira-Tore complex, the shallower summits of the Gorringe Bank are the main attraction for fishing fleets. The wreckfish *Polyprion americanus* and the European conger, *Conger conger*, are captured during spring and summer, while in autumn and winter the swordfish *Xiphias gladius* and the black scabbard fish *Aphanopus carbo* are the main targeted species (Hermida and Delgado, 2016; Campos et al., 2019). Nevertheless, it seems that these fisheries may have reached their limits of geographic expansion and are already overexploited (Hermida and Delgado, 2016). For this reason, the design of these two new MPAs should help balance the exploitation by fisheries and conserve these seamount habitats (Probert et al., 2007).

For the purpose of MPA design, it is necessary to understand population dynamics and the hydrodynamic processes related to seamounts. During the last years, several studies have been focused on describing seamounts biological communities and assessing patterns of benthic biodiversity and marine biogeography (Fock et al., 2002; Wienberg et al., 2013; Christiansen et al., 2015). Samadi et al. (2006) suggested that the genetic exchange between submarine mountains is more frequent than previously assumed and may be related to the dispersal transport induced by ocean currents. The extent to which populations are connected is also determined by the scale, intensity, direction, and frequency of the dispersal pathways (physical factors) and by the post-settlement mortality, growth, and condition from settlement to successful reproduction (biological factors; Pineda et al., 2007; Etter and Bower, 2015). However, the wide variety of interconnected mechanisms that promote or prevent the movement of individuals and their contribution to the gene pool are still poorly known (Shank, 2010). Recent methodological advances in larval tagging, parentage analysis, and otolith microchemistry shed some light on marine connectivity over relatively short spatial and temporal scales. Nonetheless, these methodologies are very expensive since they require intensive spatial and temporal sampling. On the other hand, biophysical numerical models offer the possibility to track virtual particles over longer spatial and temporal scales. This type of approach will contribute to identify the main physical processes that serve to connect or isolate seamount populations (Shank, 2010) as well as to determine their source–sink relationships (Holstein et al., 2014).

In the northeast Atlantic Ocean, several studies focused on comprehending the oceanographic phenomena, as well as the transport and retention mechanisms, around several Portuguese small islands and archipelagos (e.g., Caldeira et al., 2002; Barbosa-Aguiar et al., 2011; Sala et al., 2013, 2016; Caldeira and Reis, 2017). However, none of them focused on the connectivity between seamount complexes. To better understand how persistent oceanographic features affect the recruitment and the connectivity between Madeira-Tore and Great Meteor seamount populations, our study investigates the physical connectivity patterns in the region. For this purpose, a series of numerical experiments was performed using the Connectivity Modeling System (CMS), an off-line Lagrangian tool, attached to an ocean circulation model (as described in detail in section "Data and Methods"). The results of the different numerical experiments are presented in section "Results," and the general discussion and main conclusions are in section "Discussion and conclusions."

MATERIALS AND METHODS

Study Area and Oceanographic Context

Within the northeast (NE) Atlantic region (**Figure 1a**), the Great Meteor complex is located in the mid-Atlantic ridge, ∼900 km to the south of the Azores, and it is constituted by a series of extinct volcanoes rising from depths greater than 4,500 m to less than 300 m (Beckmann and Mohn, 2002; Geldmacher et al., 2006). The ancient volcanic cones are aligned in a north–south

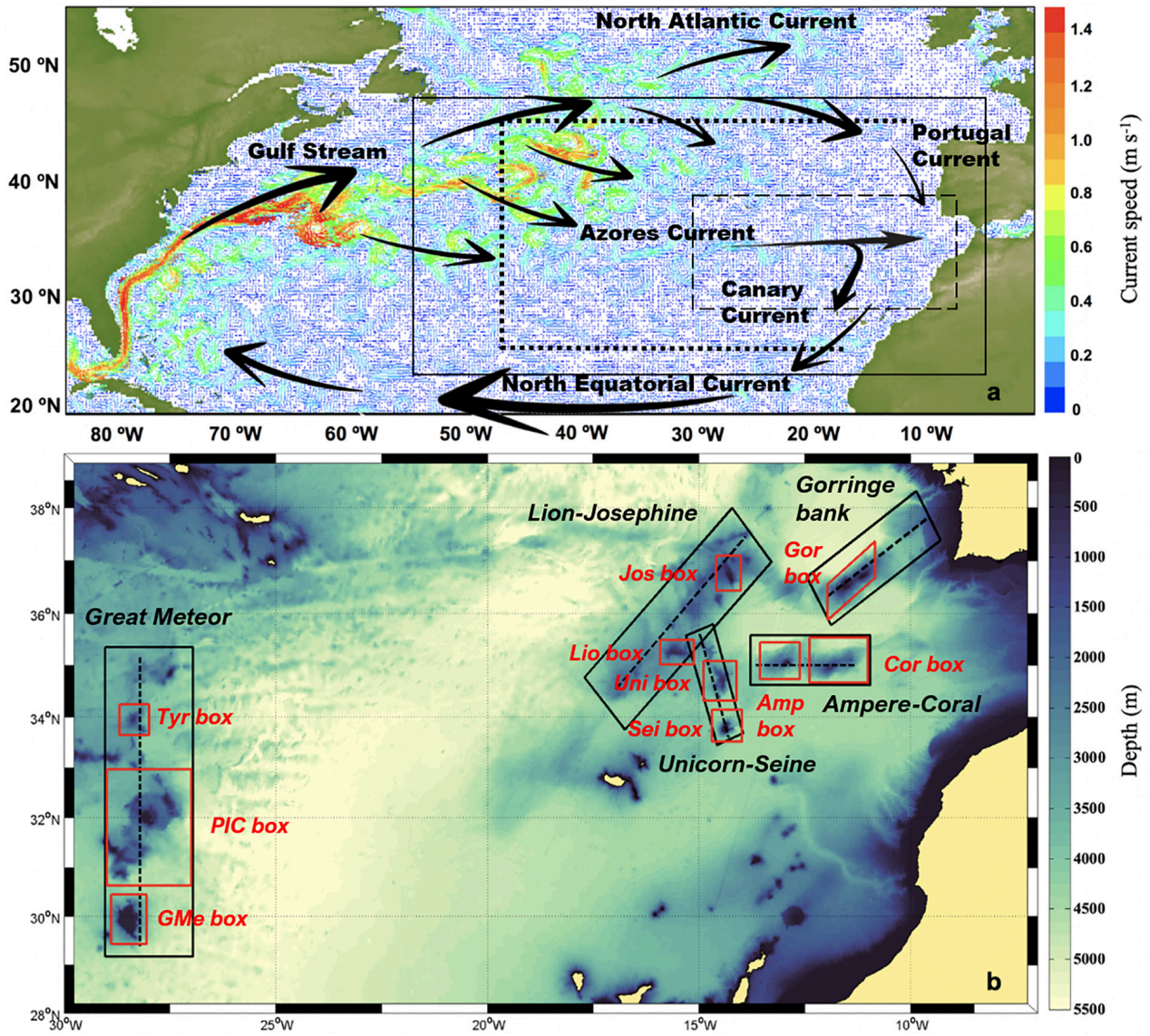


FIGURE 1 | (a) Representative map of the study area that includes the North Atlantic Subtropical Gyre and its associated currents: the Gulf Stream, the North Atlantic Current, the Portugal Current, the Azores Current, the Canary Current, and the North Equatorial Current. The solid line defines the HYCOM domain. The dotted lines represent the release boundaries for the particle retention experiment. **(b)** Zoomed-in view of the area that contains the seamounts under study [the dashed line on panel **(a)**]. The dashed lines represent the release lines for the reverse particle experiment. The black boxes represent the sink boxes for the particle retention experiment. The red boxes represent the connectivity polygons defined for the connectivity study.

orientation. This assembly includes Atlantis, Plateau, Irving, Cruiser, Tyro, Hyères, and the Great Meteor, as well as the smaller Small-Meteor and the Closs bank (**Figure 1b**). In turn, Madeira-Tore complex, located ∼700 km off the northwestern African coast, is a northeast-aligned submarine ridge in the central east Atlantic that rises from more than 4,000 m in water depth to ∼35 m below the sea surface (**Figure 1b**). Several hypotheses have been proposed for its origin (Tucholke and Ludwig, 1982; Morgan, 1983; Peirce and Barton, 1991; Royden, 1993; King and Anderson, 1998), but there is a lack of age and geochemical data (Geldmacher et al., 2006). The complex is composed of the Gorringe bank (with two mountain tops: Gettysburg and Ormonde), Seine, Josephine, Lion, and Unicorn seamounts. The present study is mainly focused on the best-studied groups in this area: Great Meteor, Plateau–Irving–Cruiser (PIC), Tyro, Lion-Josephine, Unicorn-Seine, and Gorringe bank. Additionally, Ampere and Coral seamounts were included due to their proximity to the Madeira-Tore complex.

These deep-sea areas exist in a highly variable oceanographic environment characterized by the prevailing ocean currents and the mesoscale phenomena that result from the interaction of passing ocean flows with the seamount bathymetry. Both

TABLE 1 | Summary statistics, including the correlation coefficient (*r*), root mean square error (RMSE), reliability index (RI), average error (AE), average absolute error (AAE), and the modeling efficiency (MEF), of the sensitivity tests performed throughout the study.

	r	RMSE	RI	AE	AAE	MEF
Particle retention study						
All vs. half of the number of particles	1.00	0.21	1.05	−0.08	0.12	1.00
Connectivity study						
All vs. half of the number of particles (2D)	1.00	0.01	1.08	0.00	0.00	1.00
All vs. half of the number of particles (3D)	1.00	0.01	1.10	0.00	0.00	1.00
Uniform vs. random release event (2D)	0.98	0.03	1.13	0.01	0.01	0.95
Constant vs. random depth (2D vs. 3D)	1.00	0.01	1.11	0.00	0.01	0.99
Model vs. observations						
–	0.93	0.05	1.33	−0.01	0.02	0.85

2D corresponds to 5 m depth and 3D to the depth range of 1–10 m.

complexes, Great Meteor and Madeira-Tore, are affected by the Azores Current (AzC), which is one of the branches of the Gulf Stream (GS) that composes the North Atlantic Subtropical Gyre (**Figure 1a**; Käse and Siedler, 1982; Gould, 1985; Onken, 1992). The AzC splits in one branch that goes into the Gulf of Cádiz (GoC), toward the Strait of Gibraltar, and another that deviates southward, connecting with the Canary Current (CaC; Johnson and Stevens, 2000). The CaC also receives a small contribution from the Portugal Current (PoC; Barton et al., 2001), which spreads in the north–south direction, connecting the North Atlantic Current, the northeastward branch of the GS, and the AzC (Dietrich et al., 1980). This current regime, along with other phenomena such as ocean eddies, internal tides, and variable meteorological forcing, contributes to mesoscale variability and, ultimately, the different connectivity levels occurring between the seamounts (Clark et al., 2010; Barbosa-Aguiar et al., 2011; Caldeira and Reis, 2017). There are two main processes associated to these features: the (i) "island mass effect" (or in this case "seamount effect"; Doty and Oguri, 1956), which is responsible for the enhanced production occurring around small islands/seamounts in comparison to the surrounding waters, and the (ii) "sticky water effect" (Wolanski, 1994), which generates slower mean currents in the surrounding regions of high-density topography such as a coral reef and, on a different scale, a group of seamounts, leading to an increase of larvae recruitment and trapping in the regions of weaker flow (Clark et al., 2010; Lavelle and Mohn, 2010; Sala et al., 2016).

Ocean Model and Lagrangian Tool

In this study, we applied the HYbrid Coordinate Ocean Circulation Model (HYCOM),[1] which is capable of solving the hydrostatic primitive equations in a free surface mode (Bleck, 2002; Chassignet et al., 2007). The US Navy Research Laboratory global solutions (GLBa0.08, experiment 05.8) were used with a horizontal grid resolution of ∼9.25 km (1/12°) and 32 vertical layers. For the *off-line* Lagrangian simulations, data were extracted from a sub-domain encompassing 22° to 47° N in latitude and 55° to 5° W in longitude (solid line in **Figure 1a**).

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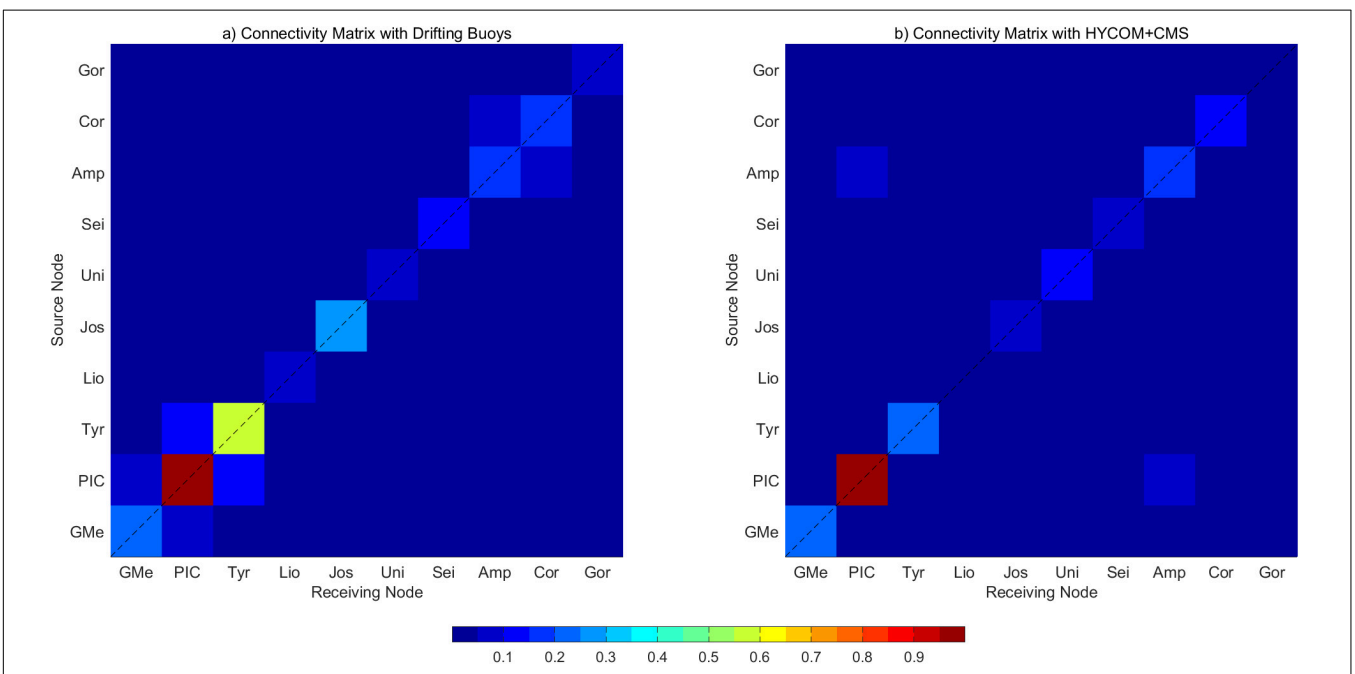


FIGURE 2 | Connectivity matrices computed for the connectivity study area and the time period from 2004 to 2012. **(a)** Connectivity matrix computed with drifting buoys data from CORIOLIS. **(b)** Connectivity matrix computed with HYCOM and CMS.

A 9-year-solution was considered (2004–2012). This model was previously validated by comparison with Argo (global array of temperature/salinity profiling floats) profiles by Sala et al. (2016), who concluded that the model ensures a good representation of the known water masses and the ocean currents in the region.

The Connectivity Modeling System (CMS v2.0; Paris et al., 2013) was used to track passive particle movements. The CMS runs *off-line*, applying the 3D velocity fields (u, v, w) of the ocean circulation model to each particle using a 4th order Runge–Kutta numerical discretization method, applied both in space and time (Van Sebille et al., 2012; Paris et al., 2013). To represent the subgrid-scale motion (physical turbulence effects) unresolved by the model, a value of 2 m^2 s^{-1} for horizontal diffusivity was added (following Sala et al., 2016). No vertical diffusivity

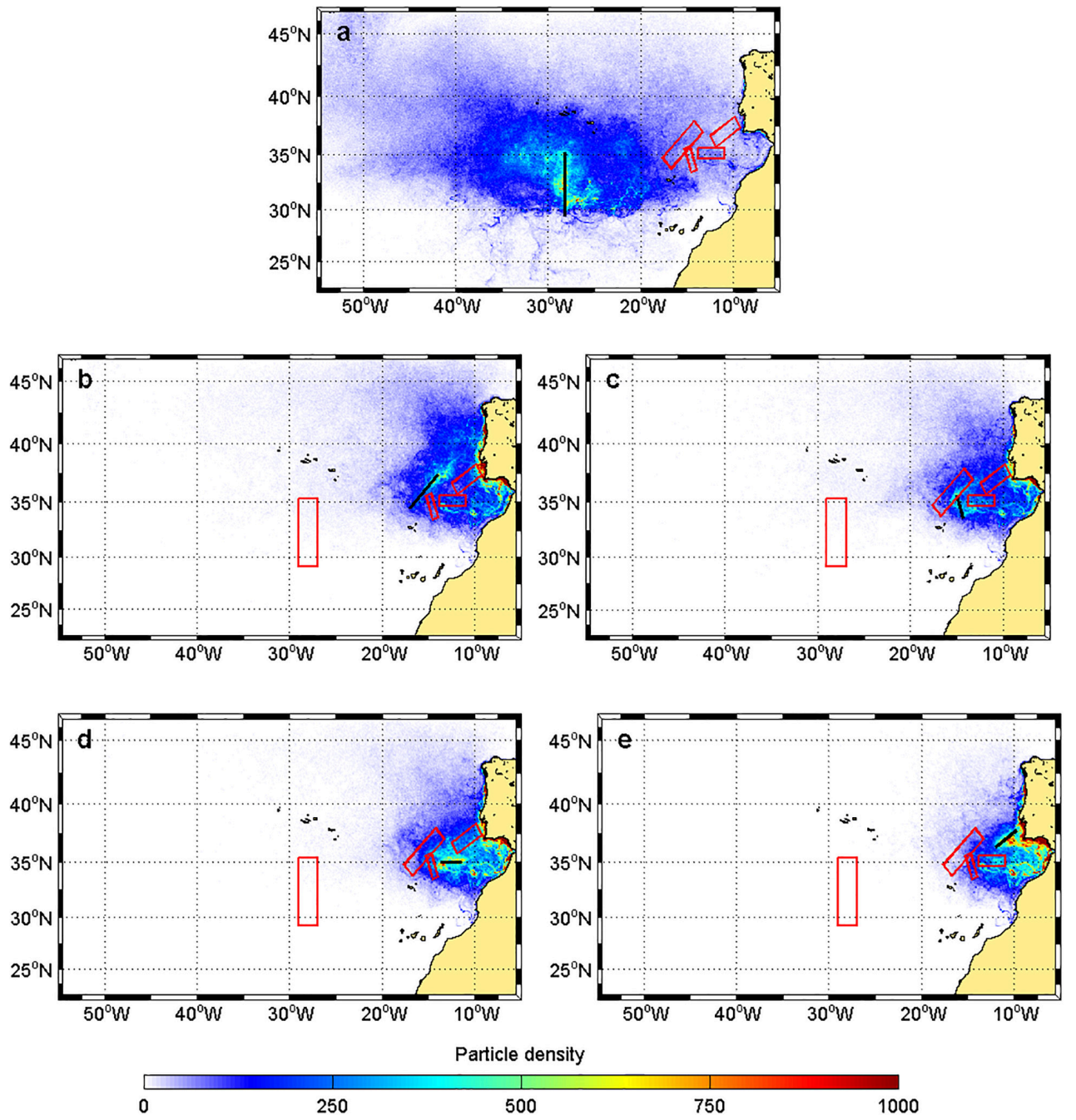


FIGURE 3 | Particle density distribution for the reverse particle tracking study at 5 m depth for particles released at the different seamounts: **(a)** Great Meteor, **(b)** Lion-Josephine, **(c)** Unicorn-Seine, **(d)** Ampere-Coral, and **(e)** Gorringe Bank. The black bar corresponds to the final destination of the particles. The red boxes represent the nearby seamounts of interest (as identified in **Figure 1b**).

was considered since these particles traveled in discrete layers while maintaining a constant depth. This Lagrangian tool was especially developed for larval dispersal modeling and to give probability estimates of population connectivity, with multiple modules available for the integration of biotic and abiotic data. Although some modules mimic larval behavior, none was activated in order to provide more accurate representations of the Lagrangian ocean circulation patterns around the Great Meteor and Madeira-Tore complexes. Therefore, the model was applied as a statistical representation of dispersal probabilities rather than as a deterministic study of individual particles and/or larval fates (Ross et al., 2016).

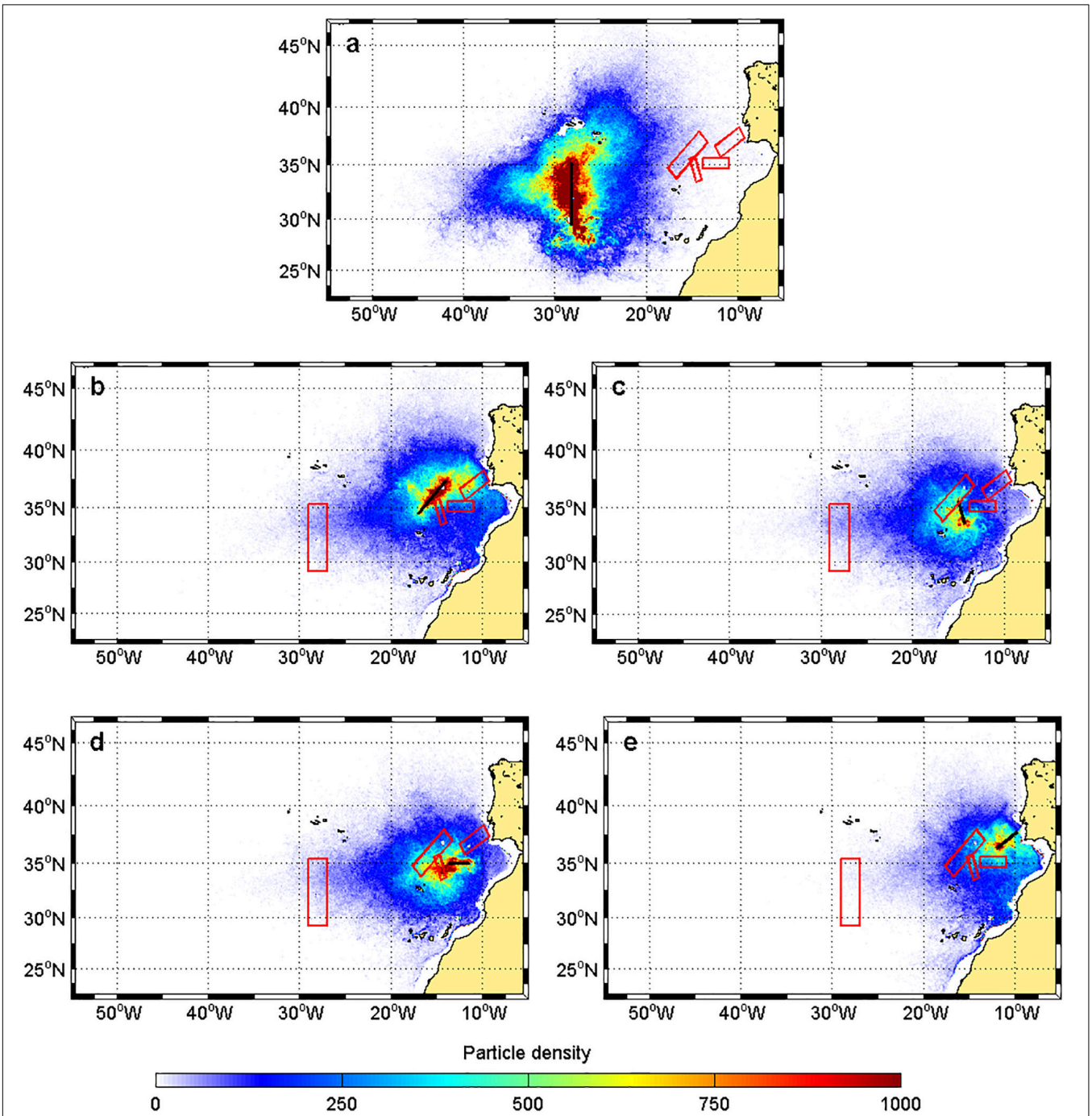


FIGURE 4 | Particle density distribution for the reverse particle tracking study at 1,000 m depth for particles released at the different seamounts: **(a)** Great Meteor, **(b)** Lion-Josephine, **(c)** Unicorn-Seine, **(d)** Ampere-Coral, and **(e)** Gorringe Bank. The black bar corresponds to the final destination of the particles. The red boxes represent the nearby seamounts of interest (as identified in **Figure 1b**).

Reverse Particle Tracking Study

This case study was carried out to determine the origin of particles reaching these submarine archipelagos, Great Meteor and Madeira-Tore (also considering the Azorean seamounts), discerning the main mesoscale phenomena that influence the transport dynamics. For each seamount, a line following their longitudinal or meridional axis was considered (depending on their orientation, dashed lines in **Figure 1b**), with several release points defined at a regular spacing of 0.05° (∼5.55 km): for Great Meteor 117 release points were considered, Lion-Josephine with 63, Unicorn-Seine with 42, and Ampere-Coral and Gorringe bank with 49 release points, adding up to a total of 320 release points. During this experiment, 10 particles were released every month at four different depth layers (5, 150, 500, and 1,000 m) at each release point, summing up to a total of 192,000 particles released at each layer. These release depths represent the common transport pathways previously identified for the northeast Atlantic Ocean by Sala et al. (2013). Trajectories of individual particles were tracked monthly ("backward" in time) from December 31, 2012 until January 1, 2008, considering that 5 years was enough time for the slowest particles to exit the model domain.

Particle Retention Study

This case study was conducted in order to evaluate the capacity of each seamount to capture and retain incoming particles. For these experiments, the particles were released from several release points regularly separated by 1° (∼111.11 km) along the model domain boundaries: the North Boundary (NB) considered 39 release points, the West Boundary (WB) with 21, and the South Boundary (SB) with 32 (dotted lines in **Figure 1a**). At each release point, 10 particles were released every month at the same depth layers as the reverse particle case study. Therefore, in the NB, a total of 23,400 particles were released, in the WB 11,400 were released, and in the SB 19,200, were released. In this case, the trajectories were monitored ("forward" in time) also at a monthly interval from January 1, 2004 until December 31, 2008.

To assess the "capture capacity" and "retention time interval" of each group of seamounts relative to incoming particles, a set of five "sink boxes" was defined: Great Meteor, Lion-Josephine, Unicorn-Seine, Ampere-Coral, and Gorringe bank (**Figure 1b**). "Capture capacity" was calculated by counting the number of particles that reached each group of seamounts (i.e., each "sink box"), while the "retention time interval" (in days) was calculated as a frequency distribution, considering the number of days that each particle spent inside a "sink box." In this experiment, the journey of a particle did not end once this particle enters a "sink box." Each particle will continue its journey until the end of the 5-year simulation or until it leaves the model domain.

Connectivity Study

This experiment analyzed the degree of connectivity between the different seamounts. For that, particles were released from the inside of 10 different 3D polygons (**Figure 1b**) at four different depth ranges following Sala et al. (2013): 1–10, 20–200, 300–500, and 600–2,000 m. Those 10 polygons represent the main seamounts that are currently the focus of this study (i.e., Great

TABLE 2 | Percentage of particles released along the domain boundaries (NB, WB, and SB) that were captured by the different sink boxes (in bold), with the corresponding percentages from each boundary, at each release depth, during the particle retention study.

Release depth	Release boundary	Great meteor		Lion-Josephine		Unicorn-Seine		Ampere-Coral		Gorringe bank	
5 m	North	**25**	65	**11**	93	**6**	93	**3**	94	**1**	97
	South		15		1		1		1		1
	West		20		6		6		5		3
150 m	North	**6**	62	**6**	75	**4**	74	**4**	68	**6**	60
	South		8		18		18		25		33
	West		31		8		8		7		7
500 m	North	**5**	41	**3**	50	**2**	47	**2**	40	**3**	30
	South		30		39		41		51		64
	West		29		10		12		9		7
1,000 m	North	**6**	26	**2**	30	**1**	25	**1**	20	**2**	9
	South		68		69		74		79		91
	West		6		1		1		1		0

TABLE 3 | Retention time interval (*d*) that at least 80% of the captured particles spent inside each sink box, at each release depth, during the particle retention study.

Release depth	Great meteor		Lion-Josephine		Unicorn-Seine		Ampere-Coral		Gorringe bank	
	Retention (*d*)	%	Retention (*d*)	%	Retention (*d*)	%	Retention (*d*)	%	Retention (*d*)	%
5 m	0–100	81	0–60	82	0–30	86	0–50	84	0–40	83
150 m	0–120	82	0–110	80	0–30	83	0–60	83	0–80	82
500 m	0–180	81	0–130	82	0–40	81	0–80	82	0–70	82
1,000 m	0–250	80	0–140	81	0–50	81	0–100	83	0–50	81

Meteor, Plateau–Irving–Cruiser, Tyro, Lion, Josephine, Unicorn, Seine, Ampere, Coral, and Gorringe bank). At each polygon, 200 release points, randomly distributed (latitudinally, longitudinally, and in depth) and fixed in time, were considered. At every point, 10 particles were released at a monthly interval for 9 years (2004–2012) and tracked "forward" in time. A particle's journey ends once it enters a polygon, but they can only settle 160 days after the release event. Connectivity matrices were calculated considering the number of particles released and captured by each polygon, reflecting the probability of a particle released from a given source box (i) to settle in a sink box (j), thus connecting the population i with the population j.

In order to quantify the physical connectivity within the network of seamounts, "source–sink indices" (SS) were calculated as the difference between the total number of particles being exported (K_{out}) and the total number of particles being imported (K_{in}) divided by the sum of the two (Holstein et al., 2014):

$$SS = \frac{K_{out} - K_{in}}{K_{out} + K_{in}}$$

where K represents the successful settlement "in" (i.e., particles imported) or "out" (i.e., particles exported) of a seamount. Negative index values ($SS < 0$) indicate that the seamount imports more particles than it exports, acting as a net sink. On the other hand, positive index values ($SS > 0$) indicate that a seamount exports more particles than it imports, acting as a net source. Meanwhile, a value equal to 0 would indicate that the seamount imports as many particles as it exports.

The "self-recruitment" (*selfr*) and "subsidy-recruitment" (*subr*) fractions of each seamount were calculated to identify which seamounts rely most on their own recruitment capacity *versus* the ones that depend more on the connections with its surroundings to maintain the local populations.

The *selfr* fraction was determined as the proportion of total recruited particles to a seamount (i) that originated from the seamount itself (Andrello et al., 2013):

$$selfr\,(i) = c(i,i) \Big/ \sum\nolimits_j c\,(i,j)$$

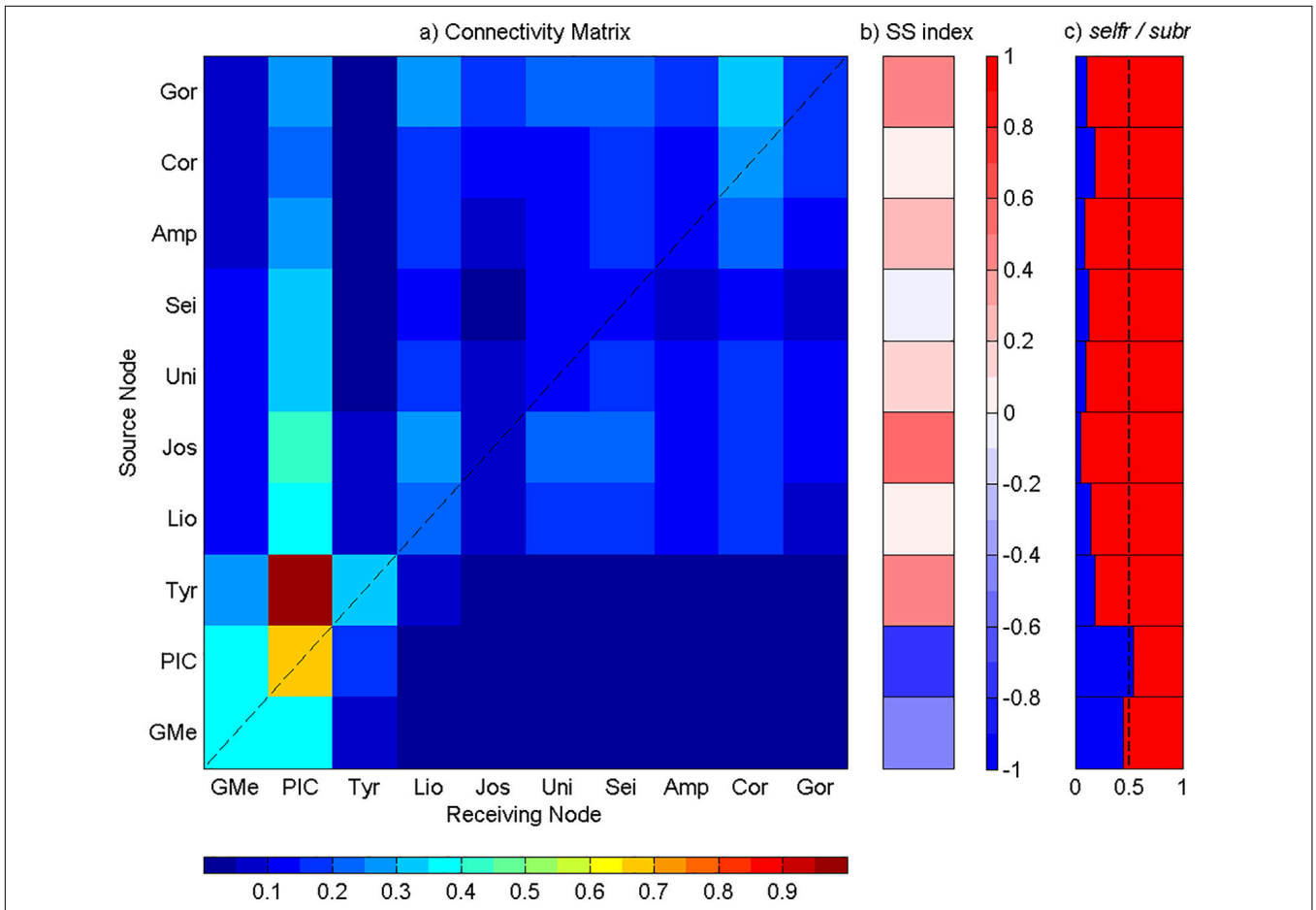


FIGURE 5 | Analysis of the connectivity among Great Meteor and Madeira-Tore complexes at the depth range of 1 to 10 m. **(a)** Connectivity matrix between the seamounts: GMe – Great Meteor; PIC – Plateau, Irving, and Cruiser; Tyr – Tyro; Lio – Lion; Jos – Josephine; Uni – Unicorn; Sei – Seine; Amp – Ampere; Cor – Coral; and Gor – Gorringe. The *y*-axis represents seamounts acting as sources and the *x*-axis represents seamounts acting as sinks. The connectivity degree increases from blue to red. **(b)** Source–sink indices for each seamount. **(c)** Self-recruitment (*selfr*, blue color) and subsidy-recruitment (*subr*, red color) fractions for each seamount. The dashed line corresponds to the reference value of 0.5.

where c is the connection probability, i.e., the fraction of particles originating in the seamount i that ended up in the same location ($c(i,i)$) or in another seamount j ($c(i,j)$).

Meanwhile, the *subr* fraction was obtained as the proportion of total recruited particles that came from the surrounding seamounts (j) (Andrello et al., 2013), calculated as:

$$subr\,(i) = \sum_{j \neq i} c\,(i,j) \Big/ \sum_{j} c\,(i,j) = 1 - selfr\,(i)$$

Thus, if *selfr* is higher (lower) than 0.5, there are more (less) particles retained by self-recruitment than by subsidy-recruitment.

Sensitivity Tests

Several sensitivity tests were performed in order to examine the limitations of the model. A first test to determine the seasonal and inter-annual variability for the capture and retention capabilities of the seamounts showed a small diversion for the bulk transport pathways. Six commonly used indices were computed to compare the model results and assess its performance: the correlation coefficient, root mean square error, reliability index, average error, average absolute error, and modeling efficiency [for more detailed information, see Stow et al. (2009)]. Notwithstanding, the tests were limited to the most superficial layer where ocean dynamics is more complex, assuming that there are no major changes with increasing depth. For the reverse particle tracking study, all possible particle pathways were recalculated with half of the particles, obtaining very similar dispersal patterns to those obtained with all the particles. For the particle retention and connectivity studies, the capture capability of each group of seamounts was recalculated through the same method, and similar results were obtained (**Table 1**). Although tens of thousands of particles were released per depth range, these tests proved that the model achieves statistical convergence using all or even half of the number of particles.

Additional sensitivity tests were performed for the connectivity study. The connectivity matrices with particles that are uniformly and randomly released (with respect to x and y coordinates) were compared, and the results were similar (**Table 1**). With matrices in which the release events were set at

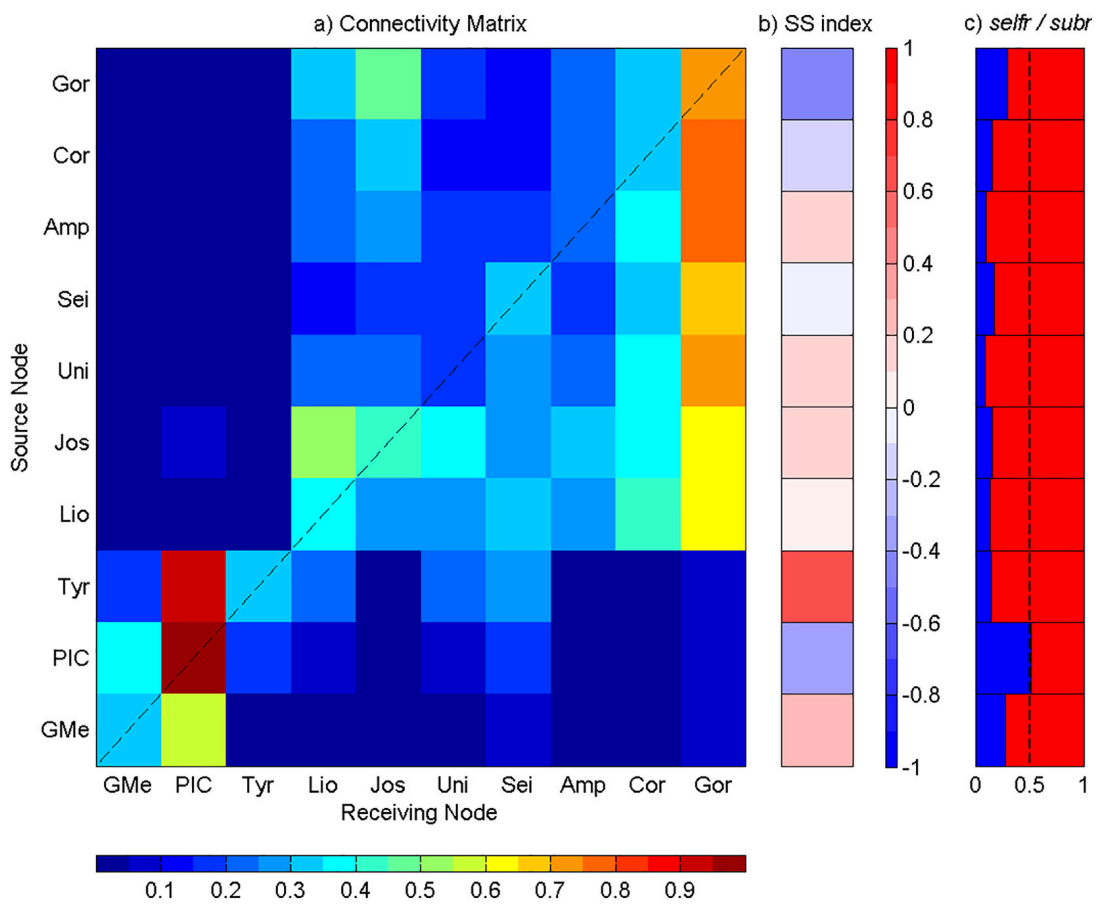


FIGURE 6 | Analysis of the connectivity among Great Meteor and Madeira-Tore complexes at the depth range of 20 to 200 m. **(a)** Connectivity matrix between the seamounts: GMe – Great Meteor; PIC – Plateau, Irving, and Cruiser; Tyr – Tyro; Lio – Lion; Jos – Josephine; Uni – Unicorn; Sei – Seine; Amp – Ampere; Cor – Coral; and Gor – Gorringe. The y-axis represents seamounts acting as sources and the x-axis represents seamounts acting as sinks. The connectivity degree increases from blue to red. **(b)** Source–sink indices for each seamount. **(c)** Self-recruitment (*selfr*, blue color) and subsidy-recruitment (*subr*, red color) fractions for each seamount. The dashed line corresponds to the reference value of 0.5.

a constant depth and at a random depth (z-coordinate) within the corresponding depth range (i.e., 1–10, 20–200, 300–500, and 600–2,000 m), the outcomes were also comparable (**Table 1**). Nevertheless, as this study is not species specific, which are often confined (due to behavior) to a certain depth range, random releases at different depth ranges were considered in order to achieve a generic approach.

Finally, a comparison between the model and surface drifting buoys data was conducted. A total of 772 drifting buoys trajectories were downloaded from the CORIOLIS database,[2] taking into account the region (dashed line in **Figure 1a**) and the study period (2004–2012). Considering the release point of each drifting buoy (i.e., longitude, latitude, and time) and its travel time (31 days maximum), a CMS experiment was performed. The resulting connectivity matrix was compared with the one obtained from the drifters (see **Figure 2**), revealing a high correlation between the ocean circulation model and the drifting buoys data (see **Table 1**).

The sensitivity studies, particularly the comparison with observations, gave the authors confidence to pursue a representative study of the physical connectivity between the NE Atlantic seamounts, of which the main findings are detailed in the section below.

[2]http://www.coriolis.eu.org

RESULTS

Reverse Particle Tracking Study

With regard to the Great Meteor complex located at ∼1,600 km from the nearest continental coast, at 5 m depth, the majority of the particles came from the west/northwest side of the domain (**Figure 3a**), whereas for the most coastal mountains (i.e., Lion-Josephine, Unicorn-Seine, Ampere-Coral, and Gorringe bank), the particles came mainly from the Iberian Peninsula (IP), GoC, and the northwest African coast (**Figures 3b–e**). A particularly high-density pathway was observed between the south IP and the Gorringe bank (**Figure 3e**). The trajectories for particles released at 150 and 500 m exhibited similar results (data not shown).

At 1,000 m depth, the particles came mostly from the west and the northeast toward the Great Meteor (**Figure 4a**). At the remaining seamounts, the particles arrived from the nearby

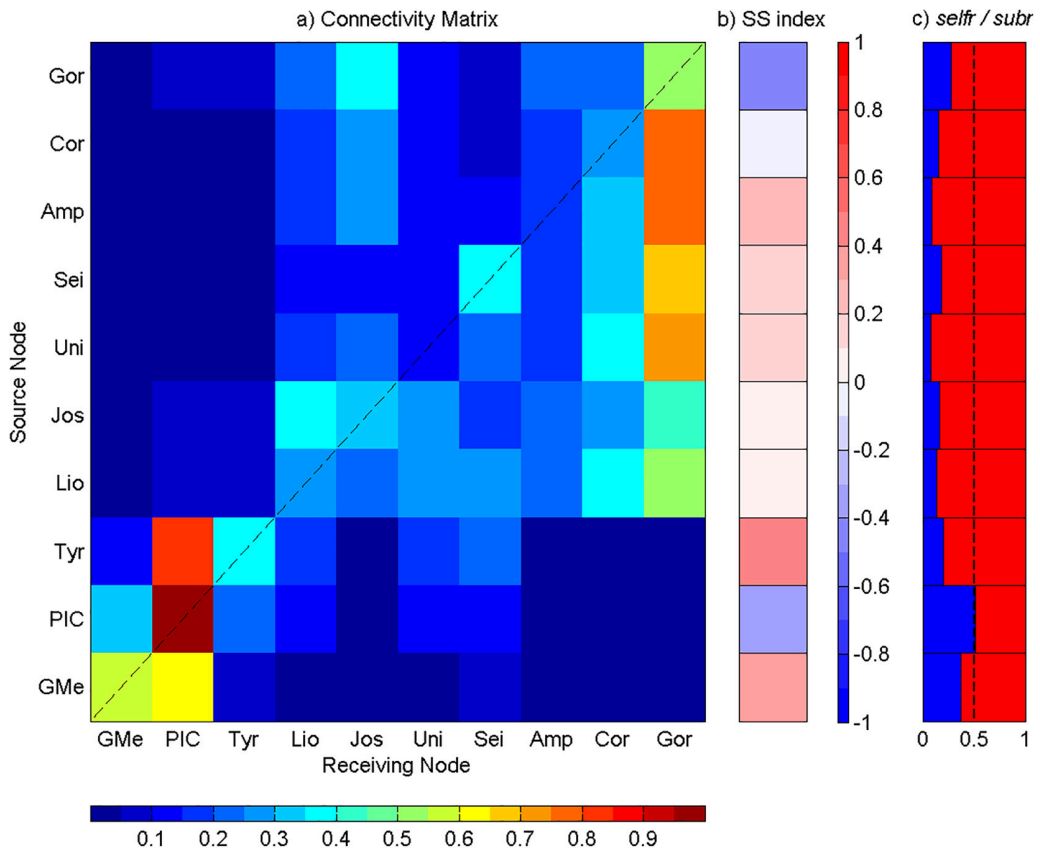


FIGURE 7 | Analysis of the connectivity among Great Meteor and Madeira-Tore complexes at the depth range of 300 to 500 m. **(a)** Connectivity matrix between the seamounts: GMe – Great Meteor; PIC – Plateau, Irving, and Cruiser; Tyr – Tyro; Lio – Lion; Jos – Josephine; Uni – Unicorn; Sei – Seine; Amp – Ampere; Cor – Coral; and Gor – Gorringe. The y-axis represents seamounts acting as sources and the x-axis represents seamounts acting as sinks. The connectivity degree increases from blue to red. **(b)** Source–sink indices for each seamount. **(c)** Self-recruitment (*selfr*, blue color) and subsidy-recruitment (*subr*, red color) fractions for each seamount. The dashed line corresponds to the reference value of 0.5.

regions (**Figures 4b,c,e**), with a major input from the southwest side (**Figures 4b,d**).

Particle Retention Capability Study

At Great Meteor, Lion-Josephine, and Unicorn-Seine seamounts, a higher percentage of particles was retained in the most superficial layer (5 m; **Table 2**). For almost all depths, the main source of particles was the NB, with the exception of the deepest layer where the SB outstood as the main contributor (**Table 2**). The captured particles spent a minimum of 30 days and a maximum of 250 days inside a box (**Table 3**). On the other hand, at Ampere-Coral and Gorringe bank, more particles were retained at intermediate waters (500 m; **Table 2**). The main origin of the total trapped particles for the first two depth layers (5 and 150 m) was the NB, whereas for the remaining two (500 and 1,000 m), the southern contribution exceeded the northern contribution (**Table 2**). The majority of the retained particles spent a minimum of 40 days and a maximum of 100 days inside one of these boxes (**Table 3**).

Connectivity Study

The connectivity matrices calculated for each depth range are presented in **Figures 5–8**. In order to be dimensionless, each element was normalized by the highest number of recruited particles. Therefore, the scale ranges from 0 to 1, with 0 being the lack of connectivity. The *X*-axis and the *Y*-axis represent the different seamounts considered in this study, geographically arranged from southwest to northeast, with the main diagonal providing self-recruitment information. It is also important to note that each row represents a release seamount (source), while each column corresponds to a settlement seamount (sink). In addition, the SS index will determine if a seamount is acting as a sink or as a source of particles. Meanwhile, the *selfr* and *subr* fractions will distinguish if a seamount relies more on self-recruitment or on subsidy-recruitment, respectively.

Particles Released Between 1 and 10 m

At this depth range, the intra-seamounts connectivity was stronger in the Great Meteor complex (i.e., Great Meteor, Plateau, Irving, Cruiser, and Tyro) than in the Madeira-Tore

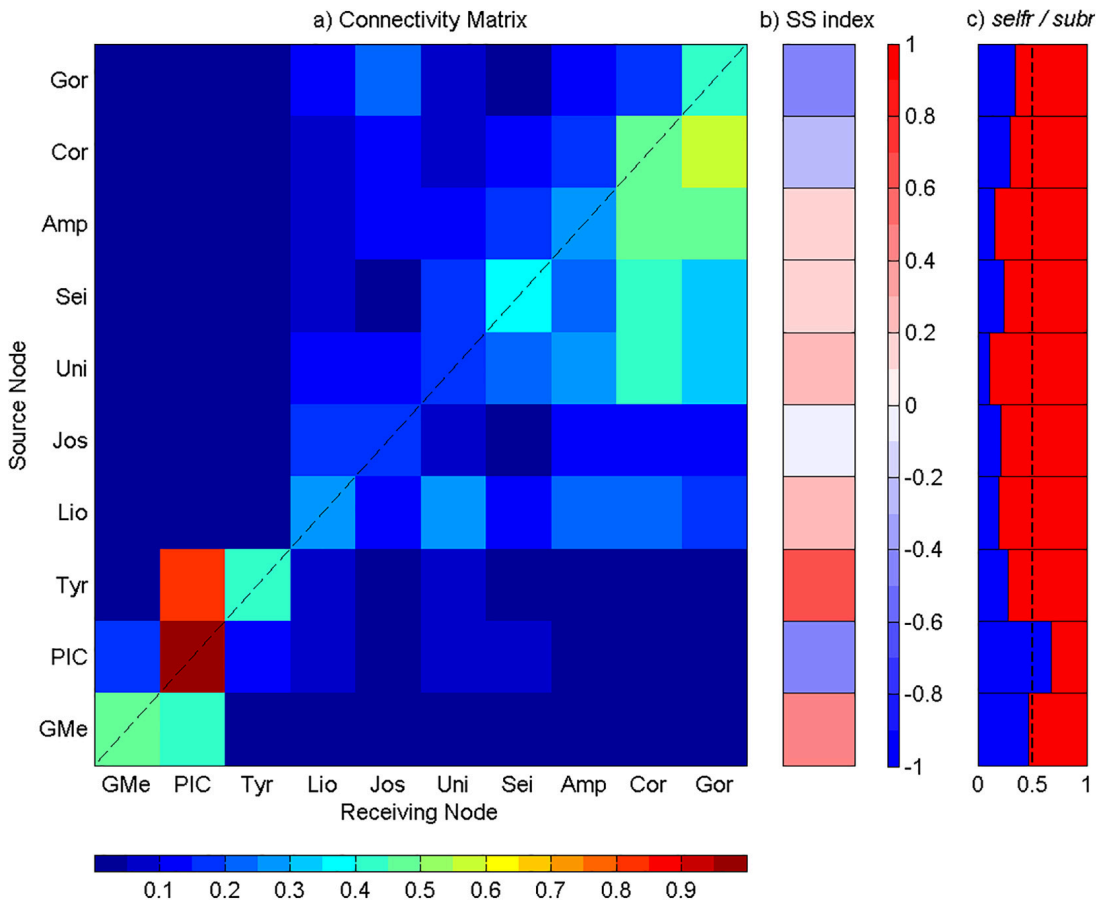


FIGURE 8 | Analysis of the connectivity among Great Meteor and Madeira-Tore complexes at the depth range of 600 to 2,000 m. **(a)** Connectivity matrix between the seamounts: GMe – Great Meteor; PIC – Plateau, Irving, and Cruiser; Tyr – Tyro; Lio – Lion; Jos – Josephine; Uni – Unicorn; Sei – Seine; Amp – Ampere; Cor – Coral; and Gor – Gorringe. The *y*-axis represents seamounts acting as sources and the *x*-axis represents seamounts acting as sinks. The connectivity degree increases from blue to red. **(b)** Source–sink indices for each seamount. **(c)** Self-recruitment (*selfr*, blue color) and subsidy-recruitment (*subr*, red color) fractions for each seamount. The dashed line corresponds to the reference value of 0.5.

complex (i.e., Lion, Josephine, Unicorn, Seine, Ampere, Coral, and Gorringe). A higher self-recruitment was found for the western group of seamounts (i.e., Great Meteor complex; main diagonal, **Figure 5a**). The Great Meteor and PIC acted as net sinks, with the highest self-recruitment (∼0.37 for both) in comparison to the other seamounts (**Figure 5a**). These results coincided with the computed SS index < 0 for both mountains, which is indicative of a sink behavior (**Figure 5b**). For the PIC mountains, the main sources of recruited particles were Tyro, Josephine, Lion, and Great Meteor seamounts. With the exception of Great Meteor, those mountains acted mainly as net sources (SS > 0) and were characterized by low *selfr* values (**Figures 5b,c**). Although the PIC seamounts acted as net sinks (SS < 0; **Figure 5b**), they also presented the highest *selfr* value, retaining slightly more of their own particles rather than from other seamounts (*selfr* > 0.5; **Figure 5c**). Tyro presented the lower value of self-recruitment of the Great Meteor complex (0.31; main diagonal, **Figure 5a**), which coincides with a positive value of SS index (i.e., acted as source; **Figure 5b**). Additionally, it revealed a relatively low value of *selfr* (**Figure 5c**). On the eastern group of seamounts, where the interaction intra-seamounts was very weak, a stronger connection occurred between the Gorringe bank and Coral patch. For the Coral patch, the highest input of particles came from Gorringe bank, followed by a high self-recruitment pattern, with a low contribution from the remaining sites (**Figure 5a**). Thus, Gorringe acted as a net source (SS > 0), with a low *selfr* fraction (**Figures 5b,c**). As expected, a higher recruitment was observed for seamounts geographically closer to the source (**Figure 5a**). Moreover, most of the recruited particles were above the main diagonal, evidencing a westward transport.

Particles Released Between 20 and 200 m

At this depth range, the intra-seamounts connectivity from both complexes was intensified, especially in the eastern complex (i.e., Madeira-Tore complex). The exchange of particles between both groups was still present, although most of the recruited particles were below the main diagonal, evidencing an eastward transport (**Figure 6a**). On the western group, at Great Meteor, the input of particles from PIC slightly exceeded its self-recruitment (**Figure 6a**). However, Great Meteor acted as a net source (SS > 0), exporting more than it imports (**Figure 6b**). Moreover, its low *selfr* fraction proved that more particles from other mountains were retained than its own (**Figure 6c**). PIC showed the highest self-recruitment value of all mountains (**Figure 6a**). Besides that, it also received a large contribution from Tyro and Great Meteor (**Figure 6b**). Thus, PIC showed a *selfr* fraction value close to 0.5, confirming that the number of particles self-recruited was similar to the number of particles imported from other seamounts (**Figure 6c**). Meanwhile, Tyro acted as a source, showing a SS index close to 1, which means that the proportion of exported particles was much larger than the imported ones (**Figure 6b**). At the eastern group of seamounts (Madeira Tore complex), the self-recruitment of almost all mountains was higher at these depths when compared to the most superficial layer. The main source of particles for Lion was Josephine, with a contribution slightly superior than its own self-recruitment (**Figure 6a**), whereas for Josephine, the input from Gorringe was

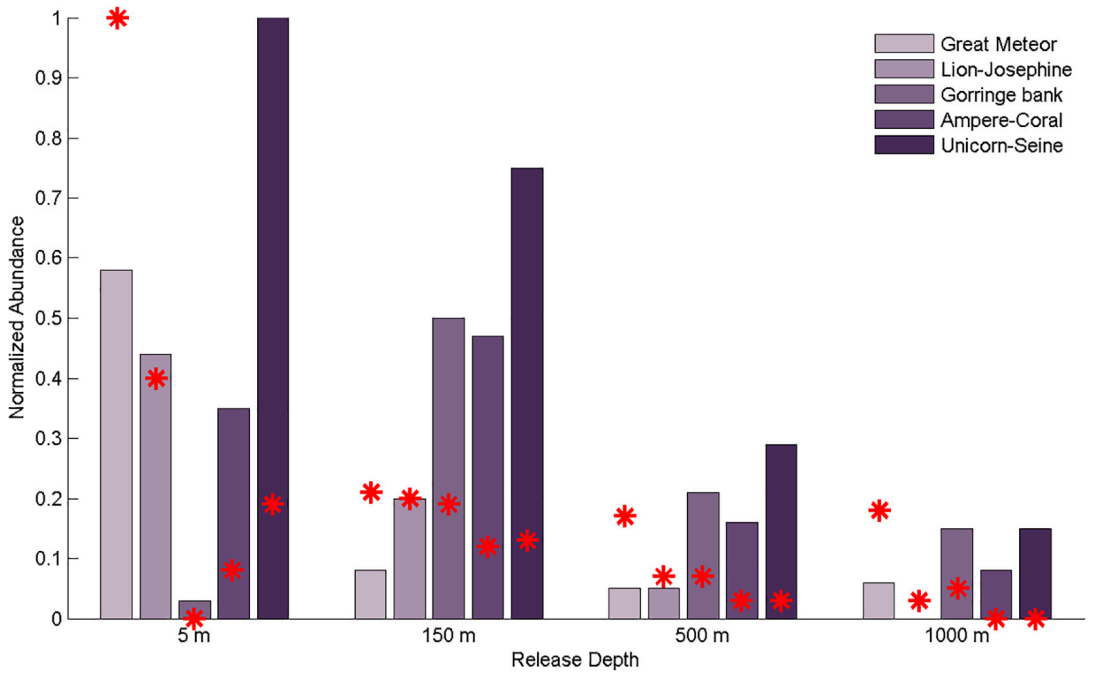


FIGURE 9 | Bar plot representing the captured particles per square kilometer, per sink box, by depth. The red stars represent the total number of captured particles per sink box. The sink boxes are arranged in descending order of sizes (i.e., Great Meteor, Lion-Josephine, Gorringe bank, Ampere-Coral, and Unicorn-Seine). Both datasets were normalized so as to be comparable.

higher than its own self-recruitment (**Figure 6a**). Meanwhile, for Unicorn, the greatest input came from Josephine and Lion (0.35 and 0.29, respectively; **Figure 6a**). For Seine seamount, self-recruitment exceeded inputs from other sources (**Figure 6a**). Lastly, Gorringe bank acted as the main sink (**Figure 6b**) for particles released by the surrounding submarine mountains (**Figure 6a**). Thus, all the eastern group seamounts, with the exception of Gorringe Bank and Coral patch, acted as net sources, albeit the relatively low values (**Figure 6b**), although at <0.5, Gorringe Bank showed the highest *selfr* fraction, importing more particles from the surrounding mountains than its own via self-recruitment (**Figure 6c**).

Particles Released Between 300 and 500 m

The results obtained at this depth-range were very similar to those presented previously. Again, a strong eastern transport was observed. Higher values of connectivity were found intra-seamounts of the western group (i.e., Great Meteor, PIC, and Tyro), while for the eastern group, the strongest connections were established mainly with Gorringe bank (**Figure 7a**). High self-recruitment was observed (**Figure 7a**) at the western group, especially in PIC, which continued to act as the main sink (SS < 0) in the Great Meteor complex (**Figures 7a,b**). PIC also presented similar values of *selfr* and *subr* fractions, with the number of self-recruited particles concurrent to the number of imported particles (**Figure 7c**). At the eastern group of seamounts, Gorringe stood out once again as the main sink for particles released in the surrounding submarine mountains, therefore with a *selfr* value lower than *subr* (**Figure 7**).

Particles Released Between 600 and 2,000 m

Once more the results obtained for this depth range were similar to the previous ranges. However, the intra-seamounts connectivity in both complexes and the eastward connectivity between them were less intense (**Figure 8a**). All mountains at the western group, particularly PIC stood out, showing a high self-recruitment (**Figure 8a**), and acting as the main sink (SS < 0) (**Figures 8a,b**). Nevertheless, the *selfr* fraction was higher than 0.5, with the number of self-recruited particles greater than the number of imported particles (**Figure 8c**). At the eastern group, a higher connectivity was observed for Unicorn, Seine, Ampere, Coral, and Gorringe Bank, with the last two seamounts acting mostly as sinks (**Figures 8a,b**).

DISCUSSION AND CONCLUSIONS

Recent studies raised concerns on the vulnerability of seamount communities to human impact due to the intrinsic biological factors characteristic of seamount species (e.g., slow growth rates or late maturation; Rogers, 2004; Clark et al., 2010). Of special distress are the consequences of the development of large-scale bottom trawl fishing for sessile fauna (Clark et al., 2010), with coral reefs being particularly vulnerable to damage (Rogers et al., 2007). In the NE Atlantic seamounts, the level of endemism in coral species is very low (<3%), which means that populations rely on external contributions. In addition, the fauna associated to them is significantly different from that recorded at the same depths on the continental slope (Hall-Spencer et al., 2007). Thus, it is necessary to advance in the protection of these (less abundant) native species. In order to further perceive how these species are sustained, understanding the influence of the oceanographic phenomena in the connectivity between the different seamounts located in this region is of special interest. This study proposes a first approximation to pursue this goal using a numerical modeling approach, focusing on the Great Meteor and Madeira-Tore complexes.

Due to the geographical location of Great Meteor and Madeira-Tore, our results highlighted the main role of the AzC and their associated eddies in the transport, dispersion, and retention of particles in this region, as well as their influence in the connectivity among the different seamounts that comprise those complexes (**Figure 1**). The Great Meteor complex, located offshore ∼1,500 km away from the African coast, is influenced by both branches of the AzC: the one that travels eastward toward the GoC and the one that veers southward near Madeira. The Madeira-Tore complex, located ∼550 km away from the IP coast, is mainly influenced by the eastward branch. When this eastward branch arrives at the GoC, it produces a front characterized by high mesoscale variability, probably being responsible for the transport of particles from the coastal regions of the GoC toward this complex (**Figures 3**, **4**). Moreover, although on a small scale, the PoC also influences the Madeira-Tore dynamics, transporting particles from the western coast of the IP to the open ocean.

The AzC and its associated eddies are the main regional features injecting particles in our study area; thus, the highest input from the north and west boundaries was expected. Our results showed that the NB was the main source of captured particles by all seamounts at the upper layers (i.e., 5 and 150 m; **Table 2**). However, the contribution from the WB was only evident at the Great Meteor complex (**Table 2**) since it is located closer to this boundary (∼2,000 km) than Madeira-Tore (∼3500 km). An intensified AzC between 150 and 500 m in depth and 32° and 35° N (Klein and Siedler, 1989; Comas-Rodríguez et al., 2011; Sala et al., 2016) resulted in the increase of captured particles from the WB by all seamounts. Due to the decrease in intensity of the AzC with depth, a lower influence was observed at 1,000 m depth. Moreover, the released particles had a maximum travel time of 5 years that proved to be insufficient to travel a greater distance (**Figure 4d** and **Table 2**). While the NB contribution decreased with depth, the contribution from the SB increased due to the intensification of the north-westward and westward transport mediated by the eddy corridors also associated with the AzC (Sangrà et al., 2009; Barbosa-Aguiar et al., 2011; Comas-Rodríguez et al., 2011; Sala et al., 2016).

The capture capacity (i.e., number of particles that reached each sink box) and the retention time interval (i.e., the number of days that each particle spent inside a sink box) were only partially related to seamount size as they depend also on the proximity of each seamount to the different source boundaries and on the predominant oceanic processes determining their oceanic pathways. As expected, the percentage of captured particles decreased with depth (**Table 2**), while the retention time increased for all boxes except at the Gorringe bank, which did

not show a clear pattern of variability (**Table 3**). In the upper mixed layer (i.e., 5 m), Great Meteor (the largest box) withheld 25% of captured particles, followed by Lion-Josephine (twice as small as the Great Meteor) with 11%. Besides the higher capture capabilities, they also had higher mean retention times. Meanwhile, Unicorn-Seine, the smallest sink box (seven times smaller than Great Meteor), showed the third highest capture capacity (6%; **Table 2**) but with a shorter retention time interval (0–30 days; **Table 3**). At the other release depths, the variability between the different sink boxes was lower (**Tables 2**, **3**). Notwithstanding, when the capture capacity per square kilometer is calculated for all the sink boxes, Unicorn-Seine stands out with the highest values at all depths (**Figure 9**). Great Meteor (the largest box) only exceeds in the most superficial layer. From 150 to 1,000 m deep, the smallest sink boxes (Gorringe bank, Ampere-Coral, and Unicorn-Seine, from large to smaller-sized seamounts) showed a capture capacity (per km^2) greater than the larger sink boxes (i.e., Great Meteor and Lion-Josephine). This higher capture capacity of the smallest sink boxes could be related to their location and orientation with respect to the incoming AzC (**Figure 1**). In addition, these aggregated seamount chains are influenced by the "sticky water effect," which increases their ability to capture and retain incoming particles, including coral eggs and fish larvae (Andutta et al., 2012). However, as their delimited areas are smaller, the particles stay for a shorter time. So, the particles are likely to be retained longer on seamounts occupying larger areas. While the Madeira-Tore complex is mainly influenced by the "sticky water effect," the Great Meteor complex, due to its orientation to the incoming AzC, must be stirring the incoming current and causing a "seamount effect," a process analogous to the "island mass effect", which enhances productivity in the lee of oceanic islands (see e.g. Dower and Mackas, 1996). Other physical processes, such as lower rates of flow during neap tides, can still induce particle retention (Andutta et al., 2012). Thus, future studies could consider variable flow rates (e.g., tidal currents).

Considering the results, the connectivity between both complexes and the intra-seamount interaction should be stronger following the direction of the predominant stream/flow. Nevertheless, it should be noted that the complexes are ∼1,000 km apart, and assuming a constant speed for the AzC of 50 cm m^{-1} (Pingree, 1997), a particle would need at least ∼23 days to travel from one complex to another. At the upper mixed layer (5 m depth), a westward connectivity was observed between Great Meteor and Madeira Tore, with PIC seamounts being the main sink (**Figure 5**). This can be related to the westward flow previously reported by Barbosa-Aguiar et al. (2011) between 18° and 24° W along 32.5° N. This counterflow feeds on a southward recirculation east of Madeira, travels westward, and veers to the south at about 24° W. However, when AzC is intensified (i.e., 20 and 500 m depth), the connectivity seemed to follow an eastward pattern from Great Meteor complex toward Madeira-Tore (**Figures 6**, **7**), whereas in deeper layers (600–2,000 m), where the currents are slower, there was almost no interaction between the two submerged archipelagos (**Figure 8**).

Regarding the intra-seamount connectivity, this interaction may depend on the submesoscale processes associated with AzC, given the almost perpendicular orientation of the Great Meteor complex (Great Meteor, PIC, and Tyro) relative to the current. In fact, previous observations have shown that the AzC recirculates in westward counterflows located both north and south of the main current, which might enable north–south as well as south–north interactions (Pingree, 1997). This intra-seamount connectivity did not vary substantially with depth. The PIC mountains always stood out with the strongest self-recruitment values, concurrently acting as the main sink for Tyro and Great Meteor, probably because of its larger volume compared with the others (see **Figure 1b**). The PIC and Great Meteor polygons are closer than PIC and Tyro, allowing a stronger interaction.

Meanwhile, the connectivity within the Madeira-Tore complex should be higher, considering that the seamounts are directly exposed to the AzC flow (**Figure 1**). At the most superficial layer, the intra-seamount connectivity was very weak. Furthermore, at this depth, all of them acted as net sources. This pattern probably relates with the fact that the particles could only settle 160 days after the release event (**Figure 5**). However, intra-seamount connectivity increased with depth, being strongest when the AzC is more intense (i.e., 20 and 500 m; **Figures 6**, **7**). Between 20 and 2000 m depth, Gorringe and Coral seamounts, the two polygons closest to the GoC, acted as prime sinks of this complex. Meanwhile, the other mountains (sited further west) continued to act as sources.

The design of MPAs seems an appropriate way to protect the Great Meteor and Madeira-Tore complexes as vulnerable habitats, helping to balance exploitation and conservation (Probert et al., 2007). According to previous studies, their design should (i) assess the necessary degree of conservation, (ii) define the goals that justify the establishment of new MPAs, (iii) integrate the biological information of threatened species, such as dispersal distances and overall distribution, and (iv) select suitable areas to create MPA networks for biodiversity conservation and fishery management (Jones et al., 2007; Clark et al., 2011). Nonetheless, to maximize the success and benefits of these ocean sanctuaries, knowledge about larval retention and connectivity should also be considered (Jones et al., 2007). In this context, our results provide valuable information for this goal. Only physical connectivity was considered in our study, and the particles behaved as passive tracers without any ecological behavior. Therefore, our results will only be relevant for species with at least one planktonic pelagic phase (i.e., unable to swim against a current). Previous studies highlighted the roles of larval behavior and duration in dispersal and connectivity control (Fox et al., 2016; Lett et al., 2019; Taninaka et al., 2019). For instance, vertical larval migration may allow deep populations from nearby seamounts to repopulate shallow areas impacted by overfishing, which might increase the intra-connectivity within each seamount system (Fox et al., 2016). On the other hand, these swimming abilities might disperse larvae over long distances (Majoris et al., 2019), possibly increasing the inter-connectivity between the two systems. Longer-living larvae are expected to travel greater distances, thus enhancing the existing connectivity pathways (Fox et al., 2016). For this reason, future studies including biological factors (i.e., diel vertical migration, reproduction season, pelagic larval duration,

and mortality rates) should target a selection of key species with known and/or well-documented behavior. Apart from focusing on a generic first study, the scientific literature on specific species behavior for Great Meteor and Madeira-Tore seamounts is virtually inexistent. On the other hand, considering that our results showed a very low connectivity between the Great Meteor and Madeira-Tore complexes, the connectivity patterns with the surrounding landscape should continue to be further investigated, for instance, in relation to the Macaronesian Islands and the western Iberian and African coasts. This will allow us to better understand the regional dynamics, including the proposed stepping-stone theory whereby the North Atlantic populations expand to the different islands through seamount chains (e.g., Cho and Shank, 2010).

SUMMARY

- The AzC and its associated eddies were identified as the main transport pathways for particles on both groups of seamounts, especially at intermediate waters.
- The Great Meteor complex was mainly affected by the AzC southward branch, while the Madeira-Tore was mainly influenced by its eastward branch.
- Low connectivity was found between the two seamount complexes.
- The inter-connectivity between seamounts increased with depth at Madeira-Tore, while minor variations were found at Great Meteor.
- The PIC seamounts from the Great Meteor complex and Gorringe and Coral from the Madeira-Tore complex led the main connectivity routes.
- Despite their size, the Madeira-Tore seamounts outstood the others with its higher capturing capacity per square kilometer, suggesting a greater influence of the "sticky water effect."
- In the Great Meteor complex, the "seamount effect" seems to be responsible for the greater retention and self-recruitment capabilities.
- These results provide a valuable first approach, from the (generic) physical point of view, to support MPA design efforts. However, since no coherent biological traits were found and/or considered, strong conclusions cannot be drawn at this stage.
- Future species-specific research including biological factors such as diel vertical migration, reproduction season, pelagic larval duration, and mortality rates are imperative.

DATA AVAILABILITY STATEMENT

The dataset analyzed in this study (HYCOM GLBa0.08, experiment 05.8), from 2004 to 2012, cannot be provided since only the latest data are publicly available. The dataset used for the sensitivity analysis was downloaded from CORIOLIS database (http://www.coriolis.eu.org/Data-Products/Data-Delivery/Data-selection), adapted to our time and spatial domains.

AUTHOR CONTRIBUTIONS

RC proposed the original ideas which lead to the design of the study. ML and IS were involved in the modeling, data collection, and analysis. All authors were involved in the writing and review process and all authors approved it for publication. An earlier version of this work was part of ML bachelor final project.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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An Assessment of Environmental Metabarcoding Protocols Aiming at Favoring Contemporary Biodiversity in Inventories of Deep-Sea Communities

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The abyssal seafloor covers more than 50% of planet Earth and is a large reservoir of still mostly undescribed biodiversity. It is increasingly targeted by resource-extraction industries and yet is drastically understudied. In such remote and hard-to-access ecosystems, environmental DNA (eDNA) metabarcoding is a useful and efficient tool for studying biodiversity and implementing environmental impact assessments. Yet, eDNA analysis outcomes may be biased toward describing past rather than present communities as sediments contain both contemporary and ancient DNA. Using commercially available kits, we investigated the impacts of five molecular processing methods on eDNA metabarcoding biodiversity inventories targeting prokaryotes (16S), unicellular eukaryotes (18S-V4), and metazoans (18S-V1, COI). As the size distribution of ancient DNA is skewed toward small fragments, we evaluated the effect of removing short DNA fragments *via* size selection and ethanol reconcentration using eDNA extracted from 10 g of sediment at five deep-sea sites. We also compare communities revealed by eDNA and environmental RNA (eRNA) co-extracted from ∼2 g of sediment at the same sites. Results show that removing short DNA fragments does not affect alpha and beta diversity estimates in any of the biological compartments investigated. Results also confirm doubts regarding the possibility to better describe *live* communities using eRNA. With ribosomal loci, eRNA, while resolving similar spatial patterns than co-extracted eDNA, resulted in significantly higher richness estimates, supporting hypotheses of increased persistence of ribosomal RNA (rRNA) in the environment and unmeasured bias due to overabundance of rRNA and RNA release. With the mitochondrial locus, eRNA detected lower metazoan richness and resolved fewer spatial patterns than co-extracted eDNA, reflecting high messenger RNA lability. Results also highlight the importance of using large amounts of sediment (≥10 g) for accurately surveying eukaryotic diversity. We conclude that eDNA should be favored over eRNA

for logistically realistic, repeatable, and reliable surveys and confirm that large sediment samples (≥10 g) deliver more complete and accurate assessments of benthic eukaryotic biodiversity and that increasing the number of biological rather than technical replicates is important to infer robust ecological patterns.

Keywords: environmental metabarcoding, RNA versus DNA, extracellular DNA, deep-sea biodiversity, benthic ecology, biomonitoring, method testing

INTRODUCTION

Environmental DNA (eDNA) metabarcoding is an increasingly used tool for biodiversity inventories and ecological surveys. Using high-throughput sequencing (HTS) and bioinformatic processing, it allows the detection or the inventory of target organisms using their DNA directly extracted from soil, water, or air samples (Taberlet et al., 2012a). As it does not require specimen isolation, it represents a practical and efficient tool in large and hard-to-access ecosystems, such as the marine realm. Besides allowing studying various biological compartments simultaneously, metabarcoding is also very effective for detecting diversity of small organisms (microorganisms, meiofauna) largely disregarded in visual biodiversity inventories due to the difficulty of their identification based on morphological features (Carugati et al., 2015).

The deep sea, covering more than 50% of Planet Earth, remains critically understudied, despite being increasingly impacted by anthropogenic activities and targeted by resource-extraction industries (Ramirez-Llodra et al., 2011). The abyssal seafloor is mostly composed of sedimentary habitats containing high numbers of small (< 1 mm) organisms, and characterized by high local and regional diversity (Grassle and Maciolek, 1992; Smith and Snelgrove, 2002). Given the increased time efficiency offered by eDNA metabarcoding and its wide taxonomic applicability, this tool is a good candidate for large-scale biodiversity surveys and environmental impact assessments (EIAs) in the deep-sea biome.

eDNA is a complex mixture of genomic DNA present in living cells, extra-organismal DNA, and extracellular DNA originating from the degradation of organic material and biological secretions (Torti et al., 2015). Extracellular DNA has been shown to be very abundant in marine sediments, representing 50–90% of the total DNA pool (Dell'Anno and Danovaro, 2005; Corinaldesi et al., 2018). However, this extracellular DNA compartment may not only contain DNA from contemporary communities. Indeed, nucleic acids can persist in marine sediments as their degradation rate decreases due to adsorption onto the sediment matrix (Corinaldesi et al., 2008; Torti et al., 2015). Low temperatures, high salt concentrations, and the absence of UV light are additional factors enhancing long-term archiving of DNA in deep-sea sediments (Torti et al., 2015; Nagler et al., 2018). Decreased rates of abiotic DNA decay can thus allow DNA persistence over millennial timescales. Indeed, up to 125,000-year-old ancient DNA (aDNA) has been reported in oxic and anoxic marine sediments at various depths (Boere et al., 2011; Coolen et al., 2013; Lejzerowicz et al., 2013a). As extracellular DNA fragment size depends on its state of degradation (Nagler et al., 2018 report overall size ranges from 80 to over 20,000 bp), aDNA fragments have generally been reported to be <1,000 bp long (Boere et al., 2011; Coolen et al., 2013; Lejzerowicz et al., 2013a; Lennon et al., 2018). Restricting molecular biodiversity assessments to large DNA fragments may thus allow avoiding the bias of aDNA in biodiversity assessments aiming at describing contemporary communities using eDNA metabarcoding.

Environmental RNA (eRNA) has been viewed as a way to avoid the problem of aDNA in eDNA biodiversity inventories because RNA is only produced by living organisms and quickly degrades when released in the environment due to spontaneous hydrolysis and the abundance of RNases (Torti et al., 2015). Few studies have investigated this in the deep-sea, with contrasting results. Investigating foraminiferal assemblages, Lejzerowicz et al. (2013b) found similar taxonomic compositions with DNA and RNA, although highlighting that RNA is more appropriate for targeting the active community component. Contrastingly, Guardiola et al. (2016) detected marked differences between RNA and DNA inventories for most eukaryotic groups but found that both biomolecules detected similar patterns of ecological differentiation, concluding that "dead" DNA did not blur patterns of community structure. Laroche et al. (2018, 2017) found stronger responses to environmental impact in alpha diversity measured with eRNA, while eDNA was better at detecting effects on community composition. Finally, long-term archived and even fossil RNA were also reported in sediment and soil (Orsi et al., 2013; Cristescu, 2019), casting doubts as to its advantage over DNA to inventory contemporary biodiversity.

The design of a sound environmental metabarcoding protocol to inventory biodiversity on the deep seafloor relies on a better understanding of the potential influence of aDNA on the different taxonomic compartments targeted. Using commercially available kits based on 2 and 10 g of sediment, we studied samples from five deep-sea sites encompassing three different habitats and spanning wide geographic ranges in order to select an optimal protocol to survey contemporary benthic deep-sea communities spanning the tree of life. We analyze eDNA and eRNA extracts *via* metabarcoding, targeting the V4–V5 regions of the 16S ribosomal RNA (rRNA) barcode (Parada et al., 2016) for prokaryotes, the 18S-V4 rRNA barcode region for micro-eukaryotes (Stoeck et al., 2010), and the 18S-V1V2 rRNA (thereafter 18S-V1) and Cytochrome c Oxidase I (COI) barcode markers for metazoans (Leray et al., 2013; Sinniger et al., 2016).

Our objectives were threefold:

(1) Evaluate the effect of removing short DNA fragments from DNA extracts obtained using a 10-g extraction kit,

(2) Compare eDNA and eRNA inventories resulting from the same samples *via* a 2-g joint extraction kit, and
(3) Assess the aforementioned kits in terms of repeatability and suitability for different taxonomic compartments.

MATERIALS AND METHODS

Collection of Samples

Sediment cores were collected from five deep-sea sites from various habitats (mud volcano, seamounts, and an area close to hydrothermal vents; **Supplementary Table S1**). Triplicate tube cores were collected with a multicorer or with a remotely operated vehicle at each sampling site. The sediment cores were sliced into layers, which were transferred into zip-lock bags, homogenized, and frozen at −80°C onboard before being shipped on dry ice to the laboratory. The first layer (0–1 cm) was used for the present analysis. In each sampling series, an empty bag was kept as a field control processed through DNA extraction and sequencing.

Nucleic Acid Extractions and Molecular Treatments

eDNA With the 10-g PowerMax Kit

DNA extractions were performed using ∼10 g of sediment with the PowerMax Soil DNA Isolation Kit (MO BIO Laboratories, Inc., Qiagen, Hilden, Germany). To increase the DNA yield, the elution buffer was left on the spin filter membrane for 10 min at room temperature before centrifugation. For field controls, the first solution of the kit was poured into the control zip lock before following the usual extraction steps. DNA extracts were stored at −80°C.

Size Selection of eDNA Extracts

Size selection of total eDNA extracted as detailed above from ∼10 g of sediment was carried out to remove small DNA fragments. NucleoMag NGS Clean-up and Size Select beads (Macherey-Nagel, Düren, Germany) were used at a ratio of 0.5 × for removing DNA fragments <1,000 bp from 500 μl of extracted eDNA. The target fragments were eluted from the beads with 100 μl elution buffer, and successful size selection was verified by electrophoresis on an Agilent TapeStation using the Genomic DNA High ScreenTape kit (Agilent Technologies, Santa Clara, CA, United States).

Ethanol Reconcentration of eDNA Extracts

A 3.5 ml aliquot of eDNA extracted from ∼10 g of sediment was reconcentrated with 7 ml of 96% ethanol (EtOH) and 200 μl of 5 M sodium chloride (NaCl), according to the guidelines in the *Hints and Troubleshooting Guide* of the PowerMax Soil DNA Isolation Kit. As this protocol does not include any incubation time, it favors large DNA fragments. The DNA pellet was washed with 1 ml 70% EtOH, centrifuged again for 15 min at 2,500 × g, and air-dried before being resuspended in 450 μl elution buffer.

Joint Environmental DNA/RNA With the 2-g RNeasy PowerSoil Kit

Joint RNA/DNA extractions were performed with the RNA PowerSoil Total RNA Isolation Kit combined with the RNeasy PowerSoil DNA elution kit (MO BIO Laboratories, Inc., Qiagen, Hilden, Germany). Between 3 and 5 g of wet and frozen sediment were used, following the manufacturer's suggestions for marine sediments (**Supplementary Table S2**). Extraction controls were performed alongside sample extractions. The RNA pellet was resuspended in 60 μl of RNase/DNase-free water. Extracted RNA was then transcribed to first-strand complementary DNA (cDNA) using the iScript Select cDNA synthesis kit (Bio-Rad Laboratories, CA, United States) with its proprietary random primer mix. Quality control 16S-V4V5, 18S-V1, and COI PCRs were performed on the RNA extracts to test for potential DNA contamination.

PCR Amplification and Sequencing

Nucleic acid extracts were normalized to 0.25 ng/μl, and 10 μl of standardized samples were used in PCR. Four primer pairs were used to amplify one mitochondrial and three rRNA barcode loci targeting metazoans (COI, 18S-V1), micro-eukaryotes (18S-V4), and prokaryotes (16S-V4V5 for homogeneity; **Supplementary Table S3**). Two metazoan mock communities (detailed in Brandt et al., 2020) were included for 18S-V1 and COI. For each sample and marker, triplicate amplicon libraries (see Supporting Information for amplification details) were prepared by ligation of Illumina adapters on 100 ng of amplicons following the Kapa Hifi HotStart NGS Library Amplification Kit (Kapa Biosystems, Wilmington, MA, United States). After quantification and quality control, library concentrations were normalized to 10 nM, and 8–9 pM of each library containing a 20% PhiX spike-in were sequenced on a HiSeq2500 (System User Guide Part #15035786) instruments in a 250 bp paired-end mode.

Bioinformatic Analyses

All bioinformatic analyses were performed using a Unix shell script (Brandt et al., 2020), available on Gitlab[1], on a home-based cluster (DATARMOR, Ifremer). The details of the pipeline, along with specific parameters used for all metabarcoding markers, are given in **Supplementary Table S4** and in Brandt et al. (2020). Pairs of Illumina reads were corrected with DADA2 v.1.10 (Callahan et al., 2016) following the online tutorial for paired-end data[2] and delivered inventories of amplicon sequence variants (ASVs). Metazoan data were further clustered into operational taxonomic units (OTUs) with swarm v2, a single-linkage clustering algorithm (Mahé et al., 2015) that aggregates sequences iteratively and locally around seed sequences based on *d*, the number of nucleotide differences, to determine coherent groups of sequences, independent of amplicon input order, allowing highly scalable and fine-scale clustering. ASVs were swarm clustered at *d*-values of 4 for 18S-V1 and 6 for COI, using the FROGS pipeline (Escudié et al., 2018).

[1]https://gitlab.ifremer.fr/abyss-project/
[2]https://benjjneb.github.io/dada2/tutorial.html

We chose to evaluate micro-eukaryote and prokaryote diversity at the ASV level due to its increasing use in the literature (Callahan et al., 2017). Although the use of OTUs may also be justified for microbial diversity depending on study objectives (Brandt et al., 2020), we did not expect an alteration of alpha and beta diversity patterns between ASV and OTU levels for the different molecular treatments investigated. ASVs and OTUs were taxonomically assigned *via* BLAST + (v2.6.0) based on minimum similarity and minimum coverage (-perc_identity 70 and –qcov_hsp 80). For ASVs, sequences obtained with DADA2 were subsequently assigned with *blastn*. For OTUs, BLAST assignment in FROGS was performed using the *affiliation_OTU.py* command. It is not uncommon for deep-sea taxa to have closest relatives in databases (even congenerics) exhibiting nucleotide divergence exceeding 20% (Shank et al., 1999; Herrera et al., 2015). Considering our interest in diverse and poorly characterized communities, more stringent BLAST thresholds were thus not implemented at this stage. However, additional filters were performed during downstream bioinformatic processing described below, and taxonomic information was used at phylum level, only when the assignment was deemed reliable at this taxonomic level. The Silva132 reference database was used for taxonomic assignment of rRNA marker genes (Quast et al., 2012), and MIDORI-UNIQUE (Machida et al., 2017) was used for COI.

Molecular inventories were refined in R v.3.5.1 (R Core Team, 2018). A blank correction was made using the *decontam* package v.1.2.1 (Davis et al., 2018), removing all clusters that were more prevalent in negative control samples than in true or mock samples. Unassigned and non-target clusters were removed. Additionally, for metazoan loci, all clusters with a terrestrial assignment (groups known to be terrestrial-only) were removed. Samples with fewer than 10,000 target reads were discarded. We performed an abundance renormalization to remove spurious ASVs/OTUs due to random tag switching (Wangensteen and Turon, 2016). The COI OTU table was further curated with LULU v.0.1 (Frøslev et al., 2017) to limit the bias due to pseudogenes, using a minimum co-occurrence of 0.93 and a minimum similarity threshold of 84%.

Statistical Analyses

Sequence tables were analyzed using R with the packages phyloseq v1.22.3 (McMurdie and Holmes, 2013), following guidelines in online tutorials[3], and vegan v2.5.2 (Oksanen et al., 2018). Alpha diversity between molecular processing methods was estimated with the number of observed target clusters in rarefied datasets. Cluster abundances were compared *via* analyses of deviances (ANODEV) on generalized linear mixed models using negative binomial distributions, as the data were overdispersed. Pairwise *post hoc* comparisons were performed *via* Tukey honestly significant difference (HSD) tests using the *emmeans* package.

Homogeneity of multivariate dispersions was evaluated with the *betapart* package v.1.5.1 (Baselga and Orme, 2012), and statistical tests performed on balanced datasets for COI as dispersions were different between 2- and 10-g datasets (**Supplementary Table S5**). Data were rarefied for metazoans and Hellinger-normalized for microbial data.

Differences in community compositions resulting from molecular processing were evaluated with Mantel tests (Jaccard and Bray-Curtis dissimilarities for metazoan and microbial taxa, respectively; Pearson's product–moment correlation; 1,000 permutations). Permutational multivariate analysis of variance (PERMANOVA) was performed on normalized datasets to evaluate the effect of molecular processing and site on community compositions using the function *adonis2* (vegan) with Jaccard dissimilarities (presence/absence) for metazoan and Bray–Curtis dissimilarities for prokaryotes and micro-eukaryotes. The rationale behind this choice is that metazoans are multicellular organisms of extremely varying numbers of cells, organelles, or ribosomal repeats in their genomes, and can also be detected through a diversity of remains. The number of reads can thus not be expected to reflect the abundance of detected OTUs. Significance was evaluated *via* marginal effects of terms using 10,000 permutations with site as a blocking factor. Pairwise *post hoc* comparisons were performed *via* the *pairwiseAdonis* package, with site as a blocking factor. Differences between samples were visualized *via* principal coordinates analysis (PCoA) based on the abovementioned dissimilarities.

Finally, taxonomic compositions in terms of cluster and read abundance were compared between molecular processing methods. In order to compare accurately phylum-level taxonomic compositions, datasets were subsampled to clusters having a minimum hit identity of 86% for rRNA loci and 80% for COI. These values were chosen as they represent approximate minimum identity for reliable phylum assignment (Stefanni et al., 2018).

RESULTS

High-Throughput Sequencing Results

A total of 70 million 18S-V1 reads, 61 million COI reads, 30 million 18S-V4 reads, and 45 million 16S-V4V5 reads were obtained from four Illumina HiSeq runs of pooled amplicon libraries built from triplicate PCR replicates of 75 sediment samples, two mock communities (for 18S-V1 and COI), three extraction blanks, and two to four PCR negative controls (**Supplementary Table S6**). One to seven sediment samples failed amplification in each dataset. These were always coming from the same sampling sites (MDW-ST117 and MDW-ST38) and predominantly comprised RNA samples (**Supplementary Table S6**). After bioinformatic processing, read numbers were reduced to 44 million for 18S-V1, 45 million for COI, 16 million for 18S-V4, and 24 million for 16S-V4V5 (**Supplementary Table S6**). For eukaryote markers, fewer reads were retained in negative controls (2–64%) than in true or mock samples (49–83%), while the opposite was observed for prokaryotes with 16S-V4V5 (62% of reads retained in control samples against 49–57% in true samples). Negative control samples (extraction and PCR blanks) contained 0.001–0.6% of total processed reads compared to 1.3–1.5% in true samples.

[3]http://joey711.github.io/phyloseq/tutorials-index.html

DNA extracts obtained from the joint DNA/RNA protocol based on the 2-g kit produced fewer eukaryotic reads than DNA extracts from the 10-g kit, while similar yields were obtained for prokaryotes. RNA extracts produced more reads than DNA extracts with the ribosomal loci, while they produced fewer reads with the mitochondrial COI locus (**Supplementary Table S6**).

After data refining, abundance renormalization (Wangensteen and Turon, 2016), and LULU curation for COI, the final datasets comprised between 8.6 and 16.2 million target reads for eukaryotes and 21.7 million prokaryote reads. Target reads delivered 4,333 and 6,031 metazoan OTUs for COI and 18S-V1 respectively, 40,868 micro-eukaryote 18S-V4 ASVs, and 138,478 prokaryote 16S-V4V5 ASVs (**Supplementary Table S6**).

Alpha Diversity Between Processing Methods

Rarefaction curves showed that a plateau was reached for all samples, suggesting an overall sequencing depth adequate to capture the diversity present (**Supplementary Figure S1**). Processing methods significantly affected the number of recovered eukaryote and prokaryote clusters, and significant variability among sites was detected for 18S-V1 for homogeneity and 18S-V4 (**Table 1** and **Supplementary Figure S2**).

Molecular processing designed to remove small DNA fragments (i.e., size selection of DNA to remove fragment <1,000 bp and EtOH reconcentration) did not significantly affect recovered cluster numbers obtained from eDNA extracted from 10 g of sediment for any of the loci investigated (**Figure 1** and **Table 1**; Tukey's HSD multiple comparisons tests, $p > 0.9$).

Extracts based on the 2-g kit resulted in more variability, reflected by greater standard errors in mean recovered cluster numbers (15–26% of the mean for eukaryotes, 7–9% for prokaryotes) than in DNA extracts based on 10 g of sediment (8–11% for eukaryotes, 3–6% for prokaryotes).

DNA extracted using the 2-g kit recovered significantly fewer eukaryotic clusters than extracts based on ∼10 g of sediment (**Figure 1** and **Table 1**), a trend consistent across most taxa (**Figure 2**). DNA 2-g extracts recovered an average of 110 ± 16 18S-V1 and 113 ± 27 COI metazoan OTUs per sample compared to 264 ± 26 (18S-V1) and 222 ± 23 (COI) in the DNA 10-g extracts. Similarly, DNA 10-g extracts recovered on average 1,117 ± 100 protistan 18S-V4 ASVs per sample compared to 595 ± 109 detected in DNA from the 2-g kit. Contrastingly to eukaryotes, all DNA methods, whether based on ∼2 or ∼10 g of sediment, resulted in comparable prokaryote ASV numbers detected (**Figures 1**, **2** and **Table 1**; $p > 0.8$), ranging from 5,330 ± 199 to 5,810 ± 170 per sample on average.

The joint RNA/DNA extracts shared 15% (COI) to 25% (18S-V1) of metazoan OTUs, 14% of protistan 18S-V4 ASVs, and 25% of prokaryotic 16S ASVs (**Supplementary Figure S3**). With COI, most unique OTUs were present in DNA extracts (74%) and RNA detected significantly fewer metazoan OTUs than co-extracted DNA (**Figure 1**, 44 ± 12 versus 113 ± 27 respectively), a trend observed in most detected metazoan phyla (**Figure 2**). Contrastingly, with ribosomal loci, most clusters were unique to RNA (56% for 18S-V1, 63% for 18S-V4, 45% for 16S; **Supplementary Figure S3**), which recovered significantly more clusters than co-extracted DNA (**Figure 1** and **Table 1**). For prokaryotes, RNA extracts even detected significantly more ASVs than DNA extracts based on 10 g of sediment (**Table 1** and **Figure 1**), a pattern observed in most prokaryotic clades, except for the Actinobacteria, Nanoarchaeaeota, Omnitrophicaeota, and Thaumarchaeota (**Figure 2**). For 18S-V4 and 18S-V1, RNA detected a cluster richness comparable to DNA 10-g extracts (Tukey's HSD multiple comparisons tests, $p > 0.16$), yet, average cluster numbers per sample were higher in RNA than in DNA 10-g extracts in numerous groups (**Figure 2**).

Effect of Molecular Processing Methods on Beta-Diversity Patterns

PERMANOVA showed that although site was the main source of variation among samples (accounting for 20–57% of variability), significant differences existed among molecular methods in terms of community structure for all loci investigated over and above any variation due to site (**Table 1**). Pairwise comparisons indicated no significant effect of small DNA fragment removal on revealed community composition (**Table 1**), and high and significant correlations in Mantel tests (r: 0.92–1.0, $p = 0.001$) confirmed the minor effect of size selection and EtOH reconcentration. Based on these results, the size-selected and EtOH-reconcentrated DNA data were removed from further analyses, and community structures of the DNA 10-g extracts were compared with those derived from co-extracted DNA/RNA using the 2-g kit.

Pairwise comparisons showed significant differences in community structures between RNA and DNA for all markers analyzed (**Table 1**). Ordinations confirmed the predominant effect of site as the first two PCoA axes mostly resolved spatial effects (**Supplementary Figure S4**) but also revealed that communities detected by RNA differed from those detected by DNA (co-extracted DNA and DNA 10-g), the level of differentiation varying among sites (**Figure 3**).

Pairwise comparisons also indicated significant differences in community structure between DNA extracts from the 2-g and 10-g kits (**Table 1**) possibly due to higher variability among replicate cores in the DNA 2-g method as seen in ordinations (**Figure 3**).

Extraction Kit Versus Nature of Nucleic Acid

PERMANOVA of the dataset containing DNA 10-g, DNA 2-g, and RNA 2-g extracts confirmed that site was the predominant effect, explaining ∼20% of variation for metazoans, 33% of variation for micro-eukaryotes, and 54% of variation for prokaryotes. The analysis also indicated that the differences observed between processing methods were predominantly due to the type of nucleic acid rather than the kit used for extraction. Nucleic acid

TABLE 1 | Changes in cluster richness and community structures with molecular processing method (DNA 10 g: DNA extracts from ∼10 g of sediment with the PowerMax Soil kit; DNA/RNA 2 g: DNA/RNA extracts from ∼2 g of sediment with the RNeasy PowerSoil kit) and site for the four studied genes.

Locus	Cluster richness			Community differentiation			
	Chi-square	*p*-value	Significant pairwise comparisons		R^2	*p*-value	Significant pairwise comparisons
18S-V1							
Molecular processing	50.3	**<0.001**	DNA2 g < RNA 2 g***	Molecular processing	0.06	**<0.001**	DNA2 g/RNA 2 g***
Site	16.2	**<0.001**	DNA 10 g > DNA 2 g***	Site	0.23	**<0.001**	DNA 10 g/DNA 2 g***
				Molecular processing × Site	0.19	0.16	DNA 10 g/RNA 2 g***
COI							
Molecular processing	57.3	**<0.001**	DNA2 g > RNA 2 g**	Molecular processing	0.09	**<0.001**	DNA2 g/RNA 2 g**
Site	2.2	0.14	DNA 10 g > DNA 2 g*	Site	0.20	**<0.001**	DNA 10 g/DNA 2 g*
			DNA 10 g > RNA 2 g***	Molecular processing × Site	0.17	**0.0013**	DNA 10 g/RNA 2 g**
18S-V4							
Molecular processing	38.3	**<0.001**	DNA2 g < RNA 2 g***	Molecular processing	0.08	**<0.001**	DNA2 g/RNA 2 g**
Site	15.9	**<0.001**	DNA 10 g > DNA 2 g**	Site	0.35	**<0.001**	DNA 10 g/DNA 2 g**
				Molecular processing × Site	0.20	**<0.001**	DNA 10 g/RNA 2 g**
16S							
Molecular processing	55.0	**<0.001**	DNA2 g < RNA 2 g***	Molecular processing	0.06	**<0.001**	DNA2 g/RNA 2 g***
Site	3.4	0.07	DNA 10 g < RNA 2 g***	Site	0.57	**<0.001**	DNA 10 g/DNA 2 g**
				Molecular processing × Site	0.14	**<0.001**	DNA 10 g/RNA 2 g***

*ANODEVs were performed on mixed models with negative binomial distributions using rarefied datasets. PERMANOVAs were calculated on normalized datasets by permuting 10,000 times with Site as a blocking factor using Jaccard dissimilarities for 18S-V1 and COI and Bray–Curtis dissimilarities for 18S-V4 and 16S. Significant p-values are in bold. For pairwise comparisons, DNA 10 g comprises all processing methods based on DNA extracted from ∼10 g of sediment, and significance codes are ***p < 0.001; **p < 0.01; *p < 0.05.*

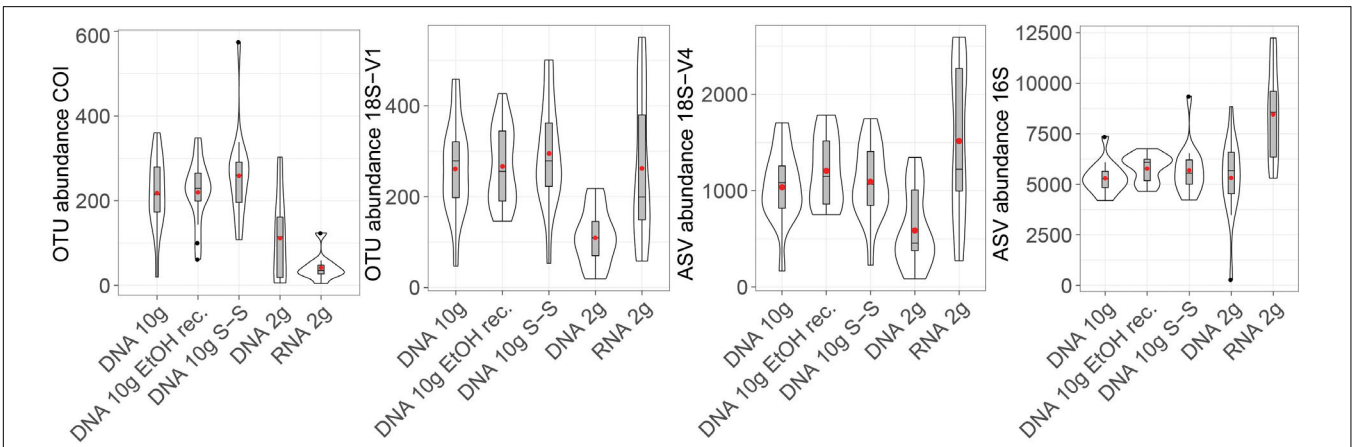


FIGURE 1 | Violin plot showing detected numbers of metazoan operational taxonomic units (OTUs) (COI, 18S-V1), micro-eukaryote (18S-V4) amplicon sequence variants (ASVs), and prokaryote (16S) ASVs recovered by the five molecular processing methods evaluated in this study (DNA 10 g: crude DNA extracts from ∼10 g of sediment with the PowerMax Soil kit; DNA 10 g EtOH rec EtOH reconcentrated 10 g DNA extracts; DNA 10 g S-S: size-selected 10 g DNA extracts; DNA/RNA 2 g: crude DNA/RNA extracts from ∼2 g of sediment with the RNeasy PowerSoil kit). Cluster abundances were calculated on rarefied datasets. Boxplots show medians with interquartile ranges. Red dots indicate mean values.

nature (DNA versus RNA) led to significant differences among assemblages for all loci, while DNA extraction kit resulted in significant differences only for 18S-V1 and 18S-V4 (**Supplementary Table S7**).

This supported observations in relative taxonomic compositions, which were more similar between samples based on DNA (**Figure 4**), a pattern consistent across cores within each site (**Supplementary Figure S5**). Expectedly, when looking at read numbers, resolved taxonomic structures were also more similar among DNA-based methods (**Supplementary Figure S6**). Comparing read and cluster abundances revealed that relative taxonomic compositions based on read numbers (**Supplementary Figure S6**) were comparable to those based on cluster numbers (**Figure 4**) for micro-eukaryotes and prokaryotes and confirmed that this was not the case for metazoans.

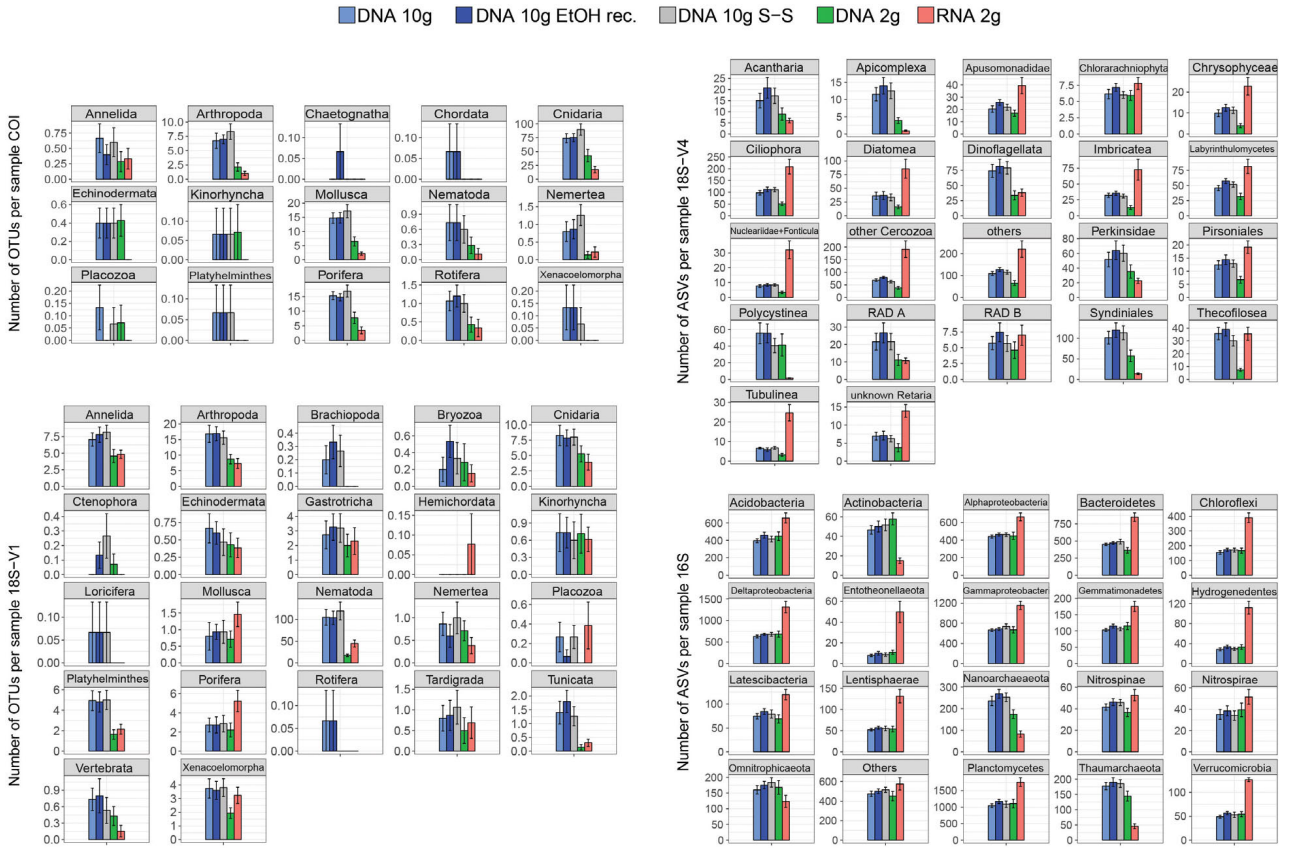


FIGURE 2 | Mean number of metazoan operational taxonomic units (OTUs) (COI, 18S-V1), protist amplicon sequence variants (ASVs) (18S-V4), and prokaryote ASVs (16S) detected per sample for each of the five processing methods (DNA 10 g: crude DNA extracts from ∼10 g of sediment with the PowerMax Soil kit; DNA 10 g EtOH rec. EtOH reconcentrated 10 g DNA extracts; DNA 10 g S-S: size-selected 10 g DNA extracts; DNA/RNA 2 g: crude DNA/RNA extracts from ∼2 g of sediment with the RNeasy PowerSoil kit). Cluster numbers were calculated on rarefied datasets. Error bars represent standard errors.

DISCUSSION

The aim of this study was to evaluate different molecular methods in order to select the most appropriate eDNA metabarcoding protocol to inventory contemporary deep-sea communities, with the lowest possible bias due to aDNA.

Using RNA rather than DNA to inventory contemporaneous communities has been suggested as a means of avoiding the bias due to long-term persistence of DNA in marine sediments. Indeed, RNA is only produced by living organisms and is thought to quickly degrade when released in the environment due to spontaneous hydrolysis and the abundance of RNases (Torti et al., 2015). Expectedly, in our COI dataset, RNA resulted in fewer OTUs (**Figure 1**) and detected fewer phyla (**Figure 2**) than co-extracted DNA. Contrastingly, for ribosomal loci, RNA detected higher cluster numbers than co-extracted DNA (**Figure 1**), resulting in more clusters per sample for most of the taxonomic groups detected (**Figure 2**). In these joint datasets, 45–63% of clusters were unique to RNA (**Supplementary Figure S2**). These unique clusters were not singleton clusters as only up to 2.2% of them had fewer than three reads, even if 5–28% had fewer than 10 reads (data not shown). Although proportions vary strongly among investigations, other studies using ribosomal loci have also reported increased recovery of OTUs in RNA datasets as well as considerable amounts of unshared OTUs between joint RNA and DNA data (Guardiola et al., 2016; Laroche et al., 2017, and references therein).

This difference observed here between COI and ribosomal loci is likely related to the nature of the targeted RNA molecule. The rapid hydrolysis of RNA mostly applies to random coils (like messenger RNA), while helical conformations (including most types of RNA, such as ribosomal RNA, transfer RNA, viral genomic RNA, or ribozymes) are less prone to hydrolysis by water molecules (Torti et al., 2015). The degradation of rRNA is thus likely to be much slower than that of messenger RNA (mRNA), which, combined with decreased digestion by RNases due to adsorption onto sediment particles (Torti et al., 2015), makes long-term persistence of rRNA possible and observed in sediments and even in fossils (Orsi et al., 2013; Cristescu, 2019). Finally, the great abundance of RNA over DNA in living organisms (e.g., 20.5% versus 3.1% in *Escherichia coli*) may also favor its persistence in the environment. This is especially true for rRNA, which is represented in a cell's RNA pool as many times

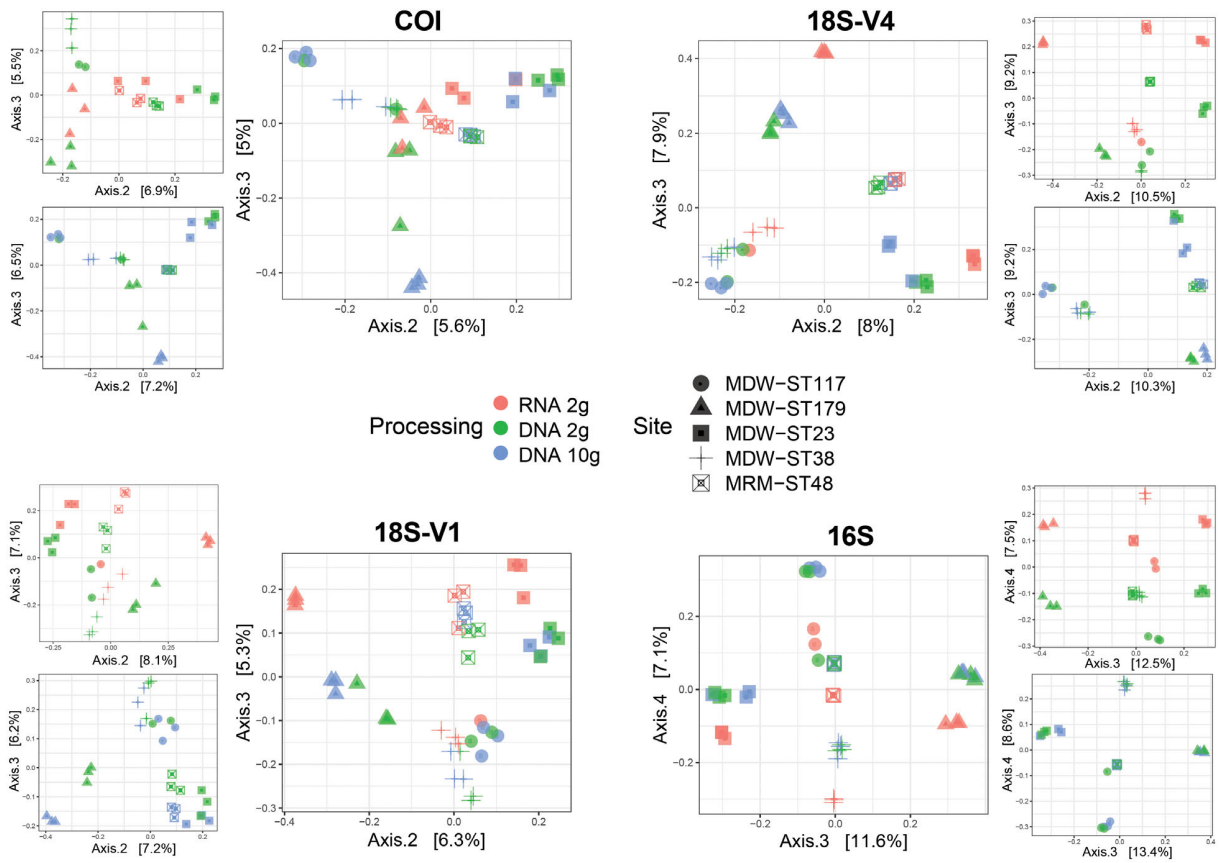


FIGURE 3 | Principal coordinates analysis (PCoA) ordinations showing community differences between RNA and DNA molecular processing methods using either RNA/DNA extracted jointly from ∼2 g of sediment (RNA 2 g/DNA 2 g) or DNA extracted from ∼10 g of sediment (DNA 10 g) in five deep-sea sites using four barcode markers targeting metazoans (COI, 18S-V1), micro-eukaryotes (18S-V4), and prokaryotes (16S). PCoAs were calculated using Jaccard dissimilarities for metazoans and Bray–Curtis dissimilarities for unicellular organisms. Inserts show pairwise PCoAs.

as there are ribosomes, while only being present in a few copies (10–150) in the genome (Torti et al., 2015).

While RNA has been reported as an effective way to depict the active community compartment (Baldrian et al., 2012; Lejzerowicz et al., 2013b; Pawlowski et al., 2014), variation in activity levels between taxonomic groups as well as differences in life histories, life strategies, and non-growth activities may confound this interpretation and generate taxonomic bias (Blazewicz et al., 2013). Instead, DNA/RNA ratios might reflect different genomic architectures (variation in rDNA copy number) among taxonomic groups rather than different relative activities (Massana et al., 2015). Thus, eRNA data need to be interpreted with caution, as some molecular clusters could be overrepresented due to increased cellular activities (Pochon et al., 2017). This could explain the higher cluster numbers detected here for ribosomal loci with eRNA compared to eDNA for several taxa (**Figure 2**).

Moreover, many of the unique RNA ASVs/OTUs may be artifacts from the reverse transcription of RNA to cDNA, a process known to generate errors that are difficult to measure and detect in bioinformatic analyses (Laroche et al., 2017) but highlighted by the greater amounts of chimeras detected in RNA extracts with ribosomal loci (**Supplementary Table S6**). This overestimation of RNA-based data will affect non-clustered data more than clustered datasets, in line with the results observed here for microbial ASVs and metazoan OTUs.

In terms of beta diversity patterns, although RNA and DNA detected significantly different communities (**Table 1**), DNA and RNA samples resolved similar spatial configurations, with samples clustering by site (**Figure 3**). This is consistent with Guardiola et al. (2016), who also reported similar patterns of ecological differentiation between DNA and RNA in deep-sea sites, although both datasets resolved different communities. Although the comparative study performed here targeted only the first 1 cm layer of sediment, the comparable results obtained by Guardiola et al. (2016) on 5 cm suggest that these findings may be expanded to deeper layers of sediments. However, spatial variation was more pronounced with DNA samples for eukaryotes, which is congruent with Laroche et al. (2017), who suggested that eDNA may be more reliable for assessing differences in community composition.

Thus, due to its suspected persistence in the environment and the unknown but potentially additional sources of bias suspected here, using eRNA for metabarcoding of deep-sea sediments does

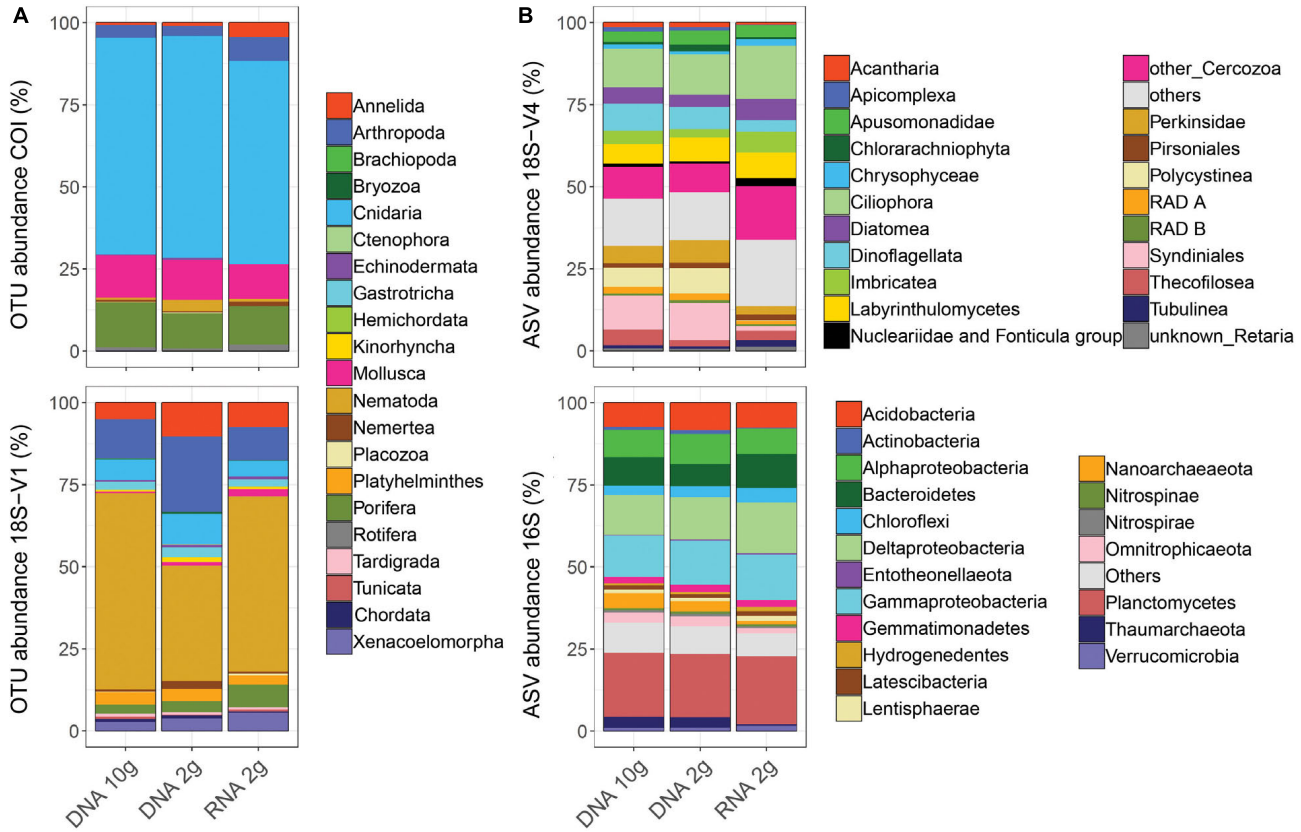


FIGURE 4 | Patterns of relative cluster abundance resolved by metabarcoding of sediment RNA and DNA from five deep-sea sites using either RNA/DNA extracted jointly from ∼2 g of sediment (RNA 2 g/DNA 2 g) or DNA extracted from ∼10 g of sediment (DNA 10 g) and using four barcode markers targeting metazoans (**A:** COI, 18S-V1), micro-eukaryotes (**B:** 18S-V4), and prokaryotes (**B:** 16S). Values were calculated on balanced datasets.

not seem to effectively address the problem of aDNA, and even less so for ribosomal loci. Other studies suggested that a more efficient way to deal with aDNA may be to use joint RNA and DNA datasets and trim for shared OTUs (Laroche et al., 2017; Pochon et al., 2017). This is however particularly stringent (given the low shared OTU proportions observed in this and other studies) and may result in a substantial number of false negatives. With COI, while mRNA may be more effectively targeting living organisms, the approach remains confronted with the taxonomic bias mentioned above, combined with higher *in vitro* lability of mRNA, making it more challenging to work with (highlighted by the increased failure of RNA extracts in this study; **Supplementary Table S6**).

Removing small DNA fragments *via* size selection (removing fragments < 1,000 bp) or EtOH reconcentration did not affect recovered cluster numbers in any of the biological compartments investigated (**Figure 1**). The methods also did not result in any significant difference in community structures (**Table 1**), suggesting that small, likely ancient, DNA fragments have a negligible impact on biodiversity inventories produced through eDNA metabarcoding. This finding is in line with results from the deep-sea (Guardiola et al., 2016; Ramírez et al., 2018) and various other habitats (Lennon et al., 2018), which showed no evidence that spatial patterns were blurred by "dead" DNA persistence, and suggested a minimal effect of extracellular DNA on estimates of taxonomic and phylogenetic diversity.

None of the methods evaluated in the present study removes DNA not enclosed in *living* cells (e.g., DNA in organelles, DNA from dead cells. . .). It is still unclear how long DNA can remain intracellular after cell death or within organelles. Future research quantifying the rate at which "dead" intracellular DNA becomes extracellular and degraded, and investigation of deeper layers of sediment, will be valuable to estimate the potential bias of archived intracellular DNA in eDNA metabarcoding inventories of extant communities. However, there is increasing evidence that DNA from non-living cells is mostly contemporary (Lennon et al., 2018). This ability to detect extant taxa that were not present in the sample at the time of collection highlights the capacity of eDNA metabarcoding to detect local presence of organisms even from their remains or excretions, and even with a small amount of environmental material.

It remains to be elucidated whether more cost- and time-effective extraction protocols specifically targeting extracellular DNA offer similar ecological resolution as total DNA kits. This is suggested to be the case for terrestrials soils (Taberlet et al., 2012b; Zinger et al., 2016), although authors have highlighted

that conclusions from these studies should be interpreted with caution as results might be influenced by actively released and ancient DNA (Nagler et al., 2018). The only available study testing this in the deep-sea showed that richness patterns were strikingly different in several metazoan phyla between extracellular DNA and total DNA. The authors suggested this to be the result of activity bias: sponges and cnidarians were overrepresented in the extracellular DNA pool because they continuously expel DNA, while nematodes were underrepresented as their cuticles shield DNA (Guardiola et al., 2016). As this comparison was performed on samples collected in two consecutive years, differences observed may partly result from temporal variation. However, another study of shallow and mesobenthic macroinvertebrates showed that targeting solely the extracellular eDNA compartment of marine sediments led to the detection of more than 100 taxa fewer than bulk metabarcoding or morphology, suggesting that extracellular DNA may not be adequate for marine sediments (Aylagas et al., 2016).

Larger amounts of sediment (≥10 g) allowed detecting significantly more eukaryotic clusters. This was not true for prokaryotes, for which both ∼2 and ∼10 g of sediment detected similar numbers of ASVs (**Table 1** and **Figure 1**). It may be suggested that in the joint RNA/DNA kit, DNA elution occurring after RNA elution induces partial DNA loss. However, such effect would be expected to equally affect eu- and prokaryotes, which was not the case here, supporting the fact that the quantity of the starting material significantly affects results for eukaryotes. The importance of adjusting the amount of starting material to the biological compartment investigated has already been documented (Creer et al., 2016; Dopheide et al., 2019), and this study confirms that while 2–5 g of deep-sea sediment may be enough to capture prokaryote diversity, microbial eukaryotes and metazoans are more effectively surveyed with larger sediment volumes.

Finally, the ∼2-g protocols were generally associated with higher variability among replicate cores for all loci investigated (**Figures 1**, **3**). This variability increases confidence intervals, reduces statistical power, and increases the risk of not identifying differences among communities, and thus impacts in EIA studies (Type II errors). Small-scale (centimeters to meters) patchiness has often been reported in the deep-sea (Grassle and Maciolek, 1992; Smith and Snelgrove, 2002; Lejzerowicz et al., 2014). While technical (PCR) replicates allow increasing taxon detection probability (decrease false positives), this within-site variability can only be mitigated by collecting more biological replicates per sampling station and using a sufficiently high amount of starting material to extract nucleic acids.

DATA AVAILABILITY STATEMENT

The data for this work has been submitted to the European Nucleotide Archive (ENA) under the following project: PRJEB33873. Please refer to the sample metadata in **Supplementary Material** to download samples from ENA. Additionally, the full dataset, including raw sequences, databases, ASV/OTU tables, and scripts (Gitlab link) are available through https://doi.org/10.12770/cf00aa7b-67e7-49c4-8939-038c4a9d887f.

AUTHOR CONTRIBUTIONS

MB, CL-H, and SA-H designed the study. MB, JP, and CL-H carried out the laboratory work. MB and BT performed the bioinformatic analyses. MB, BT, and NH performed the statistical analyses. MB and SA-H wrote the manuscript. All authors contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00234/full#supplementary-material

DATA SHEET S1 | Supplementary material tables (S1 to S7) and figures (S1 to S6).

DATA SHEET S2 | Sample metadata.

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Spatial Self-Organization as a New Perspective on Cold-Water Coral Mound Development

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Cold-water corals build extensive reefs on the seafloor that are oases of biodiversity, biomass, and organic matter processing rates. The reefs baffle sediments, and when coral growth and sedimentation outweigh ambient sedimentation, carbonate mounds of tens to hundreds of meters high and several kilometers wide can form. Because coral mounds form over ten-thousands of years, their development process remains elusive. While several environmental factors influence mound development, the mounds also have a major impact on their environment. This feedback between environment and mounds, and how this drives mound development is the focus of this paper. Based on the similarity of spatial coral mound patterns and patterns in self-organized ecosystems, we provide a new perspective on coral mound development. In accordance with the theory of self-organization through scale-dependent feedbacks, we first elicit the processes that are known to affect mound development, and might cause scale-dependent feedbacks. Then we demonstrate this concept with model output from a study on the Logachev area, SW Rockall Trough margin. Spatial patterns in mound provinces are the result of a complex set of interacting processes. Spatial self-organization provides a framework in which to place and compare these processes, so as to assess if and how they contribute to pattern formation in coral mounds.

Keywords: oceanography, pattern-formation, self-organization, cold-water corals, carbonate mounds

INTRODUCTION

Cold-water coral ecosystems are true oases amidst a deep-sea desert, with higher biodiversity (Henry and Roberts, 2007), biomass (Bongiorni et al., 2010; Demopoulos et al., 2014) and organic matter processing rates (Cathalot et al., 2015; de Froe et al., 2019) as compared to the off-reef soft-sediment seafloor at similar water depth.

When scleractinian cold-water corals grow, they build a structurally complex framework consisting of a mosaic of living corals, dead coral branches, associated fauna and coral rubble. The reef framework reduces the current velocity (Mienis et al., 2019) and thereby stimulates settling of

fine particles between the coral branches (Dorschel et al., 2005; de Haas et al., 2009). When coral growth and sediment accumulation within the framework outweighs "ambient" sedimentation of the off-reef seafloor, carbonate mounds, of tens to hundreds of meters high and several kilometers wide, are formed on geological time scales (Dorschel et al., 2005; Douarin et al., 2014; Van der Land et al., 2014; Wienberg and Titschack, 2017). Hence, coral mound formation is tightly linked to coral growth and sediment infill (Roberts et al., 2006).

The remoteness of the deep sea and the slow growth rate of mounds make it difficult to obtain insight in the processes that govern mound formation through observations alone. Environmental parameters, such as hydrodynamics, organic matter concentration and particle supply can be measured directly (e.g., Mienis et al., 2007; Davies et al., 2009; Wagner et al., 2011), but often only at a few locations and for a limited amount of time. Long sediment cores reveal information on mound growth and non-growth periods, but do not convey information on the governing environmental parameters or from periods when erosion prevailed (Hebbeln et al., 2019). Multi-beam or side-scan sonar maps provide spatial configurations of coral mounds on the seafloor, but this retrieves little information on their temporal dynamics and the underlying processes. A conceptual framework in which insights from these various data sources can be integrated may represent an interesting step forward.

Here, we provide a new perspective on cold-water coral mound formation which could serve as such a conceptual framework. It is based on the theory of spatial self-organization, a theory that is well-rooted in terrestrial and coastal sciences (Rietkerk and van de Koppel, 2008), but that has found little application for deep-sea ecosystems so far. Specifically, we hypothesize that coral mounds form on the seafloor through the interplay of positive and negative feedbacks. Positive feedbacks are processes that increasingly stimulate mound growth as they grow bigger and we will argue that these positive feedbacks act primarily at the local scale. In contrast, negative feedbacks result in an inhibitory effect on mound formation and we will argue that these act at some distance from the mound. Provided that environmental conditions are suitable for coral growth and mound development, we propose that these scale-dependent positive and negative feedbacks shape the mounds and their orientation on the seafloor.

THEORY OF SPATIAL SELF-ORGANIZATION

How scale-dependent feedbacks shape the environment is described by Alan Turing, in his attempt to explain the breaking of spherical symmetry during embryonic development (Turing, 1990). Since then, scale-dependent feedbacks have been used to explain how a variety of biological systems are shaped (Camazine et al., 2001), such as the synchronized flashing of fireflies, beehives, the appearance of animal skin (Kondo, 2002) and shells (Meinhardt, 1995), and in many ecological systems (Rietkerk and van de Koppel, 2008).

Probably the best-studied ecological example is arid vegetation. Aerial photography shows that in dry climates, vegetation forms a conspicuous spatial pattern of alternating vegetation bands and bare soil (**Figure 1A**). The mechanisms driving this pattern formation is that when water runs down a slope it is caught by a tussock of vegetation. Vegetation increases water infiltration with its roots, that serve as channels in the soil, thereby stimulating its own growth; a local-scale positive feedback. At the same time, the enhanced water infiltration reduces water supply downslope of the tussock, so vegetation growth is inhibited behind the tussock; a negative feedback at some distance. The interplay of these feedbacks creates a patterned state: on sloping terrain alternating bands of vegetation and bare soil appear, and under other environmental conditions, vegetation spots, mazes and gap patterns exist (Rietkerk et al., 2002). The initial distribution of the organism is here insignificant for pattern formation, because the organisms takes over the process of pattern formation, through scale-dependent feedbacks.

Regular patterns formed via spatial self-organization are also found in the marine environment, e.g., mussel beds (**Figure 1B**) and tropical coral reefs (**Figure 1C**). Settlement of young mussels is enhanced on existing mussel patches, as larvae need to attach to hard substrate with byssal threads (i.e., local-scale positive feedback). Downstream of a feeding mussel-patch however, water gets depleted of food, inhibiting mussel growth behind the patch (i.e., negative feedback at a distance). In a predominantly unidirectional current, these two feedbacks can cause the formation of bands of mussels from an initially random distribution of mussels (van de Koppel et al., 2005). Regular bands, called "spurs and grooves," in tropical coral reefs are also thought to be caused by a positive and a negative feedback. The spurs are favorable habitat for corals and/or coralline algae, which heighten the spur by accretion, similar to cold-water coral mounds. In the grooves, however, sediment erodes (Gischler, 2010). Spots and maze (or "reticulate") patterns are also seen in tropical coral reefs (Schlager and Purkis, 2015).

Interestingly, multi-beam and side-scan sonar topography maps of the deep seafloor of cold-water coral mound provinces from around the world, show regular bands, ridges and spots (**Figures 1D–F**) that are surprisingly similar to the systems that are known to be governed by spatial self-organization. For example, cold-water coral mounds on the Norwegian shelf, probably originating from the start of the Holocene, show ridge- and spot-like patterns (**Figure 1D**; Bøe et al., 2016). In the Gulf of Mexico, individual reefs align in a maze- and ridge-like pattern (**Figures 1E,D**; Hebbeln et al., 2014), where the mounds are subjected to a current that regularly shifts about 30 degrees. The shift in current direction is thought to be the cause of this maze pattern as the ridges appear to align in both current directions (Hebbeln et al., 2014). Finally, coral mound structures in the Florida Strait (**Figure 1F**; Correa et al., 2012) are subjected to a unidirectional current and bear strong resemblance to the bands in the mussel bed (**Figure 1B**), albeit at a different scale. Other examples of cold-water coral mound patterns are also mentioned in the literature. Somoza et al. (2014), for example, report coral mounds that are lined up in ridges, alternated by bare sediments,

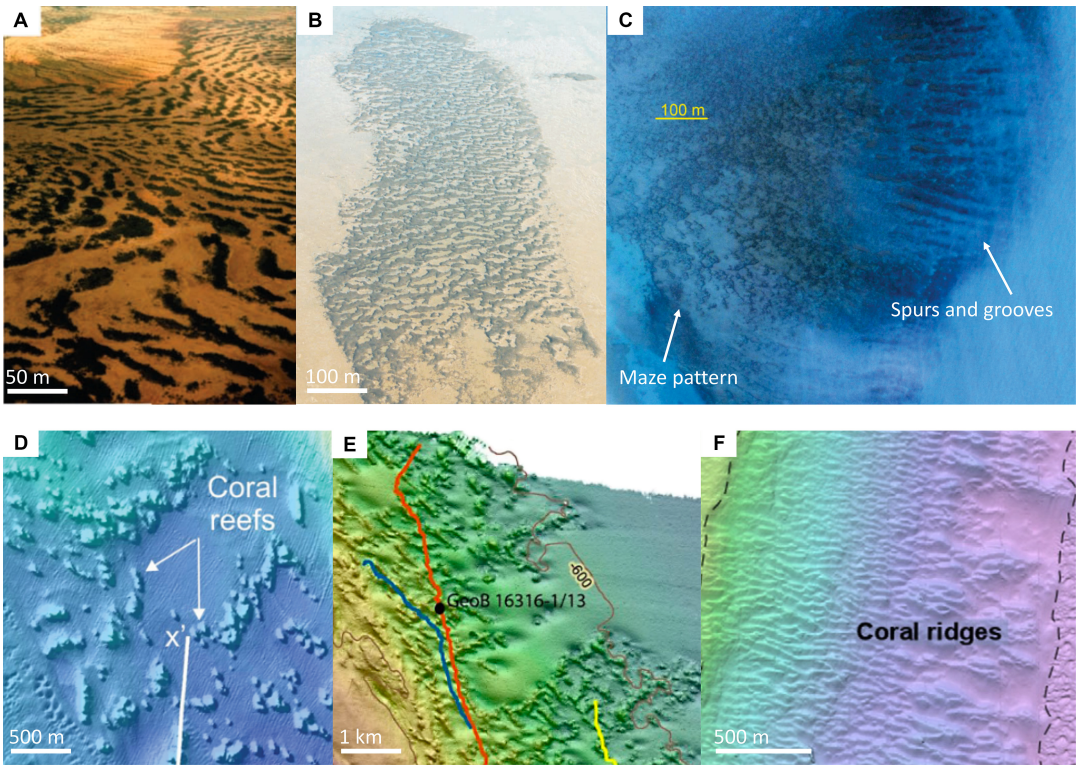


FIGURE 1 | Spatial patterns in natural systems. **(A)** Arid vegetation forming regular bands (adapted from Rietkerk et al., 2004. Reprinted with permission from AAAS). **(B)** Regular bands in a young mussel bed (adapted from van de Koppel et al., 2005. ©2005 by University of Chicago Press). **(C)** Maze (or "reticulate") patterns, and a banded pattern called "spurs and grooves," in tropical coral reefs (adapted from Schlager and Purkis, 2015. ©2014 The Authors. Sedimentology. ©2014 International Association of Sedimentologists). **(D)** Coral reefs in northern Norway, Hola reef, clustering into bands (adapted from Bøe et al., 2016. ©2016 The Geological Society of London). The white line with X' is the start of a sub-bottom profile transect. **(E)** Coral ridges in the Gulf of Mexico, Campeche coral mound Province, forming a maze pattern (adapted from Hebbeln et al., 2014. ©2014 The Authors. CC Attribution 3.0 License). Depth contours are shown for 500 m (left) and 600 m (right). Colored lines denote (parts of) ROV dives. GeoB is a station number. **(F)** Coral ridges near Miami (adapted from Correa et al., 2012. ©2012. With permission from Elsevier). Dashed lines mark the area of the slope, which is covered in coral ridges. Miami Terrace is on the left and the base on the right. The terrace also features coral ridges, but the base is covered in sand dunes. Approximate scales are indicated.

and White et al. (2007) found that mound clusters are oriented toward the strongest currents.

SPATIAL SELF-ORGANIZATION THEORY APPLIED TO COLD-WATER CORAL MOUNDS

If the coral mound patterns, as identified in the previous section, are indeed the result of spatial-self organization, then we should be able to identify positive feedbacks and negative feedbacks that act at different spatial scales. The positive and negative feedbacks can be visualized as in **Figure 2A** and are "scale-dependent," as the feedback changes from positive (green) to negative (yellow) with increasing distance from the mound.

Positive Feedbacks on Coral Mound Growth

Several mechanisms causing positive feedbacks can be found in the literature regarding coral mounds. The presence of coral reef framework has a positive effect on mound development, because it baffles suspended sediment and stimulates mound growth (Dorschel et al., 2007; Mienis et al., 2009a; Hebbeln et al., 2016) and stability (Titschack et al., 2015). Furthermore, settlement of coral larvae is greatly enhanced on coral mounds because of the presence of dead coral framework, shells and other debris from reef dwellers (Freiwald, 2002). Cold-water corals are passive suspension feeders and thus depend on water currents to intercept suspended food particles. Coral mounds have a positive effect on coral growth by accelerating currents and enhancing turbulence, because of the formation of lee waves and non-linear hydrodynamic features such as hydraulic jumps and internal bores (Mohn et al., 2014; Van Haren et al., 2014; Mienis et al., 2009b). Such internal waves can cause vertical water excursions of as much as 200 m (Mienis et al., 2007), which enhance downward transport of nutritious particles to the mounds (Duineveld et al., 2007; Davies et al., 2009; Kenchington et al., 2017). This effect becomes stronger for larger mounds, highlighting the positive feedback effect (Cyr et al., 2016). The accelerated currents and turbulent mixing increase the encounter rate of suspended

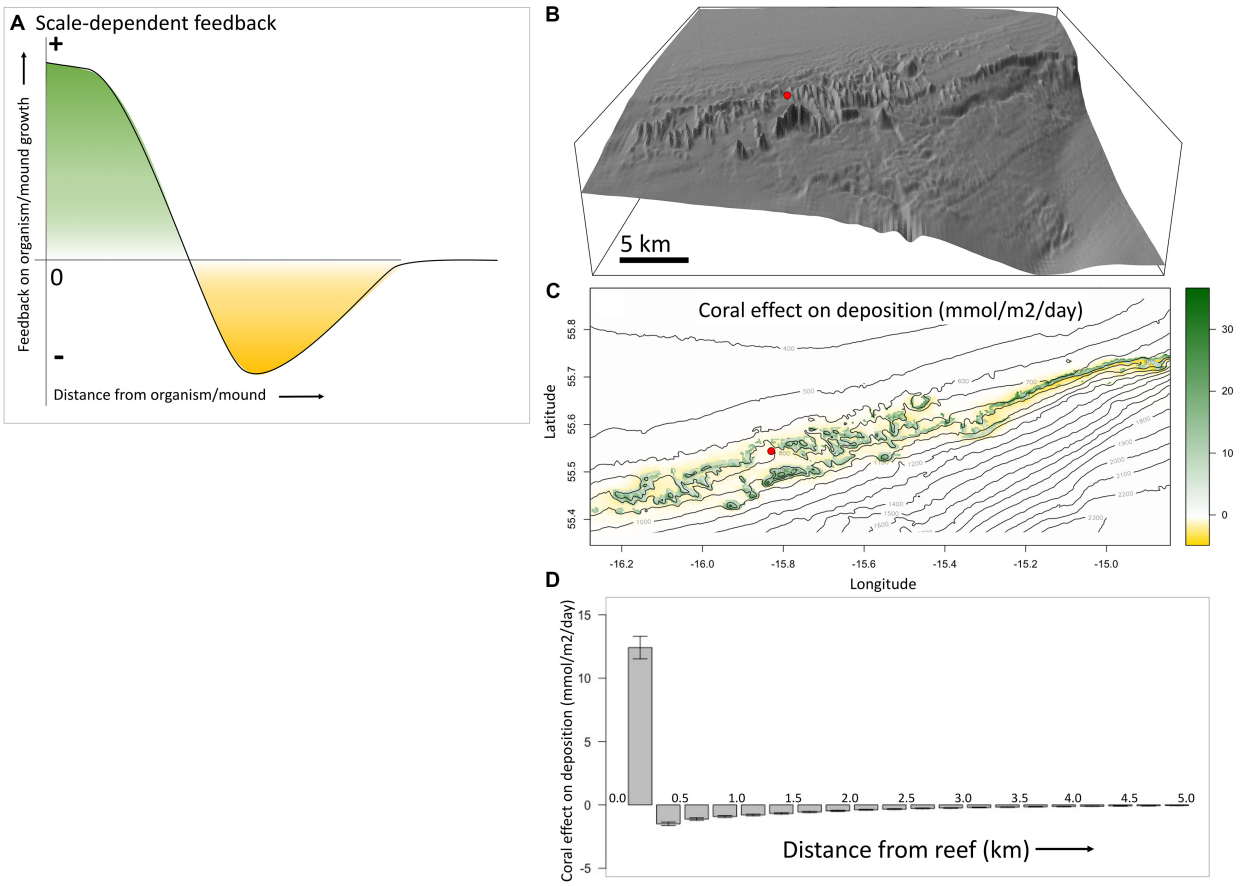


FIGURE 2 | Scale-dependent feedbacks visualized. **(A)** Depicted are the proposed scale-dependent feedbacks as caused by the presence of coral mounds, in a classic scale-dependent feedback figure (e.g., Figure 1B in Rietkerk and van de Koppel, 2008). Near the mound there is a positive feedback (green) on reef-, and therefore mound-, growth, whereas there is a negative feedback (yellow) at a larger distance from the mound. **(B)** The study area of the Southwest Rockall Trough (Logachev) area. The red circle serves as a reference to the map in panel **(C)**. **(C)** The effect of coral presence on organic carbon deposition (mmol m^{-2} day^{-1}) is mapped, with positive effects in green and negative effects in yellow. It shows a positive effect of reefs on their food supply on the mounds, and a negative effect around the mounds. **(D)** This classic scale-dependent feedback plot shows the average effect of coral reefs on their food supply, with error bars showing the 95% confidence level. Locally (distance = 0) there is a mean positive effect on deposition and until about 3 km from the reefs there is a mean negative effect. These feedbacks are illustrated using model output from Soetaert et al. (2016), for the SW Rockall Trough margin.

particles with coral feeding tentacles, and thereby likely enhance coral growth.

Negative Feedbacks on Coral Mound Growth

Negative feedbacks are also reported in the literature, and, typically, negative feedbacks are dominant over positive feedbacks, at some distance from the mound. One such scale-dependent negative feedback is caused by the filtering activity of the cold-water coral reef community that depletes the water of food particles around or downstream of the reefs (Wagner et al., 2011; Soetaert et al., 2016). Another negative feedback might come from erosional forces such as scouring, the process whereby sediment is eroded away around the base of mounds, due to the acceleration of currents. Indeed, larger mounds have larger and deeper scour marks (Lim et al., 2018), suggesting that lateral mound development is increasingly hampered by these erosional forces. By inhibiting lateral mound development, such a scale-dependent feedback can shape mounds into self-organized patterns.

Another erosional force, hydraulic drag, may also be an important factor in shaping coral mounds. A model for the Eastern Rockall Trough mounds explained the elliptical shape of the mounds as well as the mound-size distribution, using hydraulic drag. The negative feedback from drag increases as mounds grow, preventing further mound growth as soon as it becomes stronger than reef growth (O'Reilly et al., 2003).

Within coral mound provinces, i.e., areas where several coral mounds exist together, it seems that mound tops are situated around the same depth (Mienis et al., 2006; Wheeler et al., 2007). Several mechanisms have been put forward to explain this observation. At the South-West Rockall Trough margin, the presence of intermediate nepheloid layers (INL) around the tops of the coral mounds has been linked to higher turbidity and increased food supply toward the corals (Kenyon et al., 2003;

Mienis et al., 2007). The depth of mound-tops has also been linked to the presence of the permanent thermocline and water mass boundaries, which may provide favorable conditions by enhanced current speeds and vertical movement of isopycnals through internal waves (White and Dorschel, 2010; Hebbeln et al., 2014; Matos et al., 2017; Wang et al., 2019).

Visualizing Feedbacks Using the SW Rockall Trough Margin as Case-Study

The concept of scale-dependent feedbacks acting on coral mound formation can be demonstrated based on a model study on the Logachev area (**Figure 2B**), SW Rockall Trough margin (Soetaert et al., 2016). Here, food supply mechanisms to coral mounds were investigated by combining various modeling techniques. Hydrodynamics in the area, simulated in 3D (Mohn et al., 2014), was used to model organic matter dynamics in the water column, including export production, 3D-advective transport, decay, and sinking. The original paper considered two scenarios, one with organic matter uptake by reef organisms and one without uptake by reef organisms. We used the difference between both scenarios to demonstrate the net feedback caused by the suspension feeding activity of the reef community on organic matter deposition (**Figures 2C,D**).

In **Figure 2C** we plotted the effect of corals on their own food supply on a bathymetric map of the area. The mounds appear in green, because the reefs have a local positive effect on organic matter deposition. Around the mounds, depletion of organic matter by reef filtering is colored yellow. These effects can also be plotted in a classic scale-dependent feedback plot (**Figure 2D**). This shows the effect at increasing distance from the reefs, averaged over bins of 0.25 km. On the reefs, at a distance of 0–0.25 km from the reefs, the average effect is positive. At a distance of 0.25–0.5 km from the reefs the average effect is negative. The strength of the negative effect decreases until it is gone at about a distance of 3 km from the reefs.

DISCUSSION

Inherited or Self-Organized Patterns

An alternative hypothesis that could explain patterns in cold-water coral mounds, is that corals colonized pre-existing (inherited) patterns. Such patterns can come from heterogeneity in landscape suitability. For example, in arid vegetation, the self-organized pattern can be distorted by patches of rock, where plants cannot settle (Sheffer et al., 2013). Sheffer et al. (2013) show that arid vegetation patterns in nature are likely a mixture of inherited and self-organized patterns and that the probability of occurrence of self-organized patterns increases as the area suitable for plant establishment increases. Coral larvae settle only on hard substrate and therefore seem bound to follow pre-existing patterns of hard substrate. Antecedent karst, for example, can explain patterns in some tropical coral reefs (Schlager and Purkis, 2015). However, as they grow into reefs, corals start to supply their own suitable substrate. This process is subject to positive and negative scale-dependent feedbacks, as described in this paper, that shape reefs into patterns. Indeed, Schlager and Purkis (2015) show that many patterns in tropical coral reefs cannot be explained by patterns in the underlying topography.

Pre-existing patterns could also be formed by physical processes, such as sand waves and ripples, which are often observed close to coral mounds (e.g., Mienis et al., 2006; Correa et al., 2012; Lim et al., 2018). However, an inherited pattern would require that cold-water corals follow the pre-existing topography without changing it. Correa et al. (2012) show that the shape and distribution of coral ridges cannot be explained by pre-existing patterns. Moreover, the coral ridges have their steepest slope facing the current, which is the reverse of sand ripples that have their steepest slope at the lee side. So, even if corals initially inherited the sand wave pattern, coral growth subsequently changed the bathymetry by stabilizing the sediment, exerting scale-dependent feedbacks and "self-organizing" the system into its current state. This is a known process in another self-organized system: dune development, in which crescent-shaped "barchan dunes" have their crest facing the wind, but reverse their shape when colonized by vegetation that stabilizes the sand (Tsoar and Blumberg, 2002).

From Initial Settlement to Full-Grown Coral Mound

A possible sequence of events leading to self-organized patterns, could be as follows. Cold-water corals initially settle on available hard substrate. If the environment is favorable enough, they form into bush-like coral colonies that grow outward and aggregate to form complex three-dimensional reefs. At this point, coral structures create their own suitable environment, and underlying hard substrate becomes inconsequential for further settlement and growth: new corals can settle on dead coral rubble and coral framework can grow outward from established coral colonies. If the environment permits, reefs can start forming mounds, a process that, we argue, is shaped by scale-dependent feedbacks that cause the formation of self-organized patterns, such as coral ridges.

At the early mound formation stage, the initial distribution pattern gets lost as positive and negative scale-dependent feedbacks start to dominate. Larger mounds would then negatively affect nearby, smaller mounds, inhibiting coral growth on the latter. This implies the co-occurrence of large mounds with thriving corals, next to smaller mounds with degraded coral cover. Evidence for such co-occurence is reported in literature (e.g., Foubert and Henriet, 2009; De Clippele et al., 2017), but is not ubiquitous. This may be, because observations have not yet been interpreted in light of this process. Another reason may be an observation bias, as larger mounds are surveyed preferentially above the seabed in between mounds. Furthermore, larger mounds may also outcompete smaller mounds, while leaving little evidence of the smaller, dead mounds, through three non-mutually exclusive processes: (1) erosion of the smaller mounds, (2) burial after they became inactive, and (3) clustering of smaller mounds into larger mounds.

Evidence of mounds eroded away would be hard to find, but is not unlikely given that large mounds form on time scales

of thousands to millions of years. Mound burial is reported, with several studies showing the presence of living mounds close to buried mounds, e.g., on the Moroccan margin (Vandorpe et al., 2017), the Magellan province (Huvenne et al., 2007), West Melilla mound Province (Iacono et al., 2014), and the SW Rockall Trough margin (Mienis et al., 2006). Clustering of smaller mounds to form larger mounds, has also been observed (e.g., De Mol et al., 2002; de Haas et al., 2009; Lim et al., 2018). Vandorpe et al. (2017) even write that, by clustering into larger features, small coral mounds can enhance coral mound growth, by intensifying bottom currents locally. They describe a scale-dependent feedback, supporting the idea of coral mound self-organization.

Contribution of Processes to Scale-Dependent Feedbacks

Coral mound development is the outcome of a complex set of interacting processes. However, for some processes it may be unclear whether they are influenced by the mounds, or even whether they have a positive or negative effect. For instance, sedimentation is usually seen as an external factor, but it might be enhanced by mound presence, similarly as food particles. While sedimentation is necessary for mound growth and thus enhances mound development in most cases, if cold-water coral growth declines, it could also limit mound development by burying the coral reefs (De Mol et al., 2002; Foubert et al., 2008). Coral mounds are often situated in a high energy regime. The mobility of the sediments in such environments can restrict lateral mound development by burying the corals at the base (Dorschel et al., 2007; Mienis et al., 2007). While scour is a process that can restrict lateral mound growth (see above), it may also have a positive effect on mound development, as the accelerated currents can uncover hard substrates such as rocks in the sediment. Hard substrates are necessary for initial coral settlement and can therefore stimulate coral seabed colonization (Lim et al., 2018).

There are also processes that influence coral growth and coral mound development, but that do not trigger feedbacks because they are not affected by the presence of mounds or corals. An example is the type of sediment that is deposited on the coral mounds (Foubert et al., 2008; Pirlet et al., 2011; Hebbeln et al., 2016). Other external factors that influence cold-water coral growth, and that are beyond control of corals, are temperature (Freiwald and Roberts, 2005), water density (Flögel et al., 2014), oxygen (Dodds et al., 2007; Wienberg et al., 2018), and aragonite saturation state (Guinotte et al., 2006; Roberts et al., 2006). Although these factors play a major role, they merely set the scene, i.e. they determine whether or not corals can possibly occur in a region. Based on our hypothesis, it is only when presence of coral or mounds themselves can affect environmental factors, that interesting patterns may emerge.

OUTLOOK

Rapid cold-water coral extinction events are frequently observed in geological records. Such "tipping-points" are a well-known (theoretical) response of self-organized systems to a gradual change in environmental conditions. However, how self-organized systems respond to changing environmental conditions and how spatial patterns link to resilience, has recently become a topic of debate. Current belief is that the resilience of self-organized systems is not governed by a single tipping point, but by a cascade of destabilizations.

Coral mounds may provide an interesting new case to study resilience of systems governed by scale-dependent feedbacks. Mound structures remain for thousands of years even after coral reef extinction. This may facilitate recolonization as is indeed demonstrated by long cores drilled in the mounds that document sequences of individual coral growth periods, interrupted by periods without coral growth. An interesting topic is then to study the impact that scale-dependent feedbacks have for the resilience of coral systems, and how this will affect these enigmatic deep-sea environments in the near and far future.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://doi.org/10.1594/PANGAEA.911414.

AUTHOR CONTRIBUTIONS

JK, DO, and KS initiated the study idea. KS provided the model output data. A-SK analyzed the data and wrote the manuscript. All authors contributed with in-depth knowledge from their respective fields and experience, contributed to manuscript revision, read and approved the submitted version.

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Crumbling Reefs and Cold-Water Coral Habitat Loss in a Future Ocean: Evidence of "Coralporosis" as an Indicator of Habitat Integrity

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Ocean acidification is a threat to the net growth of tropical and deep-sea coral reefs, due to gradual changes in the balance between reef growth and loss processes. Here we go beyond identification of coral dissolution induced by ocean acidification and identify a mechanism that will lead to a loss of habitat in cold-water coral reef habitats on an ecosystem-scale. To quantify this, we present *in situ* and year-long laboratory evidence detailing the type of habitat shift that can be expected (*in situ* evidence), the mechanisms underlying this (*in situ* and laboratory evidence), and the timescale within which the process begins (laboratory evidence). Through application of engineering principals, we detail how increased porosity in structurally critical sections of coral framework will lead to crumbling of load-bearing material, and a potential collapse and loss of complexity of the larger habitat. Importantly, *in situ* evidence highlights that cold-water corals can survive beneath the aragonite saturation horizon, but in a fundamentally different way to what is currently considered a biogenic cold-water coral reef, with a loss of the majority of reef habitat. The shift from a habitat with high 3-dimensional complexity provided by both live and dead coral framework, to a habitat restricted primarily to live coral colonies with lower 3-dimensional complexity represents the main threat to cold-water coral reefs of the future and the biodiversity they support. Ocean acidification can cause ecosystem-scale habitat loss for the majority of cold-water coral reefs.

Keywords: deep-sea coral, ocean acidification, coral, habitat loss and degradation, *Lophelia pertusa*, dissolution

INTRODUCTION

Ocean acidification is of concern to both tropical and cold-water coral (CWC) reefs (Secretariat of the Convention on Biological Diversity [CBD], 2014). It can cause a reduction in the growth rate of live coral (Kline et al., 2019), and dissolution of dead coral skeletons (skeletons no longer covered in soft tissue) either directly (Hennige et al., 2015a) or indirectly through increasing rates of bioerosion

(Wisshak et al., 2012; Davidson et al., 2018). This can lead to a reduction in the net growth rate in the case of tropical coral reefs (Albright et al., 2018; Eyre et al., 2018; Kline et al., 2019). For CWC reefs, the severity of the threat of ocean acidification is vastly different to that projected for tropical reefs due to two factors: (1) CWC reef habitats and the biodiversity provision afforded by them is mostly provided by dead coral skeletal framework and exposed rubble ("live" coral has soft-tissue covering the skeleton whilst "dead" coral is when soft-tissue is no longer present, and the skeleton is exposed to seawater). (2) The aragonite saturation horizon (ASH), which is the depth at which aragonite (the polymorph of calcium carbonate commonly precipitated by scleractinian corals) becomes undersaturated, will rise above the majority of CWC reefs over the coming decades. Ocean acidification can thus have a *direct* and potentially rapid impact on the major load-bearing fraction of these habitats; the dead coral skeletons.

While tropical reefs are projected to experience reduced aragonite saturation levels in addition to large diel fluctuations from biological activity (Shaw et al., 2012), they will not be exposed to seawater that is permanently undersaturated with respect to aragonite ($\Omega_{Arag} < 1$), unlike the majority of CWC reefs. CWCs are typically restricted to oceanic waters and temperatures between 4°C and 12°C, which is ∼50–1000 m at high latitudes, and down to 4000 m beneath warm water masses at low latitudes (Roberts et al., 2006). The reefs and carbonate mounds they form can be up to 300 m high, several kilometres in diameter (Roberts et al., 2006), and have a global distribution (Freiwald et al., 2005). Projected ocean acidification due to rising atmospheric concentrations of CO_2 (Secretariat of the Convention on Biological Diversity [CBD], 2014) will drive the ASH shallower (Perez et al., 2018), leaving ∼70% of these CWC reefs in permanently aragonite undersaturated water by the end of the century (year 2099 with CO_2 concentrations of 788 ppmv) (Guinotte et al., 2006).

The particular concern is whether CWC reef habitat will persist once the ASH shoals past them, given that the majority of these reefs are currently above the ASH (over 95% in pre-industrial times; Guinotte et al., 2006). This leaves us with the question of whether CWC reef habitat will persist once the ASH shoals past them. One possibility is that gradual dissolution of exposed skeletal material (when exposed to aragonite undersaturation) could be countered by sustained live coral growth rates and sediment infilling, meaning little difference to reef structures. Conversely, dissolution of the supporting, dead coral framework that sits above infilled sediment/rubble and below live coral could lead to a rapid degradation of habitats and a dramatic loss in habitat complexity if it occurs faster than sediment infilling. To understand what future impacts of a shoaling ASH may be, it is crucial that we look at current CWC reefs that are found below the ASH (Thresher et al., 2011; Baco et al., 2017).

While the vast majority of cold-water reefs occur in the North Atlantic where the ASH can extend to ∼2000 m, small patchy reefs do exist in the North Pacific (Hardin et al., 1994; Baco et al., 2017; Gómez et al., 2018; Salgado et al., 2018) where the ASH occurs at depths from ∼50 to 600 m. This shallow ASH is a consequence of global thermohaline circulation (Feely et al., 2004), anthropogenic input of carbon dioxide (Feely et al., 2008), and regional upwelling of CO_2-rich older water masses onto the continental shelf (Feely et al., 2008). Pacific localities, like the Southern California Bight, are projected to experience rapid shoaling of the ASH (Gruber et al., 2012; Hauri et al., 2013; Osborne et al., 2019), meaning corals in these systems are at the forefront of environmental change. CWC in these localities are currently in conditions that are analogous to the water chemistry that most CWC reefs will experience by the year 2099 (Guinotte et al., 2006). Therefore, the Southern California Bight provides a "natural laboratory" for assessing projected impacts of ocean acidification on CWC ecosystems.

When we look at coral habitats in the Southern Californian Bight (**Figure 1**), it is clear that there is a shift between the *L. pertusa* habitats above and below the ASH, with a marked absence of dead coral and low habitat complexity in habitats below the ASH (**Figure 1b**). The occurrence of live coral below the ASH in general complements research on *L. pertusa* to date, indicating that live coral can continue to calcify under projected temperature and ocean acidification conditions (McCulloch et al., 2012a,b; Hennige et al., 2014b, 2015a; Lunden et al., 2014; Movilla et al., 2014). However, whether the acclimatory cost of this can be met in the long-term is still debatable, with different laboratory studies highlighting different processes depending on time scales of the experiments, energetic input, presence of additional stressors or species of framework forming CWC (Hennige et al., 2015a; Büscher et al., 2017; Gammon et al., 2018).

Regardless, focus on just live corals ignores the larger and more serious ecosystem-scale threat to these habitats and associated biodiversity from a shoaling ASH; the potentially rapid loss of structural integrity and habitat complexity (**Figure 2**). This is of particular concern as high biodiversity associated with CWC reefs is strongly related to their structural complexity (Henry and Roberts, 2007, 2015; Kazanidis et al., 2015). The majority of a CWC habitat is typically exposed dead coral (Vad et al., 2017) sitting on top of solid substrate or consolidated sediment and rubble, with the living coral concentrated at the outermost parts of the reef above the dead coral, where the coral can access and capture passing prey (Roberts et al., 2006, 2009). The complexity of CWC reefs not only sustains locally high species diversity (alpha diversity) but the hydrodynamic regimes and spatial mosaic of macro- and micro-habitats within the reefs also drives high species turnover (beta diversity) (Henry and Roberts, 2007, 2015). Interweaving coral branches create many small cavities for fish and invertebrates (e.g., **Figure 1a**) and provide important refuge and spawning sites for vulnerable low fecundity fish, including deep-water sharks (Henry et al., 2013). Furthermore, coral framework baffles mobile sediment leading over time to substantial deep-water coral reef and coral carbonate mound development (Roberts et al., 2006). The ability of dead coral framework to support living colonies by sustaining external loads is therefore of paramount importance not only for CWC habitat complexity and its ability to support other species, but also for reef and mound formation.

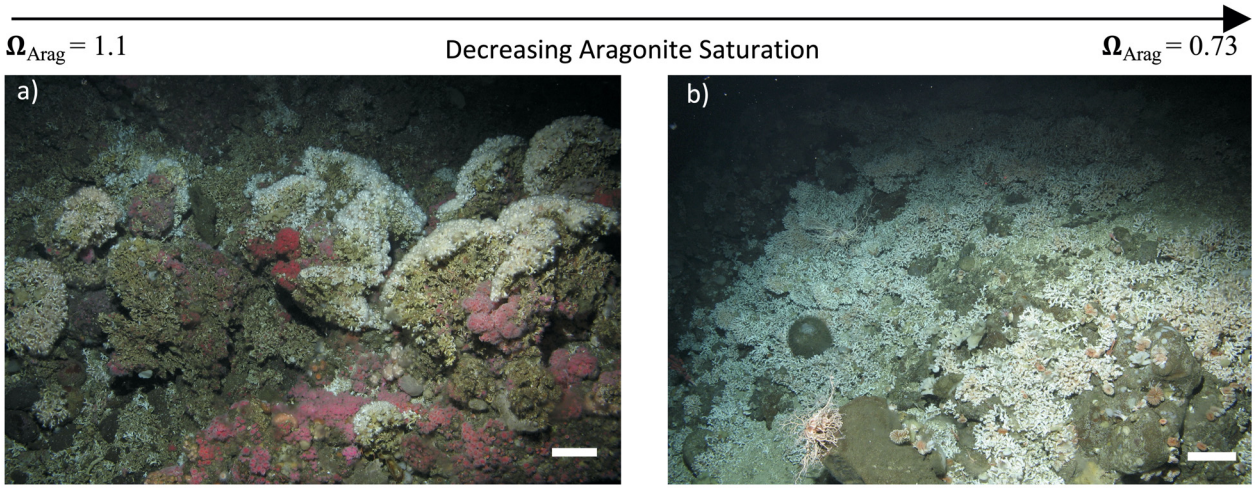


FIGURE 1 | The CWC *Lophelia pertusa* above and below the ASH in the Southern California Bight. Scale bars are 20 cm. **(a)** Example image of *L. pertusa* reef above the ASH, with substantial 3-dimensionally complex cohesive reef framework consisting of live coral (white crowns) and dead coral (brown/grey foundations). **(b)** Example of live *L. pertusa* colonies providing low habitat complexity on exposed rock. No dead framework is evident. Aragonite saturation states (Ω_{Arag}) are indicated. Image stills in **(a,b)** were taken alongside ROV footage of sites with further site details in **Supplementary Table 1**.

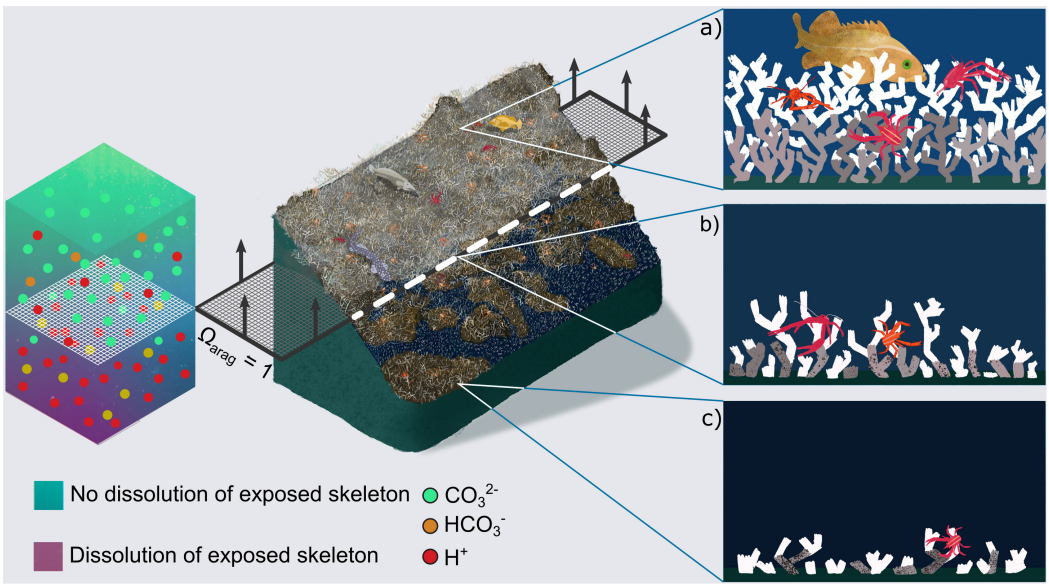


FIGURE 2 | Concept of cold-water coral habitat loss in a future ocean. Central image shows *Lophelia pertusa* reefs under present day conditions (top), and their projected habitat loss in a future ocean, once the aragonite saturation horizon (ASH, dashed layer at $\Omega_{Arag} = 1$) rises above them. A qualitative chemistry scale bar indicates dissolution of exposed aragonite beneath the horizon driven by increased [H^+] and decreased [CO_3^{2-}] ions. Arrows on the dashed layer indicate projected direction of ASH movement driven by ocean acidification. Panels on the right zoom into areas of present day and future reefs related to the position of the ASH. **(a)** Shows a healthy reef with substantial live (white) and dead (grey) coral framework (**Figure 1a**). In **(b)** porosity has started to appear in the dead, exposed skeletal framework leading to crumbling. In **(c)** exposed skeletal framework exhibits large porosity and is unable to support complex 3D habitat, although high abundances of live coral can still exist (**Figure 1b**).

The Underlying Mechanism

To understand how a 3-dimensionally complex *L. pertusa* reef can shift to become a habitat with low complexity and low biodiversity support (**Figures 1**, **2**), we need to consider the stability of live and dead coral in a way that is scalable to larger reef framework. For this, we model dissolution (resulting in an increase of skeletal porosity) in a coral (**Figure 3A**) simplified as a hollow beam fixed at its base with a load (e.g., water current) applied from the side (**Figure 3B**). Such a construct is reproducible and scalable from a single coral branch to a complex 3-Dimensional framework through computational and mathematical modelling (**Supplementary Figure 8**). In a hollow

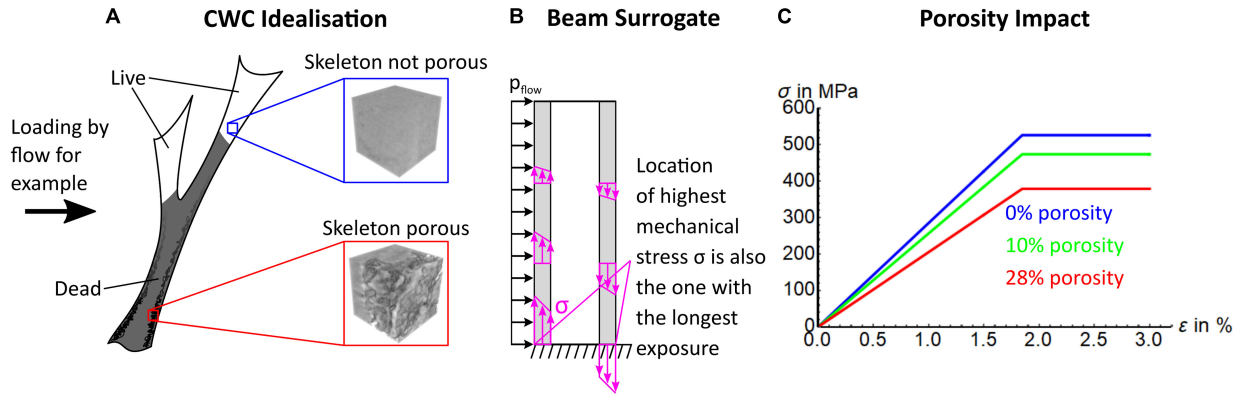


FIGURE 3 | Modelling of coral structural integrity. **(A)** An idealised representation of a CWC coral with live and dead fractions, with inlays indicating expected occurrences of porosity. **(B)** Represents a coral as a hollow beam with force applied from one direction (e.g., water flow, p_{flow}). This beam surrogate, loaded with force perpendicular to the long axis illustrates that the highest stress due to bending occurs at the outer walls (purple arrows, with length representing extent of stress). **(C)** Theoretical stress (σ) vs. strain (ε) curves of maximum bearable mechanical stress of a representative volume of an CWC skeleton (blue and red box in **A**) is reduced by increasing porosity. Note, yield strain stays the same as we assumed the same impact of porosity on yield strength and stiffness. This is a simplification for illustrational purposes.

beam coral surrogate, the critical point of failure (represented by greatest length of stress arrow (σ) in **Figure 3B**) is located at the outer surface at the base. Loss of material by increasing porosity specifically in those locations increases the fragility of the whole structure at its weakest point, leading to early onset of mechanical failure (crumbling and collapse) of the foundation framework within reef structures. Stress under the same applied load will always be higher toward the fixed base of a beam (**Figure 3B**), which is also the site of the oldest material, potentially subjected to dissolution for the longest time. Stress (σ) vs. strain (ε) curves of a representative volume element of coral skeleton demonstrates that such an increase in porosity in the skeleton leads to a decrease in apparent skeleton stiffness (initial slope) and maximum bearable mechanical stress (flat part of σ vs. ε curves, **Figure 3C**), equating to reduced stiffness and strength of the coral wall and, thus, the whole sample. The result of this process is observed in *in situ* reefs living below the ASH with little or no dead reef framework and only low structural height of living coral (**Figure 1**). The exact timescale when this becomes critical for 3D reef framework relative to exposure intensity and duration is yet to be determined, and here we present the progression of this process from *in situ* and long-term mesocosm experiments.

MATERIALS AND METHODS

Methods below describe the collection of *in situ* data, treatments of experimentally incubated corals, and material analysis of both *in situ* and experimental corals. *In situ* sampling included coral collection, water chemistry and habitat video analysis. Analysis of the skeletons includes: synchrotron radiation computed tomography for high resolution imagery; Raman imaging and X-ray diffraction for biomineralisation; skeletal density; nanoindentation to determine stiffness and hardness of materials; and using a simple 1D constitutive model to examine the effects of porosity.

Submersible Surveys

National Oceanic and Atmospheric Administration's (NOAA's) National Marine Fisheries Service (NMFS) Southwest Fisheries Science Centers (SWFSC) has conducted hundreds of remotely operated vehicle (ROV) surveys throughout the Southern California Bight since 2000. SWFSC Fishery Resource Division (FRD) conducted most of these dives using an ROV, the Phantom DS4 ROV (Deep Ocean Engineering, Inc.), equipped with a forward-looking video camera and high-resolution still camera (Scorpio, Insite Pacific). Dives in 2012 employed the HDHV ROV, equipped with high-definition video and still cameras. Dives from 2003 to 2012 (n = 570) were evaluated for *L. pertusa* presence using photographs and video. Many other surveys were conducted by SWFSC Fisheries Ecology Division (FED) using the human occupied research submersible Delta. The submersible dives from 2002 (n = 112) were used to document presence of *L. pertusa*. Dives were conducted following the methods described by Yoklavich et al. (2007). Four additional dives were conducted in 2010 by FED in the Channel Islands National Marine Sanctuary (CINMS) using the Kraken ROV in 2010 (Yoklavich et al., 2011). Follow up surveys by NOAA National Centers for Coastal Ocean Science (NCCOS) targeted 13 locations of known *L. pertusa* occurrences in 2014 and 2015 using Marine Applied Research and Exploration's (MARE) Beagle ROV (Caldow et al., 2015).

Coral Photo/Video Analysis

Locations of *L. pertusa* were identified by reviewing both video footage for sub dives and a large photographic database (n = 47,380) derived from SWFSC's combined surveys. When *L. pertusa* was identified in the photo database, those dives were marked for full video review seeking additional occurrences (n = 58). Video footage from 116 dives in 2002 (n = 112) and 2010 (n = 4) were reviewed for *L. pertusa* occurrence. Surveys in 2014 and 2015 (n = 28) targeted regions of known

L. pertusa depth and/or location. New occurrences were added if not already documented from the previous surveys. Discrete occurrences were defined as occurrences of *L. pertusa* separated by at least 3 min, or on a distinctly different substrate. Coral aggregations were categorically defined as 'reef building' when framework (live and dead coral with vertical relief) was present and aggregations were >1 m^2, as 'patchy aggregations' when there was no framework and coral patches were 50 cm^2–1 m^2, as 'sparse live patches' when coral patches were <50 cm^2, and 'rubble only' when no live coral was present.

Sampling

One collection was taken in 2010 using the Kraken ROV (M2-10-02-Lophelia, later designated as Smithsonian Sample UNSM1148068). Remaining sample collections were all taken with the MARE Beagle ROV in 2014 and 2015 under NOAA National Marine Sanctuaries permit number CINMS-2015-002. Samples were transported to the surface under ambient conditions. Upon reaching the surface, each collection was immediately subsampled for live, frozen, dry and 95% ethanol preservation.

Hydrographic Data

Conductivity, Temperature, Depth (CTD) and hydrographic upcast data between January 2007 and November 2015 were obtained from quarterly surveys conducted by the California Cooperative Oceanic Fisheries Investigation (CalCOFI, 2019). ArcGIS Desktop (10.1, ESRI) was used to calculate the nearest station to each coral occurrence and values at closest depth were used in analyses. The maximum distance between a CalCOFI station and *L. pertusa* occurrence was 35.5 km, and most were within 25 km. ROV temperature and salinity data were also available for most occurrences and used to evaluate the efficacy of using CalCOFI stations for predicting benthic conditions. CTD (Citadel CTD, Teledyne RDI) temperature data from the ROV was available for 81 of the occurrences; the ROV mean temperature of 9.03 ± 0.98°C was closely aligned with the mean temperature calculated from CalCOFI of 9.04 ± 0.41°C.

Carbonate Chemistry

Aragonite saturation states (Ω_{Arag}), dissolved inorganic carbon (DIC), pH, [CO_3^{2-}] and total alkalinity (TA) of seawater were calculated empirically using algorithms (Alin et al., 2012) and directly through water sampling using CTD-rosette in 2010 and 2015. The empirical relationships ($r^2 > 0.98$ for all but TA; TA $r^2 = 0.927$) developed by Alin et al. (2012) were specific to the southern California Current System. They use temperature (T), oxygen (O), salinity (S), and potential density (σ_Θ) to estimate various parameters of the carbonate system. Reference values ($T_r = 10.28$°C, $O_r = 127.80$ μmol kg^{-1}, $S_r = 33.83$, $\sigma_{\Theta r} = 25.97$) represent average temperature, oxygen, salinity and potential density values over the study area and were restricted to depths of *L. pertusa* occurrences. In April 2015, CTD-rosette casts were conducted directly adjacent to *L. pertusa* aggregations in CINMS (Caldow et al., 2015; Hennige et al., 2020). Total alkalinity was determined by potentiometric titration and DIC by coulometric titration. Additional carbonate parameters were calculated in CO2SYS (Lewis and Wallace, 1998). Aragonite saturation values from 2010 (D. Lipski, NOAA unpublished data) were associated with a habitat characterisation of Piggy Bank described in Yoklavich et al. (2011), Caldow et al. (2015), Hennige et al. (2020). Note the close match between Ω_{Arag} values collected from water samples (red circles) and the empirical algorithms (box plots) in **Supplementary Figure 2**.

Experimentally Incubated Samples

Live and dead *L. pertusa* specimens collected from the Mingulay Reef Complex were subjected to 12 month incubations under five different scenarios in Hennige et al. (2015a); (i) 9°C 380 ppm (the ambient environment); (ii) 9°C 750 ppm (ambient temperature, elevated CO_2); (iii) 12°C 750 ppm (elevated temperature, elevated CO_2); (iv) 12°C 380 ppm (elevated temperature and ambient CO_2); and (v) 9°C 1000 ppm (ambient temperature, elevated CO_2). At the end of the experiment, samples were dried and stored for subsequent skeletal analysis here. For each treatment, there were four replicate systems, each comprising four 5 l tanks connected to a 60 l sump (Hennige et al., 2015a,b).

Synchrotron Radiation Micro-Computed Tomography Imaging

Synchrotron radiation micro-computed tomography scans (SRμCT) were performed at the Diamond Light Source at the Harwell Science and Innovation Campus, Oxfordshire, United Kingdom (sessions MT19794 and MT20412) on the I13-2 Diamond-Manchester branchline of I13 beamline. The Insertion Device (ID) source positioned in the electron beam orbit generates X-rays ∼250 m from the sample position. The X-ray beam passed through a horizontally reflecting platinum X-ray mirror before reaching the sample. Propagation based phase contrast imaging was performed with a pink beam centred on an energy of 27 keV. This allowed the reduction of dose to the samples, i.e., using higher photon energies reduced the absorption of the X-ray by the specimen, and retrieved phase-sensitive images that reveal gradients and de-mineralisation profiles. A 500 μm $CdWO_4$ scintillator converted X-rays into visible light, and a pco Edge 5.5 camera with 1.25x Olympus objective focussed onto the scintillator was used to generate the images. This combination of optics resulted in a voxel size of $2.6 \times 2.6 \times 2.6$ μm^3. We gathered 2500 projections between 0° and 180° at an angular increment of 0.072°, an exposure time per projection of 0.05 s, and a distance between sample and camera objective of 100 mm. In total, 75 live and dead corallites from the 10 sites of ∼200 mm^3 were scanned yielding reconstructed datasets of $2160 \times 2560 \times 2560$ voxels in 32 bit. Data reconstruction was performed using Savu, a modular reconstruction pipeline with a plugin style architecture (Atwood et al., 2015; Wadeson and Basham, 2016) that makes use of the ASTRA toolbox (van Aarle et al., 2015, 2016). Custom software was developed in Python (Python Software Foundation, version 2.7.) using Numpy (Oliphant, 2007) and skimage (van der Walt et al., 2014) libraries to determine porosity ρ. To do so, images were cropped and smoothed slice-wise with a Gaussian filter with a standard deviation of 1. Subsequently, a threshold value

was determined on the middle 500 slices of the corallite, i.e., a significant portion of the scanned volume, using an automatic thresholding algorithm (Otsu, 1979). The porous coral volume (CV) was determined by counting all voxels above the threshold. Afterward, slice-wise closing was performed omitting planar porosity larger than 2500 pixels, i.e., parasitic pores or grown structural connections. Non-porous total volume (TV) was determined by counting all voxels in the closed, thresholded image, and porosity was determined as $\rho = 1 - CV/TV$ (see **Supplementary Figure 5**). Note, this represents a conservative measure, as we used whole mid-portions of corallite volumes as volumes of interest. If smaller volumes of interest are used, porosity was found to be considerably higher.

To verify findings, we sampled corals from previous laboratory mesocosms (Hennige et al., 2015a) and obtained SRμCT datasets at the same voxel size (session MT20412). We adapted our SRμCT scanning protocol based on previous experience so that exposure time per projection, and distance between camera and sample were increased to 0.07 s and 150 mm, respectively. A benefit of using a synchrotron is that image acquisition, reconstruction, and analyses are not affected by detection artefacts and no measurable effects on resulting images were detected from different shutter times. Porosity was calculated similar to the *in situ* samples but using 300 slides instead of 500 due to limited computational resources in this instance. Porosity was then correlated with aragonite saturation in Gnu R using a log-conversion of the non-linear data.

Nanoindentation

This technique was used to calculate plain strain modulus (stiffness), hardness, and a surrogate for ductility calculated as plastic mechanical work divided by total mechanical work. Stiffness relates to the ability of a material to resist elastic deformation, where it will return to its original state when an applied force is removed. Hardness is used here as a surrogate measure of yield strength (due to a lack of data) which represents the threshold where the material would start to be irreversibly deformed. We use the ratio between plastic mechanical work, i.e., dissipated energy, and total mechanical work of the indentation process as a surrogate measure for ductility (Spiesz et al., 2012; Mirzaali et al., 2016).

Sample Preparation

Forty Five samples of *L. pertusa* were analysed, 23 of which were dead and 22 were covered with living tissue. Soft-tissue was removed with a water jet and skeletal samples were prepared following previous protocols for mineralised tissues (Wolfram et al., 2010; Mirzaali et al., 2016). Samples were cut into sections for moulding using a Dremel. Sections were embedded, not infiltrated, in EpoHeat epoxy (Buehler). The resin cured under vacuum for 60 min to fill the intra-septal space. Once the resin had cured, the sample discs were extracted from the mould and cut with a precision bandsaw (Exakt) so that a longitudinal section of the coral was exposed at the surface. Samples were ground parallel using P1200 silicon carbide paper for 10 min intervals with intermediate checks. Once samples were parallel, they were polished with increasing grades of silicon carbide paper P1200, P2000, and P4000 for 8, 10, and 15 min at 300 rpm, respectively, and polished with 0.25 μm diamond paste for 8 min. Between each step, samples were cleaned in an ultrasound bath for 7 min.

Indentation was performed using a Berkovich diamond tip mounted to a depth-sensing, force controlled nanoindenter (Hysitron). The force applied to the tip followed a monotonic ramp up to 50 mN over the course of 60 s. At that point, force was held constant for 30 s before being totally unloaded in 7.5 s (Wolfram et al., 2010; Mirzaali et al., 2016). Each sample was indented 35 times in seven groupings of five indents. Each group of five was at a different transverse location, and each indent in a group was at a different radial location. Indentations were sufficiently spaced to avoid interference between indentations and were placed at least seven-times the indentation depth away from the embedding interface, thus avoiding embedding effects (Wolfram et al., 2010). In total, 1635 indentations were carried out. Indents were grouped, as no significant difference was measured between radial and transverse locations ($p > 0.78$). Scipy's trapezoidal method (Jones et al., 2001) was used in Python (Python Software Foundation, version 2.7.) to integrate force-depth curves to calculate work. The integration was carried out for the loading and holding section to find total indentation work (W_{tot}) while elastic work (W_e) was found by integrating the unloading section. The difference between total indentation work (W_{tot}) and elastic work (W_e) gives dissipated energy, i.e., plastic work (W_{pl}). The indenter was tested on a fused quartz sample to check its calibration, the same sample used to produce the tip area function. The measured value for plain strain modulus was 69.34 GPa, where the reference value for the sample supplied was 69.6 GPa. Hardness was within 10% of the reference value. In total, 476 indentations could not be used for analysis due to failed indentations, potentially as a result of holes (submicroscopic porosity, potentially the dark areas around the pores in the inlay in **Figure 4G**) not visible when assigning the indentation position, or due to surface roughness from the preparation protocol (Fischer-Cripps, 2002). To check the latter, roughness was tested on $n = 10$ samples with an electric surface roughness tester (Taylor Hobson Talysurf 5–120) working on a carrier modulating principle. We tested five samples where failed indentations had occurred and five samples where all indentations were successfully completed. No significant difference in roughness ($p = 1$) was found, and median roughness (R_a) of the samples was 2.3 nm (2.0–3.3 nm). Surface quality was considered sufficient for indentations >500 nm as conducted in this study.

Raman Imaging and Electron Backscatter Diffraction

To assess the biomineralisation aspects we used three live and three dead samples from each of the 10 sites resulting in a total of 60 samples. Samples were embedded, not infiltrated, in EpoHeat epoxy (Buehler). Resin was cured under vacuum for 60 min and cross-sectioned using a slow saw. Samples were polished using progressive grits of silicone carbide paper (P320, P1200, P2500, P4000), micropolished using alpha aluminium oxide at

1 and 0.3 μm, and fine-polished with 0.06 μm amorphous colloidal silica (Buehler) on a short nap to remove any residual damaged surface layers (Hennige et al., 2015a). To assess the compositional properties of the skeleton, Raman spectroscopy was used (Hennige et al., 2014a, 2015a) with a Renishaw inVia Raman Spectrometer equipped with a Leica DM 2500M microscope and 785 nm laser, with the aragonite peak centred at 1085 cm^{-1}. Full Width Half Maximum (FWHM) measurements of the aragonite peak at 1085 cm^{-1} were collected at the outside tips of newly grown polyps, as close as possible to the sample edge (∼5 μm). Electron Backscatter Diffraction (EBSD) was used to investigate crystal composition. A FEI Quanta 200F field emission scanning electron microscope (SEM) equipped with a TSL EBSD system (Hennige et al., 2015a). Grain CI tolerance was 5 with a minimum grain size of 2 pixels, neighbour CI correlation was 0.05. The Kikuchi patterns were indexed using the Orientation Imaging Microscopy (OIM) Data Collection database, which contains structure files of aragonite. OIM maps were subject to two clean-up algorithm procedures to ensure reliable data were displayed, where grain CI standardisation was applied with a grain tolerance of 5, minimum grain size of 2 pixels, and neighbour CI correlation of 0.2. Further partitioning of data was applied with only grains of CI Fit and displayed in the resultant OIM map to remove background noise from the final dataset (Cusack et al., 2008).

Gravitational Density Measurement

Skeletal density was determined using a pycnometer with methanol (COH_4) on four dead and four live samples representing the extremes of the sample spectrum. Pycnometers are used to measure relative density (Swartz, 1962; Titschack et al., 2016) of the solid phase in granular materials excluding the confounding impact of the pore phase. Samples were ball milled (Retsch MM 200) at a frequency of 25 Hz for 40 min to attain ∼1 μm grain size. Therefore, the investigated particle volume was ∼1 μm^3 which is at least an order of magnitude smaller than the SRμCT porosity measurements which were obtained at a voxel size of 2.6 μm. Pycnometer volume was then determined measuring the dry weight of the pycnometer with a high precision lab scale (SE 203-LW, VWR). After the room temperature was determined, the pycnometer was filled with methanol and filled weight was measured m_{sf}. Density of methanol was determined in ambient conditions using the pycnometer volume of V_s = 24.808 cm^3 as $\rho_{meth} = \frac{(m_{sf} - m_s)}{V_s}$. Subsequently, the pycnometer was emptied, dried and a CWC sample ball milled to a grain size of ∼1 μm was inserted. Combined weight of CWC dust and pycnometer m_p was measured, and sample weight $m_e = m_p - m_s$ calculated. Methanol was added, then the pycnometer was vacuumed to remove potential air bubbles and closed. The combined weight $m_1 = m_s + m_e + m_{meth}$ was then measured. Volume of the coral material was determined as $V_e = V_s - \frac{(m_1 - m_s - m_e)}{\rho_{meth}}$ so that the density of the coral material ρ_e was calculated as $\rho_e = \frac{m_e}{V_e}$. One sample was not usable due to lack of material available for the measurement. A *post hoc* power analysis (pwr package, Gnu R) (R Development Core Team, 2008) validated the number of used samples. To detect a significant difference of 10% in the material density, which we deemed necessary to trigger significant differences in mechanical response, $n = 3.45$ specimens would have been needed. For the power analysis, we used a joint standard deviation of 0.1 g/cm^3, a power of 0.8, and a significance level of 0.05 for a two-sample test. Joint standard deviation was larger than the one encountered for the used groups. Accounting for the lost sample in the power analyses with different group sizes indicated that groups of $n_1 = 2.98$ and $n_2 = 4$ were sufficient for the analyses.

X-Ray Diffraction

X-ray diffraction samples in three groups [live, dead, and samples with both live and dead parts (hybrid)] were ground to powder in a mortar, and deposited manually as a thin layer onto a Si510 wafer in an L510 PMMA sample holder. XRD was performed using the Bruker D8 Advance diffractometer Bragg-Brentano geometry with a Lynxeye position-sensitive detector, Cu Kα radiation, and sample spinning. Parameters used include divergence slit V12, scatter screen height 5 mm, 45 kV, 40 mA, and detector settings: LL 0.11, W 0.14. Measurements were performed via a coupled scan 10°–110° with step size 0.020° and a counting time per step of 2 s. The diffractograms were analysed using the Bruker software DiffracSuite.EVA v4.2. Crystalline structures were assigned through comparison of experimentally determined peak positions and intensities with the ICDD pdf4 database. Thereafter, results were refined using the Profex/BGMN Rietveld refinement software, for which complete XRD patterns were used. Five specimens per group were tested.

Constitutive Modelling for Illustrating the Effect of Porosity

We illustrate the effect of increasing porosity with a 1D linear elastic-plastic material model. A previously implemented model was used (Mirzaali et al., 2015), without damage and asymmetric yield stresses but with an ideal plasticity (Lemaitre and Chaboche, 2000). Stiffness of the coral material was obtained from the nanoindentation experiments and subjected to increasing amounts of porosity, so that $E = (1 - CV/TV)E^*$, with CV/TV the volume fraction of a region of interest in the skeletal wall. Yield stress or strength have not yet been reported for coral material on micron-sized volumes. Yield stress here was estimated based on a comparison with the extracellular matrix in bone, another mineralised tissue. Since hardness is a yield surrogate, the ratio between strength in bone tissue (Mirzaali et al., 2015) and hardness determined by microindentation were used to estimate the yield stress, so that $\sigma_y = (1 - CV/TV)\sigma_y^{est}$. Although it is clear that micromechanical strength experiments such as those determined by Schwiedrzik et al. (2014) and Groetsch et al. (2019) need to be performed to fully understand the non-linear mechanical behaviour of CWC, the estimation of the micromechanical yield stress done here is sufficient to illustrate the effect of increasing porosity on load bearing capacity. Furthermore, we assume that stiffness and strength are affected in the same way by porosity so that the yield strain is the

same for increasing porosities. This is not necessarily the case as has been shown for bone tissue (Wolfram et al., 2012).

Statistical Analysis

Descriptive statistics and statistical testing were performed using Gnu R (R06) (R Development Core Team, 2008). A significance level of $p = 0.01$ was chosen before comparisons were made. Normality was checked using Shapiro-Wilk normality tests and rejected ($p < 10^{-5}$). This was verified by Q-Q plots of the quantiles of the collected data vs. the quantiles of the normal distribution which showed non-linear curves. Therefore, median and range were chosen for descriptive statistics and non-parametric Wilcoxon rank-sum tests were used in groupwise comparisons (Crawley, 2005). R's linear regression model was used to investigate regressions between continuous variables, e.g., plain strain modulus and aragonite concentration. *Post hoc* power analyses were performed using R's pwr library and methods (see section "Gravitational Density Measurement").

RESULTS

In situ Evidence: The Southern California Bight

Lophelia pertusa occurrences were documented across the Southern California Bight in visual fisheries surveys conducted using remotely operated vehicles (ROV) from 2002 to 2012 (Salgado et al., 2018) and in targeted, follow-on visual surveys in 2015 (Caldow et al., 2015). *L. pertusa* was found on most banks, seamounts and ridges surrounding the Channel Islands (**Supplementary Figure 1**, with corresponding location data in **Supplementary Table 1**). Though widely distributed, with numerous occurrences ($n = 132$) at 313–66 m depth, the majority of sites had only sparse live or dead patches ($<1\ m^2$). Occurrences of reef building coral assemblages (with live and dead skeleton framework) increased nearly 4-fold (from 5 to 18%) from below to above the ASH ($n = 181$ data points, **Supplementary Table 1**). The highest frequency and abundance of coral was found in the Channel Islands National Marine Sanctuary (CINMS) on the peak of the Piggy Bank Seamount and along the ridge of the Footprint feature (**Supplementary Figure 1**). Studies in 2014 and 2015 targeted these sites for water sampling and included the biological samples analysed in this manuscript. Temperatures in these regions closely match those reported globally for *L. pertusa* (9.12 ± 0.95°C *SD*), but oxygen concentrations are relatively low (2.1 ± 1 ml/l; range 0.65–5.3 ml/l).

Aragonite saturation (Ω_{Arag}) values from 2007 to 2015 near Southern California Bight *L. pertusa* sites were between 0.72 and 1.86, the lowest Ω_{Arag} conditions recorded for *L. pertusa* to date (**Supplementary Table 1**). *L. pertusa* sites that had substantial cohesive reef framework consisting of live and dead coral (**Figure 1a**) were limited to shallow sites (169–65 m, $n = 14$ sites). At depths of 169 meters mean Ω_{Arag} was 0.9 ± 0.09 with a range of 0.79–1.04. At 65 meters mean Ω_{Arag} was 1.3 ± 0.25 with a range of 0.92–2.05. Based on long-term repeat estimates of carbonate chemistry (see section "Materials and Methods"), sites below 170 m are likely to experience persistent aragonite undersaturation ($\Omega_{Arag} < 1$ in $> 90\%$ of estimated Ω_{Arag} from 2007 to 2015; **Supplementary Figure 2**), corresponding closely to the depth below which dead reef framework was absent. The Piggy Bank site (293 m; $\Omega_{Arag} = 0.73$) had high abundance of live *L. pertusa* blanketing the seafloor but lacked structural complexity due to absence of dead framework (**Figure 1b**). The decrease in habitat complexity observed with decreasing Ω_{Arag} (**Figure 1b**) strongly indicates that the foundation framework of the reef is dissolving or structurally failing under low Ω_{Arag} conditions once soft-tissue has retracted. Thus, the foundation framework is unable to support larger reef frameworks. To quantify how decreasing Ω_{Arag} affected the structural integrity of corals, samples from the CINMS within the Southern California Bight were collected for structural analysis from reef (macro) to crystal (micro) length scales (**Supplementary Figure 3**).

Structural and Compositional Analysis of *in situ* Corals

L. pertusa branches from above and below the ASH within CINMS were characterised by profuse budding with thin, fragile calices and little-to-no branching. The structural and mechanical properties of these corals were assessed by evaluating porosity, chemical composition, stiffness, hardness, ductility and density from crystal-to-reef scales. Results are presented as images (**Figures 4**, **5**) and graphically (**Supplementary Figure 4**).

Porosity

Porosity of the *L. pertusa* skeletal material was analysed with synchrotron radiation micro-computed tomography (SRμCT). The SRμCT images highlighted increased skeletal porosity in dead coral skeleton (dark pore-areas appearing in the coral skeleton) exposed to aragonite undersaturated water [**Figure 4A** and **Supplementary Video 1** (from corals below ASH) and **Supplementary Video 2** (from experimentally incubated corals)]. Live coral exhibited no skeletal porosity, regardless of whether it was above or below the ASH when sampled (**Figure 4**). Dead samples from below the ASH exhibited increased skeletal porosity on both the outer walls and inner walls (**Figures 4C–E**). In cases where skeletons included both soft-tissue covered and non-covered portions, porosity was visible only in the exposed sections of skeleton (**Figures 4F–I**). Porosity (**Figure 5** and **Supplementary Figure 5**) increased in dead framework once the protective soft-tissue layer had retracted (**Supplementary Figure 6**). Skeletal mass density did not statistically differ between live and dead samples (**Supplementary Figure 7**).

Porosity and Material Structural Properties (Stiffness, Hardness, and Ductility)

To understand coral skeletal behaviour over time scales, it is critical to understand both the presence/absence (**Figure 5A**) and structural properties (**Figure 5B** and **Supplementary Figure 4**) of the "building blocks" of coral skeletal material under different environmental conditions. Results below indicate that while material is lost (increasing porosity), the structural properties of the material on the microscale do not change. This means that the loss of structural integrity for whole coral samples is

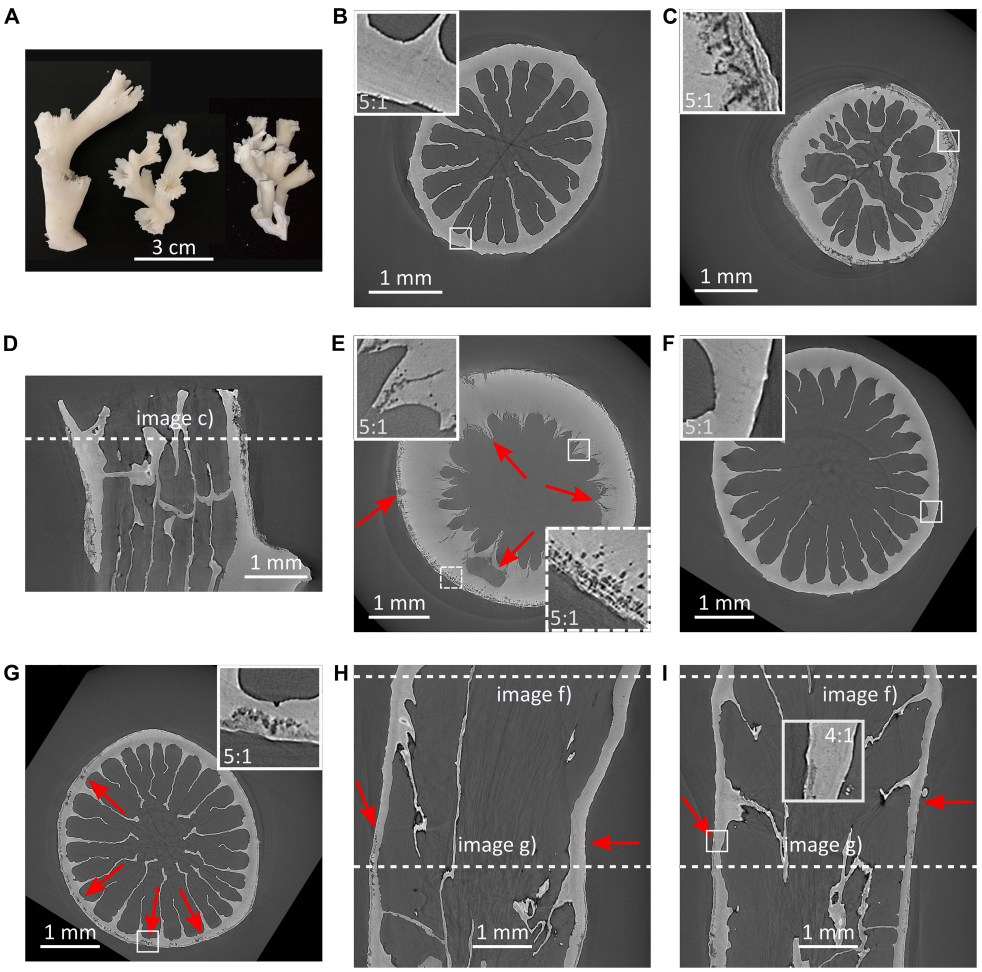


FIGURE 4 | Dissolution and porosity increase in *Lophelia pertusa*. **(A)** *L. pertusa* specimens from the NE Atlantic (left, middle) and the Southern California Bight (right) highlighting morphological variability of this species; **(B)** transverse SRμCT cross-section of live coral with protective tissue from below the ASH; **(C)** transverse SRμCT cross-section of dead coral without protective tissue from below the ASH, resorption zones are clearly visible at rim including break away patches; **(D)** longitudinal cross-section of coral in **(C)**; **(E)** transverse SRμCT cross-section of coral from below ASH showing large porosity from borers and dissolution of internal structures (red arrows skeleton indicating dark pore-areas); **(F,G)** SRμCT images showing dissolution in a specimen from below the ASH that was alive and protected by tissue at the top **(F)**, and exposed skeleton toward the bottom **(G–I)**, where **(I)** is a longitudinal cross-section perpendicular to **(H)**. Red arrows indicate onset of porosity in **(H,I)**.

driven by loss of material rather than a change in the underlying material behaviour.

Porosity is significantly higher in dead samples compared to live samples from below the ASH (**Figure 5A**, $p < 10^{-5}$). Instances of porosity in live samples (e.g., orange dots > 1 at an aragonite saturation of 0.7 in **Figure 5A**) are driven by small patches of tissue retraction and exposed skeleton in some samples (**Figures 4H,I**). Stiffness, hardness, and ductility are three mechanical characteristics of a material measured at micrometre length scales through nanoindentation (Fischer-Cripps, 2002; Mirzaali et al., 2016), where a diamond tip is pressed into the material with a known force (see "Materials and Methods"). Hardness and ductility allow evaluation of the material's ability to resist plastic deformation and, ultimately, failure. Skeletal material in live and dead samples across sites (above and below ASH) did not statistically differ with regard to stiffness or hardness (**Figure 5B**, $p = 0.081$ and $p = 0.729$, **Supplementary Figure 4B**) but median ductility was 2.5% higher in the dead samples ($p < 10^{-5}$) than in the live samples (**Supplementary Figure 4D**).

While the above effects are demonstrated and modelled on individual branches of coral, the models and units used are scalable (**Supplementary Figure 8**). Units can be modified in multiple dimensions (e.g., length, width, wall thickness) and joined together through computational and mathematical modelling to construct a framework for habitat-scale interrogation.

Mineral Composition

Mineral composition was also assessed across environmental gradients, to assess whether the *type* of calcium carbonate varied. *L. pertusa* coral skeletons across sites and in live and

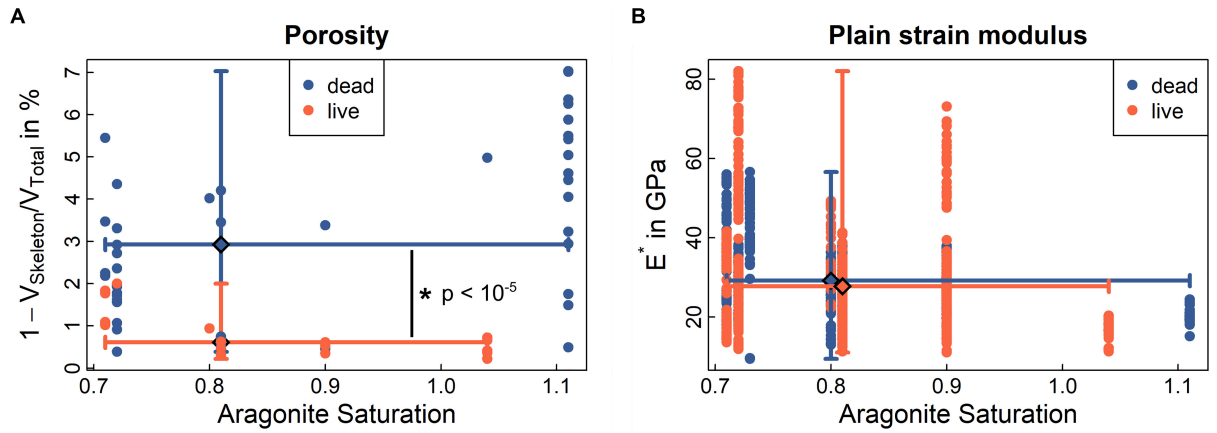


FIGURE 5 | Porosity and mechanics of CINMS *Lophelia pertusa*. The Figure shows **(A)** porosity of the skeletal volume, and **(B)** stiffness (plain strain modulus) of the skeletal material. Data represented as medians with min/max error bars for both axes at respective median (large diamond). Significant differences between live and dead samples are indicated by *. See also **Supplementary Figure 4** for Raman crystallinity, electron back scatter diffractions and other material chemistry of samples. Solid lines indicate ranges (min-max) around the median (large diamond) for ordinate and abscissa for live and dead samples, respectively.

dead samples were primarily composed of aragonitic crystals (**Supplementary Figure 6C**), but crystals were smaller in live corals exposed to aragonite undersaturated conditions than those in live corals exposed to oversaturated conditions. This is indicated by more black areas in **Supplementary Figures 4, 9**, where post-processing to determine alignment of crystals could not distinguish between data noise and individual crystals (crystal size below detection minimum). In live corals, we observed samples containing pure polymorphs of aragonite (X-Ray diffraction, see "Materials and Methods"). In the recently dead coral skeletons tested, we found mean weight percentages of 99% aragonite and 1% calcite. Compositional analysis by Raman spectroscopy did not reveal any differences between live and dead samples from different aragonite saturation conditions (**Supplementary Figure 4**). The absence of a difference in the compositional properties between live and dead samples indicates that the variation observed in the micromechanical properties is due to testing differently oriented crystal arrangements ("sclerodermites," **Supplementary Figure 3**). This held true for all samples above or below the ASH and along our Ω_{Arag} range, ruling out a systematic difference in the mechanical properties of the building material. Furthermore, this lack of difference in the micromechanical properties indicates that similar skeletal properties can be achieved with varying crystal sizes, indicating that the mineralisation process is very robust.

Evidence From Controlled Laboratory Experiments

To provide greater context to analysis of *in situ* samples and to understand the weakening mechanisms and timeline, we reanalysed existing live and dead *L. pertusa* samples from previous experiments (Hennige et al., 2015a), where corals from the Mingulay Reef Complex (North Atlantic) were collected and different subsamples were subjected to projected changes in temperature and Ω_{Arag} for 12 months, ranging from $\Omega_{Arag} = 1.46$ to $\Omega_{Arag} = 0.76$. At the start of the experiment, all live corals had complete soft-tissue coverage, but following 12 months of experimentation, some fragments experienced soft-tissue retraction leaving parts of their skeleton exposed to seawater (**Supplementary Figure 10**). Coral that was alive did not exhibit an increase in porosity with increasing acidity (decreasing Ω_{Arag}) over 12 months, with the exception of small patches under elevated CO_2 conditions where soft-tissue retraction was evident (**Figure 6**). Coral that was collected alive with subsequent soft-tissue removal prior to placement in experimental treatments (classified here as dead skeleton) exhibited clear increases in porosity over the whole exposed skeleton as Ω_{Arag} decreased (**Figure 6**). This matches our observations from *in situ* samples in **Figure 4** and provides a timescale that these impacts can be observed in as little as 12 months once a critical aragonite saturation has been reached. Porosity values of 28% ($27.9 \pm 7.9\%$) were determined from $n = 10$, $(130\ \mu m)^3$ volumes of interest in dead coral walls following exposure to the lowest aragonite saturation conditions (0.76 ± 0.1) for 12 months (Hennige et al., 2015a).

DISCUSSION

Habitat Loss

Here we demonstrate that *Lophelia pertusa* reefs living in aragonite undersaturated conditions analogous to those projected for most reefs by 2100 exhibit far less habitat complexity than *L. pertusa* reefs living above the saturation horizon. This is driven by loss of dead coral material that usually forms part of the visible habitat structure (**Figure 1**). Through experimental evidence, we go beyond identification of dissolution, and demonstrate the rapid onset of the process (quantified from 12 month experiments) in the "building blocks" of coral framework (individual coral branches), and the

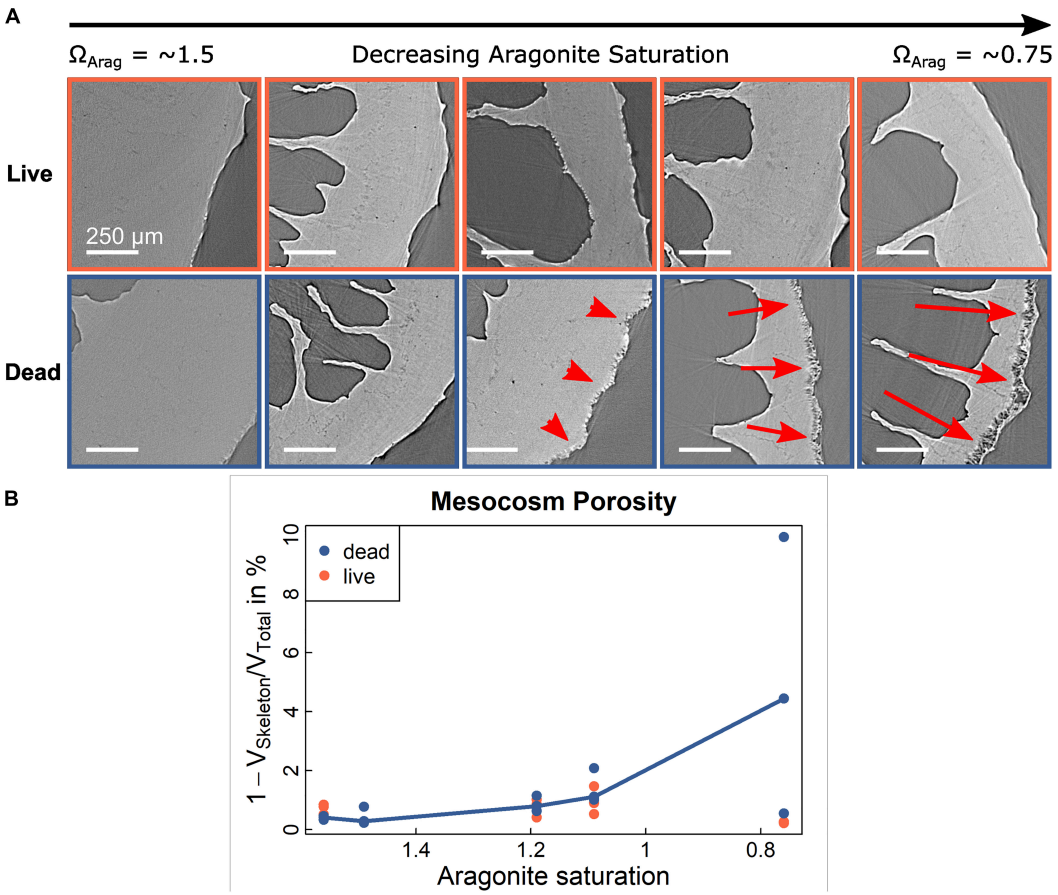


FIGURE 6 | Porosity in experimentally incubated *Lophelia pertusa*. **(A)** SRµCT cross-section images of corals from Mingulay Reef Complex (Hennige et al., 2015a) subjected to different treatments of increased levels of CO_2 during 12 month laboratory incubations. **(B)** corresponding porosity analyses shows a significant, non-linear relation between porosity [red arrows in **(A)**] and aragonite saturation in dead samples (p = 0.0008, r^2 = 0.59) but no significant relationship (p = 0.67) for live samples. Relationship is illustrated by multi-linear curve connecting the medians.

mechanism that could lead to potentially rapid ecosystem-scale habitat loss in the near future (**Figures 3–5**). Porosity in the dead skeleton leads to a weakening of the coral (also noted in tropical examples; Scott and Risk, 1988). On the scale of a colony, which both baffles mobile sediments and supports the larger, complex reef structure, loss of structural integrity could contribute to a crumbling of the larger habitat resulting in smaller aggregations of live coral with less 3-dimensional complexity and massively reduced reef/mound-building potential (**Figure 2** and **Supplementary Table 1**, *in situ* Results). Importantly, it is the *location* of the porosity in addition to the extent that underlies this process, meaning that even relatively small changes can lead to significant structural weakening. While breaking of coral under its own weight and normal bio-erosion are established (but sporadic) ways in which CWC patch reefs can expand under normal conditions (Wilson, 1979), the systemic weakening and ultimate loss of the foundation framework from ocean acidification would prevent future reef and mound growth, and lead to an ecosystem-scale habitat loss for existing coral reefs. Existing mound structure, where carbonates are buried within sediment, would not be subject to such crumbling effects.

This ecosystem-scale habitat loss, leading to a shift from one habitat type (high complexity with high biodiversity support) to another (low complexity with low biodiversity support), is generally very different from the processes described in tropical corals, where the main threat is a change in growth rates of live coral combined with greater bioerosion efficacy. While increased acidity and enhanced bioerosion activities can also lead to decreased structural integrity and density in tropical corals (Scott and Risk, 1988; Enochs et al., 2014), the risk to the overall habitat on the ecosystem scale is arguably the long-term reduction in net coral reef growth, as opposed to structural failure-induced loss of the critical (and visibly often the largest component) dead part of CWC reefs. A key part of this is the aragonite undersaturation that CWC reefs will be subjected to, and the vastly slower growth rates of the branching CWC *L. pertusa* compared to branching tropical analogs. While bioerosion is a key process on reefs through prograding and propagation of corals in both tropical and deep-sea corals (Wilson, 1979; Tunnicliffe, 1981), it is unclear how well CWC would fare if living coral "fell" (following loss of habitat integrity) into habitat areas with water flow inadequate for heterotrophic feeding

(Purser et al., 2010), as unlike tropical coral, they cannot acquire photosynthetic carbon.

Mechanical and Mineral Properties of CWC Skeletons

With regard to skeletal stiffness and hardness, our data were comparable to those recorded in shallow-water zooxanthellate corals around localised volcanic acidification sites with low pH conditions (Fantazzini et al., 2015; Pasquini et al., 2015), where Fantazzini et al. (2015) reported an ∼8% difference in stiffness but no difference in hardness over 0.4 pH points. While similar, results are not directly comparable to CWC investigated here due to the higher aragonite saturation ($\Omega_{Arag} > 1$) of the volcanic sites used, and the zooxanthellate nature of the shallow corals. Here, *L. pertusa* skeletal material properties measured at the micrometre length scale changed very little across aragonite saturation for live or dead samples, but exposed, dead coral skeleton showed significantly increased porosity driven by dissolution in aragonite undersaturated conditions (**Figure 5**). This is contrasted by no significant difference in skeletal mass density between live and dead samples from above and below the ASH. Other studies (e.g., Mollica et al., 2018) have measured a decrease in coral skeletal density due to ocean acidification, and the contrast to results here can be explained by length scale. When using a clinical type CT scanner, typical resolution is orders of magnitude larger than the porosity observed here. Porosity assessed using clinical type CT scanners would be visible through a lower X-ray attenuation, which translates into a lower density. The combined effect of constant skeletal mass density on a micrometre length scale with increased skeletal porosity, as identified here, explains lowered *macroscopic*, skeletal mass density. This further underlines the important finding that the mineralised skeleton produced below the ASH is of similar quality compared to that above the ASH. The processes observed here in CWC occurred in both thin and thick coral branches. For instance, Mingulay corals had thicker morphotypes than those sampled from the Pacific (**Figure 4**; Form and Riebesell, 2012; Hennige et al., 2014b, 2015a; Büscher et al., 2017).

In instances where calcite (1%) was observed in recently dead coral skeletons, it is possible that calcite incorporation is linked to aragonite precipitation (Farfan et al., 2018). While changes in Electron Backscatter Diffraction (EBSD) results here were driven by changes in crystal size rather than type, recent work (Farfan et al., 2018) has also shown that in some cases the incorporation of calcite in *L. pertusa* can be up to 3%, with highest values found in dead samples from deep sites. The decrease in crystal size in corals from below the ASH is consistent with observations (Hennige et al., 2015a), where *L. pertusa* samples were incubated in mesocosms of projected future conditions.

Challenges and Opportunities

While we demonstrate here that accumulation of significant porosity is rapid (12 month laboratory incubations), and that the likely impacts of this can be seen at a large scale through *in situ* evidence, there are a number of factors to integrate into future work to be able to determine *when* CWC habitats will undergo ecosystem scale changes with regard to their complexity. Timescales are key, and while significant porosity is observed within 12 months, to model when that will have reef-scale impacts we need to quantify the linear/non-linear progression of porosity under different scenarios. Scaling up from our conceptual models to reef-scale habitats will be achieved through computational and mathematical techniques, which can build directly upon findings we have conceptualised here (e.g., **Supplementary Figure 8**). Timescales of coral degradation in large habitat structures are also important to consider, as over a long period of time, dead coral framework will be biofouled and infilled with sediment. As *in situ* evidence demonstrates, once in aragonite undersaturated water, CWC habitats have reduced complexity. Given this, it seems plausible that loss of dead coral material outpaces amelioration by sediment infilling or biofouling, but the rate of growth:loss (and carbonate budgets as a whole) are a critical challenge for the field to address. An important contributor to this process is bioerosion (Wisshak et al., 2012; Büscher et al., 2019), which will contribute significantly to a weakening of the coral structure (Tunnicliffe, 1979). While no bioerosion was observed in experimentally incubated samples here, bioerosion was evident in some samples collected *in situ* (e.g., **Figure 4E**). Including the *rate* of bioerosion contribution will be important for future models as it will contribute significantly to the rate of structural weakening and crumbling of reefs overall.

Underlying these processes is the need for greater understanding of the rates of seawater carbonate chemistry changes. The progression and timescale of increased porosity *in situ* will depend on whether the aragonite undersaturation of the water is consistent (does it fluctuate above or below $\Omega_{Arag} = 1$), biological respiration enhancing localised acidification, dissolution of carbonates (Sarma et al., 2002), the coverage of exposed skeletal material by sediment or manganese oxide, and the extent of change of other key environmental variables such as temperature (a key determinant of carbonate chemistry) and deoxygenation (which may contribute to increased skeletal exposure through death or tissue retraction of the live coral). Given the lack of dead skeletal framework in **Figure 1b**, it seems likely that the timescales of material loss and habitat crumbling are faster than any mitigating processes, but to determine risk of habitat loss, repeated measure studies on live and dead coral, and refined models are needed.

CONCLUSION

The techniques used in this investigation to measure and model "porosis" in CWC build upon those routinely used to examine bone porosis (osteoporosis). The parallels that can be drawn as a result of this are of benefit to modelling "porosis" in CWC, as the independent variables investigated in this study, such as aragonite saturation, seem to offer a potential predicting metric if quantified locally over sufficient time scales. This would allow adaptation of diagnostic principals (Currey, 2002; Kanis et al., 2008; Hernlund et al., 2013; Engelke et al., 2016; Mirzaali et al., 2016; International Osteoporosis Foundation [IOF], 2019; Lefèvre et al., 2019) to model "coralporosis" and to identify tipping

points of CWC habitat loss (Dakos et al., 2019). While we describe the potentially rapid detrimental effects of ocean acidification to CWC reefs of the future along with the underlying mechanisms, it is this ability to model such changes that may give us powerful monitoring tools for deep-sea reefs. As we develop models supported by refined projections of changes in aragonite saturation, timescales of change and quantification of the proportion of CWC habitat comprised of dead (at risk) material, this will ultimately support future conservation and management efforts of these vulnerable marine ecosystems by indicating *which* ecosystems are at risk, *when* they will be at risk, and *how* much of an impact this will have upon associated biodiversity.

DATA AVAILABILITY STATEMENT

Data supporting the conclusions of this article are available through the authors and through the British Oceanographic Data Centre (Hennige et al., 2020).

AUTHOR CONTRIBUTIONS

SH, UW, LW, JMR, FM, and PE designed the concept of this manuscript. SH, LW, NK, UW, ES, AG, SS, and M-EA-T conducted the experimental analysis. All authors were involved in discussion. PE solicited funding for the fieldwork and led the *in situ* sampling effort, with assistance from LW.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00668/full#supplementary-material

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Recognising Stakeholder Conflict and Encouraging Consensus of 'Science-Based Management' Approaches for Marine Biodiversity Beyond National Jurisdiction (BBNJ)

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Areas beyond national jurisdiction (ABNJ) encompass the seabed, subsoil and water column beyond coastal State jurisdiction and marine biodiversity beyond national jurisdiction (BBNJ) is rich and varied. From providing sustenance and supporting livelihoods, to absorbing anthropogenic carbon dioxide emissions, ABNJ ecosystems are vital to the wellbeing of humankind. However, an enhanced understanding of BBNJ and its significance has not equated to its successful conservation and sustainable use. Negotiations for a new international legally binding instrument for the conservation and sustainable use of BBNJ have scoped applicable principles for a future agreement, including the use of best available science and science-based approaches. But there remains a lack of convergence on what science-based approaches would look like, or how they would be operationalised. In order to negotiate and implement a meaningful BBNJ treaty that can meet conservation and sustainable use objectives, stakeholder perceptions must be identified, and areas of divergence must be overcome. This study uses Q-methodology to reveal and analyse the diversity of perceptions that exist amongst key stakeholders regarding what it means to operationalise science-based approaches for the conservation and sustainable use of BBNJ. The Q-study features 25 stakeholder interviews and 30 Q-study participants revealing four different perceptions, each of which represent a different interpretation of what science-based management means in the context of BBNJ. Across these perceptions, there were areas of stakeholder consensus (e.g., regarding the benefits of integrative management, the application of precautionary approaches when data are insufficient, and the issues pertaining to the trustworthiness and credibility of science) and areas of stakeholder conflict (e.g., regarding the definition, function and authority of science within current and future BBNJ governance processes). Key implications of this study include the evidencing of fundamental tensions between differing perceptions of the authority of science and between conservation and sustainable use objectives, that may be fueling stakeholder conflict, and the subsequent proposal of integrative and highly participatory management approaches to operationalise science-based management of BBNJ.

Keywords: marine biodiversity, BBNJ, stakeholders, science-based approaches, Q-methodology, marine biodiversity beyond national jurisdiction, marine governance, science-policy interface

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INTRODUCTION

Areas beyond national jurisdiction[1] (ABNJ) encompass more than 64% of the ocean's surface and 95% of its volume. Once perceived as too vast to possibly incur human induced harm, it is now recognised that ABNJ are under threat. Based on the limited sampling of deep-sea ecosystems, it is evident that many deep-sea species mature slowly and produce fewer offspring than those located in shallow-water, and as such are characterised by increased levels of vulnerability (Gage and Tyler, 1991). Anthropogenic threats and pressures on ABNJ ecosystems, such as resource exploitation (e.g., fisheries, potential future deep-sea mining and bioprospecting Halpern et al., 2008) and global climate change (e.g. ocean acidification and deoxygenation (Sweetman et al., 2017; Levin et al., 2020) can impact biodiversity. There also exists a discrepancy between the pace of increasing human activities in ABNJ and scientific understanding of its unique ecosystems (Blasiak and Yagi, 2016). Indeed, recent work has highlighted huge uncertainties in our understanding of deep and open-ocean ecosystems, such as the mesopelagic realm (St John et al., 2016). While technological advancements may claim to have enabled the proliferation of deep-sea research and subsequently the volume of scientific evidence (Visalli et al., 2020), merely accumulating more evidence does not necessarily equate to improved management in practice (Fazey et al., 2014).

In response to increasing global concern for marine biodiversity beyond national jurisdiction (BBNJ), international actors are currently negotiating a new implementing agreement under the *United Nations Convention on the Law of the Sea* for the conservation and sustainable use of BBNJ (hereafter, the BBNJ Agreement) (United Nations General Assembly, 2017). Through the ongoing negotiating sessions for a new BBNJ Agreement, potential governance principles and approaches have emerged, including emphasis on, "*a science-based approach, using the best available scientific information and knowledge*"(United Nations, 2018). Science-based approaches, or evidence-based approaches are now regarded as central to environmental governance and aim to embed science in the content, outcomes and process of decision-making (Rousseau, 2012; Bainbridge, 2014). Despite the seemingly clear stakeholder approval of using a science-based approach (Earth Negotiations Bulletin, 2019) it is not clear what this would look like in practice. Consequently, the ambiguity surrounding the operationalisation of this term represents a significant bottleneck to creating functional governance structures for ABNJ. Resolving this ambiguity is not purely a matter of agreeing on definitions. Policy decisions are never objective – they unavoidably reflect the socio-economic, cultural, and institutional contexts and values under which they arise (Rosenau, 1993). Understanding stakeholder values and priorities, along with what stakeholders deem to be socially and politically acceptable, is essential for effective environmental governance (Addams and Proops, 2000; Loring and Hinzman, 2018). This is especially true for BBNJ governance, where the scientific data are limited and the inherent transboundary nature of BBNJ results in a wide range of stakeholders, each with unique sets of values. Designing and implementing successful governance structures and policies for ABNJ requires negotiators to balance diverse perceptions and find a *"sweet spot"* between an Agreement that is robust enough to adequately protect BBNJ, but not so demanding as to impede State and stakeholder participation (De Santo et al., 2019). While understanding stakeholder perceptions is particularly important for BBNJ governance, to date initiatives to understand and overcome divergence are poorly documented and are often employed on an *ad hoc* basis.

To address this knowledge gap, this study uses Q-methodology to analyse the breadth and nature of existing stakeholder perceptions regarding operationalising science-based management of BBNJ and identifies key areas of conflict and consensus that may affect future policy design decisions. As Q-methodology is an emerging methodological approach in marine studies, this paper begins with a brief introduction to Q-methodology, followed by our study design, results, and discussion. This research will highlight the trends, opportunities and management implications suggested by these data. Findings of this research include four emergent factors which represent four different perceptions of how science-based approaches should be operationalised for BBNJ governance, as well as key areas of stakeholder consensus and conflict.

METHODOLOGY AND MATERIALS

Q-Methodology

Q-methodology is a quali-quantitative methodology that originated in the field of psychology (Brown, 1980) but is now used in a wide array of fields to understand the range of stakeholder perceptions in reference to contested issues [e.g., education (Rodl et al., 2020), medicine (Hammami et al., 2020), and environment (Moros et al., 2020)]. Q-methodology combines statistical analysis in the form of a data-reduction technique applied to pseudo-ranking data with the analysis of qualitative data obtained during the ranking exercise to reveal core perceptions. The combination of quantitative and qualitative data additionally enables researchers using Q-methodology to analyse the apparent scope for compromise between different stakeholder perceptions because it reveals specific areas of consensus and conflict that exist in relation to the focus of the study. As such, Q-methodology is apt for investigating complex policy topics (Cairns et al., 2014). **Figure 1** illustrates the six general stages of a Q-methodology study, as outlined by Watts and Stenner (2012).

Detailed Methods

Identifying the Concourse

The concourse is a collection of perceptions about the issue in question, taken verbatim from real-world sources, known as 'statements', that together represent as completely as is possible the entire spectrum of perceptions that exist in relation to the contested issue.

[1]As mandated by the United Nations Convention on the Law of the Sea, areas beyond national jurisdiction refers to the seabed, subsoil and adjacent water column beyond the 200 nautical mile lines and extended continental shelves that delineate coastal State jurisdiction (United Nations, 1982).

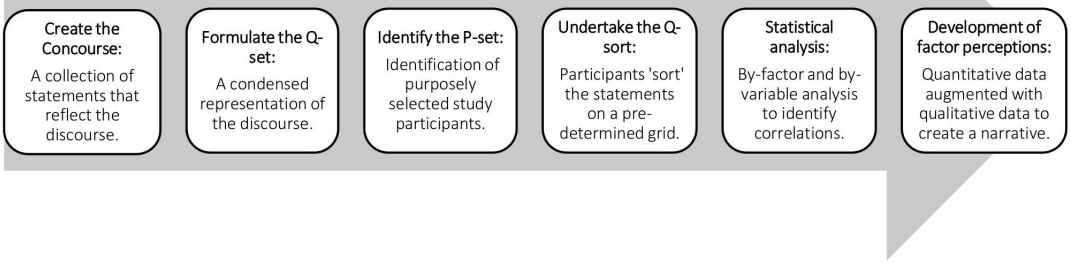


FIGURE 1 | The basic stages of a Q-methodology study: As described by Watts and Stenner (2012), Q-methodology studies start with the creation of the 'concourse', followed by formulation of the Q-set, identification of the P-set, the Q-sort, and statistical analysis and factor perception development.

The concourse for this study was identified exclusively from semi-structured interviews with stakeholders actively engaged in BBNJ issues. Semi-structured interviews were conducted at the second session of the intergovernmental conference for BBNJ (New York City, March 2019) as well as via online video conferencing (April-June 2019). In total, twenty-five stakeholder interviews were conducted with participants spanning the employment demographic groups of non-governmental organisation (NGO), intergovernmental organisation (IGO), science researcher, law and policy researcher, ABNJ industry experts, and state/delegations. Prior to the commencement of interviews, this research received approval by appropriate ethics committees and all participants were provided with written documentation of their rights as a participant. Interviews were transcribed verbatim and transcripts were supplied to participants who were given an opportunity to amend factual errors or areas of miscommunication. From the final interview transcripts, a total of 403 statements were extracted to form the concourse.

Creating the Q-Set

The Q-set is the collection of statements selected from the concourse that participants will eventually 'sort' during the Q-sort. The Q-set is formed by taking a representative sample of the statements within the concourse that together, represents the diversity of issues and strengths of opinion found within the concourse.

This study uses the steps of the basic policy cycle to categorise the statements in the concourse. These steps are: (1) undertaking science; (2) analysis, translation and advice; (3) decision-making; and (4) implementation and monitoring. The policy cycle was used as it allows for the investigation of stakeholder perceptions of the flow of science throughout the entire policy cycle. Statements within each of the stages were identified, via thematic coding, and were divided into sub-issues. Duplicate statements and statements deemed unsuitable were eliminated. The remaining statements were screened for ease of communicability through a pilot study. Statements flagged as unclear or confusing were either removed or altered to improve the clarity, whilst taking care not to change the latent meaning of the statement. The final Q-set consisted of forty-two statements (n = 42) spanning the basic policy cycle stages, as shown in **Figure 2**.

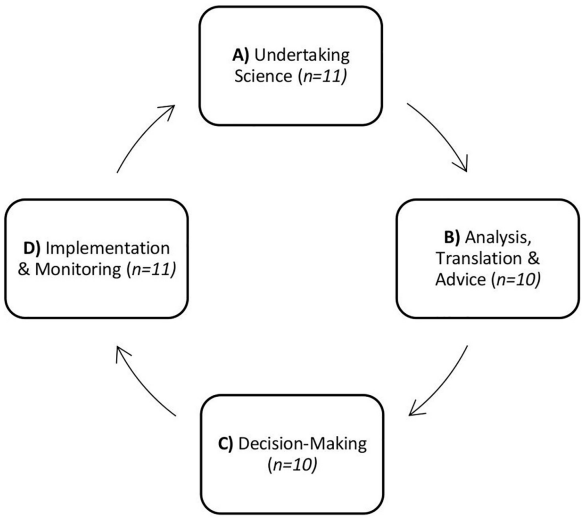


FIGURE 2 | Statement selection for the final Q-set per policy cycle stage: Division of statements under the concourse matrix (n=statements). The basic policy cycle depicts a policy process under which scientific evidence is undertaken **(A)**, analysed and translated into usable metrics and presented to policymakers **(B)** for use in decision-making **(C)** and is ultimately reflected in the implementation and monitoring of management measures **(D)**.

Identifying the P-Set

The P-set is the collection of key stakeholders who are asked to participate in the Q-study. The way in which the study participants are chosen highlights the most significant difference between Q-methodology and other, more conventional forms of surveying human attitudes (i.e., 'R' studies). The individuals who constitute the P-set are chosen very intentionally because they are knowledgeable stakeholders. In Q-methodology, the goal of the research is to use a set of relevant people and a sample of

opinion statements to draw conclusions about the 'population' of perceptions from which the sample was taken. Q-methodology is not designed to produce results that can be generalised to a larger population (of humans), and therefore requires a smaller number of human participants to produce statistically meaningful results than traditional 'R' studies (Watts and Stenner, 2012).

The P-set was comprised of individuals with a high level of knowledge of the BBNJ process. To ensure that a wide range of perceptions were captured in the Q-study, care was taken to ensure that the P-set consisted of participants from a wide range of employment demographic groups (as stated above). Criteria for participation were: (1) participation in the BBNJ negotiations (gleaned from personal contact or via the official participant list for the conference); (2) an occupation that is directly related to BBNJ issues; and (3) the authoring of BBNJ relevant peer-reviewed publications. The standard of eligibility was the fulfilment of one or more criteria. Of the originally identified potential participants, thirty participants (*P-set=30)* agreed to participate in the Q-study, including 17 participants who participated in the semi-structured interviews.

The Q-Sort

During the Q-sort stage, participants rank the Q-set statements based on their relative level of agreement with the opinion expressed in the statement by placing the statement onto a pre-defined grid. The grid is structured in a quasi-normal distribution, labelled on a continuum across the columns in the grid (Watts and Stenner, 2012). Because this continuum exists across columns, but not the rows, the data generated represent pseudo-ranking data. Each completed grid represents a single data point in the study and is accompanied by qualitative data explaining the reasons the statements were sorted in a particular way.

Our Q-sort was conducted online, utilising HTMLQ software[2] and used an eleven-point quasi-normal distribution grid with a score continuum of −5 to +5 (**Figure 3**). A shallow kurtosis was chosen for grid design, as the P-set were deemed to be highly knowledgeable, and therefore a shallow distribution would allow for the investigation of nuances within the discourse (Watts and Stenner, 2012). The grid was labelled 'Most UNLIKE How I Think' corresponding to the ranking of −5 and 'Most LIKE How I Think' corresponding to the ranking of +5. Prior to commencement, participants were provided with an information package with detailed instructions and participant information. Participants were asked to provide explanations for the placement of the highest and lowest ranking statements.

Statistical Analysis

The statistical analysis stage of a Q-methodology study uses a multivariate data reduction technique to produce a correlation matrix which represents the level of association between Q-sorts (Brown, 1980). The outcome is a set of 'factors', which each represent a broad perception. Q-sorts that share similar sorting patterns end up 'loading' onto the same 'factors' in similar ways. Q-sorts that load in a statistically significant way[3] onto a factor are referred to as 'factor exemplars' and become the focus of the qualitative analysis (Watts and Stenner, 2012). Q-sorts that load onto more than one factor are considered confounded and factors that do not load strongly onto any factor are considered outliers. During the analysis, the emergent correlation scores for individual statements are standardised into z-scores. The ranking implied by these z-scores is used to generate an 'idealised' Q-sort and corresponding factor scores for each statement for each factor. *Z*-scores are also used to test and analyse the degree of difference (i.e., consensus and/or conflict) between each of the factors extracted during the analysis and statements that are characterised by polarised sorting (i.e., a statement in which different participants either strongly agree or strongly disagree with) can be seen as areas of conflict between participants. Identified factors are tested against the following criteria:

(1) Eigenvalues: The eigenvalue for each factor must be greater than one for a factor to be accepted, as an Eigenvalue of less than one accounts for less study variance than one Q-sort (Kaiser, 1960) (Yeomans and Golder, 1982).
(2) Percentage of explanatory variance: The cumulative variance of extracted factors must be greater than 35% (Kilne, 1994).
(3) Number of Q-sorts flagged: A minimum of two Q-sorts must be flagged per factor (Watts and Stenner, 2012).
(4) Humphrey's rule: The cross-product of each factor's two highest loadings (either positive or negative) must exceed twice the standard error value (Eq. 1) (Humphreys and Maontanelli, 1975).

$$Humphrey's\ Rule\ Threshold = \frac{2}{\sqrt{n}},$$
$$where\ n = number\ of\ statements \quad (1)$$

This study's Q-sort data were input into a matrix which underwent a principle components analysis with a varimax rotation using the qmethod package in R Studio. Pearson's correlation coefficient was used in the data reduction process. The initial correlation matrix between Q-sorts were tested against the aforementioned criteria and 5 different possible factor solutions were identified. Preliminary analysis was undertaken for each viable factor solution and researcher abduction was applied in order to determine the best solution. All possible factor solutions were examined and compared to determine if a significant component of the discourse was included with the addition of more factors. This reduction exercise included analysis of

[2]HTMLQ is an open source application created by Aproxima and released under the Massachusetts Institute of Technology license Copyright (Aproxima Gesellschaft Für Markt- Und Sozialforschung Weimar, 2014-2015).

[3]The R package qmethod, used in this study, applies two tests by default to determine whether a Q-sort has loaded onto a factor in a statistically significant way. The first test compares the factor loading for a Q-sort with a particular, minimum threshold. This threshold is set to be $1.96 * 1/\sqrt{n}$, where 'n' is the number of statements in the Q-methodology study. The second test compares the strength with which a Q-sort has loaded onto one factor with the strength with which the same Q-sort has loaded onto the other factors extracted in the analysis. Only those Q-sorts that load by a sufficiently large margin onto a single factor (as compared to the other factors) are considered to have passed this test. Q-sorts must pass both tests to be considered statistically significant by R.

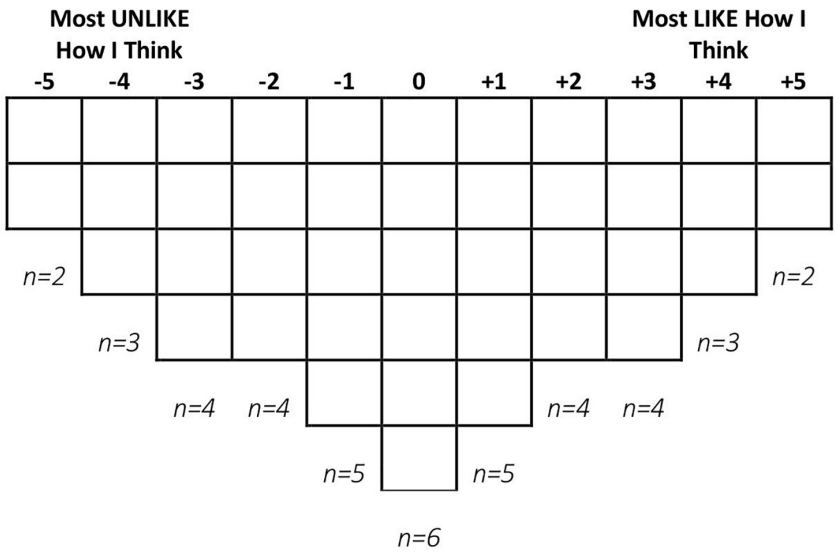


FIGURE 3 | Quasi-normal distribution grid utilised in Q-study: Participants 'sort' statements (*n*) by placing them into a column of a pre-defined, quasi-normal distributed grid based on their personal perceptions.

the number of total Q-sorts included or excluded under each solution (i.e. the solution that had the least number of outlying and confounded Q-sorts) and the uniqueness and/or similarity between the factor's perceptions.

Development of Factor Perceptions

The development of factor perceptions relies on researcher abduction, by which quantitative results (which identify the number of factors, the idealised Q-sorts, the factor exemplars, and the specific consensus and conflict issues) are augmented with qualitative data to form a narrative describing the perceptions that are reflected in the emergent factors (Brown, 1980).

The development of factor perceptions involved the examination of the idealised Q-sort and factor scores for each statement per factor, the identification of distinguishing statements, and considerations of polarised sorting of statements amongst factors. Qualitative data in the form of pre-study semi-structured interviews of Q-study participants and in-situ sorting explanations by the P-set of the most and least salient statements were gathered from factor exemplars. Through the augmentation of the statistical outputs with qualitative data, abduction was used to create a social discourse or factor perception for each factor.

Key Assumptions

This methodology generates an indicative 'snap-shot' of stakeholder perceptions regarding science-based approaches to BBNJ. The perceptions revealed through Q-methodology will evolve over time as the context, scope and direction of the BBNJ negotiations change and evolve. Thus, it is assumed that perceptions identified in this study may change overtime. Furthermore, undertaking the Q-study online (as opposed to in-person) has unique trade-offs. Online studies are accessible and alleviate the spatial and temporal constraints of in-person studies, however the researcher is not able to investigate subtle participant reactions to statements or ask further questions about sorting behaviour. As such, this study primarily utilises quantitative results and augments these with qualitative data.

TABLE 1 | Composition of factors (F), illustrating the employment demographic group of factor exemplars and the total number of exemplars per factor (in bold).

Employment Demographic Group	F1	F2	F3	F4
NGO	2	2	0	0
IGO	2	0	2	0
Science Researcher	3	0	1	2
Law & Policy Researcher	1	2	0	0
State/Delegate	1	2	1	1
Industry Experts	1	1	0	1
Total	**10**	**8**	**4**	**4**

RESULTS

Overview

It was determined that a 4-factor solution was the qualitatively optimal solution and reflected the breadth of identified perceptions. Under this solution, one Q-sort was an outlier and an additional three Q-sorts were confounded. In total, ten exemplars loaded onto Factor 1, eight onto Factor 2, and four onto each Factor 3 and 4 (**Table 1**). It is notable that none of the employment demographic groups loaded exclusively onto a single factor, highlighting heterogeneity of perception within, as well as across, each of these categories of stakeholder. The z-scores, idealised Q-sort scores (IQS) and distinguishing statements for the 4-factor solution (hereafter, the Q-results) were produced for each factor (**Table 2**). Together, the factors explain 50.94% of the variance in the data. The qualitative analysis of each factor resulted in the following emergent perceptions:

TABLE 2 | *Z*-scores (ZSC) and idealised Q-sort scores (IQS) for factors (F).

Statements	F1		F2		F3		F4		Significance					
	ZSC	IQS	ZSC	IQS	ZSC	IQS	ZSC	IQS	F1:F2	F1:F3	F1:F4	F2:F3	F2:F4	F3:F4
In order to regulate human interactions in the ocean, science must provide baseline data.	1.06	3	0.34	1	0.92	3	0.67	2						
The role of science in the BBNJ process is to assist in monitoring once an instrument has been put into place.	−2.34	−5	−0.42	−1	−0.56	−2	−0.66	−2	****	****	****			
Science-based management of BBNJ would look like having a rigorous EIA process.	−0.43	−1	0.60	2	−0.12	−1	−0.64	−2	***			*	***	
We need more data from people in local communities who are actually experiencing the impacts.	0.56	2	−0.49	−2	−0.39	−2	−0.12	0	***	**	*			
Traditional knowledge is just as credible for some elements as Western knowledge is for others.	0.65	2	0.44	1	−1.59	−4	−0.05	0		****	*	****		***
Data is perceived as having hidden agendas if it comes from a conservation-oriented source.	−0.62	−2	−0.88	−2	−0.86	−3	−0.54	−1						
It is problematic that a lot of our data is collected by ABNJ industry.	−0.91	−3	−0.47	−1	−0.26	−1	−1.47	−4						
We do not have a global scientific community big enough to tackle all the BBNJ knowledge gaps.	−1.36	−4	−0.14	0	−1.95	−5	−1.91	−5	****	*		****	****	
We do not have enough data to implement ecosystem-based approaches in ABNJ.	−0.97	−3	−1.98	−5	−2.32	−5	−0.96	−3						
A major problem is that we currently use the data that we do have ineffectively.	−0.07	0	−0.79	−2	0.17	0	0.39	1	**			**	***	
You cannot do ecosystem-based management under the current sectoral management regime.	−1.90	−5	1.74	5	−0.27	−1	−1.64	−4	****	****		****	****	***
In order to define science-based management, we need to bring more disciplines into the discourse.	−0.06	0	0.13	0	−0.58	−2	1.78	5			****	*	****	****
Marine spatial planning is a useful tool for implementing science-based management.	0.80	3	0.37	1	0.52	1	0.93	3						
Lack of data should not stop us from making sensible management decisions.	1.53	4	1.60	5	1.21	4	1.35	4						
We must consider what a country needs as opposed to imposing science on them.	0.24	1	0.31	0	−1.08	−3	0.57	1		***		***		****
Summaries for policymakers are either too simplistic without much content or too complex for policymakers to understand.	−0.20	−1	−1.46	−4	0.03	0	−1.80	−5						
Science-based management is hindered by the lack of communication between different departments within states.	0.12	0	0.39	1	0.57	1	2.21	5			****		****	****
Scientists have difficulties communicating their science to different audiences.	0.71	3	−0.23	0	−0.26	−1	−0.71	−3	***	***	****			
If a policymaker fails to listen to scientific advice, it is a political failure not a scientific failure.	0.21	1	−1.14	−3	−1.22	−3	−1.44	−4	****	****	****			

(Continued)

TABLE 2 | Continued

Statements	F1		F2		F3		F4		Significance					
	ZSC	IQS	ZSC	IQS	ZSC	IQS	ZSC	IQS	F1:F2	F1:F3	F1:F4	F2:F3	F2:F4	F3:F4
Even when the science is clear, it is difficult to get the policymakers to take that science on-board.	0.36	1	0.72	2	1.49	4	−0.25	−1		***	*	**	**	****
Barriers are overcome by scientists and policymakers getting to know one another in informal settings.	0.97	3	−0.45	−1	0.63	1	1.39	4	****			***	****	*
It makes it difficult to use science when scientists disagree amongst themselves.	−1.63	−4	−1.08	−3	−0.60	−2	−1.11	−3						
It is a challenge to articulate the science into a real-world management response.	−0.51	−2	−0.34	−1	−0.29	−1	1.11	3			****		****	***
People will always pick and choose the scientific evidence that supports their priorities.	−0.21	−1	−1.31	−4	1.16	4	0.70	2	***	***	**	****	****	
Policymakers are not clear enough about what science they need.	0.06	0	−1.13	−3	−0.03	0	−0.64	−2						
The problem with science is that as humans we like to be certain, and science is inherently not.	−0.73	−3	−1.44	−4	0.76	2	0.51	1	**	****	***	****	****	
Often, policymakers do not understand what is feasible from the scientific community.	0.47	1	−0.68	−2	0.68	2	−0.29	−1						
Side events provide a good opportunity for the uptake of science by policymakers.	0.67	2	−0.99	−3	0.80	3	0.07	0	****		*	****	***	*
NGOs are an important vehicle for bringing science into the BBNJ process.	−0.04	0	0.52	1	0.93	3	−0.22	0						
In the negotiations we have diplomats and politicians but not enough scientists.	−0.50	−1	−0.08	0	0.61	1	−0.66	−2		***		*		***
I think there is a strong presence of science within the BBNJ negotiations.	−1.37	−4	−1.81	−5	−1.74	−4	0.87	3			****		****	****
Currently, we are getting a more developed perspective of the science.	−0.51	−1	0.09	0	−1.45	−3	−0.55	−1	*	**		****	*	**
The more you can put science on an equal footing within the decision-making hierarchy, the better.	−0.71	−3	0.88	2	1.57	5	−0.48	−1	****	****		*	***	****
We need a science body at the global level to provide common scientific standards.	0.63	2	1.31	3	0.65	2	−0.92	−3	**		****	*	****	***
Strengthening the financing mechanisms of a BBNJ instrument is crucial.	−0.67	−2	1.13	3	1.50	5	0.10	0	****	****	**		***	***
The best available science needs to be widely available for everyone to access.	1.86	5	1.51	4	0.53	1	1.38	4		***		**		*
Data sharing should be an obligation under a BBNJ Agreement.	1.85	4	1.34	4	−0.09	0	0.10	1	*	****	****	****	***	
It is crucial that a BBNJ Agreement enhances the transfer of marine technology between states.	0.37	1	1.09	3	0.27	0	0.76	2						
A BBNJ instrument must be flexible to accommodate the science that will come in the future.	2.10	5	0.81	2	0.98	3	0.77	2	****	***	***			
We should coordinate existing scientific programmes to drive the implementation of a BBNJ Agreement.	−0.15	0	1.00	3	0.52	0	0.04	0						

(Continued)

TABLE 2 | Continued

Statements	F1		F2		F3		F4		Significance					
	ZSC	IQS	ZSC	IQS	ZSC	IQS	ZSC	IQS	F1:F2	F1:F3	F1:F4	F2:F3	F2:F4	F3:F4
We need to manage BBNJ at an ocean basin scale because ecosystems are ecologically connected across ocean basins.	1.21	4	1.42	4	0.67	2	1.24	3						
While we need some form of global science body, the science needs to be driven from a regional level.	−0.55	−2	−0.44	−1	−1.51	−4	0.14	1		***	*	***		****

*Asterisks signify statistically significant differences between pairs of factors in the strength of perception pertaining to each statement. *p-value of < 0.05; **p-value of < 0.01; ***p-value of < 0.001; ****p-value of < 0.0001.*

Factor 1: Enhancing Not Undermining

Science-based management can be operationalised by enhancing the existing system through a more effective science-policy interface and a greater dissemination of knowledge. Factor 1 does not see sectoral management as the most significant barrier, but instead highlights communication failures as an impediment to science-based approaches.

Factor 2: The Global Idealist

Successful science-based management requires top-down approaches in order to enhance equality amongst states and to fix the currently fragmented regime. Factor 2 suggests that science-based approaches cannot be achieved under the current sectoral regime, and that an adequately funded global science body is necessary to achieve BBNJ objectives.

Factor 3: Trust in Science

Political barriers, such as actor bias, hinder science-based management and therefore a future BBNJ Agreement should use science as a neutral platform. Factor 3 suggests that science-based approaches can be achieved by enhancing the authority of science within the decision-making process amongst all stakeholders.

Factor 4: More Than Just Science

Science-based management can be achieved by including more disciplines, particularly socio-economic research. Factor 4 suggests a bottom-up approach which can better account for socio-economic interests and priorities.

Each of these are elaborated on below, with special attention paid to the core themes within each perspective.

Factor 1: Enhancing, Not Undermining

Factor 1 explains 16.14% of the study variance and has an eigenvalue of 4.84. The composite reliability score for Factor 1 is 98%. Ten participants are exemplars for this factor, accounting for one-third of the total P-set. There are no apparent employment demographic connections defining the composition of Factor 1, with exemplars from all six employment demographic groups.

The Status Quo. . . but Better!

The ranking of the statement, *'you cannot do ecosystem-based management under the current sectoral regime*' is particularly significant to interpret Factor 1. With an IQS of -5, exemplars suggest that ecosystem-based approaches can be successful under sectoral management through the enhancement of cross-sector communication and data sharing. Exemplars recommended that barriers to science-based management approaches could be overcome by individual sectors having more consideration of the impacts that they have on other sectors. Factor 1 takes a realist view, noting that sectoral management is unavoidable, with sectoral organisation the norm for industry, academia and governments. Factor 1 exemplars posit that some actors use the limitations of a sectoral regime as an excuse for inaction. Instead, it is suggested that ecosystem-based management and other science-based approaches could be successful under the sectoral regime if the sectors have common strategies and objectives, which a future BBNJ Agreement could provide.

A Well-Connected Science-Policy Interface

The perception revealed in Factor 1 is that poor communication between scientists and policymakers is a significant barrier to implementing science-based approaches in ABNJ. With an IQS of +3, the statement, *'scientists have difficulties communicating their science to different audiences*', is a distinguishing statement for Factor 1 (compared to Factor 2: 0, Factor 3: −1, Factor 4: −3). One factor exemplar noted that, *"there is a big divide between. . . the science being produced and how much of this science is actually being translated into language metrics that managers and policy makers can understand and then apply."* Furthermore, Factor 1 is also distinguished by its indifference to the statement, *'if a policymaker fails to listen to scientific advice, it is a political failure not a scientific failure*' (compared to Factor 2: −3, Factor 3: −3, Factor 4: −4). As such, Factor 1 suggests that science-based approaches are hindered by the failure of scientists to communicate properly and policymakers to listen. Indeed, one factor exemplar posited that science-based management of BBNJ, *"would be a system where the science can directly influence the policy and vice versa."*

Dissemination of Knowledge Through Obligatory Data Sharing

Factor 1 suggests that enhanced data sharing procedures are vital to the success of science-based management. This is demonstrated through the corresponding IQS of +5 for the statement, '*the best available science needs to be widely available*

for everyone to access.' Furthermore, a distinguishing statement for Factor 1 is, *'data sharing should be an obligation under a BBNJ Agreement'* (IQS +4), which signifies a desire for enhanced responsibility to share data. Factor exemplars emphasised that data sharing is fundamental for all aspects of a future BBNJ Agreement to support decision-making. One exemplar posited that when creating ocean laws and policies, *"the laws of nature should be our model,"* concluding that, *"this is why good science is needed by decision-makers."* Moreover, Factor 1 emphasises the importance of the dissemination of data for informing policy decisions, with one exemplar noting that, *"the further you get towards knowledge and advice, the more diversified become the possible policies that can be chosen."*

Factor 2: The Global Idealist

Factor 2 explains 15.42% of the study variance and has an eigenvalue of 4.61. The composite reliability score for Factor 2 is 97%. It is the second most densely populated factor group and has eight factor exemplars. Notably, no individual from the science researcher or IGO employment demographic groups loaded significantly onto this factor. Furthermore, Factor 2 is the only factor that does not have an exemplar from the science researcher demographic group.

BBNJ and Equality

Factor 2 emphasises the importance of equality between states. Similar to Factor 1, this includes data sharing, but the emphasis on equality of access is broader for Factor 2, than just ensuring access to scientific data. While Factor 1 exemplars referenced informing policy as the benefits of data sharing, an emergent viewpoint from Factor 2 is that data sharing is to enhance equality of access to marine technology and data amongst states. One factor exemplar noted that, "*the non-availability of science…would be detrimental to the maximization of the common good, unfair, unethical*". Factor 2 emphasises global equality, as is demonstrated through the highest corresponding IQS amongst factors (+3) for the statement, *'it is crucial that a BBNJ Agreement enhances the transfer of marine technology between states'*. Factor exemplars posited that, *"for equity and adequate management in all parts of the globe, technology transfer is very important"*. Factor 2 has a corresponding IQS of +3 for the statement, *'strengthening the financing mechanisms of a BBNJ instrument is crucial'* (compared to Factor 1: −2). Indeed, Factor 2 exemplars explicitly reference financial capacity as a prerequisite to conduct scientific observations, build global capacity and transfer technology between states and posited that, *"in science there are gaps in terms of how much science we can conduct, due to funding and capacity."*

The Status Quo Does Not Work

The results suggest that Factor 2 has a globalised perception of operationalising science-based management, with factor exemplars demonstrating an inclination for a centralised, top-down approach. Factor 2 emphasises the failure of the current sectorally managed regime to implement science-based approaches, such as ecosystem-based management. With a corresponding IQS of +5, the statement, *'you cannot do ecosystem-based management under the current sectoral management regime'* is a distinguishing statement for Factor 2 and contrasts with that of Factor 1 (−5). Factor exemplars expressed doubt that, *"rational integrated management"* could take place under the currently fragmented regime. Instead, a cross-sectoral and holistic approach was touted as the ideal to address the geographical, thematic and institutional gaps that exist under the current regime. The distinguishing statement, *'we need a science body at the global level to provide common scientific standards'* has the highest corresponding IQS (+3) of all four factor groups. One factor exemplar posited that, *"the scientific method…can provide us with some common ground in order to proceed when we have differences in opinions."*

Factor 3: Trust in Science

Factor 3 explains 9.93% of the study variance and has an eigenvalue of 2.98. The composite reliability score for Factor 3 is 94%. There are four factor exemplars for Factor 3, consisting of participants from the IGO, science researcher and state/delegation employment demographic groups. No participants from the NGO or law/policy researcher demographics loaded significantly onto Factor 3.

Science-Based Management Is Hindered by Politics

With a corresponding IQS of −5 for both of the statements, *'we do not have enough data to implement ecosystem-based approaches in ABNJ'* and, *'we do not have a global scientific community big enough to tackle all the BBNJ knowledge gaps'*, Factor 3 does not perceive the current status of available scientific data as a barrier. Indeed, factor exemplars suggest that, *"we have enough knowledge and enough scientists to start the job"*. Instead, Factor 3 emphasises that the barriers to operationalising science-based approaches for BBNJ are political in nature. Factor 3 has a corresponding IQS of +4 for the distinguishing statement, *'even when the science is clear, it is difficult to get the policymakers to take that science on-board'* (compared to Factor 1: 1, Factor 4: −1). Highlighting the political nature of BBNJ resource use, one factor exemplar posited that you cannot, "*ask for a science-based approach and then overlook the science and establish quotas based on your national interests,*" and continued that, *"it may not give you the quotas that you desire or the mining sites that you desire but I do not think you can have it both ways."* This viewpoint is further demonstrated by the corresponding IQS of +4 for the statement, *'people will always pick and choose the scientific evidence that supports their priorities'* (compared to Factor 1: −1, Factor 2: −4).

Barriers Can Be Overcome by Putting Science on an Equal Footing

Factor 3 calls for an enhanced role of science, scientists and research within the decision-making process. Significant to the viewpoint of Factor 3 is the statement, *'in the negotiations we have diplomats and politicians but not enough scientists,'* which distinguishes Factor 3 only. Factor exemplars commented that, *"the scientific community is the only actor who can provide the necessary knowledge to gather and synthesize this information and make it actionable for policymakers."* It was further posited that the scientific community has been, "*absent in these negotiations.*"

Factor exemplars noted that the minimal presence of science in the negotiations is, *"one of the biggest weaknesses of the BBNJ process."* Moreover, it was suggested that while scientists play an important role, they are, *"tucked away at the back of the room"*. As such, Factor 3 suggests that science-based approaches can be achieved by enhancing the role and authority of science and scientists. This is further supported by the corresponding IQS of +5 for the distinguishing statement, *'the more you can put science on an equal footing within the decision-making hierarchy, the better'* (compared to Factor 1: −3, Factor 4: −1).

Factor 4: More Than Just Science

Factor 4 explains 9.45% of the study variance and has an eigenvalue of 2.83. The composite reliability score for Factor 4 is 94%. There are four factor exemplars for Factor 4, including participants from the employment demographic groups of ABNJ industry experts, state/delegate and science researcher.

De-Centralised Approaches Account for Socio-Economic Interests

Factor 4 demonstrates an aversion to a centralised approach to science-based management. As such, the statement, *'we need a science body at the global level to provide common scientific standards'* distinguishes Factor 4 with an IQS of −3 (compared to Factor 2: +3). The view that we should enhance the current system as opposed to imposing a top-down governance structure is further demonstrated by the corresponding IQS of −4 for the statement, *'you cannot do ecosystem-based management under the current sectoral management regime'* (compared to Factor 2: +5). Factor exemplars note that, *"as long as sectors are talking together and interacting at a national, regional and global level it is entirely possible to not only do ecosystem based management but do it better"*. Factor 4 posits that enhanced integration and interactions between sectors is the optimal solution because it can consider, *"other elements, like social elements and economic interests and priorities"*. The distinguishing statement, *'in order to define science-based management, we need to bring more disciplines into the discourse'*, further demonstrates this with a corresponding IQS of +5 (compared to Factor 1: 0, Factor 2: 0, Factor 3: −2). Factor exemplars highlight the need to include a wide scope of disciplines, including socio-economic research. To facilitate a wider inclusion of disciplines, Factor 4 suggests that ABNJ industry can play a role in data collection, which is demonstrated by the corresponding IQS of −4 for the statement, *'it is problematic that a lot of our data is collected by ABNJ industry'*.

It Is Not Only About Making the Science Available, but Making the Right Science Available

Distinguishing Factor 4 only, the statement, *'it is a challenge to articulate the science into a real-world management response'*, has a corresponding IQS of +3 (compared to Factor 1: −2, Factor 2: −1, Factor 3: −1). However, Factor 4 suggests that it is not the sole fault of policymakers. Coupled with the lowest IQS amongst factors for the statements, *'if a policymaker fails to listen to scientific advice, it is a political failure not a scientific failure'* and, *'even when the science is clear, it is difficult to get the policymakers to take that science on-board,'* Factor 4 highlights the importance of the availability of policy-relevant and salient science. One factor exemplar suggested that while policymakers may be clear about the science that they need, external factors such as personal research interests, institutional incentives to publish novel work and poor understanding of how policy functions, amongst others, could negatively influence the undertaking of salient research. Factor exemplars posited that, *"if the science is presented and is sufficiently tuned to the policymakers understanding, then there is not a problem"* and continued, *"the problem is making sure that the right science is available."*

Identified Areas of Consensus and Conflict

One indication of the level of consensus and conflict between factors comes from the relative perception of each statement by each factor. Statements for which there is not a significantly different relative ranking across the factors can be considered to be areas of consensus. All other statements represent areas of varying degrees of conflict. Another way to conceive of relative consensus is to consider the standard deviation between factor z-scores per statement. As demonstrated in **Table 3**, the Q-results highlight three true consensus points, three areas of broad consensus, and three areas of broad conflict. Each of these areas of consensus/conflict were identified using a combination of quantitative and qualitative information.

Areas of Consensus

Areas of consensus emerged regarding the application of integrative approaches to operationalise science-based management. The statement, *'marine spatial planning is a useful tool for implementing science-based management'* enjoys true consensus across factors with a standard deviation of ±0.26 amongst factor z-scores. The IQS for this statement range from +1 to +3, which suggests a neutral-positive perception of the use of marine spatial planning to operationalise science-based approaches for BBNJ. Participants expressed perceived benefits of MSP in ABNJ, suggesting that, *"if you have an integrated approach to MSP then you will be able to understand not only what you have and what is going on, but the different uses, conflicts and opportunities."* Participants posited that while MSP has not received much focus in the negotiations, the basic principles that characterise MSP are being discussed. It was noted that you cannot achieve BBNJ objectives without some degree of integration, spatial planning, stakeholder cooperation and area-based management tools (ABMTs).

The perceived benefits of integrative approaches also emerged regarding the statement, '*we need to manage BBNJ at an ocean basin scale because ecosystems are ecologically connected across ocean basins',* which enjoyed broad consensus amongst factors. With IQS ranging from +2 to +4, participants posited that integrative approaches that took into consideration ecological connectivity were vital to meet conservation and sustainable use objectives. One participant noted that, *"oceans are complex ecosystems and you cannot manage oceans without a real understanding on how the big flows and processes interconnect."* Another noted that, "*interconnectivity is an essential characteristic*

TABLE 3 | Identified consensus and conflict statements: Statements sorted by standard deviation (variance across factor *z*-scores for each statement), with corresponding idealised Q-sort scores (IQS) for each factor (*F*) and category of consensus or conflict (Trend).

Statement	IQS				SD	Trend
	F1	F2	F3	F4		
Data is perceived as having hidden agendas if it comes from a conservation-oriented source.	−2	−2	−3	−1	0.17	True Consensus
Lack of data should not stop us from making sensible management decisions.	+4	+5	+4	+4	0.18	True Consensus
Marine spatial planning is a useful tool for implementing science-based management.	+3	+1	+1	+3	0.26	True Consensus
We need to manage BBNJ at an ocean basin scale because ecosystems are ecologically connected across ocean basins.	+4	+4	+2	+3	0.32	Broad Consensus
It makes it difficult to use science when scientists disagree amongst themselves.	−4	−3	−2	−3	0.42	Broad Consensus
It is problematic that a lot of our data is collected by ABNJ industry.	−3	−1	−1	−4	0.46	Broad Consensus
We do not have enough data to implement ecosystem-based approaches in ABNJ.	−3	−5	−5	−3	0.58	Broad Consensus
The more you can put science on an equal footing within the decision-making hierarchy, the better.	−3	+2	+5	−1	1.09	Broad Conflict
I think there is a strong presence of science within the BBNJ negotiations.	−4	−5	−4	+3	1.27	Broad Conflict
You cannot do ecosystem-based management under the current sectoral management regime.	−5	+5	−1	−4	1.66	Broad Conflict

of ocean ecosystems." Other participants highlighted that governing BBNJ at an ocean basin scale would not only reflect ecosystems, but would also reflect similar political desires and capacities of coastal states, and that governing BBNJ at an ocean basin scale is, "*where political realities and coastal states interests best align."*

Consensus also emerged regarding the application of precautionary approaches for ABNJ. The treatment of the statement, *'lack of data should not stop us from making sensible management decisions'* enjoys true consensus, with a standard deviation of ±0.18 amongst factor z-scores and IQS ranging from +4 to +5. These data suggest approval for precautionary approaches to be employed when data are lacking. Participants noted that, *"to be proactive, we should make management decisions even when anecdotal evidences indicate necessity for management."* Furthermore, it was highlighted that this is an important aspect of the precautionary approach and that one should always strive to make the best possible decisions with the data available. Another participant suggested that, "'*best available science' should not mean that we wait for perfect information before acting*" and other participants posited that waiting for, "*the 'right amount' of information…has delayed management and conservation actions throughout global and regional frameworks."*

Similarly, the broad disagreement with the statement, *'we do not have enough data to implement ecosystem-based approaches in ABNJ' (*IQS ranging from −3 to −5*)* demonstrates broad consensus within these data about the capacity to take actions to manage BBNJ, rather than deferring it to the future. Participants posited that, *"even with limited data we can implement an approach based on precaution".* One participant noted that the existing data is, "*more than enough to support the implementation of ecosystem-based approaches*" but continued that, "*what we are lacking is the appropriate set of legal and policy tools that enable and sustain those approaches."*

Complementary to this is the general disagreement with the statement, *'it makes it difficult to use science when scientists disagree amongst themselves' (*IQS ranging from −2 to −4*).* This shared disagreement demonstrates that there is broad consensus within these data regarding the usefulness of scientific data, despite uncertainty within that data. Participants noted that, *"there will always be some scientists who disagree."* Other participants suggested that, *"this is the nature of science- scientists make hypotheses and…others test them."* It was furthered that science is not the only discipline that faces disagreements or uncertainty, and that disagreement should not be used as an excuse for non-action in relation to the conservation and sustainable use of BBNJ.

Lastly, consensus emerged regarding perceived trust and credibility of scientific data collected by different key stakeholder groups. With a standard deviation of ±0.17 between factor z-scores, the disagreement with the statement, *'data is perceived as having hidden agendas if it comes from a conservation-oriented source'* is a point of true consensus amongst factors. As shown in **Table 3**, the IQS range from −1 to −3 and demonstrate that this statement has a neutral-negative perception across all factors. Similarly, broad consensus emerged in relation to the treatment of the statement, '*it is problematic that a lot of our data is collected by ABNJ industry'*. With IQS ranging from −1 to −4, these data suggest that participants perceived industry-sourced data as credible.

Areas of Conflict

These data suggest that there is conflict amongst stakeholder perceptions surrounding the status and authority of science in relation to BBNJ governance. The statement, *'you cannot do ecosystem-based management under the current sectoral management regime'* demonstrates broad conflict within these data, which is demonstrated by a standard deviation amongst factor z-scores of ±1.66. This statement does not distinguish all factors but presents conflict in perceptions between Factor 1 and Factor 4 versus Factor 2. Exemplars from Factor 1 and 4 (IQS of −5 and −4, respectively) noted that science-based approaches, such as ecosystem-based management, were completely possible under sectoral management (which they considered to be the reality of ocean governance), and in some instances the superior option to a centralised regime. Other participants ranked this statement negatively because they believed that sectoral barriers represented one of many obstacles, and that blaming the sectoral

regime, *"seems to provide an excuse."* In contrast, exemplars from Factor 2 who agreed with this statement suggest that sectoral management is a significant barrier to operationalising science-based approaches and is plagued with fragmentation, both geographically, thematically and substantively. Participants noted that while there has been some improvement, *"many sectoral bodies cannot or are reluctant to undertake ecosystem-based approaches."* It was furthered that, *"we need a cross sectoral approach…to be able to effectively address all regions and all features of the marine biodiversity in ABNJ."*

There is also conflict surrounding perceptions of the current role of science, and the role that it *should have* in the context of a BBNJ Agreement. These disagreements exist despite the aforementioned consensus surrounding the usefulness of existing scientific data and the importance of a precautionary approach to managing BBNJ. For example, perceptions differed in relation to the statement, '*I think there is a strong presence of science within the BBNJ negotiations.*' Factors 1, 2 and 3 disagree with the statement (IQS of −4, −5, −4, respectively), while Factor 4 moderately agrees with it (IQS of +3). Some participants disagreed because they felt that science had been under-represented in the BBNJ negotiation process. This is illustrated by the quote from a Factor 3 exemplar: *"there has been a very weak presence of science throughout the Preparatory Committees and the Intergovernmental Conferences."* Other participants disagreed with the statement because they were uncertain about how science was being used in practice. For example, a Factor 1 exemplar noted that, *"although there is a consensus…regarding the importance of science, it is quite unclear how science is utilized in decision making."*

However, Factor 1 and 4 disagree with the statement, *'the more you can put science on an equal footing within the decision-making hierarchy, the better,'* whereas Factors 2 and 3 agree with it. Considering these two insights together shows that while Factors 1,2 and 3 perceive science to have a weak presence within the BBNJ negotiations, they differ as to whether this is a problem that needs to be addressed going forwards. Exemplars from Factors 2 and 3 who had a positive perception of this statement posited that, "*the alternative to putting science on an equal footing…is the current status quo which allows a wide range of industries to operate without supervision in the high seas."* It was further noted that putting science onto an equal playing field would, "*avoid politicization of the decision making process when considering proposals for new ABMTs."* Exemplars from Factors 2 and 3 further posited that putting science on an equal footing was important because making decisions that are, *"based on the best available science will ensure that the best decisions are taken for the effective long term conservation of marine biodiversity."* This suggests that the perspectives connected with Factors 2 and 3 are associated with a particular value system – one that in the evaluation of any trade-off would, by default, prioritise marine biodiversity. In contrast, Factors 1 and 4 seem to hold value systems that do not give such exclusive primacy to marine biodiversity. For example, exemplars posited that, "*science needs to underpin the BBNJ negotiations but needs to be balanced with economic needs and societal expectations."* Seeing this as a potential area of conflicting value system is an important insight.

DISCUSSION

This study uses Q-methodology to investigate stakeholder perceptions of science-based management of BBNJ. Thirty highly knowledgeable stakeholders ranging from six different employment demographic groups undertook the Q-study, which produced four factors. Factor 1 emphasises a desire to enhance the existing system through a more effective science-policy interface. In contrast, Factor 2 favours a global, centralised approach to science-based management and has a strong focus on global equality, enhanced funding and technology transfer between states. Factor 3 emphasises the importance of enhancing science in the decision-making hierarchy and the use of science to neutralise perceived political bias. Factor 4 suggests that operationalising science-based approaches is a bottom-up task that requires wider input from other disciplines, including socio-economic research. Ultimately, these findings point to a significant level of disagreement amongst key stakeholders regarding the operationalisation of science-based approaches for the conservation and sustainable use of BBNJ.

Achieving the consensus required to effectively implement science-based approaches for BBNJ will not be an easy feat but is of paramount importance. When mandating the negotiating sessions for a BBNJ Agreement, the UN General Assembly Resolution 72/249 stipulated that actors, *"shall exhaust every effort in good faith to reach agreement on substantive matters by consensus"* (United Nations General Assembly, 2017). While areas of consensus can be used as rallying points to build momentum behind desired policy options or to maintain enthusiasm during difficult discussions, a tactic employed to good effect by the President of the Conference, achieving consensus is not an end in itself. Consensus is crucial as participatory processes, such as consensus-built decision-making, can support the acceptance and implementation of future regulatory measures (Maisley, 2013). When trying to build consensus, it is important to understand where there are conflicting perceptions, as well as the differing motivations attached to the polarised views. Identifying areas of stakeholder conflict and the underlying causation can aid in achieving a mutually agreeable (and more abideable) middle ground for BBNJ management options. Here, we highlight the key implications of our study of stakeholder perceptions and the minute nuances and motivations that may drive these perceptions, to unearth ways forward for operationalising science-based approaches for BBNJ.

Implications of Identified Conflict

When investigating existing stakeholder perceptions of science-based approaches for BBNJ, our study highlights significant conflict around:

(1) The authority, status, and definition of 'science' within the BBNJ process.
(2) The extent to which conservation goals or sustainable use goals are emphasised by stakeholders.

Regarding (1), all four factors displayed differing perceptions of the ideal role and authority of science under a future BBNJ Agreement. This finding reflects a well-known science-policy conundrum. Frequently, scientists are asked to provide scientific evidence and advice on complex environmental issues, yet their role in the policy process is often *ad hoc* or undefined (Spruijt et al., 2014). While the authority and role of science often remains uncertain, the perceived importance of science in decision-making is well recognised. However, mere appreciation that science is an important tenet of decision-making will not operationalise science-based approaches. Our study shows that opposition to the current sectoral governance structure is coupled with a higher prioritisation of the need for a global science body and a call for putting science on an equal footing in the decision-making hierarchy. Interestingly, this identified area of conflict closely reflects the polarised debate surrounding a 'duty to not undermine' that has afflicted the negotiations since they began (Scanlon, 2017). Brought into fruition through UN General Assembly Resolution 69/292 (United Nations General Assembly, 2015) it is widely recognised that a future BBNJ Agreement shall not reduce the effectiveness of existing instruments, frameworks and bodies. The duty to not undermine and the complexity of the existing policy and institutional landscape highlight a significant challenge for implementing science-based approaches under a future Agreement. The draft text offers potential modalities that could support science-based approaches for BBNJ, such as a Scientific and Technical Body feeding into and supporting a Conference of the Parties, and a Clearing House Mechanism. Our results suggest that defining the role of science and framing it within an institutional structure is important for moving science-based approaches from aspirations to obligations.

Regarding (2), our results suggest that the underlying conflict around the role and authority of science may be fueled by the extent to which a particular stakeholder/stakeholder group is motivated by the 'conservation' of BBNJ or the 'sustainable use' of BBNJ. Notably, participants with aligned values regarding the benefits of a sectoral approach to governance believe that this approach is beneficial for incorporating socio-economic concerns. Opponents of sectoral governance highlight that preservation of species and ecosystem health objectives cannot be met under a decentralised and fragmented regime. However, ocean management is inherently a societal activity (Christie, 2011), and therefore management must reflect diverse activities and goals (i.e., both conservation and sustainable use objectives). As such, it follows that both BBNJ governance and the science that informs decision-making should accurately reflect the diversity of ocean users and their priorities. Scientific evidence is crucial for informing both the conservation and sustainable use of marine biodiversity and can act as a neutral mediator between the two factions. As Harden-Davies (2018) posits, science can offer universally applicable principles that can be applied to BBNJ governance and, "*can offer a safe "port" in a sometimes stormy sea of discussions.*" The promotion of more disciplines within the BBNJ process, could ensure that there is available and salient science that reflects varying stakeholder priorities to support the BBNJ process. However, our results suggest that there are differing perceptions regarding which disciplines should be included (and/or excluded) when defining 'best-available science.' Notably, similar divergence exists in the negotiations. The draft text presents two possible options- a narrow definition calling for the, "*use of the best available 'science'*" and a more inclusive definition calling for the, "*use of best available 'scientific information and relevant traditional knowledge of indigenous peoples and local communities'*"(United Nations, 2019). Our results suggest that the promotion of inclusive terminology that reflects diverse knowledge systems and stakeholder values, may help enhance support for science-based approaches under a future BBNJ Agreement. Indeed, there is evidence that existing international processes, such as the UN's Convention on Biological Diversity and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have been successful in incorporating diverse knowledge systems into their science-policy processes (Tengö et al., 2017).

Implications of Identified Consensus

When investigating emergent stakeholder consensus regarding science-based management of BBNJ, our study highlights apparent consensus regarding:

(1) The perceived trust and credibility of science and precautionary approaches.
(2) The perceived benefits of integrative and participatory management approaches for BBNJ.

Regarding (1), our results highlight areas of consensus regarding certain basic principles, including the application of precautionary approaches and the trustworthiness and credibility of science. In what is now a rapidly changing ocean, scientific evidence is often complex, incomplete or uncertain, which can complicate science-policy interactions. While scientific uncertainty and gaps in understanding are often considered the crux of successful science-policy interfaces (Esch et al., 2018), our findings suggest that precaution in the face of uncertainty is becoming entrenched within international fora. Indeed, a key finding of this research is the general appreciation and call for precautionary approaches when data are insufficient. Furthermore, participants were generally accepting of non-academic sources of scientific data, which has significant implications for the BBNJ knowledgebase. Consensus emerged around the perceived credibility of conservation and industry-oriented sources. Regarding conservation-oriented data, our results reflect similar findings concerning the perceived usefulness of the workshops and side events provided by civil society throughout the BBNJ process (Blasiak et al., 2017). Moreover, our findings regarding the perceived credibility of industry-sourced data present unique opportunities for implementing science-based approaches for BBNJ. While data collected from industry stakeholders, such as fisheries, oil and gas or deep-sea mining, is often perceived as less credible, our work suggests that BBNJ stakeholders may be open to

utilising these data sources. Ocean industries operate tens of thousands of maritime vessels and platforms worldwide, which can potentially provide valuable infrastructure for cost effective data collection (Holthus, 2018; Murray et al., 2018).[4] Apart from supporting science-based management by bolstering the BBNJ knowledgebase, framing ABNJ industries as valuable stakeholders could also enhance multi-stakeholder engagement in the BBNJ process which could help align fundamental values between the 'conservation' and 'sustainable use' of BBNJ.

Regarding (2), our Q-results highlight consensus regarding the application of integrative and participatory management approaches. There appears to be general participant agreement regarding the application of integrative approaches, such as MSP, to operationalise science-based management of BBNJ. While MSP has received minimal attention within the negotiations thus far, this approach to marine governance could be considered under ABMTs (Wright et al., 2019). Within the Q-results, the application of MSP received a neutral-positive reaction from participants and was generally supported in interview data. This highlights an opportunity to build on stakeholder support through enhanced communication of the benefits that MSP could provide. The neutral-positive ranking could suggest that the introduction of MSP as a tool to operationalise science-based management would not receive strong pushback or opposition. Indeed, many of the core components that make up MSP are already included in the negotiations, albeit under different branding. This is significant because integrated and inclusive governance approaches could enhance scientific coordination in ABNJ and provide an avenue for overcoming the aforementioned conflict regarding the role and authority of science. It also corresponds with an internationally recognised awareness that stakeholder involvement is a prerequisite for the perceived legitimacy of international environmental regulations (Maisley, 2013). Building on these findings, integrative and highly participatory management approaches could provide an optimal platform to institutionalise science-based management approaches for BBNJ and should be actively promoted in the negotiations.

Implications for the BBNJ Negotiations

It has long been recognised that value systems can drive conflict (Druckman et al., 1988). This suggests that the BBNJ process and the future BBNJ Agreement will inevitably be a consensus reflection of the underlying values held by key stakeholders. Therefore, there is significant merit in explicitly and formally addressing these value systems as a part of progressing the BBNJ negotiations, rather than allowing them to implicitly influence the process. Our results suggest that BBNJ stakeholders generally value scientific input, despite uncertainty. This not only provides a strong foundation for delegations to push for the inclusion of robust science-based approaches, but also presents a unified rallying point. With only one scheduled negotiating session remaining, negotiators will inevitably have to engage in difficult discussions, rife with divergence. Notwithstanding the fact that much is ultimately down to States' political will and realpolitik, recognising and openly addressing areas of divergence will be an important element of participatory decision-making, both for the negotiations and under a future BBNJ regime.

[4]However, there are barriers to free and open access to industry collected datasets, which would need to be overcome to fully optimise multi-stakeholder benefits (Murray et al., 2018).

CONCLUSION

While there is a general consensus that science-based approaches are beneficial, it is important to understand what this entails and enshrine these approaches within a robust international BBNJ Agreement. This study uses Q-methodology to assess existing stakeholder perceptions of operationalising science-based management approaches for BBNJ. Ultimately, we highlight areas of conflict amongst stakeholder perceptions, especially regarding the role, authority and definition of science within the BBNJ process. Despite these obvious areas of conflict, areas of stakeholder consensus also emerged. Our study suggests a general acceptance of scientific uncertainty and the application of precaution, as well as a perceived benefit of integrative approaches. Key implications of this research include the evidencing of fundamental tensions between differing perceptions of the authority and definition of science and between conservation and sustainable use objectives, which may be fueling stakeholder conflict. Furthermore, this research highlights actionable ways forward and suggests that integrative and highly participatory management approaches are required to operationalise effective science-based management of BBNJ. Insights can help resolve conflict and build a stronger BBNJ Agreement.

DATA AVAILABILITY STATEMENT

The raw statistical data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by GeoSciences Ethics Committee, University of Edinburgh. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

CG, JR, and DJ conceived the study and research question. CG was the lead investigator of the research and designed and undertook the data collection and analysis. CB provided

Q-methodology expertise. JR procured the funding for the research. CG led the writing and drafted the text for the manuscript. All authors contributed to the draft text and revision of the manuscript.

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Tourist Preferences for Seamount Conservation in the Galapagos Marine Reserve

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Seamounts provide oases of hard substrate in the deep sea that are frequently associated with locally enhanced biological productivity and diversity. There is now increasing recognition of their ecological and socio-economic importance. However, management strategies for these habitats are constrained not only by limited ecological understanding but by the general public's understanding of the pressures facing these ecosystems. This study adds to the growing literature on willingness to pay for conservation of deep-sea ecosystems and species by undertaking a stated preference survey to assess tourist's awareness of seamounts and their preferences for protection within the Galapagos Marine Reserve. Visitors' perceptions of seamount biodiversity must be studied because tourists are key drivers of the Galapagos economy and account for 41% of the Marine Reserve budget. Our survey captured the attitudes, perceptions and willingness to pay of tourists for an increase in the entrance fee to the Galapagos Marine Reserve. Results showed tourists were willing to pay on average US$48.93 in addition to existing entrance fees. The results of this study support the willingness to develop a multiuse management plan for the Galapagos Marine Reserve, balancing conservation, local communities livelihoods and sustainable tourism. Our results evidence a willingness to support and fund conservation, which is of critical importance to both the Galapagos National Park and local non-governmental organizations heavily reliant for their work on entrance fees and donations respectively. Overall, the conclusion from this study is that, despite limited knowledge, visitors of the Galapagos Islands attach positive and significant values to the conservation of seamount biodiversity.

Keywords: seamounts, deep-sea, marine conservation, contingent valuation, ecosystem services, Galapagos Marine Reserve, MPAs

HIGHLIGHTS

- Respondents were willing to pay on average US$48.93 in increased entrance fees to the Galapagos Marine Reserve.
- Tourists placed equal emphasis on management plans which aimed to benefit local people's livelihoods, science and tourism.

INTRODUCTION

Offshore seamounts are prevalent and pervasive underwater ecosystems and make up one of the largest biomes of the deep-sea (Staudigel et al., 2010; Wessel et al., 2010). Seamounts are extinct underwater volcanoes that may rise hundreds or even thousands of meters above the surrounding seafloor. While estimates vary, it is believed that there may be over 100,000 seamounts greater than 1 km high that remain uncharted globally (Wessel et al., 2010). Seamount habitats and biodiversity have gained increased academic interest because of their unique ecological and socioeconomic value (Ramirez-Llodra, 2020). They provide many ecosystem services that present use and non-use values to human populations such as fisheries, biodiversity and habitat conservation (for current and future generations), mining, pharmaceuticals and cultural and recreational values (Ressurreição and Giacomello, 2013). Yet, in recent decades, human pressures on seamounts, notably the physical damage caused by bottom trawling, has threatened their biodiversity and resilience (Rogers, 2019). Several of the cold-water corals that can dominate seamount benthic communities are also highly vulnerable to ocean acidification and projected increased temperatures (Roberts and Cairns, 2014; Roberts et al., 2016). Damage to seamounts and their overexploitation can also have widespread consequences on human's food security and medicinal use (Pitcher et al., 2007). Any additional or new activity, or the intensification of an ongoing activity, could become the tipping point for the collapse of a seamount ecosystem. Therefore, growing awareness of human pressures on seamounts, coupled with their important ecological roles in maintaining biodiversity and food webs (Morato et al., 2010) has made seamounts management and conservation a growing policy priority. It is important to recognize that significant gaps remain in our current knowledge of global seamount ecology and biodiversity largely due to their depth and remoteness limiting research (Danovaro et al., 2020). The limited seamount communities surveyed to date and the lack of understanding of their ecological connectivity greatly impedes our assessment of the impacts of human activities on seamounts, as well as the effectiveness of management strategies (Morato et al., 2010; Clark et al., 2012).

Beyond the lack of fundamental scientific knowledge, there are significant additional barriers to seamount ecosystem management. There is a need for comprehensive and effective governance frameworks for marine biodiversity in the high seas (Marsac et al., 2019). The limited frameworks to support these complex ecosystems is also challenged with the difficulty of managing human activities in the high seas, including monitoring, control and surveillance (De Santo, 2018). The magnitude of threats posed to seamounts, and other ecosystems characteristic of areas beyond national jurisdiction, have made their sustainable management a major international policy priority. At the time of writing the United Nations was negotiating an international legally binding instrument under the UN Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (General Assembly resolution 72/249, the 'Biodiversity Beyond National Jurisdiction or BBNJ process).

One option to assist decision-makers in managing the conflicts that arise between the management of human activities and the conservation in the high seas is recognizing and quantifying the economic value of biodiversity (TEEB, 2010). Economic valuations can be used to assess ecosystem services and the value of their benefits to humans (Tinch et al., 2019), which are critical inputs to conduct a cost-benefit analysis in support conservation or restoration interventions (O'Connor et al., 2020a). By incorporating ecosystem service measurements on a quantitative interdisciplinary scale (including monetary, biophysical, and social) it is now feasible to produce practical information to inform well-informed decisions guiding sustainable use of seamount ecosystems (Ainscough et al., 2019). However, in comparison to terrestrial and coastal habitats, there are comparatively few studies which undertake a socio-economic valuation of marine ecosystems, especially in relation seamounts (Jobstvogt et al., 2014). This poses serious challenges for decision-makers responsible for identifying seamount management options, specifically for policies that are centered on maximizing human welfare, or specifically, use values stemming from ecosystem services (Potts et al., 2014). Without including socio-economic knowledge of these ecosystems, management considerations risk failure (Saarikoski et al., 2018). A lack of understanding of the nature of public support for seamount conservation might further hamper the adoption and effectivity of such measures. This is particularly the case given that the known benefits of deep-sea ecosystems lack widespread public awareness (O'Connor et al., 2020b).

Our research contributes to a better understanding of the benefits and values supported by seamount ecosystems. Although the use-values (i.e., economic value) of seamount ecosystem services are important components to take into consideration for management, this study considers primarily the non-use values (i.e., social value) provided by Galapagos seamounts using a stated preference survey to understand visitors preferences for conservation of seamounts in the Galapagos (Gillespie and Bennett, 2011). Little is known about the value of seamount ecosystem benefits, posing serious challenges to the Directorate of the Galapagos National Park when considering options for their future management (DPNG, 2014). Individuals assign Non-use values to economic goods, even if they never have and never will make use of these goods. This type of value is commonly applied to the value of natural habitats, biodiversity or cultural heritage sites (Arrow and Fisher, 1974; Costanza et al., 2014). Different types of Non-use values usually refer to an individual's willingness to pay for preserving goods for future use even if the individual has no use for it (option value), preserving a good for future generations (bequest value), or just for purely altruistic motivations (altruistic value) (Walsh et al., 1984).

To date, there is one known valuation study in the Galapagos focusing on ecosystem services provided by mangroves and our research adds further evidence to the policy and conservation-oriented valuations in the management of the Galapagos archipelago (Tanner et al., 2019).

Specifically, our research:

(1) Adds to the evidence base on the relative importance of non-use values for Marine Protected Areas.
(2) Explores the potential influence of tourists' willingness to pay for seamount conservation in the Galapagos Marine Reserve.
(3) Identifies knowledge gaps and recommendations for future research into management measures applicable to seamounts in the Galapagos which we can build on in future research.

Our study is now possible as a result of new information on the ecology of deep seamount communities collected through deep-sea surveys in 2015 and 2016 (Salinas-de-León et al., 2020) and its findings help inform the practical policies that will be essential to ensure sustainable management of ecosystems in the deep and open ocean, e.g., via any new UN 'BBNJ' treaty. The recent findings of new species can be understood given the isolated and volcanic nature of the Galapagos archipelago, standing approximately 1000 km into the Pacific ocean, representing an oasis of life in the vastness of the ETP abyssal (ocean zone > 3000 m deep) plain. Beneath the surface, hundreds of seamounts provide ecosystem services of biodiversity provisioning, due to a confluence of warm and cold oceanic currents, which gives rise to a unique mixture of marine biodiversity (Banks, 2002). Seamounts are recognized to enhance productivity, providing fisheries provisioning services to the local fishing fleet and recreational ecosystems services to the thriving tourism sector at the heart of the archipelago's economy (Engie and Quiroga, 2014; Marin Jarrin et al., 2018).

CONTEXT OF STUDY: GALAPAGOS ISLAND AND SEAMOUNT CONSERVATION

The Galapagos Islands are celebrated for their ecologic and historical importance by declaring the Galapagos National Park as a UNESCO World Heritage Site in 1979. The Galapagos Marine Reserve (GMR) represents one of the largest and most biodiverse marine protected areas in the world and spans more than 138,000 square kilometers around the archipelago (**Figure 1**). To regulate the different uses of the marine reserve and ensure biodiversity conservation, the first zoning plan was created in 2000. The plan organized the coastline in sectors according to management/use subzones (fishing, tourism and conservation). The zoning plan divided the GMR into three zones: Zone 1–the multiple-use zone, which includes the deep waters of the GMR, Zone 2–the limited use zone, which consists of coastal waters (<300 m), islets and rocks, and seamounts and Zone 3–port zones. Zone 2 has four management subzones: 2.1 Conservation subzone, 2.2 Tourism subzone, 2.3 Fishing subzone, and 2.4 Areas of Special Temporal Management. At the time of preparation of this manuscript, the Galapagos national park Directorate is debating the new zonification for the GMR, which should become enforced by 2020. This new system aims to divide the archipelago into multi-use protected area: sustainable use (sustainable fishing), conservation (non-extractive activities such as tourism), intangible (only research) and transition areas (**Figure 1**).

In the last decade, numerous deep-sea exploration cruises took place in the GMR, providing comprehensive datasets, based on physical sampling and video surveys, enabling scientists to characterize these unknown remote ecosystems. These efforts are being led by CDF in collaboration with GNP and numerous international research institutes (Darwin Foundation, 2020). The recent discovery of both new marine species and endemics show that seamount ecosystems should be specially considered for conservation (Salinas-de-León et al., 2020).

TOURISTS PERCEPTIONS AND MANAGEMENT PREFERENCES

The Galapagos Islands are internationally known for their unique ecosystems. This has created a thriving tourist industry, which is a key source of income for the local economy (Epler, 2007; Walsh and Mena, 2013). In 2019 the Galapagos hosted a total of 271,238 tourists a sharp increase from 42,000 received in 1989 (Galapagos National Park [GNP], 2020). However, according to Pizzitutti et al. (2014) tourism is also the main driver of change on Galapagos, affecting the social and ecological systems and is considered one of the principal drivers of invasive species introduced into the archipelago (Toral-Granda et al., 2017). If the number of international visitors and the supporting facilities continues to grow rapidly, there will be a need to question how this will affect the pristine biodiversity, natural environment and the social setting of the Galapagos Islands (Jones, 2013; Pizzitutti et al., 2014).

Entrance fees are amongst the most widespread revenue sources from national park visits and are associated with the management and protection of MPAs (Lindberg and Halpenny, 2001). Visitor entrance fees are the main source of income for the GMR and thus directly support conservation of the island, contributing an average of 41% of the budget for the conservation of protected areas (Galapagos National Park [GNP], 2014). Thus, the growth of marine tourism represents a favorable avenue to explore marine conservation funding mechanisms for deep-sea seamounts in the Galapagos, especially the case with the rise of local tourism champions whose self-interest is aligned with ecosystem services protection (Tanner et al., 2019). For this to happen, however, a better understanding of tourists' perception and attitudes toward the support for deep-sea seamounts is needed to design effective funding and conservation initiatives.

Consequently, we explore whether people are willing to pay an increased entrance fee to the Galapagos National Park which would provide additional conservation revenues for seamount conservation and associated biodiversity. We are specifically interested in how preferences are affected by respondent's knowledge of seamounts, their attitudes and perceptions toward seamount and marine conservation and how these measures can provide recommendations for ecosystem-based management scenarios employed by the National Park. The visitor fees are

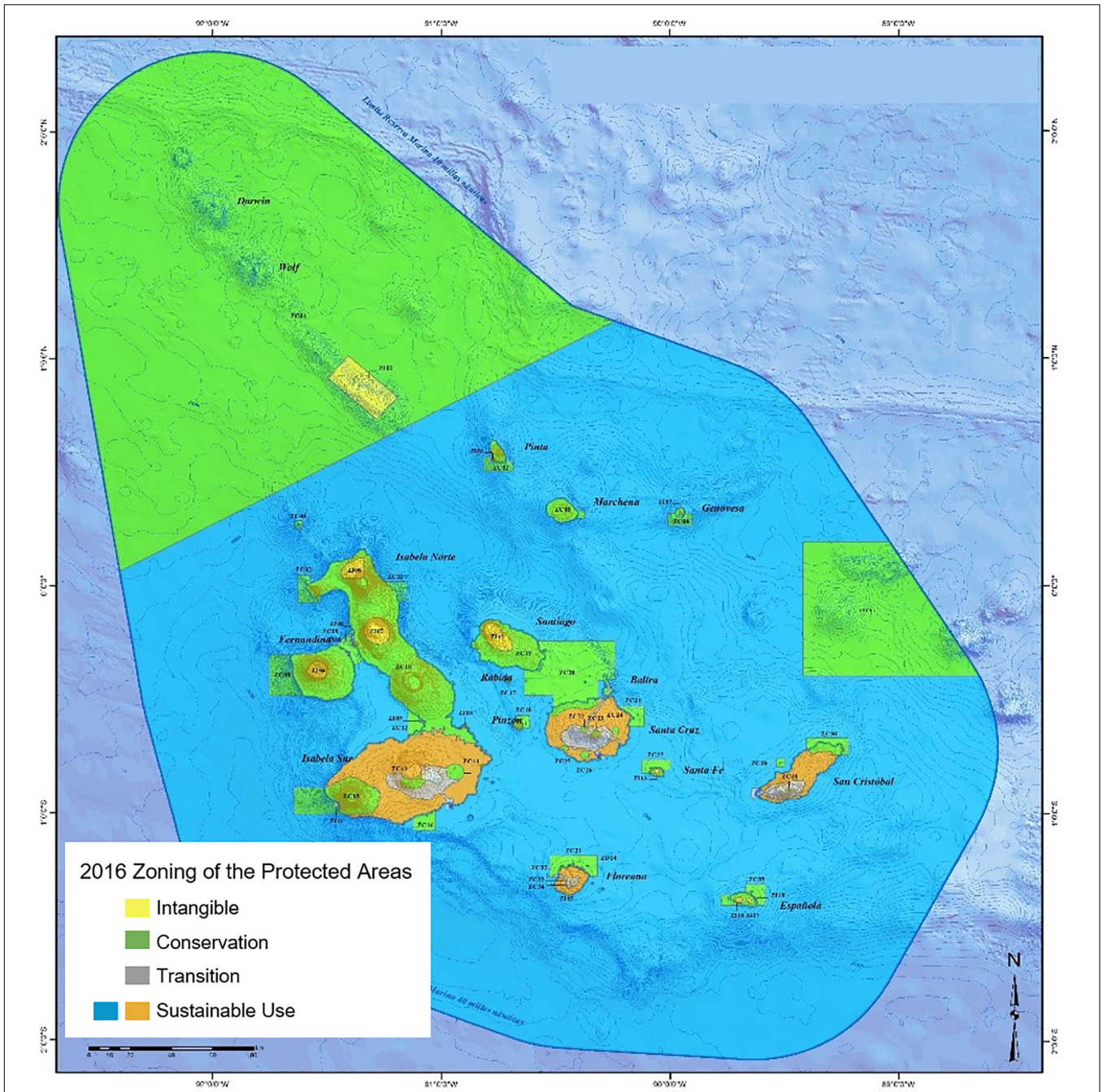


FIGURE 1 | Map of the Galapagos Marine Reserve with proposed Zoning Plan. Source: Galapagos National Park.

therefore not expected to resemble the true value that tourists attach to deep-sea seamounts in the Galapagos Archipelago but rather provide recommendations for potential conservation mechanisms that might capture and monetize the surplus "welfare" experienced by tourists. Due to lack of economic and social research on deep-sea seamounts in the Galapagos, we aim to test hypotheses which provide insight into both key survey design issues (e.g., geographical and financial scoping) and policy questions (e.g., where and how to protect seamount ecosystems?). Given the rapidly growing number of stated preference environmental valuation studies and their use in policymaking, it is important to arrive at a better understanding of the environment before implementing management efforts. This study identifies the interests and information needs of potential management measure for seamounts in the future.

There are various stated preference studies which have shown that visitors to protected areas are generally willing to pay much higher fees than are currently charged to support marine

conservation due to increasing tourism demand and increased desired to support conservation of species and ecosystems (Rivera-Planter and Muñoz-Piña, 2005; Moyle et al., 2017; Banerjee et al., 2018). More recently, valuation work has focused on how we can value biodiversity and ecosystem services in the deep sea (Ressurreição et al., 2011; Jobstvogt et al., 2014). One of the major challenges of estimating the value of deep-sea biodiversity stems from the public's unfamiliarity with the deep-sea environment (Jobstvogt et al., 2014). Poor understanding of complex ecological concepts such as biodiversity among members of the public also underpins many valuation challenges (Laurila-Pant et al., 2015). Evidence from this research is encouraging, limited knowledge does not equate to limited interest.

We recognize that seamounts and their associated biodiversity are an unfamiliar good for many respondents, and critics of stated preference methods argue that familiarity with the good is essential for providing meaningful responses to valuation questions (Carson et al., 2001). For seamounts, it is unlikely that respondents will have well-defined preferences before elicitation and instead preferences are constructed during the survey process (Gregory et al., 1995; Gregory and Slovic, 1997). Providing information to respondents who have little prior knowledge of the good is a crucial aspect of the survey and Mitchell and Carson (1989) identified information provision as "amongst the most important and most problematic sources of error" in contingent valuation. In our survey, we were interested whether the respondent's prior knowledge of seamounts leads to a higher or lower willingness to pay estimate than those who are not aware of seamounts. We were careful to ensure no cue was provided that their knowledge of seamounts was correct or incorrect. Also, we tested whether respondent's self-judged prior knowledge of the information presented to them during the survey affected their willingness to pay to avoid and control for scenario rejection or adjustment (Cameron et al., 2011).

MATERIALS AND METHODS

Survey Overview

To better understand tourist's perceptions and attitudes toward conservation of seamounts and their associated biodiversity a contingent valuation survey was designed and implemented to respondents in the Galapagos Archipelago. The survey aimed to understand initial willingness to pay values which would guide further research at the Galapagos National Park regarding the tourist's management preferences. Contingent valuation is a stated preference technique, which uses questionnaires to create a realistic, but hypothetical market, for respondents to indicate their willingness to pay for a change in an environmental good (Mitchell and Carson, 1989). Scenarios are constructed which offer different policy alternatives to the current *status quo*. The respondent is asked to state whether they would support an alternative policy option depending on what the new policy will provide, how this will be delivered and how much it will cost (Carson, 2000). If the study is well designed and carefully tested in advance the answers to the survey should reveal the respondent's true willingness to pay for a given change. Our respondents are asked whether they would support an increase in the entrance fee to the GMR with the additional revenues used to fund research programs into seamount conservation and diversity.

Survey Design

The contingent valuation survey was designed following the recommendations of Johnston et al. (2017). A single questionnaire was produced to capture the attitudes, perceptions and willingness to pay of foreign and national tourists. Respondents were first provided with an introduction to the survey, followed by two questions to assess their prior knowledge and awareness of seamounts. Respondents were asked if they recognized a seamount and then were asked to define the term "seamount." Following this, respondents received specific information the importance of the GMR as one of the largest and most diverse marine protected areas in the world, an introduction to seamounts, their associated biodiversity and their contribution to marine ecosystem services. In this manner, we present a clear baseline or *status quo* scenario, which is a central requirement in stated preference questionnaires (Johnston et al., 2017). This was followed by self-evaluation of participant's knowledge of seamounts and whether they already knew the information provided to them (using a 5-point Likert rating scale from "I knew everything" through to "I knew nothing"). This allowed us to test the respondent's perceived knowledge of seamounts and whether this influenced their willingness to pay, to evaluate whether respondents are adjusting or reinterpreting the presented information according to their subjective perceptions (Johnston et al., 2017).

The next stage of the survey aimed to identify social values that could be used in the resource allocation decision-making process. Respondents were presented with a photographic catalog of seamount species and asked to express which species they preferred for the allocation of conservation funds to deep-sea species. The images were screenshots from video transects during the Nautilus Cruise Galapagos Platform Expedition between 25 June and 26 July 2015. To ensure a representative sample, 10 species of invertebrates (annelids, xenophyophores, molluscs, anthropods, cnidarians, ctenophores, echinoderms, hemichordates, sponges, and tunicates) and five species of vertebrates (chordates) were used. Below each image, key information was presented, including the phylum, the scientific and known name and depth range. Each species was presented with a fact on their biological characteristics, ecological importance or human uses. Finally, four species were identified as "new species" because these species were discoveries from the Nautilus expedition (Salinas-de-León et al., 2020). A copy of the Figure is provided in the **Supplementary Material**.

This was followed by the willingness to pay question. Respondents were then presented with the elicitation scenario:

> *The Galapagos National Park is under the management of the Galapagos National Park Directorate. In the near future, they are proposing to increase the tourist entry fee in order to allocate more funds for deep-sea seamount conservation. The generated funds will be used for seamounts conservation projects, education and outreach [. . .] Please select the maximum amount you would*

definitely be willing to pay (USD) in additional entrance fees to fund seamount biodiversity conservation programs, education and outreach.

Willingness to pay was elicited using a payment card format. Respondents were presented with values ranging from US$0 to US$100 and asked to select the maximum value they were willing to pay in additional entrance fees to enter the Galapagos National Park (or to specify another amount if above US$100). The payment vehicle was the increase in tourist fee to the Galapagos National Park. The payment card format was justified as at the time of the survey the exact increase in the entrance fee was unknown. The bid vector is shown in **Table 1**.

To foster a level of incentive compatibility, our payment card was presented as a series of yes/no votes following Carson and Groves (2007) and Vossler et al. (2012). We highlighted that the cost was uncertain which is why a range of payments options was offered and respondents were told that their responses would be shared with policymakers, who are in the process of evaluating an increment in entrance fees to the Galapagos National Park. A reminder cue specifying that the results would be shared with policymakers was included:

"The price you choose will be used to inform the Galapagos National Park Directorate when deciding the allocation of future funding – so it is very important you answer the question truthfully."

This further strengthens incentive compatibly by demonstrating that the relevant authority can enforce payments by the tourist who are under the jurisdiction of the Galapagos National Park Directorate (Vossler et al., 2012). Likewise, this feature in our design allows respondents to infer that the probability that the proposed project is implemented is weakly monotonically increasing with the proportion of yes votes, which is a requirement for incentive compatibility (Vossler and Holladay, 2018). As an aside, practical issues such as budget and timing constraints, the payment card format was the most statistically efficient design for this survey although we acknowledge there is also the risk of being afflicted by both range and anchoring effects (Rowe et al., 1996; Covey et al., 2007).

A follow-up question asked respondents to state their primary motivation behind their willingness to pay bid. Respondents were asked to state their reason for a positive willingness to pay. Out of the five possible response options available, three reflected the intrinsic value of the good: (i) I want to preserve the seamount biodiversity for future generations; (ii) because the biodiversity on seamounts is unique and (iii) because the biodiversity on seamounts has a positive impact on the marine economy. The remaining two statements were understood to express personal motivations for valuing the good: (i) I want to personally contribute to projects that protect the environment and (ii) because I can afford it. To determine protest bids, those who stated a zero willingness to pay were asked their reason for doing so. Respondents with valid-zero willingness to pay would select statements regarding significance: (i) Seamount conservation is not important to me; (ii) I don't regard the environmental threats to seamounts as high and therefore conservation measures are not needed, and affordability (iii) I cannot afford it. Alternatively, statements that reflect protest-zero willingness to pay bids included: (i) conservation efforts should be funded by other sources; (ii) I don't agree with paying an entrance fee, and (iii) I don't agree with how the Galapagos National Park Directorate allocates tax funds. This approach is generally taken to maximize the validity of our valuation exercise, by minimizing different possible biases present in stated preference approaches (Bishop and Boyle, 2017).

Follow up questions focused on the individual's attitudes and perceptions regarding different aspects of marine conservation. Respondents were asked to rate how urgent they think seamount biodiversity conservation is, and their preferred management objective for the Galapagos National Park. Finally, respondents were asked about their socio-demographic characteristics. These questions aimed to collect information necessary to develop a set of tourist profiles which could be compared against previous visitor surveys undertaken in the Galapagos Islands and to control for possible covariates which are explanatory of observed willingness to pay changes. A full copy of the survey is available in the **Supplementary Material**.

The survey was designed by the research team and initially pre-tested with staff and students at the University of Edinburgh. This pre-test aimed to ensure readability and understanding of the payment vehicle and a credible and understandable scenario to respondents, whilst minimizing respondent fatigue (Champ et al., 2003). A pilot survey with tourists was then undertaken with 45 individuals on the National Geographic Islander cruise ship on May 25, 2017. Following this pilot exercise, minor changes were made to the final survey, including adding three more questions that capture participant's attitudes toward marine conservation. The final survey of 125 individuals was conducted between 29 May and 16 June 2017. Three main locations were used to administer surveys: (1) Charles Darwin Research Station, (2) Gus Angermeyer Pier and Ferry Terminal and (3) Tortuga Bay Beach. For sampling locations (1) and (2) the interviewer approached each individual/group who arrived and asked them

TABLE 1 | Payment card and bid vectors shown to the respondents.

Please select the maximum amount you would realistically be willing to pay (USD) in additional entrance fees to fund seamount biodiversity conservation programs.
$0
$5
$10
$15
$20
$25
$30
$35
$40
$45
$50
$60–70
$80–100
I am prepared to pay more than $100

to take part in the survey. For location (3), the interviewer randomly selected individuals and groups on the beach. This mixed-approach was taken to maximize the potential number of respondents in the sampling period. Unfortunately, our interviewer did not record how many individuals she approached to complete the survey but who refused. We recognize this would be a useful measure for future survey work. Respondents were approached by a trained interviewer and guided through the survey. The interviewer could respond to any questions asked by the respondent. Each interview took 12–15 min to complete. The target populations included foreign tourists (non-resident and Andean Community or Mercosur residents) and tourists who are citizens or residents of Ecuador. Sampling took place exclusively on Santa Cruz Island because it is the tourist hub of the archipelago (Epler, 2007). Tourists were required to be 18 years of age or older to complete the questionnaire and both English and Spanish translations of the survey were used. Most foreign tourists come from the United States, United Kingdom, and Europe, and therefore were approached using the English questionnaire, while national tourists were approached using the Spanish version.

Empirical Approach

Responses were analyzed using Stata (Version 16). Based on the recommendations of Bateman et al. (2002), datasets were analyzed to differentiate between genuine zero bids and protest zero bids. Mean and median willingness to pay were compared, before and after the exclusion of protest responses. The determinants of WTP were analyzed using both the Tobit and Interval regression model. The Tobit model, or censored regression model, is designed to estimate linear relationships between variables when there is either left or right censoring in the dependent variable (UCLA: Long and Freese, 2014). For WTP surveys left-hand censoring is appropriate as it takes into account respondents who are not prepared to pay toward the scheme. However, our survey used a payment ladder to elicit WTP and it is recognized that estimates from the Tobit model can result in a biased average valuation, as the expected values between the upper and lower bounds of the payment cards are unknown (Cameron and Huppert, 1989). Interval regression can overcome this issue by using the lower and upper bounds of the value chosen on the payment card (Haab and McConnell, 2002). For this survey, respondents were asked to tick the highest value they were prepared to pay. However, their true value may lie between the highest bid they chose and the next highest amount, for example, the respondent ticked $5 and the next highest was $10. In this case, their true value may lie between $5 and $10 and these bounds can be used in the interval regression estimation. Interval regression uses the lower-bound and upper-bound responses on the payment card as the dependent variables, minimizing the potential of over or underestimating WTP.

The final modeling approach considered whether multiple explanatory variables influenced WTP (Equation 1). The stated preference literature suggests that the valuation of an environmental good is impacted by a variety of socio-demographic factors and the relationship between the respondent and the good in question. Consequently, we included income, age, gender, and nationality within our modeling framework. Also, there is an expectation that the respondent's experiences with the good in question and their personal motivations, will affect WTP (Cameron and Englin, 1997; LaRiviere et al., 2014; Needham et al., 2018). As such, we include the time that the respondent has spent on the Galapagos (measured in days), whether they are a member of an environmental group and their motivation for being willing to pay. Furthermore, we were interested in two variables related to the respondent's knowledge of the seamount. Firstly, if the respondent was aware of the term 'seamount' at the start of this survey. This was judged by the interviewer based on the respondent's answers to a series of opening questions about seamounts. Secondly, we included a variable which examined respondents own self judged awareness of seamounts. A list of the variables used in the modeling approach can be found in **Table 2**.

Four regressions were estimated:

(1) Tobit model with only socio-demographic characteristics.
(2) Tobit model with socio-demographic characteristics and other explanatory variables.
(3) Interval model with only socio-demographic characteristics.
(4) Interval model with socio-demographic characteristics and other explanatory variables.

Equation 1: Interval regression equation to explore which factors influence a respondent's willingness to pay for increased seamount conservation in the Galapagos.

$$WTP = b_0 + b_1 income + b_2 age + b_3 gender + b_4 nationality + b_5 days + b_6 env + b_7 priorknowledge + b_8 familiarity + b_9 motivation + b_{10} urgency + b_{11} management + \varepsilon_i$$

RESULTS

Sample Characteristics

In total 125 surveys were completed. Of the 125 respondents sampled, 81 were foreign tourists, eight were from the Mercosur and Andean Community of Nations, and 36 were Ecuadorian nationals. We removed the eight respondents from the Mercosur and Andean Community of Nations from our subsequent analysis as we felt the number of respondents from this region was too low to include in our analysis. The three tourism categories (Foreign, Mercosur and Andean Community of Nations and Ecuadorian nationals) each pay a different amount to enter the GNP. We felt this difference in entry fee would influence the respondent's willingness to pay, hence we wanted to include nationality as a control variable within our analysis. Despite removing eight of the respondents, we can conclude that our sample, despite its small size, is representative of the general characteristics of the Galapagos tourist's population (**Table 3**). We compared our sample descriptive statistics with annual visitation data reported by the Galapagos National Park for 2019 (Galapagos National Park [GNP], 2020). In 2019, 67% of all visitors were foreign with the remaining 33% being Ecuadorian. The gender breakdown of visitors is in favor of females at 55 to 45. In our sample, Ecuadorian tourists represent 31% of all

TABLE 2 | Variables used in the estimation process.

Socio-Demographic Variables	
Income	Household income:
Age	Age of respondents: 18 – 25,26 – 35, 36 – 45, 46 – 55, 56 – 65, and over 66
Gender	0 = Male, 1 = Female
Nationality	0 = Ecuadorian National 1 = Foreign tourist
Additional variables	
ENV	Member of an environmental group 0 = No, 1 = Yes
Days	Days spent on the Island
Prior	Whether the respondent was familiar with the term seamount prior to the survey (as judged by the interviewer): 0 = No 1 = Yes
Familiarity	The respondent's perception of how much they already knew about the information presented to them: 0 = I knew less than half of the information presented to me 1 = I knew more than half of the information presented to me
Motivation	Respondents reason for being willing to pay: 1 = Biodiversity is beneficial for the marine economy 2 = Biodiversity is unique 3 = I want to preserve for future generations 4 = I can afford to 5 = other reason 6 = I want to personally contribute to projects that benefit the marine environment (warm glow effect)
Urgency	Response to whether seamount conservation is urgent or not: 1 = Unsure 2 = Not urgent at all 3 = Urgent or very urgent
Management	Respondents preference for the management of the Galapagos Marine Reserve: 1 = Equally important 2 = Promotes science 3 = Supports livelihoods 4 = Tourism focus

TABLE 3 | Descriptive statistics for socio-demographic variables.

Variables	Number of respondents
Income	
Up to $20,000	10
$20,001–40,000	20
$40,001–60,000	15
More than $60,000	70
Gender	
Male	55
Female	62
Age	
18–25	27
26–35	40
36–45	15
46–55	13
56–65	14
66–75	8
Nationality	
Ecuadorian	36
Foreign	81
Education	
High school	16
Undergraduate Degree	58
Postgraduate Degree	37
Further education	6
Economic activity	
Working	70
Studying	14
Unemployed	18
Retired	15
Employment sector: mining, oil and gas, fisheries or tourism?	
No	102
Yes	15
Member of environmental group	
No	99
Yes	18
Number of visits	
First visit	101
Two and three visits	9
Four and five visits	4
More than five visits	3

respondents, with the remaining 69% being of a foreign origin. The corresponding gender breakdown of our sample is 53 to 47 in favor of females. On average on 2019 the age of visitors to Galapagos is 35 years, which is also the biggest age bracket in our sample (34.2% are between 26 and 35). Likewise, the United States of America is the biggest nationality amongst foreign tourists, for both official data and our sample. Hundred and one of the respondents were visiting the area for the first time, with nine respondents on their second or third visit, four on their third or fourth visit and three having visited five times or more to ensure sufficient involvement of the local community in the management planning process.

Knowledge of Seamounts, Attitudes and Perceptions Toward Seamount and Marine Conservation

The analysis revealed the majority of respondents (76%) were unfamiliar with the term seamount as judged by the survey interviewer (**Table 4**). The self-evaluation of seamount ecosystems revealed that 85% of the respondents felt that they knew only half or less of the information discussed in the survey introduction. Across the sample, only 3% stated they did not think seamount conservation was urgent, although 15% of the sample were unsure. Across the sample, 53% of respondents favored the development of an integrative management plan that equally addresses the social objectives of marine management in the Galapagos.

When respondents were asked to list the two most important marine environmental problems that came to mind, the main responses identified pollution (45%), overfishing (23%), climate change (15%) and wildlife conservation (8%) as the most important problems. The terms pollution combines mentions of "pollution," "water quality," "chemical and oil pollution," and

TABLE 4 | A comparison of seamount knowledge and conservation priorities between foreign and local tourists.

Variables	Number of respondents
Perceived prior knowledge of seamounts	
Detailed knowledge of seamounts	28
No knowledge of seamounts	89
Self-evaluation of seamount information	
Knew more than half the information	18
Knew less than half the information	99
Conservation Urgency	
Not urgent	3
Moderately urgent	30
Urgent or very urgent	66
I don't know	18
Management Plan Preference	
Promote science	26
Tourism	23
Livelihoods	6
Equal importance	62
Allocation of funds	
Charismatic or uncharismatic	
Charismatic	55
Uncharismatic	62
Common or new	
Common	27
New	90
Human or eco	
Human	43
Ecological	74
Medical research or fisheries	
Medical	103
Fisheries	14
Species: Scientific name (Common name)	
Yoda sp. (Acorn Worm)	5
Ophiocten spp. (Brittle Star)	9
Pontinus clemensi (Brujo, Scorpionfish)	4
Victogorgia sp. (Octocoral)	14
Aulacoctena (Comb Jelly)	2
Paromola cf. rathbunae (Crab)	12
Teuthidodrilus sp. (Marine Worm)	13
Graneledone sp. (Octopus)	7
Trachichthyidae spp. (Orange Roughy)	1
Lophiidae spp. (Paco, Goosefish)	1
Phellodermidae family (Sea Sponge)	8
Unknown (Sea Squirt)	4
Bathyraja spp. (Stingray)	7
Chaunacidae spp. (Toadfish)	16
Unknown – xenophyophore (Foraminifera)	14

"sewage." The term climate change covers responses of "climate change," "sea-level rise," and "ocean acidification"; and the term wildlife conservation includes responses within the category of biodiversity loss. This open-ended question provides insight into the ways that the tourists frame their main concerns in terms of marine impacts.

When respondents were asked their preference for the allocation of conservation funds to deep-sea species our results show that tourists were equally divided when it came to charismatic versus uncharismatic species protection. A much greater proportion of respondents favored the new species (77%) over the more known species (23%). When respondents were asked to choose a single deep-sea species to allocate conservation funds to, the most popular species was the toadfish (14%) followed by the octocoral and the xenophyophore (12% each), the squid worm (11%) and the crab (10%).

Willingness to Pay

Of the 117 respondents, 94% were willing to pay toward increased seamount conservation through an increase in visitor fee. Responses to the bid vectors presented on the payment card are shown in **Figure 2**. Hundred and ten of the 117 respondents accepted the first level on the payment card "$5". The number of respondents accepting the bid level gradually declines between $5 and $50 with a marked decline in respondents accepting a bid level above $60 or more. Nine respondents were willing to pay over $100. 7 respondents were not willing to pay, and based on the debriefing questions, three respondents were considered protest bidders because they thought conservation efforts should be funded by other sources. Beyond that, four were considered genuine zero bidders (**Table 5**). Enhancing seamount biodiversity conservation for the benefit of future generations was the most frequently expressed motive for wanting to pay for increased entrance fees followed by existence values and use-values (**Table 5**). Across all datasets, mean and median values were calculated before and after the removal of protest responses. The exclusion of the protest zero bids had a US$1.29 impact on mean willingness to pay and it was decided to include these in the final regression analysis. The total sample mean willingness to pay was estimated at US$48.93 (CI = US$40.08–US$57.78) (calculated using the lower bound willingness to pay from the payment card).

Table 5 shows the results of the regression analysis and **Table 6** shows the predicted mean willingness to pay based on the four different modeling approaches. The predicted mean willingness to pay varies between $48.83 (Model 1) and $54.56 (Model 4). The use of the Interval Regression Model increases the predicted willingness to pay and reduces the standard error of the estimate. The inclusion of additional explanatory variables has no significant effect on the predicted willingness to pay.

Several key results emerge from this analysis. Firstly, the results show that respondents prefer a management scenario which places equal emphasis on all three management plan aspects: promoting tourism, securing livelihoods and promoting science. Respondents are WTP $22 less for a program which focuses on science only and $24 less for a program focusing on tourism.

Secondly, in terms of urgency of conservation, there is a significant difference in WTP between respondents who are "unsure" compared to those who believe conservation is urgent at some level. There is no significant difference in WTP between those who think it is moderately urgent or very urgent.

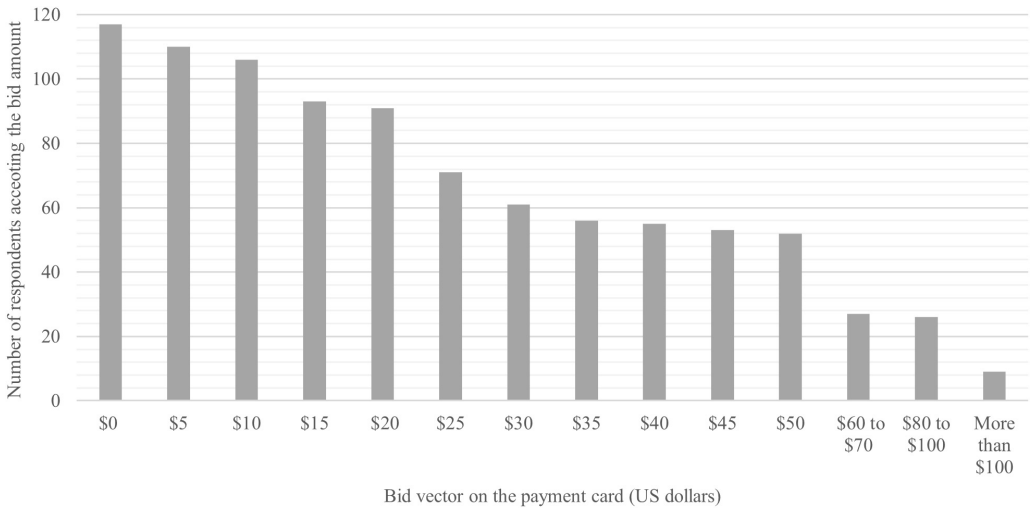


FIGURE 2 | Responses to the bid vectors on the payment card.

TABLE 5 | Overview of willingness to pay responses including protest bidders.

	Number of respondents
Whether a respondent is willing to pay?	
Yes	110
No	7
Protest responses	
Protest bidders (total)[a]	3
Genuine zero bidders (total)[a]	4
Positive willingness to pay (total)[b]	110
Reason for expressing a positive willingness to pay	
I want to preserve the seamount biodiversity for future generations (bequest value)	49
Because the biodiversity on seamounts is unique (existence value)	21
Because the biodiversity on seamounts has a positive impact on the marine economy (direct-use value)	9
I want to personally contribute to projects that protect the environment (warm glow)	24
Because I can afford it (warm glow)	5
Other (specify)	2
No response	7

[a] *Respondents could only tick one motive for their negative willingness to pay for seamount biodiversity conservation.* [b] *Respondents could only tick one motive for their positive willingness to pay for seamount biodiversity conservation.*

A third finding is a difference in willingness to pay when we considered self-assessed awareness and actual knowledge of seamounts (as assessed by the interviewer). Respondents who had higher knowledge of seamounts, as judged by the interviewer, were prepared to pay significantly more toward their conservation than those who were not familiar with seamounts ($32.35, Model 4). In contrast, respondents who stated they were familiar with the information presented to them during the survey were willing to pay less than those who stated they were not familiar ($-30.81, Model 4).

Finally, socio-demographic statistics have a limited effect on WTP. We find no significant effect of gender and a weak signal of age with those in the oldest age group willing to pay more than those in the youngest age group. There is a mixed effect for income. We find that those in the highest income band (more than $60,000) are prepared to pay significantly more than those in the lowest category. However, respondents in the $20,000–$40,000 band are willing to pay less than those in the lowest income band (−$23.26, Model 4). We find that foreign tourists are willing to pay $49 more than Ecuadorian tourists.

DISCUSSION AND CONCLUSION

This study aimed to explore tourist perceptions and attitudes toward conservation of seamounts at the Galapagos Marine Reserve (GMR). The survey aimed to understand tourist's preferences and willingness to pay values which would inform local policymaking and conservation agendas. To do this we designed and implemented a contingent valuation survey to assess whether tourists would be willing to pay an increased entrance fee to the reserve and which management options tourists would prefer. Our study tested respondent's prior awareness of seamounts, provided them with information on seamounts and asked them to assess their own familiarity with this information before eliciting their willingness to pay for entrance fees for the GMR. We also assessed their motivations for contributing to conservation efforts and their preferences for the allocation of conservation funds to deep-sea species.

TABLE 6 | A comparison of results from Tobit and Interval regression estimation for exploring public willingness to pay for seamount conservation.

Variables	Tobit (1)	Tobit (2)	Interval (3)	Interval (4)
Income: baseline less than $20,000				
$20,001–40,000	−40.14*** (12.05)	−23.00* (11.82)	−34.63*** (11.09)	−23.26** (11.60)
$40,001–60,000	−5.35 (12.55)	−11.87 (12.62)	−6.03 (11.82)	−12.06 (12.38)
More than $60,000	26.91*** (10.03)	21.11** (10.01)	24.79*** (9.41)	20.32** (9.81)
Gender: baseline: female				
Male	7.08 (7.87)	7.48 (7.71)	6.15 (7.34)	7.40 (7.57)
Age: baseline 18 – 25				
26–35	6.90 (10.32)	10.80 (9.68)	8.17 (9.64)	10.38 (9.50)
36–45	2.05 (13.32)	−5.30 (13.08)	2.91 (12.45)	−5.51 (12.82)
46–55	7.33 (14.01)	0.60 (13.15)	7.25 (13.09)	0.82 (12.90)
56–65	16.19 (13.75)	6.52 (12.94)	16.04 (12.94)	6.47 (12.70)
66–75	52.64*** (16.69)	34.87** (15.69)	51.31*** (15.70)	34.25** (15.38)
Nationality: baseline Ecuadorian				
Foreign	58.51*** (9.52)	50.02*** (9.26)	57.29*** (8.93)	49.93*** (9.08)
Member of environmental group		4.93 (11.35)		4.27 (11.13)
Number of days spent at the GMR		0.00 (0.32)		0.02 (0.31)
Respondent has prior knowledge of seamounts (assessed by the survey interviewer)		33.33*** (11.84)		32.35*** (11.62)
Respondent knew most of the information presented to them in the survey (self-assessed)		−32.60** (12.53)		−30.81** (12.30)
Reason for positive willingness to pay: baseline biodiversity benefits marine sectors				
Biodiversity is unique		−3.34 (15.79)		−4.29 (15.50)
I want to preserve for future generations		−2.10 (13.62)		−3.70 (13.37)
I can afford to		23.67 (22.11)		22.87 (21.69)
Other reason		−9.46 (29.62)		−11.67 (29.04)
Personally, contribute to projects that protect the environment		−7.61 (14.95)		−8.48 (14.68)
Conservation urgency: Baseline unsure				
Moderately urgent		26.74** (12.31)		26.67** (12.07)
Very urgent or urgent		21.61* (11.39)		21.38* (11.17)
Preferred management option baseline: balance of all three				
Promote science		−22.09** (9.55)		−21.74** (9.37)
Support livelihoods		−5.42 (18.44)		−5.49 (18.09)
Tourism focus		−24.76** (10.35)		−23.93** (10.16)
Constant	−4.75 (12.08)	−4.56 (20.48)	−0.32 (11.28)	−0.51 (20.10)
Observations	117	110	117	110

*Standard errors in parentheses ***p < 0.01, **p < 0.05, *p < 0.1.*

Our results show respondents were willing to pay an increase in their entrance fee to the benefit of seamount conservation, ranging from US$40 to US$57. This result is comparable with that obtained by Jobstvogt et al. (2014) on the attitudes of the Scottish public toward deep-sea biodiversity, who found that 90% of respondents wished to protect deep-sea biodiversity for the benefit of future generations. However, the value is significantly lower than Ressurreição et al. (2011) who reported a willingness to pay €405–605 per person to prevent 10–25% reductions in deep-sea species richness. From a marine management perspective, we find that an integrative management plan was viewed as most favorable with 53% of respondents favoring this approach and respondents were willing to pay $25 more to fund a program with this focus, compared to either a tourism or research science-focused plan. From this perspective, tourists recognize the need to balance multiple activities including fishing, tourism and conservation, to achieve sustainability. Our results place equal emphasis on all three management plans. The new management plan and zoning of the Galapagos Marine Reserve from 2016 support zones for the sustainable use of the marine resources ("sustainable use") maintain other zones with non-extraction activities ("conservation use") and other pristine

zones of exclusive research use ("intangible"), although this plan is yet to be implemented.

The effect of socio-demographic characteristics on willingness to pay did not conform to the usual expectations in stated preference surveys. The relationship between income and willingness to pay was inconsistent which raises some questions about the validity of our results and whether people considered their budget constraints. A previous study on shark conservation in the Galapagos by Cárdenas and Lew (2016) also found a negative income effect. One explanation for this insignificant result is when we consider that the majority of tourists, irrespective of their wealth, are drawn to the Galapagos for its pristine nature (Mathis and Rose, 2016) and have already committed a significant amount of their household budget on the trip. As such, they are less concerned about what they spend when they reach the island and are more motivated by keeping the islands in their pristine state, at whatever cost. A second explanation for the insignificant results for the coefficients is the relatively small sample size (125 responses) and this may have led to insignificant coefficients for our socio-demographic variables. Indeed, we recognize one of the main limitations of our study is the small sample size (125 responses, of which 117 were used for the analysis) and will have reduced the statistical power in our chosen modeling approaches. Our study was undertaken as face-to-face interviews and to reduce interview bias we chose to use only one interviewer; however, this reduced the number of responses which could be collected within the 2-week sampling timeframe. We also recognize that this is one of the first studies of its kind in the Galapagos, with the first discrete-choice experiment held in 2011 yielding 252 responses (Mejía and Brandt, 2015). This survey suggests that with more sampling time available, a larger number of responses could be collected for future research. We encourage caution in the broader implementation of our results to policymaking in the Galapagos and instead see this study as a pilot in which a more in-depth study of local and tourist values for the GNP could be captured. The main stakeholders for the GMR are the tourism and local fishing sectors (all fishing in the GMR is restricted only to Galápagos residents and locally registered vessels), the conservation and science sector (both local and international), the Ecuadorian Navy and the Galápagos National Park Service (GNPS), who have the official responsibilities for managing the reserve. As tourism is one of the main stakeholders this study provides relevant information for future management and policy recommendations, particularly with the new entrance fees in Galapagos. As the GMR management plan stipulates the need to take into account the precautionary principle and to provide for adaptive management based on a solid scientific basis, stakeholder participation and sustainable use the information from this study can be useful for the updating of the management planning process.

We also found a significant difference in willingness to pay between foreign visitors and Ecuadorian nationals with foreign tourists willing to pay significantly more, although given the small sample size of local tourists surveyed any inference made of this group should be made with caution. A higher allocation of funds by foreign tourists for marine conservation is reported in some studies (Arin and Kramer, 2002; Yeo, 2004). Foreign tourists expressed that snorkeling and diving and viewing land-based wildlife as their primary reason to visit the Galapagos. These tourists were interested in visiting the islands to interact with and appreciate the natural environment and thus were prepared to pay more to protect it. A limitation of our study is that it focused only on Galapagos tourists, and the sample under-represents national tourism. As such, to the extent visitors to other islands differ from Galapagos tourists in terms of their support for species conservation, the results may not be easily generalized beyond our study site. We also recognize that many of the foreign tourists only visit the island once in their lifetime which could undermine the validity of our elicitation format, however, we did ensure that the sample was representative of tourists which do visit the island. Our calculated willingness to pay (between US$40 to US$57 per person), is lower than the increased planned entrance fee agreed by the Galapagos National Park for 2020. Entrance fees for international tourists are set to increase to US$200 from US$100. This increase is greater than the willingness to pay calculated within our dataset and suggests the values we elicited were on the lower bound of individuals true valuations.

The majority of those who participated in our survey stated they had very little knowledge of seamounts as assessed by the interviewer. We find that respondents who did have prior knowledge of seamounts, as assessed by the survey interviewer, were willing to pay $33 more than those who did not have prior knowledge. This result is in line with what is expected of *ex ante* knowledge and its relationship with WTP (Cameron and Englin, 1997). In contrast, respondents who stated they were familiar with the information presented to them were willing to pay less than those who were unfamiliar. These results at first appear to be contrasting. What we find is that respondents are less confident in their knowledge (stating their awareness of the information) but are knowledgeable (as assessed by the researcher) are prepared to pay the most. It could be argued that the unfamiliar nature of seamount biodiversity undermines the use of stated preferences methods to assess the non-use values of biodiversity. However, here we follow the argument of Ready et al. (1995), who state that participants gain information during the process of a contingent valuation survey and can develop preferences for the good in question. This is also in line with literature in the psychology field, which suggests that preferences are first constructed by the respondent for unfamiliar goods during the interview process itself (Schkade and Payne, 1994). Also, Meinard and Grill (2011) state that there is no literature which supports the claim that people without pre-existing preferences for a good are incapable of expressing their true willingness to pay.

It can be argued then that our results also provide support for existing hypothetical bias, which can arise when respondents report a WTP that exceeds what they actually pay using their own money in laboratory or field experiments (Loomis, 2011). Hypothetical bias has been linked to the familiarity of the good being valued (Vossler and Kerkvliet, 2003;

Vossler et al., 2003), with it being minimized when the good and the context can be made familiar and meaningful to respondents (Schläpfer and Fischhoff, 2010). As the WTP of respondents who self-assessed as more familiar with the good is lower than those who didn't, this finding supports the thesis that familiarity plays an important role in both reducing hypothetical bias and ensuring more robust results. Our approach of controlling for *ex ante* knowledge, with both subjective and objective (third-party) measures is thus an advisable methodological addition when conducting stated preference surveys on intrinsically unfamiliar goods such as remote deep-sea ecosystems. This result also suggests that more investment in education to create awareness of deep-sea conservation could be undertaken as part of future management efforts. For example, tourist cruises which include Remotely Operated Underwater Vehicles (ROVs) could showcase deep-sea biodiversity as part of the cruise. Through citizen science approaches, these activities can enhance scientific knowledge, as well as increasing awareness and providing additional funding streams for the conservation of deep-sea and seamount ecosystems.

Despite controlling for prior knowledge and familiarity, there is concern that some respondents are expressing a "warm glow" effect (Becker, 1974). The warm glow effect involves respondents stating their WTP for environmental goods as a way of 'purchasing moral satisfaction' (Czajkowski and Hanley, 2009). Within the survey, we asked respondents their main reason for expressing a positive willingness to pay and characterized these statements as either "warm glow" or not. Of these, we perceived 29 respondents as expressing "warm glow" motivations. Other empirical studies have recognized this phenomenon of impure altruism (Nunes and Schokkaert, 2003; Kirkbride-Smith et al., 2016), which is suggested to be more common among tourists on vacation (Polak and Shashar, 2013). This result is comparable with that obtained by Ressurreição et al. (2012) on pubic preferences for marine species in the Azores islands (Portugal), Gulf of Gdańsk (Poland), and Isles of Scilly (United Kingdom), who found that respondents saw the conservation of biodiversity as a moral obligation to take action on behalf of future generations. Thus, individuals with a taste for this warm glow derive utility from "doing the right thing" rather than from the good in question, though most (60%) tourists in this present study expressed the motivation of bequest and existence value as the main driver of willingness to pay. We found that these measures of warm glow had no significant impact on respondents stated willingness to pay. However, respondents who deem seamount conservation as "urgent" do express a significantly higher willingness to pay than those who are unsure or do not consider it urgent. This alone does not fully confirm warm glow effect, although when we consider that prior to the survey many respondents had very little knowledge of seamounts and therefore would not be concerned about their decline it suggests some degree of hypothetical bias. This highlights the challenge within the valuation of unfamiliar goods between providing sufficient information needed to establish "baseline conditions" and over-loading respondents with superfluous detail (Needham et al., 2018). Given the challenges of valuing unfamiliar goods such as seamount biodiversity, it is no surprise that most empirical studies have focused on measuring non-use values of more familiar habitats such as shallow-water coral reefs and charismatic species such as sharks and mammals (see Casey et al., 2010; Ressurreição et al., 2012; Matsiori et al., 2013; Cazabon-Mannette et al., 2017). Comparing the mean willingness to pay estimates presented in **Table 7** to our estimate (US$52) (**Table 8**) reveals the public's interest in protecting seamount ecosystems – even though they do not see or "directly" experience seamount biodiversity as they do with coral reefs, marine mammals and turtles. This conclusion is strengthened when we consider respondent's response rates concerning their preferences for the allocation of conservation funds to seamount species. Moreover, our results show that tourists were equally divided when it came to charismatic versus uncharismatic species protection – therefore challenging the commonly held view that charismatic species have a stronger influence on human preferences for biodiversity conservation than less charismatic species (Ressurreição et al., 2011). However, small differences in the valuations of marine mammals compared to invertebrates were also found by Ressurreição et al. (2011).

TABLE 7 | A comparison of predicted willingness to pay across the four estimated regression models.

Model	Mean	Standard Error	95% Conf. Interval
Tobit 1 (sociodemographic variables only)	48.83	2.82	43.25 – 54.42
Tobit 2 (all explanatory variables)	52.05	3.13	45.84 – 58.25
Interval regression 3 (sociodemographic variables only)	52.47	2.69	47.15 – 57.80
Interval regression 4 (all explanatory variables)	54.56	3.08	48.46 – 60.66

The key issues that threaten the sustainability of seamount biodiversity stem from our limited ecological understanding of seamount communities (Morato et al., 2010). This lack of knowledge is further compounded by limited information on the social and economic benefits of protecting deep-sea species. In the Galapagos, this has led to a clear bias toward the conservation of certain biomes that deliver direct-use values including rocky nearshore environments and sandy beaches (Edgar et al., 2004). Furthermore, there is a disproportionate allocation of funds for the conservation of charismatic species, such as sharks and penguins, that generate high economic returns to society (Vinueza et al., 2014). Moreover, there are no current studies that evaluate the use values provided by seamounts by small-scale deep-sea fisheries and "Pesca Vivencial" or sport fishing. Hence, a major challenge to implement seamount biodiversity conservation has been to demonstrate that direct links exist between seamount species and direct benefits to society. Due to the fact, the very few individuals have "direct" experiences of the seamounts, the economic valuation of seamount biodiversity using only direct-use ecosystem services and ignoring cultural services, would undervalue the good rather than support its conservation. From this perspective, the Directorate of the Galapagos National Park could recognize the need to include non-use benefits in the valuation of

TABLE 8 | Selected papers and key findings of marine species valuation studies using the contingent valuation method.

Author(s) (year)	Location	Users	Good Valued	Mean Willingness to Pay Range (a)	Frequency of Payment	Units	Survey
Aanesen et al., 2015	Norway	Public	Cold-Water Coral	$364–381	Annual	H	2014
Casey et al., 2010 Kirkbride-Smith et al., 2016	Riviera Maya, Mexico	Tourists	Coral Reef	$42–58	Per visit	I	2005
	Barbados, West Indies	Tourists	Coral Reef	$16–21	Per visit	I	2013
Jobstvogt et al., 2014	Scotland	Public	Deep-Sea Biodiversity	$111–122	Annual	H	2012
Ressurreição et al., 2011	The Azores	Residents and Tourists	Invertebrates	$63–108	One-time	I	2007
Ressurreição et al., 2011	The Azores	Residents and Tourists	Mammals	$79–136	One-time	I	2007
Cazabon-Mannette et al., 2017	Tobago	Tourists	Sea Turtles	$31	Per visit	I	2007–2010
Schuhmann et al., 2019	Barbados	Tourists	Coastal and Marine resources	$36–52	Per Visit	I	2015
Susilo et al., 2017	Indonesia	Residents	Mangrove ecosystems	$2.57 – 2.58	One-time	I	2016
Armstrong et al., 2019	Ireland, Norway	Public	Cold Water Coral	$36.83 – 45.80	One-time	I	N/A
Grafeld et al., 2016	Guam	Divers	Coral Reef	$10	One-time	I	2013

[a]*Willingness to pay is reported in U.S. dollars (all values converted using average annual currency conversion rates). Units refer to the value's unit measurement in terms of household (H) or individual (I).*

seamount ecosystems, especially when our study leads to the conclusion that people experience a significant increase in their willingness to pay for seamount conservation through an increase in entrance fees.

The findings of our study provide a basis for understanding trade-offs between benefits from conservation and commercial uses of seamount biodiversity. The high non-use value that we identified justifies the need to ensure that cultural services are consistent with provisioning services in the rezoning of the archipelago's marine reserve. This is explicitly being discussed in a current re-zoning plan that addresses areas within the GMR as exclusive conservation zones or rather zones for sustainable use. Possible income through increased entrance fees stemming from non-use values for diverse ecosystems supports the case for enhancing conservation. Furthermore, as the major economic sector in the Galapagos, tourism has a vested interested in the conservation of ecosystems, since their economic incentives are aligned with conservation. The rise of a locally owned ecotourism sector is a positive development both for the local economy and ecosystem conservation and we argue that seamount biodiversity conservation can be managed as part of the wider objective of promoting sustainable tourism. The symbiotic relationship that exists between tourism and conservation in the Galapagos, places a high economic value on the existence of seamount biodiversity (Mathis and Rose, 2016) and we should protect these systems for the sake of conserving biological diversity in the Galapagos Marine Reserve, as well as for their economic importance.

On a broader scope, the findings of this study are timely for the debate over raising the entrance fee into the Galapagos National Park. The majority of tourists expressed the willingness to pay increased entrance fees to improve conservation efforts. Based on the predicted mean willingness to pay of foreign and national tourists and the total number of tourists who entered the Galapagos in 2016, over USD$11.2 million in additional revenue could be generated. Potential revenue from increasing tourist entry fees can, therefore, be a feasible avenue through which funding for conservation-oriented research, outreach campaigns and marketing can occur. Critically, funds stemming from entrance fees are assigned to various governmental agencies, not exclusively the Galapagos National Park, that are conservation and management oriented. Furthermore, research is almost exclusively carried out by non-governmental and academic institutions, such as the Charles Darwin Foundation, which don't receive access to these funds. It is thus important for visitors to know what conservation projects they are financing and which they are not. Upon entry into the Galapagos National Park, we suggest that tourists are presented with a pamphlet that outlines current research projects and specifies how funds from entrance fees are distributed amongst conservation priorities. Not only will this help to justify the fee payment, but it will also serve to educate tourists on important areas of conservation before their trip starts. Moreover, it will also avoid a possible "crowding out effect" on donations to the local NGOs which they depend upon since entrance fees do not fund the research they conduct. This is important because increasing tourists' knowledge of the host-area will help to increase their support for nature conservation, and also highlight key areas not covered by their entrance fees.

Conclusion

Overall, our findings suggest that tourists would support the development of a multiuse management plan for the Galapagos Marine Reserve. This plan balances conservation, local communities and sustainable tourism. Visitors to the Galapagos Islands attach positive and significant values to the conservation of seamount biodiversity. From a policy perceptive, our results show that the non-use values people associated with species protection need to be incorporated alongside the direct-use values for better management of marine protected areas.

Additionally, the results show that overlooking the non-use values provided will lead to undervaluation of marine ecosystems and their services. As the new multiuse zoning plan for the Galapagos Marine Reserve is soon to be implemented, it is very timely to consider user preferences that combine conservation, sustainable fishing and sustainable tourism into the management plan. Tourism is also the main driver of the Galápagos economy, accounting for 78% of all employment, compared to less than 5% in fishing. The tourism sector is a main stakeholder to the Galapagos islands, but successful management plan should take into account other relevant stakeholders such as the local communities. The Galápagos Special Law (1998) established the GMR's overarching objective – the protection of the archipelago's marine biodiversity, both in terms of its intrinsic (preservation) and utilitarian (fisheries and tourism) values (Galápagos National Park Service [GNPS], 1998). The Management Plan states that the main aim of the GMR is to "protect and conserve the coastal-marine ecosystems of the archipelago and their biological diversity for the benefit of humanity, the local population, science and education." (Galápagos National Park Service [GNPS], 1998). As this study was focused on tourism preferences, we, therefore, recommend performing additional studies to local communities such as fisheries to include their view into policy recommendations. One of the main purposes of the tourist visiting Galapagos is nature-tourism. Lack of awareness on the importance to support local communities is probably one of the main reasons that tourist did not include livelihoods in the management plan. Conclusions on this part should be taken with precaution, and additional efforts should be made to increase the awareness of tourist with the local community and livelihoods.

Although WTP studies are normally hypothetical in nature, i.e., depend on people's opinions (Carson et al., 2001) they can be useful for management and have been extensively used globally. Therefore, our study can be used to inform policymakers of one avenue toward sustainably managing seamounts while being mindful of the need to consider livelihoods, conservation and tourisms into the equation. Knowing what we know about environmental funds of GMR, tourism funds dedicated to the conservation of seamounts would seem an important and practical step to ensure the protection of the diverse pelagic ecosystems, offshore seamounts, and ocean trenches globally. Thus our findings have relevance beyond the Galapagos as they give insights into the motivations people have to see the sustainable management of poorly known deep-sea ecosystems. Recent work shows members of the public in Norway and Scotland are supportive of deep-sea marine conservation, despite overall low levels of prior understanding (Ankamah-Yeboah et al., 2020). It is important that this public goodwill translates through national and international policy processes and those decisions are informed by the best available scientific information. In the context of the BBNJ treaty negotiations, while stakeholders show varying opinions on the role science plays, there is evidence of consensus regarding the benefits of integrative management, the application of precautionary approaches when data are insufficient, and the perceived trustworthiness and credibility of science (Gaebel et al., 2020). Our study reiterates and amplifies these positive messages. People prioritize sustainable management and we need to support and nurture the human and technical capacities beyond developed economies so all have access to the information to make informed policy choices.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

SI was the main manuscript author and wrote the abstract, discussion, and conclusion. TI designed the survey and collected the data as part of her Masters Dissertation at the University of Edinburgh under the supervision of JR, KN, and PM-P. PM-P supervised the collection of the data and design of the survey, reviewed the manuscript, and provided the input into the abstract, discussion, and conclusion. KN assisted in the survey design, undertook the data analysis, and wrote the methods and results. MT assisted in the data analysis and the writing of the methods and results, as well as providing comment on the manuscript. JR was the primary supervisor of SI's project, re-drafted the manuscript, and provided direction on the project. All the authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.602767/full#supplementary-material

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frontiers in Marine Science

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North Atlantic Basin-Scale Multi-Criteria Assessment Database to Inform Effective Management and Protection of Vulnerable Marine Ecosystems

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INTRODUCTION

The identification of areas that fit the Food and Agriculture Organization of the United Nations (FAO) criteria to define what constitutes a Vulnerable Marine Ecosystem (VME) has been the main policy driver for the protection of deep-sea environments in Areas Beyond National Jurisdictions (United Nations General Assembly, 2006; FAO, 2009) in relation to bottom fisheries. At the same time, the Convention on Biological Diversity advocates for the implementation of representative networks of Marine Protected Areas (MPAs) in the open ocean and the deep sea, and calls for the identification of Ecologically or Biologically Significant marine Areas (EBSAs; Convention on Biological Diversity, 2008, Decision IX/20). Although VMEs and EBSAs are conceptually different, Ardron et al. (2014) argue that the designation of VMEs, EBSAs, and large open-ocean MPAs should be aligned to ensure that VMEs are incorporated within area-based management tools.

The International Council for the Exploration of the Sea (ICES) adopted a Multi-Criteria Assessment (MCA) methodology for informing the identification of VMEs in the North-East

Atlantic (ICES, 2016a,b; Morato et al., 2018). The MCA is a taxa-dependent spatial method that incorporates the fact that not all VME indicators are equally vulnerable to human impacts, and thus should not be weighted equally. By including a measure of the confidence associated with each VME record, this methodology also considers some of the uncertainties associated with the sampling methodologies, the reported taxonomy, and data quality issues. Equally important, it highlights areas in the North Atlantic that have been poorly sampled and that require further attention. Finally, this methodology also allows for the evaluation and comparison of VME index with spatial fisheries data that may directly generate significant adverse impacts on VMEs. Although the VME Index has been used since 2018 in ICES advice, several caveats and limitations have been identified (ICES, 2018, 2019, 2020). The main criticism refers to the fact that the VME index signals the presence of VME indicator taxa that are considered to be the most important rather than showing the likelihood of an area containing a spatially explicit VME. Also, concerns over the abundance scores adopted have been raised and it has been suggested that abundance thresholds should be defined for each VME indicator. It is, therefore, recognized that improvements of the VME index and the way actual VMEs are identified are still necessary.

The identification of representative areas that can form a network of MPAs in the deep sea requires ocean basin-scale approaches grounded on ocean basin-scale datasets. In this regard, the H2020 ATLAS project (GA 678760) performed a unique trans-Atlantic assessment of deep-water ecosystems to inform Atlantic Ocean basin-scale governance. The ATLAS project compiled the best available data on VME indicator taxa for the North Atlantic (Ramiro-Sánchez et al., 2020) in order to assist with the identification of locations that may constitute VMEs and EBSAs, as a precursor to the development of a North Atlantic wide network of MPAs. Here, we applied the ICES MCA method to the ATLAS VME indicator taxa database to produce and make publicly available a new "North Atlantic Ocean basin-scale VME index dataset," facilitating further consultation and use by scientists, managers, or other relevant stakeholders.

DATA COMPILATION AND METHODS

The MCA VME assessment method described in Morato et al. (2018) was applied to the deep waters of the North Atlantic basin, from 18°N to 76°N and from 36°E to 98°W. This area is one of the best studied deep-water regions in the world with respect to both VMEs and fishing effort. ATLAS compiled the best available information on *bona fide* VMEs and VME indicator taxa for the North Atlantic Ocean from public databases such as the Ocean Biogeographic Information System portal[1] (OBIS), the NOAA Deep Sea Coral Data Portal[2], the ICES Vulnerable Marine Ecosystems data portal[3], and the InterRidge Vents Database[4]. The ATLAS VME indicator database (Ramiro-Sánchez et al., 2020), was complemented with records from existing institutional databases from the partners involved in the ATLAS project, and is currently comprised of ∼455,000 records distributed in both sides of the North Atlantic: 38,400 records from the ATLAS partners, 315,000 from OBIS, 71,500 from NOAA, 30,000 from ICES, and 100 from InterRidge.

We applied the MCA method described in Morato et al. (2018) to the ATLAS VME database in order to assess and map the likelihood of presence of VMEs in the North Atlantic Ocean. This methodology aggregates data compiled from different sources to provide a spatially gridded index that combines how intrinsically vulnerable and abundant VME indicators are, along with the uncertainty associated with the gridded index. The MCA method comprised six main steps described below.

Assign a VME Indicator Score to VME Indicators

First, we adopted the VME indicator scores described in Morato et al. (2018) that assessed each of the thirteen VME indicator types (ICES, 2016b) against the five FAO criteria for defining what constitutes a VME (FAO, 2009); i.e., rarity, functionality, fragility, life-history, and structural complexity. The VME indicator scores represent a proxy for the intrinsic vulnerability of the VME indicator types to human impacts and range from low (1.48) to high (4.47).

Compile the Best Available Data on *bona fide* VMEs

Bona fide VMEs are spatially explicit areas that have been recently surveyed with video systems or other scientific trawl surveys and qualitatively identified as VMEs using local expert judgment. The areas containing *bona fide* VMEs were compiled from the ICES VME database and complemented by the ATLAS partners based on their best available information (Combes et al., 2019) and compiled from the list of known hydrothermal vents from the InterRidge Vents Database v.3.4. *Bona fide* VMEs have been described in multiple sources (Abad et al., 2007; Rengstorf et al., 2013; Kenchington et al., 2014, 2017, 2018a,b; NAFO, 2016; Rueda et al., 2016; Brooke et al., 2017; CSA et al., 2017; Hourigan et al., 2017; Van den Beld et al., 2017; De la Torriente et al., 2018; Combes et al., 2019; Kazanidis et al., 2019; Ramiro-Sánchez et al., 2019; Durán Muñoz et al., 2020; MAREANO Cold water coral reefs; ICES VME dataset[3]) and included:

(1) *Lophelia pertusa* and *Madrepora oculata* reefs in the Norwegian Sea, Porcupine, Rockall and Hatton Banks, the Bay of Biscay, the Gulf of Cádiz, the Davis Strait, and Cape Lookout;
(2) sea pen communities in the Bay of Biscay, the Gulf of Cádiz, the Davis Strait, and the Flemish Cap;
(3) cold-water coral gardens in the Gulf of Cádiz, the Azores, the Davis Strait, and Baltimore and Norfolk canyons;

[1]https://obis.org/
[2]https://deepseacoraldata.noaa.gov/
[3]http://www.ices.dk/marine-data/data-portals/Pages/vulnerable-marine-ecosystems.aspx
[4]https://vents-data.interridge.org/

(4) deep-sea sponge aggregations in the Faroe Shetland Channel, Gulf of Cádiz, the Azores, the Davis Strait, the Flemish Cap, and the Tropic Seamount, and
(5) all known active hydrothermal vent fields, including the recently discovered Luso hydrothermal vent field in the Azores.

Assigning Abundance Score to VME Indicator Records

We adopted the abundance score methodology described in Morato et al. (2018), where records with abundance data were evaluated against VME encounter thresholds defined by NEAFC (Recommendation 19:2014 and 09:2015) and the EU (Regulation 2016/2336) for live corals (30 kg) and live sponges (400 kg). For other VME indicator taxa (e.g., anemones) the encounter threshold value defined for live corals was used. If the reported abundance was over the encounter threshold, the MCA assigned an abundance score of 5. When the reported abundance was below the encounter threshold, but above 1 kg of corals or 60 kg of sponges, an abundance score of 3 was assigned. Otherwise, a value of 1 was assigned. If no data for abundance were available, a score of 0 was allocated.

Assigning a Spatially Gridded VME Index

As described in Morato et al. (2018), the VME index combines the intrinsic vulnerability (VME indicator scores) and the abundance of the VME indicators (abundance score). The *bona fide* VMEs identified in the ATLAS VME database received the maximum VME index of 5. A VME index calculated from the VME indicator score (90% weight) and the abundance score (10% weight) was assigned to the remaining records. The VME index assigned to each VME indicator record was then aggregated to a grid of 25 × 25 km cells using the maximum VME index value per cell and assigned to three classes computed with the Jenks natural breaks classification method (Low "VME index": <2.7; Medium: 2.7–3.7; High: 3.7–4.5).

Assigning a Confidence Index

A data confidence index associated with the "VME index" was estimated using the methodology described in Morato et al. (2018). Low confidence was given to confidence scores smaller than 0.32, medium confidence to scores between 0.32 and 0.77, and high confidence to scores > 0.77.

Assigning Portfolio Categories Based on the VME Index and Fishing Intensity

The VME index and fishing intensity of individual cells can be summarized and classified into four main categories: Low VME index–Low fishing; Low VME index–High fishing; High VME index–Low fishing; High VME index–High fishing (Morato et al., 2018). These categories can assist during the discussions toward the development of area-based management tools. We used a proxy of fishing intensity derived from the average annual catch per km^2 of bottom contact gears over the period 2010–2015, based on the catch data obtained from Watson and Tidd (2018). Values were then log-transformed, re-scaled between 1 and 5, and categorized as low fishing intensity (≤3.31) and high fishing intensity (>3.31) using Jenks natural breaks. To assign portfolio categories, the adopted threshold for the VME Index was also computed with Jenks natural breaks (i.e., Low VME index ≤ 3.7 and High VME index > 3.7).

NORTH ATLANTIC BASIN-SCALE VME INDEX DATASET

The dataset presented here allowed to apply the MCA methodology developed by Morato et al. (2018) to the scale of the whole North Atlantic Ocean. The resulting basin-scale datasets of the VME Index and Confidence Index (**Figure 1**) and of the classification among the four portfolio categories (**Figure 2**) at the scale of the North Atlantic Ocean were deposited in ZENODO and are publicly available at: http://doi.org/10.5281/zenodo.4279776. The caveats of the MCA methodology are discussed in Morato et al. (2018). This dataset integrates the largest amount of information available on VME indicator taxa and *bona fide* VMEs for the North Atlantic. It can be used to inform deep-sea fisheries management, systematic conversation planning initiatives, or area-based management discussions, including those referred to as other effective area-based conservation measures (OECMs), at the North Atlantic basin-scale. However, this dataset also highlighted that the Eastern and Mid Atlantic are, generally, less sampled when compared to the Western Atlantic. Namely, the Mid-Atlantic Ridge beyond National Jurisdictions from Iceland down to the Azores is still one of the areas with remarked limited publicly available information. It also highlighted reduced sampling efforts in most abyssal areas. The limited coverage of the North Atlantic basin-scale VME index dataset also highlights the importance of using complementary datasets such as, for example, those produced with species distribution or habitat suitability models (e.g., Morato et al., 2020).

Although we make the North Atlantic basin-scale VME index dataset publicly available for ATLAS partners and other users, the ICES VME database should always be considered as the primary source for the VME index information since it is regularly updated with new information provided by the ICES member countries.

The VME index dataset (**Figure 1A**; **Supplementary Figures 1–5**) contained high numbers of VME habitats (*bona fide*) in the northeastern Canadian coast, the Gulf of Saint Lawrence and the northeastern American coast, which includes the well-known *Oculina* banks, *Lophelia pertusa* reefs, *Vazella pourtalesii* sponge grounds and sea-pen fields. The dataset also reported *bona fide* VMEs areas around Rockall Bank and along the Norwegian coast, which reflect the presence of large *Lophelia pertusa* reefs, and which have been extensively sampled. Besides the *bona fide* VMEs, the dataset also identified other areas with high values of VME index around the Florida-Hatteras slope, the Azores, the Reykjanes Ridge and southern Iceland, around the Strait of Gibraltar, in the Bay of Biscay, the Rockall and Hatton Banks, the Faroe Islands, and along the Norwegian coast. On the other hand, a high number

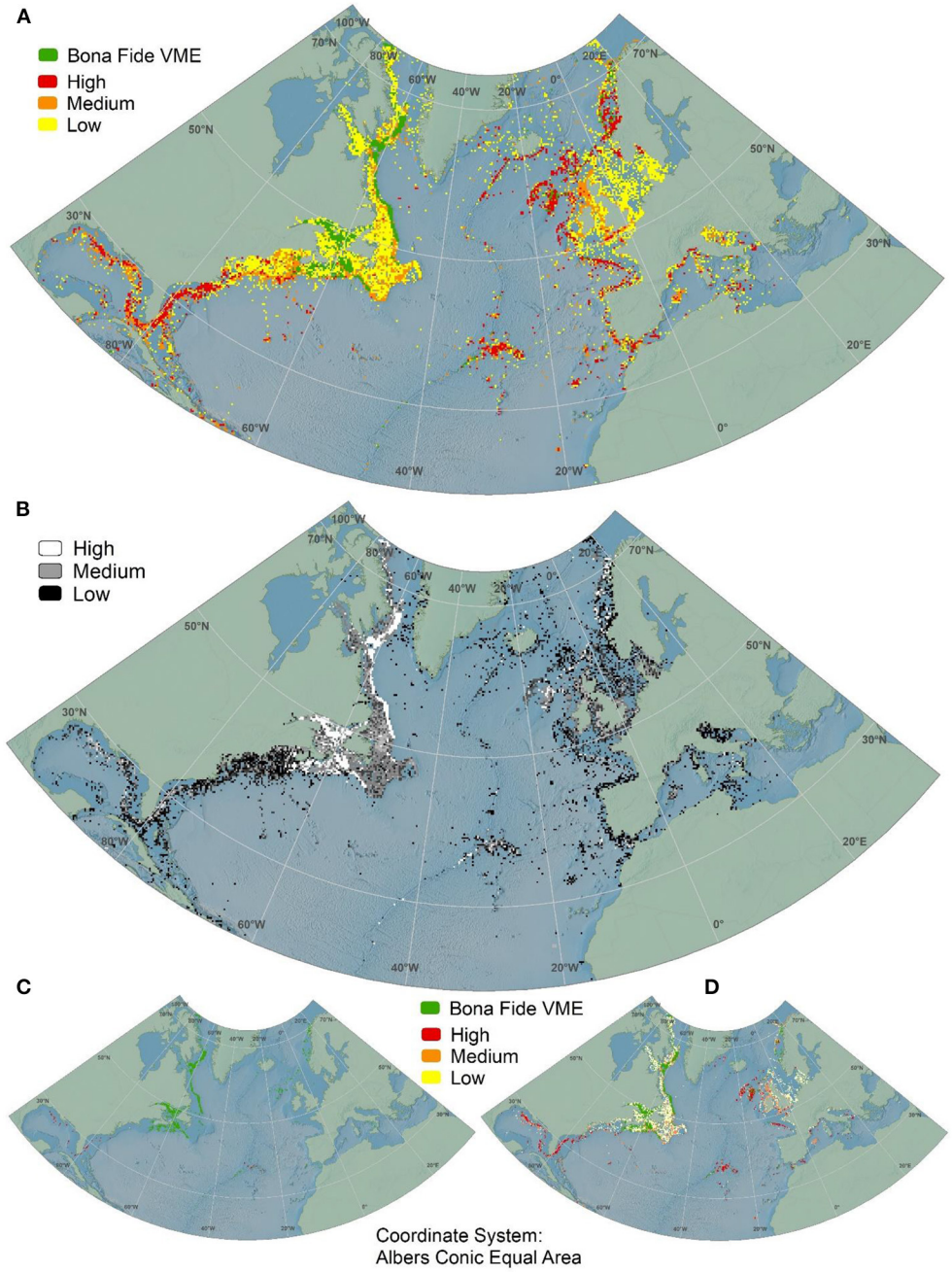


FIGURE 1 | The North Atlantic basin-scale VME and confidence indexes datasets. **(A)** VME index for all cells with data; **(B)** Confidence index for all cells with data; **(C)** VME index for cells with high confidence only; and **(D)** VME index for cells with medium and high confidence.

of low VME index areas were found in the North Sea and the English Channel, in the Irish Sea and along the shelves and slopes of the Canadian eastern coast, as well as off the northeastern American coast from the Mid-Atlantic Bight to the Gulf of Maine regions.

The VME index confidence dataset (**Figure 1B**; **Supplementary Figures 1–5**) contained mostly VME index values with low or medium confidence, highlighting a limited sampling effort in most areas. With few exceptions, high confidence areas were restricted to *bona fide* areas (**Figures 1B,C**) and small areas in the Gulf of Mexico and around Florida, around the Azores and in the Bay of Biscay. The dataset contained medium confidence values inside the Gulf of St. Lawrence, around the Flemish Cap and the Grand Banks, along most of the Canadian coast, as well as around the UK and the Rockall Bank (**Figures 1B,D**).

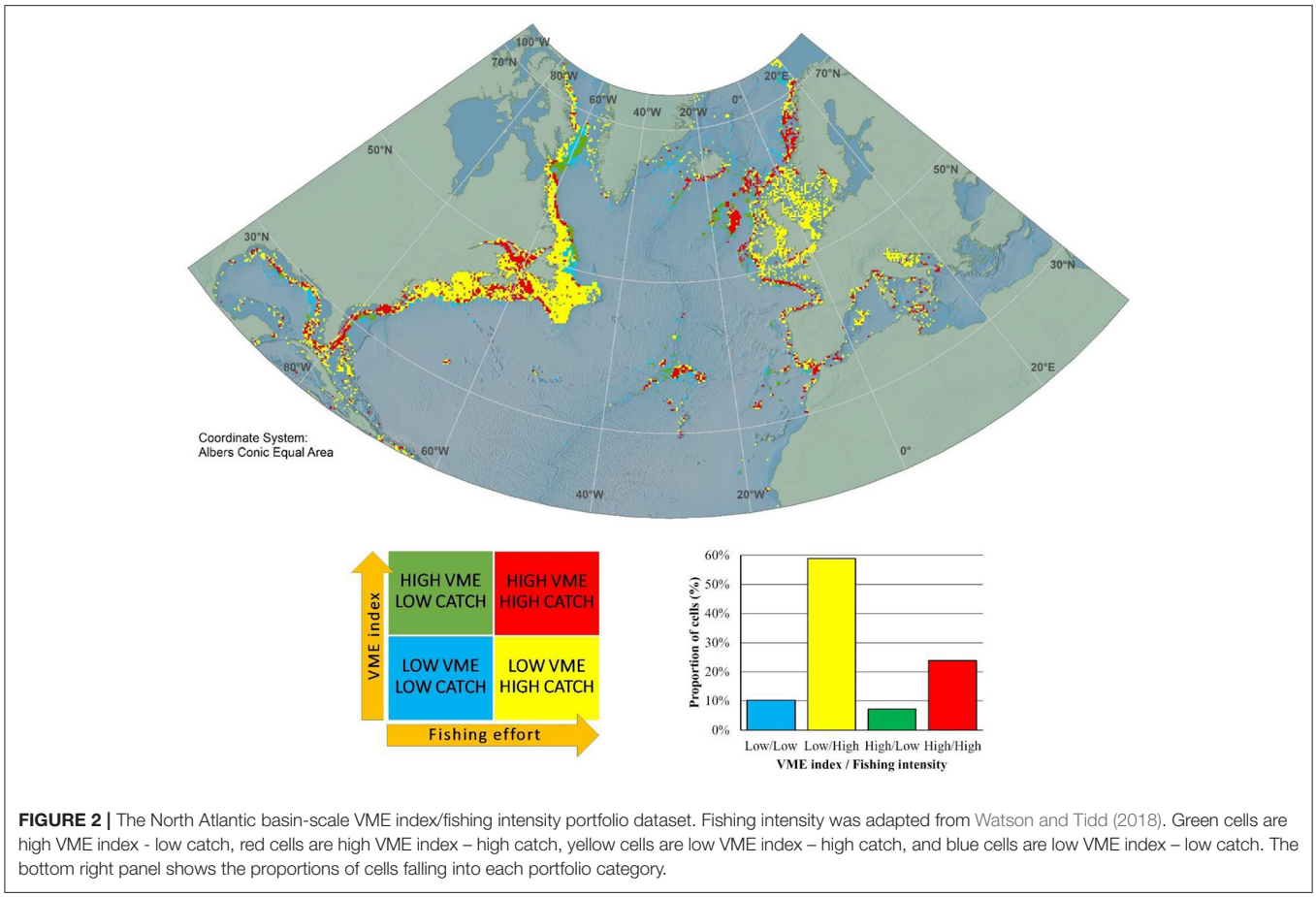


FIGURE 2 | The North Atlantic basin-scale VME index/fishing intensity portfolio dataset. Fishing intensity was adapted from Watson and Tidd (2018). Green cells are high VME index - low catch, red cells are high VME index – high catch, yellow cells are low VME index – high catch, and blue cells are low VME index – low catch. The bottom right panel shows the proportions of cells falling into each portfolio category.

The VME index/Fishing intensity portfolio dataset (**Figure 2**; **Supplementary Figure 6**) contained high catch values in most of the coastal areas of the North Atlantic, with the exceptions of the central part of the Davis Strait, north of the Flemish Cap, most of the Azores, the Denmark Strait, the southern part of the Reykjanes Ridge, the Hatton Bank and some offshore areas of the Norwegian Sea. The VME index/Fishing intensity portfolio dataset revealed a larger portion of cells categorized as Low VME index–High fishing (59%) and High VME index–High fishing (24%), with only a small portion being categorized as High VME index–Low fishing (7%). The areas where high catch overlaps with high VME index, i.e., areas of potentially significant adverse impacts, are essentially located around Florida and the Hatteras Slope, in the northeast coast of the USA, the Gulf of St. Lawrence and the southern part of the Davis Strait, some around the Azores, the northern part of Reykjanes Ridge and southern Iceland, along the coast of Norway, around the Faroe Islands, Rockall Bank and the margin of the Bay of Biscay and the Strait of Gibraltar. However, the number of cells with high fishing catch should be considered with caution because some catch might have been incorrectly spatially allocated (Watson and Tidd, 2018), highlighting the need to make high-resolution fishing effort maps publicly available.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: http://doi.org/10.5281/zenodo.4279776.

AUTHOR CONTRIBUTIONS

TMor and CP designed the work and performed the analyses. GT compiled and organized the raw data. TMor, CP, LF, and LR prepared the data report. All authors provided raw data essential for the construction of the dataset.

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SUPPLEMENTARY MATERIAL

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Systematic Conservation Planning at an Ocean Basin Scale: Identifying a Viable Network of Deep-Sea Protected Areas in the North Atlantic and the Mediterranean

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Designing conservation networks requires a well-structured framework for achieving essential objectives such as connectivity, replication or viability, and for considering local management and socioeconomic stakes. Although systematic conservation planning (SCP) approaches are increasingly used to inform such networks, their application remains challenging in large and poorly researched areas. This is especially the case in the deep sea, where SCP has rarely been applied, although growing awareness of the vulnerability of deep-sea ecosystems urges the implementation of conservation measures from local to international levels. This study aims to structure and evaluate a framework for SCP applicable to the deep sea, focusing on the identification of conservation priority networks for vulnerable marine ecosystems (VMEs), such as cold-water coral reefs, sponge grounds, or hydrothermal vents, and for key demersal fish species. Based on multi-objective prioritization, different conservation scenarios were investigated, allowing the impact of key elements such as connectivity and conservation cost to be evaluated. Our results show that continental margin slopes, the Mid-Atlantic Ridge, and deeper areas of large and productive shelves housing fishing grounds appeared as crucial zones for preserving the deep-sea biodiversity of the North Atlantic, and within the limitations imposed by the data available, of the Mediterranean. Using biologically-informed connectivity led to a more continuous and denser conservation network, without increasing the network size. Even when minimizing the overlap with socioeconomic activities, the inclusion of exploited areas was necessary to fulfil conservation objectives. Such areas included continental shelf fishing grounds for demersal fish species, and areas covered by deep-sea mining

exploration contracts for hydrothermal vent communities. Covering 17% of the study area and protecting 55% of each feature on average, the identified priority network held a high conservation potential. However, these areas still suffer from poor protection, with 30% of them benefiting from some form of recognition and 11% only from protection against trawling. Integrating them into current marine spatial planning (MSP) discussions could foster the implementation of a basin-scale conservation network for the deep sea. Overall, this work established a framework for developing large-scale systematic planning, useful for managing Areas Beyond National Jurisdiction (ABNJ).

Keywords: marine spatial planning, marine protected areas, biodiversity conservation, spatial prioritization, connectivity, vulnerable marine ecosystems, open ocean, high seas

INTRODUCTION

The deep sea hosts a large diversity of ecosystems and species (Gage and Tyler, 1991; Tyler, 2003; Danovaro et al., 2010; Ramirez-Llodra et al., 2010). The bathyal domain, which comprises continental margins and oceanic rises from about 200 m down to 3,500 m deep (UNESCO, 2009), is topographically complex, including canyons, seamounts and ridges, known to represent hotspots of benthic and demersal biodiversity (Rogers et al., 2007; De Leo et al., 2010; Würtz, 2012; Morato et al., 2013; Fernandez-Arcaya et al., 2017). These habitats offer diverse substrates for species to attach to, but also a plentiful food supply for benthic filter- and suspension-feeders, as plankton is trapped by currents on their steep slopes (Frederiksen et al., 1992; Gili et al., 1999; Genin, 2004; White et al., 2005; Mienis et al., 2007). The presence of habitat-forming species highly influences the structure and functioning of such benthic ecosystems. Cold-water corals and deep-sea sponges facilitate the development of complex benthic communities, including coral reef frameworks, coral gardens, sea-pen fields and sponge grounds, among others (Roberts et al., 2006, 2009; Buhl-Mortensen et al., 2010; Baker et al., 2012; Beazley et al., 2013; Rueda et al., 2019). Hydrothermal vents and cold seeps are other types of highly specific and unique communities whose components rely on chemosynthesis achieved by the symbiotic association of organisms (Fisher et al., 2007; Palomino et al., 2019). This mosaic of deep-sea ecosystems offers a wide array of ecological functions beyond structuring benthic communities, such as the provision of habitat, refuge and feeding resources for many demersal fish species (Baillon et al., 2012; Henry et al., 2013; Pham et al., 2015; Buhl-Mortensen et al., 2017; D'Onghia, 2019) and influences oceanic functioning through the carbon pump (Cathalot et al., 2015; Soetaert et al., 2016). Many of such ecosystem functions translate into ecosystem services, which ultimately benefit humankind (Thurber et al., 2014).

Deep-sea ecosystems are under increasing pressure from human activities (Davies et al., 2007; Ramirez-Llodra et al., 2011; Pianté and Ody, 2015; Halpern et al., 2019), whose cumulative impacts remain highly uncertain (Armstrong et al., 2019). Deep-sea fishing is known to deplete deep-water fish stocks, and to adversely impact entire benthic habitats (Koslow et al., 2000; Althaus et al., 2009; Bailey et al., 2009; Maynou and Cartes, 2012; Pusceddu et al., 2014; Aguilar et al., 2017; Clark et al., 2019). Recent advances in technology have opened the way for the biotechnology industry to access and exploit the potential of deep-sea biochemical compounds (Synnes, 2007; Skropeta and Wei, 2014). The oil and gas industry has a long history of activity in the deep sea (LaBelle, 2001) and may soon be followed by the mining industry (Sharma, 2017). Deep-sea mining targets minerals that are often found in areas supporting high biomass, such as hydrothermal vents, and is therefore likely to cause adverse impacts on these ecosystems (Van Dover, 2011; Gollner et al., 2017; Niner et al., 2018; Van Dover et al., 2018). In addition to these growing exploitation threats, the future of deep-sea species and habitats will also be influenced by forecasted changes in climate conditions, which will widely affect deep-sea ecosystem structure and functioning (Parravicini et al., 2015; Sweetman et al., 2017; Levin et al., 2020; Morato et al., 2020). In the face of these threats, certain deep-sea ecosystems have now been designated as vulnerable marine ecosystems (VMEs) following the criteria proposed by the Food and Agricultural Organization (FAO) of the United Nations (FAO, 2009). These criteria include: (1) uniqueness or rarity; (2) functional significance of the habitat; (3) fragility; (4) life history traits of component species that make recovery difficult; and (5) structural complexity. VMEs are generally identified through the type and abundance of indicator taxa such as large cold-water corals and sponges, chemosynthetic species and certain types of mud and sand fauna.

The challenge of progressing toward a sustainable exploitation of deep-water resources and the inherent fragility of deep-sea ecosystems reinforce the need to establish an adequate conservation and governance framework for the deep sea (Mengerink et al., 2014; Manea et al., 2020; Orejas et al., 2020). In recent years, a growing number of regional or international agreements, conventions and laws have addressed the need to conserve deep-sea biodiversity (Ardron et al., 2014). These include: (i) the UN Convention on Biological Diversity (CBD) leading a global effort to identify Ecologically or Biologically Significant Areas (EBSAs); (ii) the implementation by Regional Fisheries Management Organizations (RFMOs) of the United Nation General Assembly resolutions (61/105 and 64/72) calling on sovereign states to protect VMEs from fishing; (iii) the identification and protection of Areas of Particular Environmental Interest by the International Seabed Authority (ISA) in areas licensed for seabed mining; (iv) the regional

designation of marine protected areas (MPAs) by consortiums of nations such as the OSPAR Commission in the North-East Atlantic and the UNEP-MAP Protocol of the Barcelona Convention in the Mediterranean (Barcelona Convention, 1995; MedPAN & SPA/RAC, 2019); and (v) the ongoing negotiations on the new legally-binding UN Treaty to protect Biodiversity Beyond National Jurisdictions (the UN BBNJ treaty for short, Wright et al., 2019).

Despite the various measures outlined above, less than 2% of Areas Beyond National Jurisdiction (ABNJ), which are almost exclusively constituted by deep sea, are protected in the world, and the integration of the deep sea in national protection networks remains uneven and lacks foundation. Hence there is an urgent need to provide objective guidance if global marine protection objectives are to be met (i.e., the Aichi Target 11 of 10% of the oceans protected by 2020; and prospective 30% targets in the draft CBD post 2020 Global Biodiversity Framework). Meanwhile, systematic approaches for conservation planning have been called for (Ban et al., 2014; Manea et al., 2020) but only sparsely applied to the deep sea (Evans et al., 2015), essentially for sectoral purposes (deep-sea mining, see Wedding et al., 2013; Dunn et al., 2018), or in ABNJ in general (Álvarez-Romero et al., 2018a; O'Leary et al., 2019; Visalli et al., 2020).

Systematic conservation planning (SCP) is an explicit, objective-based and quantitative approach for allocating areas for biodiversity conservation (Margules and Pressey, 2000). Although it is widely used to design terrestrial protected areas and coastal MPAs, a major constraint for the development of this method at an ocean basin scale, particularly in the deep sea, is the lack of baseline data on the distribution, biogeography and connectivity of both vulnerable and exploited species (IUCN, 2019; Wright et al., 2019; Manea et al., 2020). The deep North Atlantic and the Mediterranean are some of the most sampled areas of the deep sea and thus are suitable regions to implement SCP at large spatial scales. To date, as elsewhere, the protection of these basins has been designed by incrementally protecting important and well-studied areas, and then iteratively adding *ad hoc* new areas to enhance conservation, without considering overall network coherence (Ardron et al., 2014, MedPAN & SPA/RAC, 2019). While a few studies have investigated aspects of the efficiency of the current MPA network to protect deep-sea ecosystems in parts of the North Atlantic (e.g., Johnson et al., 2014; Evans et al., 2015; Ross et al., 2017; Kenchington et al., 2019b), and the Mediterranean (Abdulla et al., 2009; Amengual and Alvarez-Berastegui, 2018; MedPAN & SPA/RAC, 2019; Manea et al., 2020), conservation planning has seldom been addressed over the full basin even though it represents the most relevant ecological scale especially for widely distributed species. Besides, climate change is likely to severely limit the effectiveness of currently existing protection measures for the deep sea (Johnson et al., 2018b) by causing significant species distribution shifts, contractions and local extinctions. This emphasizes the need to consider a large spatial scale, at which ecological and evolutionary processes take place, and it appears then crucial to propose conservation options that will provide long-term network viability and identify areas of refugia that are resilient to climate change (Johnson and Kenchington, 2019; Manea et al., 2020).

This study draws upon recent research that identified a series of ecological principles that should be used to guide the implementation of MSP for the deep environments of the Mediterranean (Manea et al., 2020), the Mid-Atlantic Ridge (Dunn et al., 2018), and addressing the conservation of VMEs (Morato et al., 2018). Even though the narrow Strait of Gibraltar can represent a dispersal barrier for several species or populations (Pascual et al., 2017), the natural connection between the North Atlantic and the Mediterranean links the deep-sea ecosystems of the two basins, for instance through the Mediterranean Outflow Water (MOW) (e.g., Boavida et al., 2019; Mosquera Giménez et al., 2019). This interdependency makes it ecologically relevant to conduct this study considering the two basins together particularly in terms of network connectivity in the face of climate change. Moreover the North Atlantic and the Mediterranean share several riverine states and a common supra-national body (EU) for law enforcement, that reinforce the relevance of addressing them together regarding MSP.

Our aim is to apply a SCP exercise to address conservation management gaps for the deep-sea biodiversity in the North Atlantic, and within the limits of data available, in the Mediterranean, in the context of climate change and ongoing international discussions on conservation management policies. Our study is thus not attempting to design a fully ecologically representative conservation network (including exhaustive pelagic, demersal and benthic compartments) but rather focuses on designing and evaluating a framework that can be re-used to better conserve deep-sea VMEs. This will be achieved by:

(1) Identifying zones of conservation importance for VMEs (especially habitat-forming cold-water corals and sponges) and commercially important demersal fish species, by taking into account predicted climate change;
(2) Evaluating the implications of considering connectivity in the conservation network design;
(3) Evaluating the implications of considering current management of human activities in the conservation network design;
(4) Assessing the efficiency of current conservation efforts and identifying priority areas that could set the baseline for the design of a robust network of MPAs.

MATERIALS AND METHODS

In the framework of two EU projects funded under the Horizon 2020 programme (ATLAS and SponGES), the generation and synthesis of (1) knowledge on the actual distribution of VMEs in the Atlantic and the Mediterranean (**Supplementary Figure 1**, Combes et al., 2019; Morato et al., 2021), (2) predictive modelling of the current and future distributions of VME indicator taxa and deep-sea fishes (Morato et al., 2020; González-Irusta, unpublished data), and (3) the modelling of larval dispersal at the scale of the North Atlantic (Gary et al., 2020) provided the basis to test the relevance of SCP to guide MSP. Furthermore, this

information was augmented with existing datasets on seafloor geomorphology and biogeography, human uses of the deep sea and the current conservation management measures being implemented over the full basin.

Systematic Conservation Planning

For a given region (i.e., an area to be managed), SCP is based primarily on an analysis of the distribution of biodiversity (species and/or habitats) while taking into account existing management of human activities. By applying spatial prioritization calculations, an SCP framework aims to select a network of areas that, if protected, would satisfy specific and quantitative conservation objectives. Various types of objectives can be set for a conservation network, such as protecting a set of species, representing the diversity of habitats, maximizing the connectivity between conservation units, or minimizing the socioeconomic cost of implementing the network (e.g., minimizing the amount of fishing grounds to close). The conservation solution emerging from prioritization depicts a suggested network of marine reserves, fishing closures, or any other designation that can suggest management measures ensuring the protection of the features of interest.

The spatial prioritization approach used in this study is similar to the widely used Marxan framework (Ball et al., 2009), and follows the steps outlined in the conceptual flow diagram shown in **Figure 1** and explained in more detail in the following subsections. Technical key terms of the prioritization approach are outlined in this paragraph.

Spatial planning scenarios are developed for a given **planning region.** The **planning region** is subdivided into a series of spatial grid cells known as **planning units (PUs)** that can be either selected or not selected by a prioritization algorithm to reach a **conservation solution**. Spatial prioritization was undertaken using an integer linear programming (ILP) algorithm available in the Prioritizr package (Hanson et al., 2019b) in the R environment (R Core Team, 2018). A number of different conservation scenarios were constructed to determine the optimal conservation network design in terms of MPA size, number and location while minimizing disruption to the existing economic activity, i.e., fishing for the **planning region**.

The **conservation features**, e.g., vulnerable species or habitats, are each assigned a **conservation target**, corresponding to the minimum percentage area of the feature distribution that is required to be protected in the **planning region**. Besides setting **conservation targets**, the other essential element of SCP is determining the socio-economic **cost** of protecting a PU. When no socioeconomic **costs** are available, an area-based **cost** (i.e., proportional to the area of each PU) can be used, which is identical for all the PUs within a regular grid. In order to balance conservation goals with socio-economic or spatial management needs, the **cost** of PUs can be varied according to acquisition **costs**, the value of foregoing economic activity (opportunity cost), or any relative measure of easiness-to-implement management (Ban and Klein, 2009). Here, the **cost** layer was varied according to the scenarios' objectives (**Figure 1**). Furthermore, spatial **constraints** and **penalties** can be factored into the solution of the conservation problem by influencing the location, size and spacing of the areas selected as part of the **conservation solution**. A **constraint** is a spatial requirement applied to the **conservation solution** that excludes or includes certain **PUs** (e.g., to include existing MPAs in the final solution). **Penalties** are associated with a specific metric, which acts as a trade-off between the **cost** of PUs. Two penalties were used here: (1) a boundary **penalty,** which increases the **cost** for more spatially fragmented solutions and thus favours larger, less numerous areas (through "clumping" of PUs) as the **penalty** is increased; and (2) a connectivity **penalty**, which applies a connectivity metric to promote better connectivity among conservation units (**Figure 1**).

The optimal **conservation solution** is determined by applying a "minimum set," i.e., a Marxan-like objective function, whose objective is to minimize the **cost** of the solution whilst ensuring that all targets (and other constraints, if any) are met (Ball et al., 2009; Hanson et al., 2019b). This can be expressed in matrix notation as:

$$\text{minimize } cx \text{ subject to } Ax \geq b$$

where x is a vector of decision variables (here, whether to select or not a PU), c is a vector of **costs** for each PU, A is the **constraint** matrix that stores the amount of each feature in each PU, b is a vector of targets for each **conservation feature**, the $\geq$ symbol indicates that the total amount of each feature in the solution must exceed the quantities in b. A conservation problem can be further modified by adding penalties acting on c (e.g., the connectivity **penalty** that decreases the **cost** of well-connected PUs), or **constraints** acting on A (e.g., the exclusion of certain PUs).

In this study, this objective function was further adjusted by imposing the completion of **conservation targets** non-solely on the total **planning area**, but also within 13 sub-regions (**Figure 2**) in order to allocate conservation units across the entire ocean basin and enhance the network replication and capture some element of geographic representativeness. Each conservation problem was solved a number of times so that it was possible to obtain a **selection frequency** with which individual PUs appeared in each solution, indicating the relative importance of PUs for achieving the conservation objectives. The resulting proposed **conservation priority networks** thus include those PUs that reached a high selection frequency, i.e., that were present in more than half or 75% of the solutions.

Planning Region

The planning region covered the Atlantic and Mediterranean basins from 18°N to 76°N and 36°E to 98°W (**Figure 2**). This area was sub-divided divided using a grid of 25 × 25 km cells, with each square representing a PU. Units that only contained seafloor deeper than 3,500 m (abyssal and hadal environments) were excluded because target VME and fish species do not occur at these depths. In contrast, shallow areas (<200 m depth) were retained, since demersal fish species occur both on margin slopes and continental shelves, and cold-water corals are often found in shallower waters on continental shelves and in fjords (Freiwald et al., 2004; Roberts et al., 2009; Buhl-Mortensen et al., 2015; Chimienti et al., 2019). PUs containing more than 20%

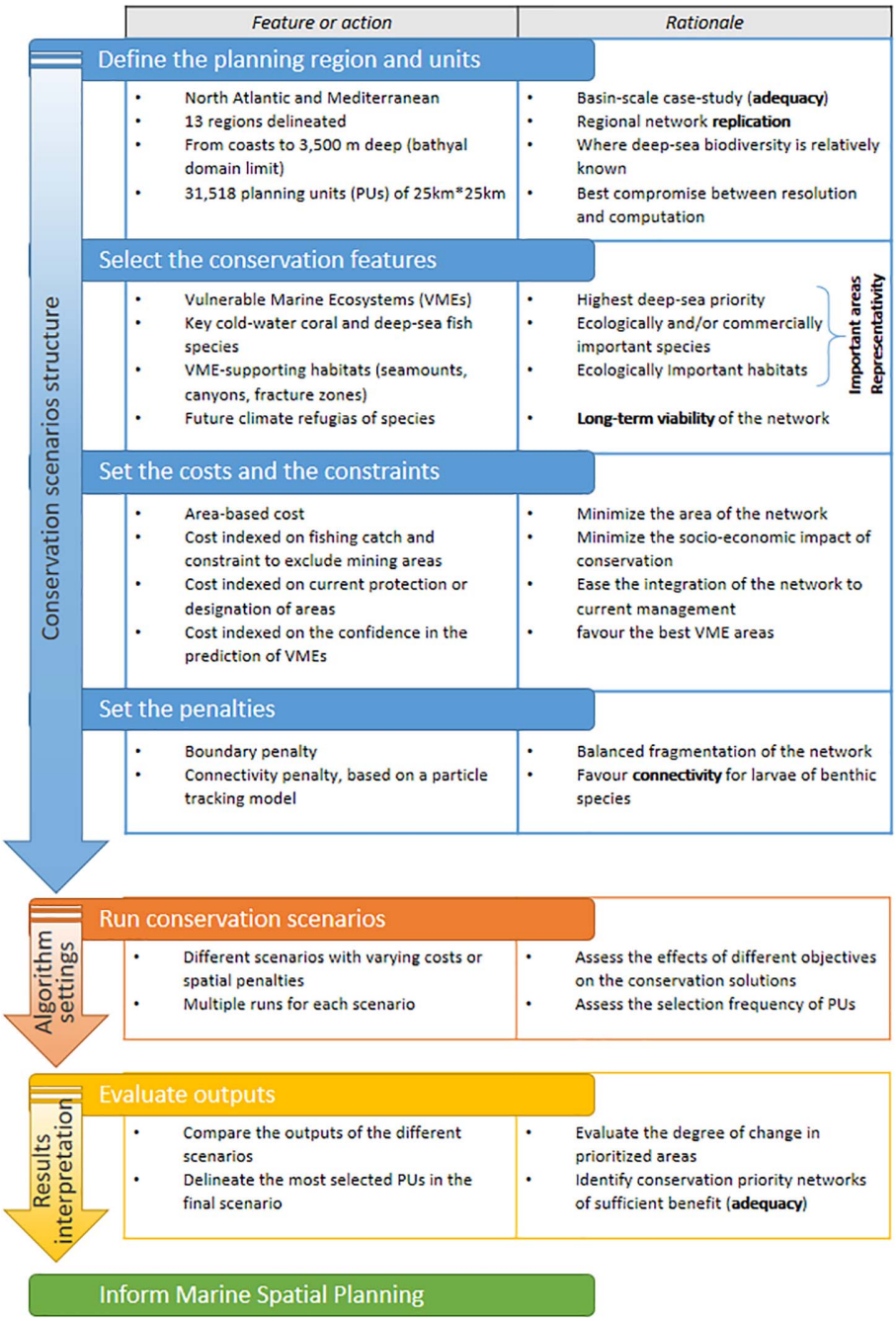


FIGURE 1 | Conceptual flow diagram of the prioritization steps of the framework. The five network criteria for ecological coherence (important areas, representativity, connectivity, replication, and adequacy and viability) as identified by the Convention on Biological Diversity (CBD, 2008), are outlined in bold.

terrestrial land cover were also excluded, leaving a total of 31,518 PUs covering 19,698,750 km^2 of the North Atlantic and the Mediterranean (**Figure 2**). Scenarios that included connectivity were run on a reduced area matching the boundaries of the VIKING20 oceanographic model (Böning et al., 2016) used as input for Lagrangian larval dispersal modelling (Gary et al., 2020). This smaller area comprised 22,347 PUs (70.9% of the total planning region, **Figure 2**). An Albers equal-area conic projection centered in the study area (origin of latitude 30°N and longitude 30°W) was used during spatial data extraction, conservation prioritization and mapping.

Given its large spatial scale, the planning region was divided into 13 sub-regions or provinces (11 in the North Atlantic and 2 in the Mediterranean) to target a geographically representative protection of species and habitats, and enhance conservation network replication. These 13 provinces (**Figure 2**) were

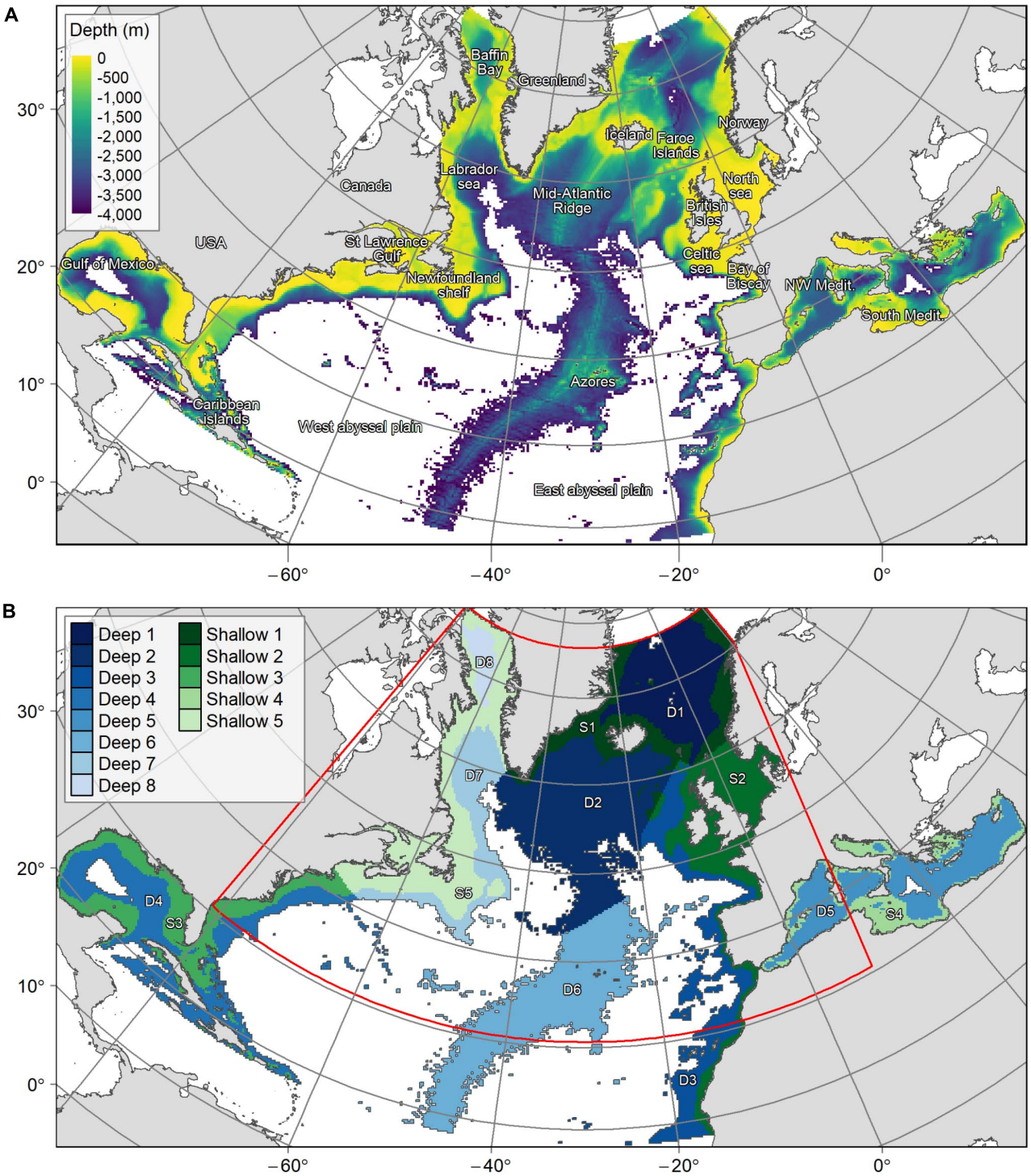


FIGURE 2 | (A) Bathymetry over the planning region. **(B)** Delimitation of the planning region into 13 "provinces." "Deep" regions represent areas with an average depth below 800 m whereas "shallow" regions have an average depth between 0 and 800 m. The red line shows the limits of the smaller planning area used for connectivity scenarios.

delineated with reference to three criteria that capture large scale habitat heterogeneity: (1) the lower bathyal Global Open Oceans and Deep Seabed (GOODS) biogeographic provinces classification (UNESCO, 2009); (2) the identification of major geographical barriers separating the abyssal plains located east and west of the Mid-Atlantic Ridge, as well as the Gibraltar

Strait separating the Atlantic from the Mediterranean; and (3) depth, distinguishing between shallow (<800 m) and deep (>800 m) areas corresponding to the upper and lower bathyal biogeographic regions (UNESCO, 2009). The shallow provinces thus include the upper bathyal zone as well as the continental shelf (<200 m), while the deep provinces represent the lower bathyal zone down to where it transitions into the abyssal domain (ca. 3,500 m). Conservation targets for each conservation feature were applied in each of the 13 provinces. This ensured that in all solutions the same percentage of each conservation feature was protected within each province across the whole planning region.

Conservation Features and Targets

Conservation Features

In our study, we considered four main types of conservation features across the North-Atlantic and the Mediterranean: (1) known *bona fide* VMEs and areas where VMEs are likely to occur, (2) predicted suitable habitat of VME indicators, (3) predicted climate change refugia for VME indicators and deep-sea fish, and (4) geomorphologic features.

Vulnerable marine ecosystems

We assembled datasets of records from both the Atlantic and the Mediterranean (Combes et al., 2019; Morato et al., 2021), based on the lists of VME indicator taxa or VME habitat defined by the ICES Working Group on Deep-water Ecology (WGDEC) and GFCM Working Group on VMEs (ICES, 2016, 2019; GFCM, 2018). Such records were compiled from the ATLAS "North Atlantic Ocean basin-scale VME index dataset" (Morato et al., 2021), which is currently comprised of ∼455,000 records distributed in both sides of the North Atlantic and within the Mediterranean: 38,400 records from the ATLAS partners[1], 315,000 from the Ocean Biogeographic Information System portal[2] (OBIS), 71,500 from the NOAA Deep Sea Coral Data Portal[3], 30,000 from the ICES VME database[4] and 100 from the InterRidge Vents Database v.3.4[5], and further complemented by a literature review to list all known cold-seep ecosystems in the North Atlantic and the Mediterranean, of which 41 occurred in the planning region (**Supplementary Text 1**).

Known *bona fide* VMEs were defined as records for which there is unequivocal evidence for a VME, e.g., hydrothermal vents and cold seeps, in-situ ROV observations of a coral reef or significant bycatch of a VME indicator species. On the other hand, areas where VMEs are likely to occur were defined as records of VME indicators that suggest the presence of a VME with varying degrees of uncertainty. Based on these records, the VME index, originally described by Morato et al. (2018), involved the calculation of two indices: (1) a VME index score based on indicator species taxonomy and abundance giving an indication of the likelihood that a PU could contain VME habitat and (2) an associated confidence score based on source data quality. Based on the combined scores, individual records could then be assigned to one one of three levels of VME likelihood (low, medium, or high) using the Jenks natural breaks classification method (Jenks, 1967). In our study, the known VMEs and the areas categorised with a "high," "medium," and "low" VME likelihood (**Supplementary Figure 1**) were each associated with a conservation target.

Vulnerable marine ecosystems species and demersal fishes: present and future predicted habitat suitability

Because the spatial distribution of VME indicators in the deep sea is still poorly known, it is common practice to incorporate the outputs of species distribution models (or habitat suitability models) in prioritization exercises (Kenchington et al., 2019a). In this study, we included the predicted habitat suitability index of a number of VME indicator species and deep-sea fish species (González-Irusta, unpublished data; Morato et al., 2020; sponge HSM unpublished data) in the prioritization approach. Six coral species and one sponge species were selected as VME indicator species because they can form diverse VME habitat types in the North Atlantic and in the Mediterranean (**Supplementary Figures 2,3**). The coral species included three scleractinians with aragonitic skeletons (the reef-building colonial species *Lophelia pertusa*[6] and *Madrepora oculata*, and the solitary cup coral *Desmophyllum dianthus*), and three octocorals with calcitic skeletons (*Acanella arbuscula*, *Acanthogorgia armata*, and *Paragorgia arborea*). The selected sponge species *Geodia barretti* is a boreal species forming sponge grounds on both sides of the Atlantic (Cárdenas et al., 2013). Six demersal fish species, occurring below 200 m depth and where the largest bottom-fisheries take place on the North Atlantic (Watson and Tidd, 2018), were also included, as securing the stocks of these highly targeted species appears essential to work toward bottom-fishing sustainability. These species were the roundnose grenadier (*Coryphaenoides rupestris*), the Atlantic cod (*Gadus morhua*), the bluemouth rockfish (*Helicolenus dactylopterus*), the American plaice (*Hippoglossoides platessoides*), the Greenland halibut (*Reinhardtius hippoglossoides*) and the beaked redfish (*Sebastes mentella*). Most occurrence records of these fish are in the northern half of the North Atlantic, thus the use of such fisheries-targeted species would only affect the SCP in this constrained latitudinal range, in contrast with the other types of conservation features that were spread through the whole planning region.

In order to assess possible climate change impacts, Morato et al. (2020) used habitat suitability modelling to forecast potential shifts in species distribution from the present-day (1951–2000) to future climate change RCP 8.5 scenarios (2081–2100) for the 12 species used in the study. The modelling approach hence resulted, for each species, in two maps

[1]The ATLAS data calls were sent to partners to inventory the VMEs emerging from their institutional databases or through ATLAS research activities. This database included *bona fide* VMEs and VME indicator taxa records for both the Atlantic and Mediterranean. Several of these VMEs have been discovered recently thus are not yet available on public data portals (Combes et al., 2019).

[2]www.iobis.org

[3]https://deepseacoraldata.noaa.gov/

[4]http://www.ices.dk/marine-data/data-portals/Pages/vulnerable-marineecosystems

[5]http://vents-data.interridge.org

[6]Recently synonymised to *Desmophyllum pertusum* (Addamo et al., 2016).

TABLE 1 | Summary of conservation target attribution for each conservation feature.

Rarity (% of planning region)	Other decision rule	Effect on target	Final target	Features
Cover ≤ 5%	–	–	60%	**Known VMEs**; **geomorphotypes:** fracture zones; seamounts; canyons
	Potential habitat reduction ≥ 70%	+20%	80% (60 + 20%)	**VME species refugia:** *A. armata*; *P. arborea*; *G. barretti*
Cover 5–10%	–	–	50%	**VME species SH:** *A. armata*; *P. arborea*; *G. barretti*
	Potential habitat reduction ≥ 70%	+20%	70% (50 + 20%)	**VMEs species refugia:** *A. arbuscula*; *L. pertusa*
	Potential habitat reduction < 70%	0	50%	**Fish refugia:** *C. rupestris*; *H. platessoides*; *G. morhua*; *R. hippoglossoides*; *S. mentella*
Cover 10–25%	–	–	30%	**VME species SH:** *A. arbuscula*; *D. dianthus*; *L. pertusa*; *M. oculata*
	Potential habitat reduction < 70%	0	30%	**VME species SH and fish refugia:** *D. dianthus*; *M. oculata*; *H. dactylopterus*
–	**Areas where VMEs are likely to occur** : VME index category	50%	50%	High VME likelihood
		30%	30%	Medium VME likelihood
		15%	15%	Low VME likelihood

The different conservation features' categories are outlined in bold. Final targets are highest when the conservation feature has low coverage/high rarity and, for species predictions, when current habitat extent is likely to suffer large reductions. For VME indicator species, the present-day predictions of suitable habitat (SH) are expressed as "VME species SH" whereas the climate refugia predictions of the same species are expressed as "VME species refugia". For demersal fishes, only the refugia predictions were considered in the prioritization.

of the predicted suitable habitat under both present and future environmental conditions (Morato et al., 2020). Given uncertainties associated with predicting future conditions and, hence, habitat suitability, future predicted species distributions were only used to identify potential species climate refugia. Climate refugia are defined as areas predicted as suitable habitat for the modelled species both during the present (1951–2000) and under future conditions (2081–2100), i.e., areas of suitable habitat that overlap between the two time periods.

While the emphasis of our study is on VME species, it is useful to consider the longer-term evolution of fisheries by including predicted climate refugia for commercial fish species. Thus, conservation scenarios included: (1) for the VME indicator species, predictions of both present suitable habitat (**Supplementary Figure 2**) and future climate refugia (**Supplementary Figure 3**) and (2) for fish species, only the prediction of climate refugia (**Supplementary Figure 4**).

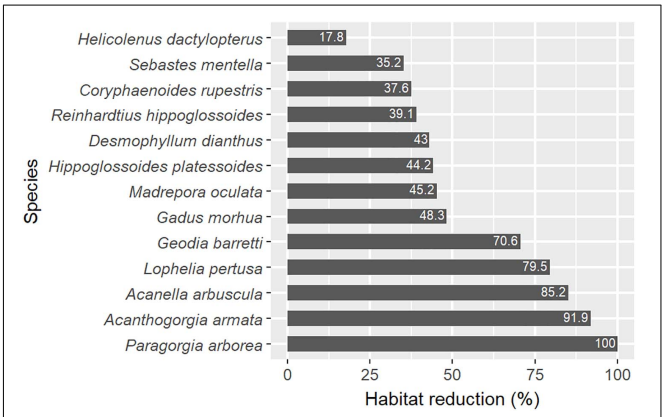


FIGURE 3 | Relative habitat reduction between present suitable habitat and future climate refugia for the 13 selected species.

Geomorphologic features

Three geomorphologic features known to provide a physical environment for VME indicator species were also considered in our planning scenarios (**Supplementary Figure 5**) (1) the seamounts extracted from Yesson et al. (2011), (2) the fracture zones along the Mid-Atlantic Ridge, determined from the GEBCO Gazetteer of Undersea Features Names[7], and (3) the shelf-incising canyons (i.e., which have a shelf origin and continue toward the margin slope), measured by their total length (km) in each PU, calculated from the dataset of Harris and Whiteway (2011).

Conservation Targets

The attribution of targets for all conservation features was based on the application of simple decision rules (**Table 1**). Firstly, conservation targets were based on the rarity of the conservation feature within the planning region (**Supplementary Table 1**); higher conservation targets being set for rarer features. The conservation targets were fixed at 60, 50, or 30% for features covering less than 5, 5–10, or 10–25% of the planning area, respectively (**Table 1**). Secondly, targets were adopted to conserve areas predicted to act as species' climate refugia. The potential reduction of species habitat in the future was estimated by comparing current and future predictions of suitable habitat for each species (**Figure 3**). Climate refugia were here chosen as the most conservative (or restrictive) representation of the future distribution of the species, as if species could not extend their habitat in areas that are currently unsuitable, thus resulting in the highest future potential reduction. For five species that were predicted to have a suitable habitat reduction under future

[7] www.gebco.net

environmental conditions of at least 70% (the three gorgonian corals, one scleractinian coral and the sponge), climate refugia were regarded as crucial areas for the species viability and thus these areas were prioritised by increasing their conservation targets by a further 20% (**Table 1**). Finally, for areas where VMEs are likely to occur a target of 15, 30, or 50% were assigned to those PUs with low, medium, or high VME index, respectively. Hence, the higher conservation targets of 70–80% were assigned to rare features (<10% cover) that act as climate refugia. Such targets were high relative to those generally used in conservation planning, from the 10% Aichi targets (CBD/COP10) to the 50% targets (Wilson, 2016; Dinerstein et al., 2017), but were here regarded as a scientific recommendation to ensure protection and buffer the uncertainties associated with habitat models and climate predictions (in line with our general approach of adopting the more conservative methods for prioritization).

Costs and Constraints

A common objective during SCP is to minimize conservation costs while achieving conservation targets (Ban and Klein, 2009). One way to achieve this is to favour solutions that promote cost-efficient management and/or minimize socio-economic impacts. In this study, we produced different scenarios based on two cost and constraints approaches: (1) constant area-based cost and (2) varying cost that accounts for current conservation measures and current bottom-fishing activities.

Area-Based Cost

A constant area-based cost, minimizing the total area of the network, is used as all the PUs have identical areas. In that case, the prioritization does not account for spatial heterogeneity in management or socio-economic activities. A cost-calibration analysis showed that increasing the value of a constant area-based cost constrained the number of PUs in solutions. The area-based cost was set either to 1 (low cost) where PUs selected to provide a solution were lowly restricted, or to 10 (high cost) which imposed a more restricted selection of PUs and a higher influence of combined costs and penalties on the solution.

Existing Conservation Measures and Ecologically or Biologically Significant Areas

Protected areas are often forcibly included in conservation solutions, so the prioritization algorithm complements the existing conservation network with new areas. In this SCP framework, we adopted a more flexible approach, by not locking-in, but rather favouring areas that already benefit from legal protection (MPAs) or that are considered as priority for conservation due to their ecological significance (EBSAs). Thus, we created an inventory of all the MPAs and EBSAs that were in place in the Atlantic and Mediterranean in 2019. These included fishing closures implemented to protect VMEs by the north Atlantic RFMOs (NAFO and NEAFC) and the GFCM in the Mediterranean, MPAs from the World Database on Protected Areas[8] (WDPA) complemented by national databases for Norway[9], Canada[10] and the United States[11], and CBD[12] EBSAs in the northwest Atlantic, Caribbean, and Mediterranean regions. These areas were subsequently categorised according to their level of protection (**Supplementary Figure 6**): (1) High – for areas restricting human activities, e.g., RFMOs' fishing closures and "marine reserves," i.e., MPAs providing full no-take zones, closed to bottom-fishing, and/or those corresponding to IUCN category "Ia" or "Ib"; (2) Medium – for areas with less restrictions such as MPAs not classified as "reserves" and a GFCM fishing restricted areas in the Gulf of Lions, France; (3) Low – for CBD EBSAs, which are indicative areas and not under any management regime. When different protection measures overlapped in the same area, the stricter protection category was retained.

Bottom-Fishing Activities

Planning units that contain areas of high economic value (e.g., fisheries) can be assigned a higher cost so they are less likely to be included in conservation solutions. We extracted the fishing catch landing value for towed bottom-impacting gears (dredges, bottom trawls, and Danish seines) using the Global Fisheries Landings database (Watson, 2017; Watson and Tidd, 2018). The 2010–2015 average annual catch rate (tonnes per square km of ocean) was calculated for each PU and then log transformed to lower the weight of extremely high catch values (**Supplementary Figure 7**). Passive bottom impacting fishing gears (e.g., traps or bottom longline) were not considered as they were fairly localised comparatively to the working spatial resolution used (25 km), their catch levels were negligible in respect to total catches, and pelagic and bottom gears were not always distinguished in the available data.

Combined Costs

The layer displaying varying costs was computed from three sets of data, which allowed the inclusion of socio-economic and spatial management aspects in the PU selection process. First, PUs cost was negatively indexed to the three levels of protection in order to favour zones that already benefit from conservation designations and acknowledge the management efforts in place. Second, PUs cost was increased in proportion to the bottom fishing catch value to penalize the selection of fishing grounds, and thus, limit the economic loss due to implementing restrictions in fished areas selected in conservation

[8] www.protectedplanet.net

[9] http://maps.imr.no/geoserver/web/. Map "coralmpa": cold-water corals MPAs in the EEZ of Norway.

[10] https://open.canada.ca/data/en/dataset/a1e18963-25dd-4219-a33f-1a38c4971250; https://open.canada.ca/data/en/dataset/44769543-7a23-4991-a53f-c2cf7c7a946f

[11] https://marineprotectedareas.noaa.gov/dataanalysis/mpainventory/; https://safmc.net/ecosystem-management/mapping-and-gis-data/. The national NOAA dataset of protected areas was complemented by the deepwater coral Habitat Areas of Particular Concern (HAPC) and grouper Special Management Zones managed on the Atlantic coast by the SAFMC.

[12] www.cbd.int/ebsa/ebsas. Considering the North-East Atlantic, a first workshop to describe EBSAs was held by the OSPAR Commission and the North East Atlantic Fisheries Commission in 2011. In 2019, a new workshop, convened by the CBD, and with input from ATLAS Partners, has taken place (CBD/SBSTTA/23/7 and 23/7/ADD1) and described 17 potential EBSAs, but have yet to be formally endorsed by CBD COP and have therefore not been included in this analysis.

solutions (i.e., fishing considered an opportunity cost). Third, PUs containing known VMEs or assigned with a medium to high VME confidence index score were given a lower **cost** value and were preferentially selected to PUs with low VME confidence due to a reduced requirement to confirm the presence of VME before designating an area as an MPA.

The PU values of the cost layer were calculated following the formula:

$$Cost\ layer = b\ (1 - (\frac{f1}{n} * c1 - \frac{f2}{n} * c2 + \frac{f3}{n} * c3))$$

where b is the PU raster layer; n is the number of features in the scenario ($n = 24$); $f1$, $f2$, and $f3$ are the number of features affected by protection measures ($f1 = 24$), fishing ($f2 = 21$) or VME confidence index ($f3 = 1$); $c1$, $c2$ and $c3$ are raster layers with protection ($c1$), fishing ($c2$) or VME confidence ($c3$) cost indices rescaled within [0,0.8].

The cost layer was computed from an area-based baseline value (b) of 10, which then was made to vary according to the weighted sum of three cost indices ($c1$, $c2$, and $c3$). These latter described the range of cost variation applied to the baseline, from 0 to 80%, either following fixed values per categories (0.25, 0.5, and 0.8 for lower to higher levels of protection; 0.5 and 0.8 for medium and high VME confidence) or a continuous gradient (fishing catch). The three indices were weighted depending on the proportion of features likely affected by each kind of cost ($\frac{f}{n}$). The protection and fishing cost indices had a high weight (1 and 0.88, respectively) as these activities potentially impact many species and habitats. On the contrary, the VME confidence index was only related to the VME feature and thus had a low importance in the final cost value (weight of 0.04).

Deep-Sea Mining Constraint

Finally, a spatial constraint consisted in the exclusion from the solutions of 106 PUs that contained deep-sea mining exploration zones, under contract with the ISA (**Supplementary Figure 7**). Scenarios including this constraint considered that SCP could not be implemented in these areas although efforts are underway to develop a Regional Environmental Management Plan for the Atlantic which will include conservation areas (International Seabed Authority, 2018).

Spatial Penalties

Spatial penalties enable trade-offs on the cost of PUs. We applied a "boundary penalty," known as the boundary length modifier (BLM) in Marxan, that penalizes solutions that are excessively fragmented (Hanson et al., 2019b). A penalty value of 0.0001 was found to provide a suitable compromise between too fragmented and too clumped solutions and was applied in all scenarios run without connectivity.

Connectivity was addressed by adding penalties to favor solutions that selected combinations of PUs with high connectivity between them (Hanson et al., 2019b). A matrix of the probability of connectivity between each pair of PUs was derived from the outputs of the ARIANE Lagrangian particle tracking model (see Gary et al., 2020). This model tracked the trajectories of almost 500 million hypothetical pelagic larvae of benthic species with ocean circulation conditions over a 50-year period (1959–2008) generated by the VIKING20 model (Böning et al., 2016). Particles were released in each PU, at the surface (20 m) and at the seabed, and at 1,000 m if water depths were deeper than 1,000 m. The different release depths were a simplified way to model different larval behaviors which have been observed in deep-sea benthic species: drifting near the seabed, swimming up to the surface, swimming clear of the seabed but not right up to the surface. Particles were passively drifting with the prevailing currents for 20 days, corresponding to the shorter end of the range of many deep-sea pelagic larval durations (PLDs) (Hilário et al., 2015). This was of sufficient duration to identify connectivity pathways that could be factored into our models, but it should be noted that in addition to the PLD, the competency period (i.e., at which time larvae start heading downward to find somewhere to settle) and larval behaviour will have significant influence on actual connectivity patterns (Gary et al., 2020). The degree of connection between PUs was calculated as the proportion of particles released from a source PU passing through any other PU within 20 days. The connectivity penalty thus favoured solutions that maximise the number of larvae retained within the conservation network.

Spatial Prioritization

Scenarios

A total of 47 scenarios were formulated for the ATLAS SCP approach, for which conservation features, conservation targets, penalties (costs and connectivity) and constraints vary. Four of the more complex scenarios are presented and compared in this paper (**Table 2**). For the "Base" scenario, the 24 features and associated conservation targets were replicated within the 13 provinces across the full planning region, and an area-based cost with a low value (1) was used during the planning exercise. The "Base" scenario was rerun in the smaller planning region used for the "Connectivity" scenario (**Figure 2B**) that was limited by the coverage of the ocean circulation model used in particle tracking and called the "Reduced Base" scenario. In the "Connectivity" scenario, the replacement of the boundary penalty by the connectivity penalty allowed us to consider larval dispersal to achieve a more resilient conservation network. The area-based cost was increased to 10 in this scenario to increase the influence of the connectivity penalty on PUs selection. The area-based cost was similarly increased for the "Reduced Base" scenario to facilitate comparisons. Finally, the "Management" scenario involved more complex costs and constraints to prioritize areas according to the current protection and uses of the deep sea. The aim was therefore to find solutions that maximize the spatial overlap with current protection measures (PUs with low cost), while minimizing the overlap with fishing (PUs with high cost) and deep-sea mining (excluded PUs).

Solving and Evaluation

The Gurobi solver (Gurobi Optimization LLC, 2018) was used to solve the prioritization problems. For most scenarios, 100

TABLE 2 | Characteristics of the implemented scenarios.

Scenario	Planning area	Penalty	Cost	Constraint
"Base"	Full	Boundary	Area-based (1)	None
"Reduced Base"	Reduced	Boundary	Area-based (10)	None
"Connectivity"	Reduced	Connectivity	Area-based (10)	None
"Management"	Full	Boundary	Varying (1.8–17)	Mining areas excluded

runs were required using the "cuts" portfolio method (Rodrigues et al., 2000; Hanson et al., 2019b), and the 30 best solutions, i.e., the less costly solutions, were picked from the 100 initial runs (see **Supplementary Figure 8** for cost evolution through solving). Connectivity problems were computationally heavy and particularly long to solve thus limits were placed on the calculations: only 30 runs with a computational time limit of 10,000 or 15,000 seconds were permitted. Outputs were evaluated using the selection frequency of PUs, reflecting how often they were included within the 30 best solutions. For each scenario, the dispersion of the number of selected PUs across the selected solutions was assessed using boxplots. The selection frequencies approach was preferred to using the binary output of a single solution, because it provides more flexibility in suggesting a conservation network solution. Thresholds of PUs selection frequency were used to determine the importance of their contribution toward the conservation objectives:

- PUs that were selected at least once across solutions contribute to the objectives;
- PUs that were selected in at least 50% of solutions make a relatively important contribution to the objectives;
- PUs that were selected in at least 75% of solutions make a highly important contribution to the objectives.

Finally, the PUs selected in at least 50–75% of solutions within the "Management" scenario were used to delineate two suggested priority networks for ocean-basin conservation. The representativeness of the prioritization elements (features, protection levels, and fishing catch) was assessed in these two priority networks and their conservation value compared with existing MPAs and CBD EBSAs.

Data Management and Access

The R code used to structure and run the scenarios, together with links to the scenarios' input layers, the conservation targets table, the connectivity matrix resulting from the 20 days PLD larvae drift modelling and the final scenarios' outputs are available online (Combes and Vaz, 2019).

RESULTS

Base Scenario

This conservation planning scenario covered the whole planning region (**Figure 2**). The PUs most frequently selected in the solutions were mainly located along the slopes of the continental margins on both sides of the Atlantic, on the southern coasts of Greenland and Iceland, along the Mid-Atlantic Ridge, on the north of the Gulf of Mexico, and for the Mediterranean, along its western coasts, the Tyrrhenian Sea and the north and west of the Ionian sea (**Figure 4**). Large shallower expanses of the upper slopes and continental shelves (northern part of the North Sea, north of the British Isles and the Canadian shelf from the St. Lawrence Gulf to Baffin Bay) were also selected but with more moderate frequency (**Figure 4**). The individual solutions computed for this scenario covered approximately 19% of the planning region on average. This distribution of PU selection frequencies in the "Base scenario" seems to fit the overall distribution pattern of the selected features (Combes and Vaz, 2019; Morato et al., 2020). With regards to the invertebrate species, their present-day distribution and particularly their future climate refugia, appear mostly on margin slopes, sometimes predicted exclusively in those areas (**Supplementary Figures 2,3**). For instance, the refugia of *A. arbuscula*, *A. armata*, *L. pertusa*, and *G. barretti*, which were all small in extent and thus had high conservation value, formed thin ribbons of highly selected PUs along the North-Atlantic margins. In general, fish species' climate refugia were located on the northern continental shelves above 500 m depth (**Supplementary Figure 4**), with some of them (*R. hippoglossoides* and *S. mentella*) exclusively found in cold waters as far as the Arctic. VME habitat and geomorphotype features displayed a more scattered distribution, mainly along margin slopes of the Atlantic, on the Mid-Atlantic Ridge and on the northern part of the Mediterranean (**Supplementary Figures 1**, **5**).

Connectivity Scenario

In order to test the influence of including connectivity in our SCP solutions, a "Reduced Base" scenario was re-run within the smaller planning region used for the connectivity scenario. The output was similar to the larger area "Base" scenario. The "Reduced Base" output (**Figure 5A**) was compared with the "Connectivity" scenario output (**Figure 5B**) that maximised connectivity. Replacing the boundary penalty with a connectivity penalty did not change the broad distribution of conservation solutions but tended to constrain selection frequencies so that less PUs contributed to the solutions (**Table 3**) resulting in highly selected areas systematically forming a continuous and compact conservation network (**Figure 5B**). Hence, the connectivity scenario conserved much less of the planning region when focusing on the PUs with selection frequencies of $\geq$50% or those that were selected at least once (21 vs. 16% and 50 vs. 32%, respectively). Both the "Reduced Base" and "Connectivity" scenarios conserved c. 10% of the planning region when only PUs with a selection frequency of $>$75% were retained. However, the use of connectivity did not affect the number of PUs in individual solutions, ranging approximately from 4,400 to 4,600 PUs (19.7–20.6% of the planning area) for both scenarios (**Figures 5A,B**).

Management Scenario

The "Management" scenario has the aim of finding solutions that maximize the selection of current conservation measures while minimizing the overlap with human activities. In this

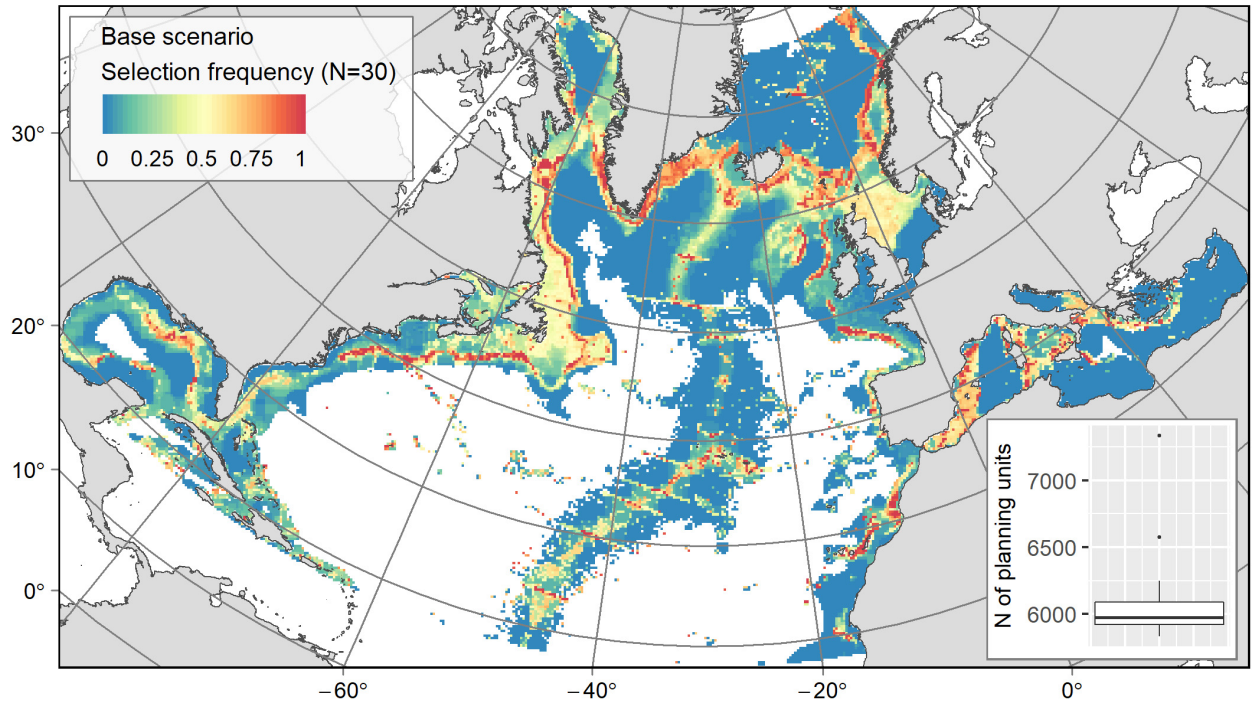


FIGURE 4 | Output from the "Base" scenario: map of PU selection frequency from the 30 solutions with a boxplot showing the number of PUs in the solutions.

scenario, the socio-economic costs were assigned to PUs ranging between 1.8 and 17, with the baseline value of 10 predominating (**Figure 6A**) based on the value of fish caught or the presence of MPAs and likely VMEs. The lower cost values (least penalised) were attributed to MPAs and fishing closures in the High Seas where bottom-fishing was absent. The lowering of cost values for MPAs inside EEZs (**Supplementary Figure 6**) was partly counterbalanced due to fishing occurring in the same areas (e.g., parts of the US shelf, Celtic Sea and North Sea, northwest Mediterranean, **Figure 6A**). The higher cost values induced by high fishing activity were found along the Atlantic coasts and on large shelf areas, such as the North Sea, Celtic Sea and the Canadian shelf, and to a lesser extent in the Mediterranean, within the Alboran Sea and the coasts of Italy (**Figure 6A**). Existing MPAs, fishing closures or CBD EBSAs cover 19.7% of the planning region, of which 4.6% are fishing closures or marine reserves, 8.7% are MPAs with lesser protection (i.e., without no-take zones or strong fishing restrictions) and 6.4% are EBSAs (which do not mandate any management measures, **Supplementary Figure 6**). Current fishing closures and reserves with adequate enforcement protect from 0 to 16.5% of the target conservation features, with an average area extent of 7.2% (**Supplementary Table 1**). Importantly, existing levels of protection of potential climate refugia for 8 of the 13 species examined in this study are currently below 6% (**Supplementary Table 1**). Deep-sea mining areas are all situated in the same province ("Deep 6," **Figure 2**), and overlap with the "hydrothermal vent fields" EBSA designated along the Mid-Atlantic Ridge almost entirely (**Supplementary Figure 6**).

While the areas selected as having conservation value in the "Management" and "Base" scenarios are broadly similar (**Figures 4**, **6B**, respectively), their selection frequency varied (**Table 3**). Indeed, 30% less PUs were selected in solutions for the "Management" scenario, while the number of highly selected PUs (≥75% of selection frequency) increased by one third (**Table 3**) as would be expected existing conservation areas were favoured in solutions by their lower cost. The percentage of PUs selected in existing MPAs and EBSAs increased from 25% in the "Base" scenario to 38% in the "Management" scenario (**Table 3**). Similarly, this was reflected in the contribution of existing MPAs and EBSAs in the conservation solutions (an increase from 7 to 15.8 %) linked to their cost premium up to −80%. In the High Seas, solutions captured fishing closures in the NAFO regulatory area: Flemish Cap, New England and Corner seamounts; and in the NEAFC regulatory area: middle and northern Mid-Atlantic Ridge and Hatton Bank (**Figure 6B**). In EEZs, the selection of MPAs and EBSAs increased where the fishing pressure was relatively low, along the coasts of the US (mainly Florida, including its cold-water coral Habitat Areas of Particular Concern and snapper MPAs) and Canada (e.g., in several cold-water coral marine refuges and cod closures) and along the northern Mediterranean coast (e.g., in the large MPAs of the Pelagos Sanctuary and the Spanish Whale Migration corridor, that are cetaceans MPAs but encompass large deep-sea ecosystems and notably canyons) (**Figures 6A,B**).

The increase of cost indexed to fishing catch, which generally occurred in coastal areas and over large shelf areas (**Supplementary Figure 7**), reduced the selection frequency of

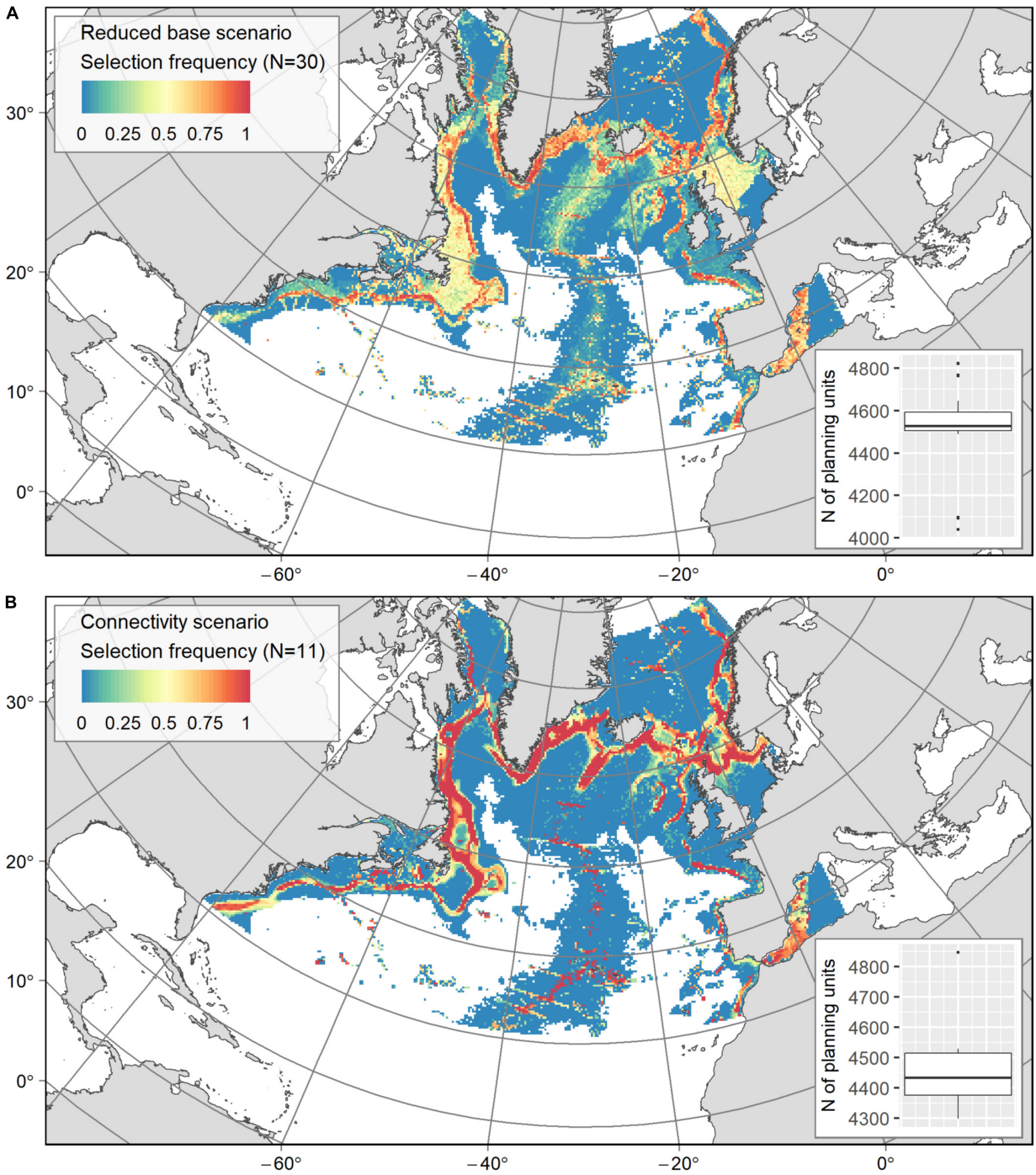


FIGURE 5 | Outputs from **(A)** the "Reduced Base" scenario and **(B)** the "Connectivity" scenario: maps of PU selection frequency from the N solutions with a boxplot showing the number of PUs in the solutions.

these areas but did not exclude them from conservation solutions, likely because they hold significant potential for demersal fish conservation (**Figure 6B**). In both the "Base" and "Management" scenario solutions, median fishing catch values in selected PUs appeared to be higher than those obtained for the planning region as a whole (**Figure 7**).

Finally, removing areas covered by existing sulphide mining exploration contracts from conservation solutions did not change the general output, because of the small size of the excluded area (**Figure 6A**). However, the loss of potential conservation area is compensated for by a strong selection of conservation PUs north of the mining exploration zone (**Figure 6B**). The "Deep

TABLE 3 | Number of selected PUs in the different conservation solutions based on selection frequency thresholds (PUs selected at least once; in ≥50% of the solutions; or in ≥75% of the solutions).

Scenario	PU selection	*N* of PUs	Relative cover (% of planning area)	% of PUs in MPAs or CBD EBSAs	% of the MPAs and CBD EBSAs being included
"Reduced Base"	Selected at least once	11,278	50.47	19.8	57.5
	≥50% of frequency	4,785	21.41	21.2	26.1
	≥75% of frequency	1,855	8.3	21.5	10.3
"Connectivity"	Selected at least once	7,170	32.08	19.9	36.8
	≥50% of frequency	3,615	16.18	19.4	18.1
	≥75% of frequency	2,384	10.67	17.6	10.8
"Base"	Selected at least once	16,907	53.64	21.7	57.6
	≥50% of frequency	5,766	18.29	24.7	22.4
	≥75% of frequency	1,947	6.18	25.0	7.6
"Management"	Selected at least once	11,900	37.76	24.1	45.0
	≥ 50% of frequency	**5,247**	**16.65**	**29.9**	**24.6**
	≥75% of frequency	**2,618**	**8.31**	**38.3**	**15.7**

*"Reduced Base" and "Connectivity" Scenario calculations are for the reduced planning region (**Figure 2**; N = 22,347 PUs) while the full planning region (N = 31,518 PUs) is used for the "Base" and "Management" scenarios. Two suggested priority networks for conservation are highlighted in bold.*

6" province contained 51.7% of all the PUs with hydrothermal vents. Sulphide exploration contracts cover 43.3% of PUs with hydrothermal vents in "Deep 6" and 23.2% of all the hydrothermal vent PUs at the basin scale. Therefore, excluding the licensed mining areas from conservation solutions removed the associated hydrothermal vents. So while the conservation target of 60% for these ecosystems –that were included in the "known VMEs"– could be achieved at the basin scale by selecting PUs further north, it was not possible to reach that target in the "Deep 6" province (with a maximum of 56.7% PUs available for conservation).

Conservation Priority Networks

Outputs from the "Management" scenario were used to identify a set of conservation priority areas (including certain existing measures) in the North Atlantic and the Mediterranean. Using selection frequency thresholds, it was possible to identify: (1) a "priority" network based on PUs that were selected in at least 50% of the scenario solutions, and (2) a "core priority" network based on PUs that were selected in at least 75% of the scenario solutions (**Figure 8**). The "priority" network, which covered 16.6% of the planning area (**Table 3**), included on average 55% of each conservation feature, exceeding the initial conservation targets in most cases (**Supplementary Table 1**). While the twice smaller "core priority" network included on average 37% of each conservation feature, falling short of the initial conservation targets, it still identified a conservation area extent 6 times higher than that currently covered by MPAs or EBSAs (**Supplementary Table 1**). The percentage of PUs in the "priority" and "core priority" networks that occurred in MPAs or EBSAs was 29.9–38.3%, respectively, with values dropping to 10.7 and 15.8%, respectively when only marine reserves and fishing closures were considered (**Table 3** and **Figure 8**). Conversely, 75.4% ("priority" network) to 84.3% ("core priority" network) of the MPAs and EBSAs (out of which 61% and 71.2% for marine reserves and fishing closures, respectively) were not located in the selected priority networks (**Table 3**).

DISCUSSION

To our knowledge, this study is among the first SCP exercises to employ a strategic approach to the conservation of deep-sea biodiversity at an ocean-basin scale. The spatial prioritization process developed here shows this strategy has the potential to facilitate the identification of conservation priority networks across the whole of the North Atlantic, and into the Mediterranean, down to depths of c. 3,500 m. Conservation features included VME indicators, such as habitat-forming cold-water coral and sponge species and commercially-important demersal fishes, as well as habitat geomorphotype proxies. We carried out a multi-objective prioritization using different approaches: inclusion of climate refugia, replication, connectivity, different costs and constraints, in order to assess their applicability in basin scale SCP. Continental margin slopes of the Atlantic, the Mid-Atlantic Ridge, the Western Mediterranean, the north and west of the Ionian Sea, together with the largest continental shelves containing fishing grounds, were identified as crucial areas for conservation management. Interestingly, the priority networks identified ostensibly to protect the coral and sponge species included in this study also encompass much of the predicted distribution of a number of other VME indicator species not included in this study, mostly occurring between 500 and 2,500 m depth (Davies and Guinotte, 2011; Yesson et al., 2012, 2017; Knudby et al., 2013; Howell et al., 2016). Priority networks to protect the cold-temperate fish species selected focused on securing their future climate refugia and did not include species found in warm-temperate, tropical or Arctic zones. Notwithstanding caveats, such as the patchy data availability usual in the deep sea, the investigated scenarios used in this SCP exercise were able to identify gaps in the current conservation network employed to protect deep-sea VMEs and demersal fishes. This may help drive future data acquisition programs, particularly in the Mediterranean,

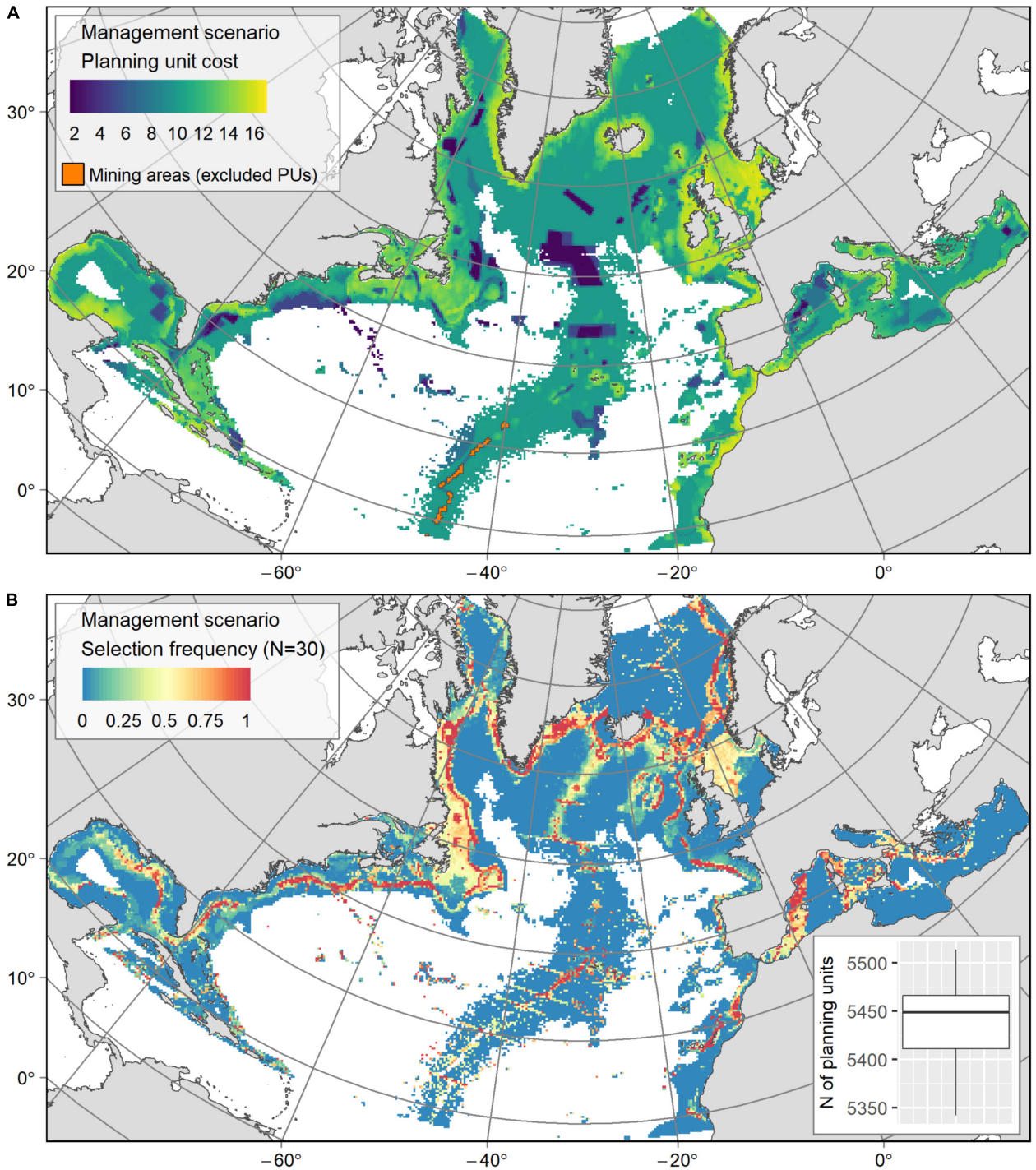


FIGURE 6 | (A) Socio-economic cost layer used in the "Management" scenario, generated from the distribution of bottom fishing catch, the presence of MPAs or CBD EBSAs and the VME confidence index. Blue PUs (cost lower than 6) highlight the MPAs in which the fishing catch was relatively low, while yellow PUs reveal areas of high fishing catch. PUs containing deep-sea mining activities (in orange) were excluded from the conservation solutions. **(B)** Output from the "Management" scenario: map of PU selection frequency from the 30 solutions with a boxplot showing the number of PUs in the solutions.

notwithstanding preliminary attempts to identify knowledge gaps and the need for transnational conservation strategies (IUCN, 2019). Repeating a systematic conservation approach similar to that used in this study could add value to regional conservation planning processes in the North Atlantic and the Mediterranean.

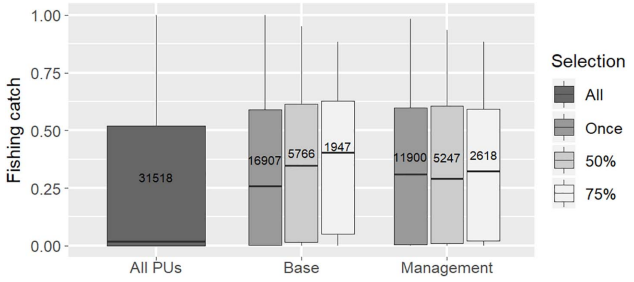


FIGURE 7 | Distribution of costs associated with the fishing catch index (log of fishing catch +1, rescaled between 0 and 1) and total number of PUs selected (in box) for all PUs and for "Base" and "Management" scenario solutions (according to frequency of PU selection in solutions: selected at least once, ≥50% or ≥75%).

Structuring a Resilient and Replicated Network

A growing number of SCP studies highlight the importance of designing resilient protection networks that integrate climate change considerations (Levy and Ban, 2013; Magris et al., 2014, 2017; Álvarez-Romero et al., 2018b; Manea et al., 2020). In our study, more than half of the conservation features considered consisted of species' future climate refugia. Accompanying conservation targets were set high so that solutions preferentially selected these areas having high resilience toward climate change. Above all, in the context of drastic widespread environmental changes such as ocean acidification, warming and deoxygenation, VME engineers like most skeleton-forming invertebrates, are facing serious declines by 2100 potentially leading to extinction (Veron, 2008; Jackson et al., 2014; Roberts et al., 2016; Morato et al., 2020). In this study, refugia for coral and sponge species were restricted to steep margin slopes, that together with seamounts, appear to be essential areas for their future conservation because they provide a large range of environmental conditions in a relatively small area (Tittensor et al., 2010; Lo Iacono et al., 2018). Such climate refugia (for fish or invertebrates) may facilitate recolonisation or colonisation of new areas, thus fostering long-term species viability. Therefore their protection should be considered a high priority for the deep sea (Manea et al., 2020; Morato et al., 2020). The ability of species to show phenotypic plasticity or genomic adaptation that may enhance their tolerance to climate change was not considered here.

Subdividing the planning region into smaller sub-regional provinces appears to be an appropriate method to ensure network replication and resilience, as well as for capturing elements of geographic representativeness in such a large planning area. A similar approach has already been implemented in large planning regions such as the Mediterranean Sea (Giakoumi et al., 2013), the Caribbean and the Gulf of Mexico (Schill et al., 2015) and the Great Barrier Reef (Fernandes et al., 2005), ensuring higher potential resilience for the target species and habitats. Replicating the targets set for conservation features within each province fosters the selection of a range of small to large patches across the basin, and avoids the issue of focusing solely on areas where the targets are most densely represented. This in turn increases the likelihood that conservation solutions cover basin scale ecoregion variability. Furthermore, such an approach could increase the preservation of a greater range of spatially-structured intraspecific diversity. For instance, good genetic diversity and unhindered gene flow are needed to ensure conservation measures and networks function optimally (Laikre et al., 2010). However, these aspects are rarely considered in conservation planning frameworks because they still represent knowledge gaps (Hanson et al., 2019a).

Finally, basin-scale prioritization can highlight the relative importance of each province in contributing to conservation at the basin scale. Regional managers should be encouraged to work together, adopting standardised approaches to ensure conservation targets at the regional level are attained so that basin scale targets can be achieved.

Assessing Connectivity

Despite the fundamental importance of genetic connectivity in the local and regional persistence of metapopulations (Kritzer and Sale, 2004; Cowen, 2006), and the strong influence of oceanographic features on patterns of larval retention or dispersal (Dubois et al., 2016), very few algorithms, most of them rather recent (Daigle et al., 2018; Fox et al., 2019; Hanson et al., 2019b), include connectivity in marine conservation prioritization exercises. There are other methods that can generate connectivity metrics between PUs (e.g., betweenness centrality, Google PageRank, eigenvector centrality, see (Daigle et al., 2018) or optimize network-wide metrics such as population persistence or average shortest paths (Kininmonth et al., 2011; Fox et al., 2019), but these are very computationally heavy and would demand considerable computing power and time if used in large-scale conservation scenarios such as the one tackled here.

In this study, our approach to integrate connectivity into SCP aimed at maximizing the recruitment of benthic species larvae within the reserve network by favouring the selection of pairs of PUs with high connectivity between them (Hanson et al., 2019b). This allowed us to carry out a preliminary exploration of the influence of connectivity on planning solutions. Using modelled larval drift trajectories in SCP can substantially promote the viability of protected populations by favouring recruitment within the reserve network (Dubois et al., 2016; Magris et al., 2018; Álvarez-Romero et al., 2018b, Manea et al., 2020); and even benefit fisheries by replenishing fishing grounds (Krueck et al., 2017).

We used the Lagrangian particle models of Gary et al. (2020) to track the larval drift of hypothetical sessile VME indicator species, which were the main focus of this exercise. Many benthic species have spatially fragmented distributions and for the vast majority, their dispersal capability is linked to pelagic larval drift and duration (Cowen and Sponaugle, 2009; Hilário et al., 2015). The species studied here show a diversity of life-history traits and their PLD, when this information is available, can vary from days to months (Brooke and Young, 2005; Maldonado, 2006; Larsson et al., 2014;

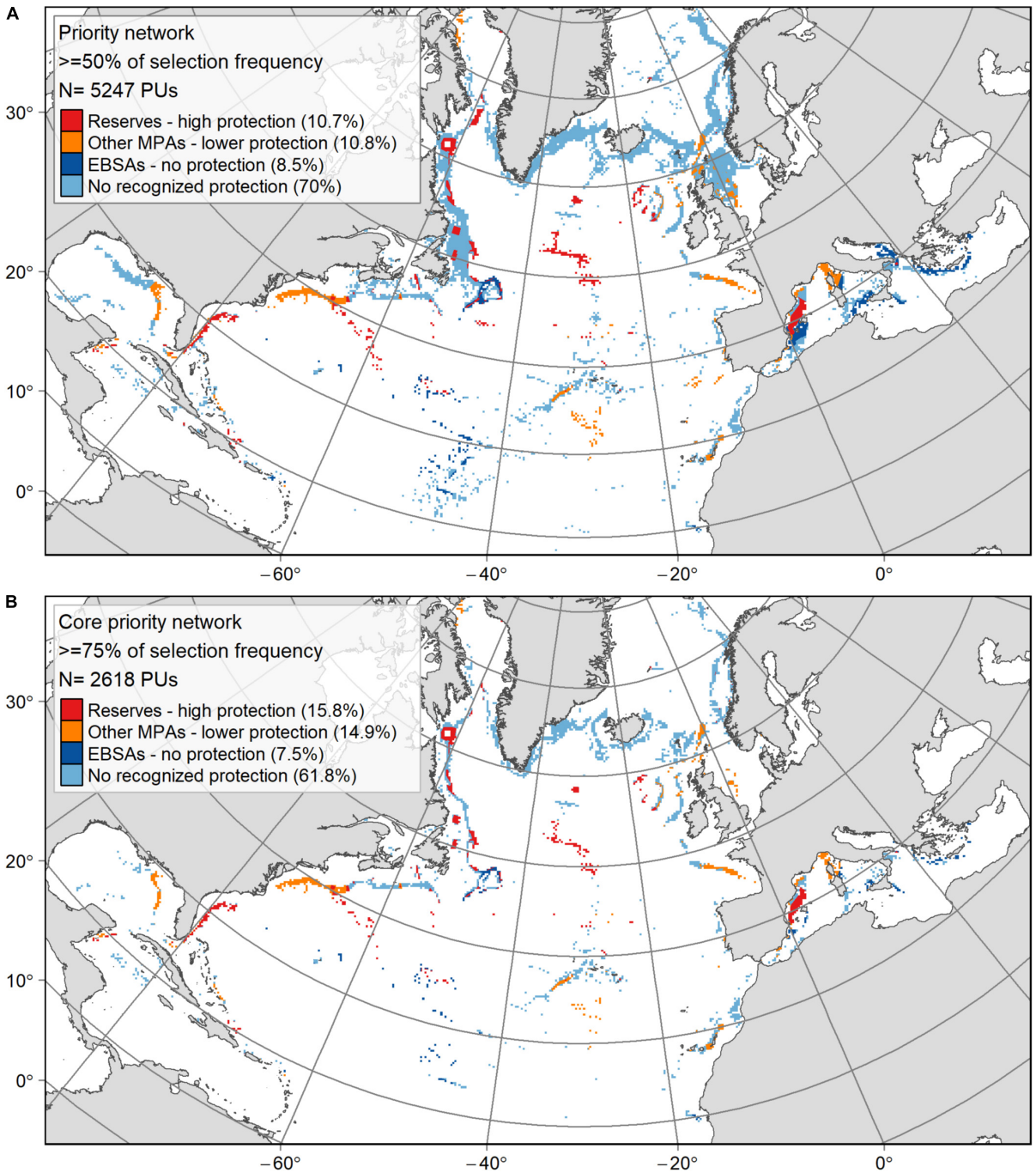


FIGURE 8 | Maps showing the priority conservation networks selected in the "Management" scenario solutions, where PUs occurred in at least 50% **(A)** or 75% **(B)** of the selection frequency. The colour categories differentiate between current spatial management and designation categories together with their contribution (% of the priority network): (1) restrictive marine reserves and RFMOs fishing closures providing a high protection; (2) other MPAs with lower protection level; (3) CBD EBSAs with no legal protection; and (4) areas that have no protection of any kind or a protection that is not recognised as an MPA by the World Database of Protected Areas or as an EBSA by the CBD.

Hilário et al., 2015; Strömberg and Larsson, 2017; Kenchington et al., 2019b). Hence, accounting for the diversity of life history traits coexisting in marine communities is a very challenging target to achieve (Gaines et al., 2010; Moffitt et al., 2011; Jonsson et al., 2016). In this study, a non-specific and simple approach was applied to model larval connectivity, likely to provide broad results that would be more relevant information for prioritization than focusing on specific

dispersal strategies. However, it is important to keep in mind that dispersal patterns may be largely deterministic as they are linked to individual species larval or adult reproductive behaviour.

Accounting for connectivity during SCP resulted in a relatively coherent and continuous network with the main priority areas linked together by "corridors" of PUs. This kind of output selects important larvae pathways and hubs (in Lagrangian dispersal modelling terms) that link populations. Certain PUs that were not retained under the "Base" scenario became very relevant in the "Connectivity" scenario. This suggests that when building a conservation network, some suboptimal areas (with a lower number or abundance of target conservation features) might be important to ensure connectivity between distant populations and maintain large-scale populations' renewal and persistence. A strong connectivity across habitats enables larvae and propagules from source areas to supply degraded deep-sea ecosystems, thus improving resilience. Furthermore, results here demonstrate that a better connected conservation network could be achieved by prioritizing PUs with high connectivity potential without the need to increase the total area of the network. Other studies found similar prioritization results, where including larval connectivity favoured the selection of more numerous or larger reserves in close proximity without increasing the solution cost or area (Magris et al., 2018; Álvarez-Romero et al., 2018b).

Whereas this study did not evaluate the performance of the current MPA network in maintaining deep-sea benthic connectivity, similar particle-tracking model assessments have been undertaken quite recently at sub-basin scale in the North Atlantic (Fox et al., 2016; Ross et al., 2017; Kenchington et al., 2019b) and at smaller scale in the Mediterranean (Basterretxea et al., 2012; Clavel-Henry et al., 2019). While the NAFO VME fishing closures in the northwest Atlantic (Kenchington et al., 2019b) and MPAs in the EEZs such as the west of the United Kingdom and Ireland (Fox et al., 2016; Ross et al., 2017) and the Mediterranean (IUCN, 2019) form networks, these are the result of *ad hoc* additions of new fisheries closures and MPAs over time without any attempt to take network properties such as connectivity into account. As in other regions (Schill et al., 2015; Magris et al., 2018), these studies demonstrate that such *ad hoc* networks fail to maintain the larval exchange pathways that are essential to replenish benthic populations. Substantial conservation network improvements could be achieved in the North Atlantic and the Mediterranean by expanding MPA networks to allow for enhanced self-recruitment and to ensure the capture of likely important sources and sinks of larval recruitment. This would result in improved within-network exchange increasing genetic variability and hence overall resilience (Ross et al., 2017; Kenchington et al., 2019b; Manea et al., 2020). However, building networks that are highly connected is extremely challenging in the deep sea since life-history traits and the behaviour of deep-sea larvae remains largely unknown (Hilário et al., 2015; Clavel-Henry et al., 2019; Kenchington et al., 2019b), thus limiting the precision of predicted connectivity patterns. Approximate estimates may be modelled, as they were here, where different release depths were used to account for larval dispersion behaviour strategies rather than model specific swimming, floating and sinking parameters.

Assessing Spatial Management and Exploitation Activities

Factoring in the costs associated with the implementation of different sizes, numbers and locations of MPAs, as well as imposing constraints to avoid areas that are already exploited or have potential to be, led to prioritization solutions that favoured the selection of a conservation network with low implementation costs while minimizing the inclusion of areas that provide economic value (e.g., for deep-sea fishing and potentially mining). This widely used approach provides a solid basis for stakeholder negotiations and eases the subsequent implementation of conservation measures by reducing conflicts between stakeholders and managers (Klein et al., 2008; Ban and Klein, 2009; Mazor et al., 2014). While the objective of such an approach is to reach a compromise between biodiversity conservation and resource exploitation or management measures in place, it can lead to a selection of areas that are sub-optimal for conservation, yet still likely to provoke less stakeholder conflict. It is therefore important to evaluate how integrating socio-economic considerations into conservation prioritisation planning will influence the solutions. There are formal methods to approach these trade-offs using multi-objective optimization methods and calculation of the Pareto frontier (Lester et al., 2013; Rassweiler et al., 2014; Fox et al., 2019), but they are generally too resource-intensive to apply to a network of this size.

It is common practice during SCP to lock-in current MPAs to ensure they are part of the conservation solution. This approach often results in sub-optimal planning solutions (Evans et al., 2015; Moore et al., 2016) because current MPAs are often designated on an *ad hoc* basis that may differ from the conservation objectives employed in more systematic planning. However, including existing MPAs in conservation prioritisation planning should lead to reduced network implementation costs and acknowledges prior efforts to conserve biodiversity (Manea et al., 2020). Indeed, strengthening the management of existing MPAs may sometimes be less costly and easier for stakeholders to accept than creating a new MPA. When favouring the selection of existing MPAs rather than locking them, a priori, into the planning solution, the MPAs that contribute to the SCP conservation objectives are likely to be included while MPAs that make no contribution will be excluded. Hence this approach enables integrating existing MPAs into conservation planning based on their contribution to the conservation objectives rather than the fact that they already exist. By analysing the MPAs (or parts of MPAs) selected in the conservation solutions, their relative contribution to the conservation network can be assessed.

Our study shows that current MPAs or EBSAs in the North Atlantic and the Mediterranean are inadequate for the preservation of deep-sea biodiversity. Even with their cost decreased down to −80%, three quarters of the MPAs or EBSAs within the planning region did not fall into the priority conservation areas identified in the "Management" scenario. Even the marine reserves and fishing closures, most

of them explicitly targeting VMEs in the North Atlantic and the Mediterranean, were predominantly excluded from the conservation solutions as only 29% of them were included in priority networks. These restrictive MPAs, with their small coverage (4.6%) and uneven distribution across the planning region, only conserve 7% of target species or habitats, a proportion that appears largely insufficient given global conservation target goals. These results agree with the previous studies in the northeast Atlantic (Johnson et al., 2014; Evans et al., 2015) and the Mediterranean (IUCN, 2019), which highlighted the lack of an efficient and representative MPA network for conserving deep-sea habitats.

While minimizing the selection of areas with socio-economic activity to avoid conflict is a goal in prioritization, it is worth noting that areas of high conservation value may be found where activities take place. In our study, this was particularly evident for Atlantic fish populations that are exploited by bottom fishing over large areas of the shelf and for specific ecosystems such as hydrothermal vents that generate polymetallic sulphides coveted by the mining industry (Fisher et al., 2007). According to the targets set during prioritization, conserving areas of future refugia for fish species could not occur without implementing new closures on the current bottom-fishing grounds. Similarly, areas currently licensed for deep-sea mining exploration are considered to be priority conservation areas in the "Base" scenario, simply because the licensed areas include all of the known hydrothermal vent fields south of the Azores EEZ (Van Dover et al., 2018) that form the largest part of the hydrothermal vent fields identified in the Mid-Atlantic Ridge EBSA. At the level of the planning region, excluding this relatively small area could be compensated for by increasing the amount of known VMEs (in particular hydrothermal vents) in other areas included in solutions. In the management scenario, however, it wasn't possible to reach the 60% conservation target for hydrothermal vents in the "Deep 6" province while excluding areas already licensed for mining. To achieve 100% of the targets, the potential contribution of some of the existing licensed areas would need to be considered.

Hydrothermal vent communities show high rates of endemism, symbiotic association, and extreme environmental adaptation that makes them extremely rare. Since deep-sea mining impacts and the recovery potential of hydrothermal vent communities are still unknown (Gollner et al., 2017; Niner et al., 2018), exploration for polymetallic sulphides could represent a critical threat to these ecosystems (Boschen et al., 2016; Van Dover et al., 2018). Furthermore, the concentration of mining operations in a particular province may prove particularly high risk if the region contributes significantly to the overall network connectivity. Finally, the mining footprint might expand in the future and further increase the potential impact already facing these hydrothermal vent ecosystems (Boschen et al., 2016; Van Dover et al., 2018).

Limitations

Although efforts were made to ensure results would be as comprehensive as possible by diversifying the types of data and objectives included in the prioritization, several limitations emerged during the study that should be considered in order to judiciously use these outputs in conservation management and to improve future SCP of the region.

As expected, the results obtained underline several limitations due to data availability and accuracy, reflecting the uneven distribution of deep-sea scientific data available for the Atlantic and Mediterranean basins. In fact, the main priority networks identified correspond to areas where data on VMEs and fish species was most available, further highlighting the need to continue improving our scientific knowledge, especially in data-poor regions. For instance, results obtained here show that the north and western sides of the Mediterranean were often selected in conservation solutions, whereas the southern and eastern parts were less represented. Such underrepresentation very likely reflects the paucity of deep-sea data in such areas, linked to an imbalance in the resources dedicated to deep-sea research and regional geopolitical issues (IUCN, 2019; Manea et al., 2020). Deep-sea exploration is generally targeted, focusing on areas of interest for resources or "anomalies" (e.g., areas of chemosynthetic activity, geological interest, or high biomass concentration), leading to patchy information about the distribution of deep-sea species and habitats. Habitat suitability models can be used to overcome the lack of observations over large geographical extents, but their results are highly reliant on the availability of species records where environmental conditions are relatively well described. The identified priority networks should be useful in providing conservation options where VMEs are known or likely to occur but should not be used in areas that are under-explored.

Another data gap relates to knowledge of intraspecific diversity (i.e., genomic and physiological data) allowing an appraisal of the species capacity to adapt to forthcoming environmental changes (Buckley et al., 2011; Feng et al., 2019), either through phenotypic plasticity or through genetic adaptation, as this may confound predictions of future habitat shifts and the location of potential climate refugia. Equally, little is known about the reproductive cycle and larval biology of most VME indicator species (but see Larsson et al., 2014; Strömberg and Larsson, 2017), making it difficult to predict changes in connectivity patterns and population renewal capacity under climate change scenarios.

Considering the current management and socio-economic data used to create the cost layer, the accuracy and resolution of the data used in this study was limited by the need to cover the entire North-Atlantic basin and the Mediterranean. Indeed, even if the global MPA datasets used were complemented by national datasets, discrepancies were found (United States, Canada, and Norway). Furthermore, not all local datasets could be properly investigated, potentially resulting in the missing of information inside some national EEZs. An example might be national fishing closures that have a high level of protection but are not internationally recognised as MPAs. In the future, the recognition of Other Effective Conservation Measures (OECMs) as MPA equivalents (Diz et al., 2018) by the CBD (CBD/COP/DEC/14/8), as applied in Canada, will help to capture some of the areas missed. Similarly, the fishing catch dataset used was of a lower resolution than other fishing datasets, such as the bottom

trawling footprint in European waters (Eigaard et al., 2017). Data homogeneity and comparability over the whole planning region, even with coarser resolution and more approximate proxies, was favoured instead of trying to integrate patchy high-resolution sub-regional datasets with the biases that it would create.

Finally, selecting PUs based on an analysis of their selection frequencies in order to identify priority networks must be done with caution. Networks delineated based on PU selection frequencies are not prioritization solutions *per se* and thus do not ensure that the conservation targets of each feature will be met. While each individual solution for a given scenario is optimised to meet the conservation targets, retaining only the PUs most often selected in the overall runs does not guarantee that all targets are met in the final network. It is then essential to evaluate if the level of target completion within the priority networks is sufficient when using this delineation method. In contrast, the selection frequency provides useful information regarding the importance of each PU through the number of times a scenario was run. For instance, a PU might be highly selected because it is irreplaceable in meeting one or several targets, contains numerous features, is essential to ensure connectivity, or is situated at the core of an important area for conservation.

Recommendations

The "priority" and "core priority" networks delineated by the selection of units with high conservation importance provide useful information to focus the attention of managers engaged in future conservation planning for the North-Atlantic and Mediterranean deep sea. Covering from 8 to 17% of the planning region, the "priority" and "core priority" networks contained on average 37–55% of each conservation feature, emphasizing their high conservation potential relative to other areas. However, ensuring an adequate conservation of all deep-sea species and habitats and not just those selected for this study will require even larger areas.

Our results reinforce the need to set more ambitious conservation targets for the ocean. The current CBD target to protect 10% of marine areas by 2020 (Aichi Target 11, CBD/COP10) will likely soon be replaced by the ambitious target of protecting 30% of marine areas by 2030 with 10% declared no-take zones (CBD/COP15, see CBD, 2020), with some already calling for a "30% by 2030" no-take target (e.g., United Kingdom, IUCN, Oceans Unite, see SCP examples for ABNJ in O'Leary et al., 2019; Visalli et al., 2020) or even to reach 50% of terrestrial and marine protection by 2050 (e.g., Nature Needs Half, see Wilson, 2016; Dinerstein et al., 2017).

Despite their obvious importance, the priority areas identified in our study are currently poorly protected since existing fishing closures and reserves cover less than 16% of their extent. Moreover, our results show that bottom fishing, particularly on continental shelves, occurs within MPAs that have low levels of restriction and of course within EBSAs, as these areas are indicative and do not have any legal protection. Marine reserves permanently closed to demersal fishing appear to be the most effective tool to guarantee the long-term conservation of deep seabed ecosystems, given that benthic ecosystems may struggle to completely recover from the impacts of even infrequent bottom-fishing events (Althaus et al., 2009; Huvenne et al., 2016; Aguilar et al., 2017; Clark et al., 2019). Moreover, reinforcing and expanding the network of no-take marine reserves in the North Atlantic and Mediterranean could also contribute to local rebuilding of commercially exploited demersal fish stocks as well as by-catch species caught during fishing (Murawski et al., 2000; Kincaid and Rose, 2017; del Otero and Marin, 2019).

In addition to the results produced above, we have developed a SCP framework that may be used by decision makers to achieve future conservation goals. The framework enables the identification of priority networks based on science that can inform various MSP and management processes at the ocean-basin scale. SCP for the deep sea can help fast-track consensus around the expansion of an MPA network by facilitating engagement with stakeholders. Identified priority networks due to their conservation importance are likely to require more stringent environmental impact assessment (EIA) thresholds with accompanying mitigation measures.

Understanding where deep-sea protective measures are most needed and what level of management is required for them to achieve their conservation goals is imperative to support the setting of more ambitious conservation targets for the ocean. The SCP framework employed here and the priority conservation networks we identified can potentially support the implementation of marine spatial planning (MSP) in the deep sea via a number of avenues:

(1) The on-going negotiation of a legally binding instrument for the conservation and sustainable use of biodiversity beyond national jurisdictions (the BBNJ process), coordinated by the UN Division of the Law of the Sea (UNGA, 2017). This BBNJ process aims to set global protection goals for ABNJ and will include guidelines for the use of area-based management tools (including MPAs) and implementation of EIA;

(2) A further iteration of the CBD EBSA process (Johnson et al., 2018a), notably to foster the description of EBSAs in ABNJ. Whilst in the Northwest Atlantic, Mediterranean and Northeast Atlantic Regional EBSA Workshops the focus was predominantly on deeper waters including ABNJ, other Regional EBSA Workshops concentrated on shallower coastal locations within national jurisdiction. A thematic deep-sea review of EBSAs, taking into account SCP suggestions could further highlight gaps and opportunities.

(3) Informing competent regional and/or sectoral organizations with a mandate to protect biodiversity – notably NAFO, NEAFC, OSPAR, the Barcelona Convention and ISA[13] – which should all aim to consolidate and expand their conservation networks to meet strategic obligations. For instance, deep-sea priority

[13] Beyond these mentioned sectoral and regional organizations, it should be noted that there are regional governance gaps in the North Atlantic. For instance the northwest Atlantic has no Regional Seas Convention and WECAFC (Western Central Fishery Commission) can provide fisheries advice but has no mandate to designate VMEs.

areas could inform the extension of the North-Atlantic fishing closure network by the relevant sectoral (RFMOs) and local (nations, EU) jurisdictional bodies. Similarly, our priority networks could contribute to the regulation of deep-sea mining regulation via the Atlantic Regional Environmental Management Plan (REMP). The ISA is required to implement the REMP and is mandated to designate Areas of Particular Environmental Interest (APEI) using SCP (Wedding et al., 2013; Lodge et al., 2014; Dunn et al., 2018) to protect specific features such as hydrothermal vents (Johnson, 2019).

(4) Informing national conservation planning exercises in many different countries by highlighting the potential contribution national conservation initiatives could make to the support of basin-scale priority conservation networks.

Finally, these results can help direct future research. The UN Decade of Ocean Science for Sustainable Development will undoubtedly have a deep-sea component. Building baseline data, ground-truthing identified priority networks, confirming their potential to promote resilience and provide refugia from climate change, should all be featured in future research programs informed by SCP. From a viability and resilience perspective, it is recommended that connectivity and climate change should be factored into the design of future conservation networks (Magris et al., 2014). By investigating in more detail the connectivity pathways of benthic species, broadly addressed here, and including areas identified as sources and sinks from population genetic studies, more robust conservation networks are possible. This study has shown that few areas that could be considered as potential climate refugia for deep-sea species currently benefit from some form of protection. Our results support the conclusions of Johnson et al. (2018b) that climate change pressures are likely to affect deep-sea oceanography and biodiversity, and thus the ability of the current protection network to preserve them.

SUMMARY/CONCLUSIONS

This study adds to previous research that promotes the use of SCP based on multi-objective prioritization (Beger et al., 2015; Magris et al., 2017; Álvarez-Romero et al., 2018b; Manea et al., 2020). It factors in multi-scale representativity (species, ecosystems, and physical habitats), regional replication, climate change resilience and population connectivity while taking into account existing spatial management and socio-economic interests (fisheries and mining).

The key findings that emerged from both the process of structuring the prioritization framework and the resulting conservation solutions are as follows:

- An in-depth and exhaustive data mining exercise is a prerequisite for successful application of SCP. Diverse data types should be collated including habitat types, species occurrence records and predicted distributions based on the outputs of habitat suitability models models. The latter facilitates testing the impact of various climate change scenarios on the future distribution of species and habitats.
- It is important to consider climate change effects during MPA design. The inclusion of predicted species climate refugia as conservation features during the planning process provides a degree of future proofing, ensuring the long-term viability, and resilience of the conservation network.
- Promoting conservation network replication by dividing the planning region into distinct sub-regions promotes environmental and geographic representativeness and potentially increases intraspecific diversity, thus strengthening overall network resilience.
- Adjusting targets to prioritize conservation features according to their rarity, ecological importance or vulnerability, or degree of data confidence provides more flexibility and accuracy than applying blanket targets across all features.
- The inclusion of connectivity in SCP is challenging, especially for remote and poorly known areas or species. Including it during prioritization can help to identify areas that do not appear as important at first sight, but play an essential role in ensuring connectivity and network coherence.
- Weighting in favour of, rather than "locking-in," current protected areas and EBSAs during prioritization builds on the existing networks while excluding any individual MPAs or EBSAs that do not contribute to the proposed SCP network.
- Taking into account economic activity in the SCP design is essential so that the selection of the conservation network minimizes the socio-economic costs of conservation, but also to assess whether prioritised conservation areas overlap with those activities which may prevent them from contributing to meeting the conservation targets. This was the case for most fish refugia that were located on existing fishing grounds, and for hydrothermal vents located within licenced deep-sea mining exploration areas.
- Identifying the priority conservation zones that most strongly contribute to the SCP objectives is a fundamental step in the development and implementation of a robust MSP approach.
- This study highlights the value of SCP in that the relatively small proportion of the planning region – here around 17% – proposed for the network ensured that on average 55% of each feature would be conserved, thus banking an extensive conservation capital.
- While VMEs are considered amongst the ecosystems most at risk from climate change and considered as a top-priority for conservation management, deep-sea biodiversity in the North Atlantic and Mediterranean is still inadequately protected.

In conclusion, this multi-objective prioritization allowed us to determine options for developing a coherent VME conservation network for the whole of the North Atlantic and the Mediterranean that could be updated as new data is gathered.

The SCP approach adopted here could be employed by stakeholders and policymakers to provide the foundation for basin-scale MSP, for example, in ABNJ, where a framework to coordinate the actions of different regional authorities and sectoral bodies is still lacking (Ardron et al., 2014; Ban et al., 2014; Wright et al., 2019). A similar approach could be used to extend such planning into adjacent areas, such as the Arctic. This study demonstrates the value of adopting a basin-wide management strategy to protect the vulnerable habitats and species found in the deep sea in a more systematic way to improve mitigation of the threats posed by bottom fishing, mining and climate change.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.17882/62541.

AUTHOR CONTRIBUTIONS

SV and MC structured the scenarios building on discussions held with participants during a workshop "Conservation management issues in ATLAS," held in Sète, France, in January 2019, with subsequent review by LM and SA-H. CD-C, AF, JG-I, and TM produced parts of the data. MC, LM, and TM compiled the data. MC conducted the analysis and wrote the first draft of the manuscript. All authors structured the objectives, framework of the study, and revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.611358/full#supplementary-material

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Distribution of Megabenthic Communities Under Contrasting Settings in Deep-Sea Cold Seeps Near Northwest Atlantic Canyons

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Cold seeps support fragile deep-sea communities of high biodiversity and are often found in areas with high commercial interest. Protecting them from encroaching human impacts (bottom trawling, oil and gas exploitation, climate change) requires an advanced understanding of the drivers shaping their spatial distribution and biodiversity. Based on the analysis of 2,075 high-quality images from six remotely operated vehicle dives, we examined cold seep megabenthic community composition, richness, density, and biodiversity at a relatively shallow (∼400 m water depth) site near Baltimore Canyon (BC) and a much deeper site (∼1,500 m) near Norfolk Canyon (NC), in the northwest Atlantic. We found sharp differences in the megabenthic composition between the sites, which were driven mostly by bathymetric gradients. At both BC and NC there were significant differences in megabenthic composition across habitats. Hard habitats in and around cold seeps had significantly higher values of species richness, density, and biodiversity than soft habitats. Depth and habitat complexity were the leading environmental variables driving megabenthic variability. The presence of microbial mats and gas bubbling sites had a statistically significant contribution to explaining megabenthic variability mainly in the shallower BC and less in the deeper NC areas examined; drivers behind this discrepancy could be related to differences between BC and NC in terms of chemical compound fluxes and megafaunal life history characteristics. Our surveys revealed marine litter, primarily from commercial fisheries. This study highlights the importance of habitat complexity for the proliferation of highly diverse cold-seep ecosystems and underscores the importance of discovery science to inform spatial management of human activities in the deep and open ocean.

Keywords: deep sea, chemosynthetic environments, vulnerable marine ecosystems (VMEs), climate change, marine conservation, marine litter, cold-water coral

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INTRODUCTION

Cold seep and hydrothermal vent communities comprise unique deep-sea ecosystems as their survival and proliferation does not depend primarily on photosynthetically produced organic matter; on the contrary these ecosystems rely on reduced chemical compounds (e.g., reduced sulfur, methane) which are released from the subsurface to the seafloor (Levin et al., 2016). Cold seeps have

a wide geographical distribution and are found across diverse geological settings such as passive continental margins (Paull et al., 1984), subduction zones (Kulm et al., 1986), and oil/gas seismic wipeout zones (Kennicutt et al., 1985).

Among the important contributors to the formation and longevity of complex ecosystems, such as cold seeps, are free-living and symbiotic microorganisms which transform the chemical compounds to organic matter (Childress et al., 1986). Dominant seep megafauna (e.g., vestimentiferan worms, bathymodiolin mussels, and vesicomyid clams) increase habitat complexity (Sibuet and Olu, 1998; Van Dover and Trask, 2000) and contribute to the establishment of cold seeps as hotspots of biodiversity and biomass (Turnipseed et al., 2003; Vanreusel et al., 2009). Seeps host meio- (63–500 μm body size), macro- (500 μm–5 cm), and megafaunal organisms (>5 cm) (Gage and Tyler, 1991) which span a wide range of ecophysiological traits (feeding, reproduction, and mobility) (Tyler and Young, 2001; Levin, 2005; Van Gaever et al., 2009). Often the species richness and biomass in seeps exceed those in adjacent sediments (e.g., Bourque et al., 2017). As a response to high structural complexity, biodiversity and biomass, cold seeps are recognized to provide many significant ecosystem goods and services, such as habitat supply and primary production (Foucher et al., 2009), biogeochemical cycling (Boetius and Wenzhöfer, 2013; Thurber et al., 2014), climate regulation (Knittel and Boetius, 2010), and carbon sequestration (Levin et al., 2015).

Research in cold seep ecosystems has documented the roles of environmental parameters in shaping community structure, mainly for macrofauna (Robinson et al., 2004; Levin, 2005; Cordes et al., 2010a,b; Levin et al., 2010; Bourque et al., 2017; Robertson et al., 2020). For example, macroinfauna have shown depth-related patterns with different communities occupying upper-bathyal (200–1,500 m) and lower-bathyal/abyssal (>1,500 m) depths (Bernardino et al., 2012). The important role of habitat in shaping seep macrofauna has also been examined. Near Baltimore Canyon (∼400 m; BC hereafter) and Norfolk Canyon (∼1,500 m; NC hereafter) in the northwest Atlantic, macrofaunal densities in microbial mats were four times greater than those in mussel beds and slope sediments (Bourque et al., 2017).

Studies on cold seep megafauna have focused on dominant species such as tube worms, bathymodiolin mussels and vesicomyid clams with studies ranging from the whole organism down to molecular levels (Kojima, 2002; Coykendall et al., 2019). The ecology of cold seep megafaunal communities is not very well known yet (Baco et al., 2010; Cordes et al., 2010a; Sen et al., 2019; Zhao et al., 2020; Dueñas et al., 2021). This knowledge gap is especially evident in the United States Atlantic Margin where widespread methane seepage has recently been discovered (Skarke et al., 2014). Habitat diversity within United States Atlantic Margin canyons and seeps was demonstrated to exert an important influence on fish assemblage structure, and some fish species exhibited close associations with cold-water coral and sponge habitats (Ross et al., 2015). However, information on the roles of habitat type (e.g., soft/hard/mixed, biogenic habitats), interspecific relationships, resource availability (e.g., presence of microbial mats) and physical oceanography in shaping megabenthic seep communities is almost absent (Turner et al., 2020). Addressing this gap is an urgent need as areas in the United States Atlantic Margin support intensive fisheries and are under consideration for future wind power and oil and gas exploration (CSA Ocean Sciences Inc. et al., 2017).

Advancing knowledge about the environmental parameters shaping the distribution and composition of cold seeps' megafauna will improve model predictions about the geographic and bathymetric distribution of cold seeps (Cordes et al., 2010b; Georgian et al., 2019) and will assist in the establishment of efficient conservation strategies for their protection (Cordes et al., 2016).

Considering the major knowledge gaps about seep megabenthos, this study focused on seep communities found in two very different bathymetric regimes, i.e., seeps adjacent to BC and NC. Three major research questions were addressed:

(1) Which are the major megabenthic taxa found in the areas?
(2) How do the community composition and structure of the megabenthos change across depth and within each seep system?
(3) How do environmental parameters such as the type of habitat and the presence of gas bubbling sites and microbial mats affect the community composition?

This study builds on previous research for BC and NC seep sites on the Mid-Atlantic Bight in the United States Mid-Atlantic Margin (e.g., Ross et al., 2015; Bourque et al., 2017; Demopoulos et al., 2019), advancing our understanding of the structure and functioning of deep-sea seep ecosystems in the northwest Atlantic.

MATERIALS AND METHODS

Study Areas

Water masses and circulation in the Mid-Atlantic Bight have been studied (Obelcz et al., 2014; CSA Ocean Sciences Inc. et al., 2017 and references therein). The major oceanic source water masses in the Mid-Atlantic Bight are Shelf Water (<200 m water depth), North Atlantic Central Water or West North Atlantic Central Water (<500 m), Labrador Sea Water (>500–1500 m), Western Atlantic Subarctic Intermediate Water (>500–1500 m), Gulf Stream (>500–1500 m), and North Atlantic Deep Water (1500 m- bottom) (see Table 5.1 in CSA Ocean Sciences Inc. et al., 2017 for water mass characteristics).

Two large methane seep environments located near similarly sized shelf-sourced canyons in the Mid-Atlantic Bight, along the United States Atlantic Margin (Obelcz et al., 2014) were explored in 2012 and 2013 (**Figure 1**). Hecker et al. (1983) first suggested a potential seep on the continental slope near BC, and this was confirmed at water depths between 366 and 450 m (CSA Ocean Sciences Inc. et al., 2017). The second seep located about 20 km south of the mouth of NC, was first identified by sonar by the NOAA vessel *Okeanos Explorer* at depths between 1,457 and 1,602 m (Skarke et al., 2014). Uranium-thorium dating on authigenic carbonates suggest seepage at Baltimore Canyon

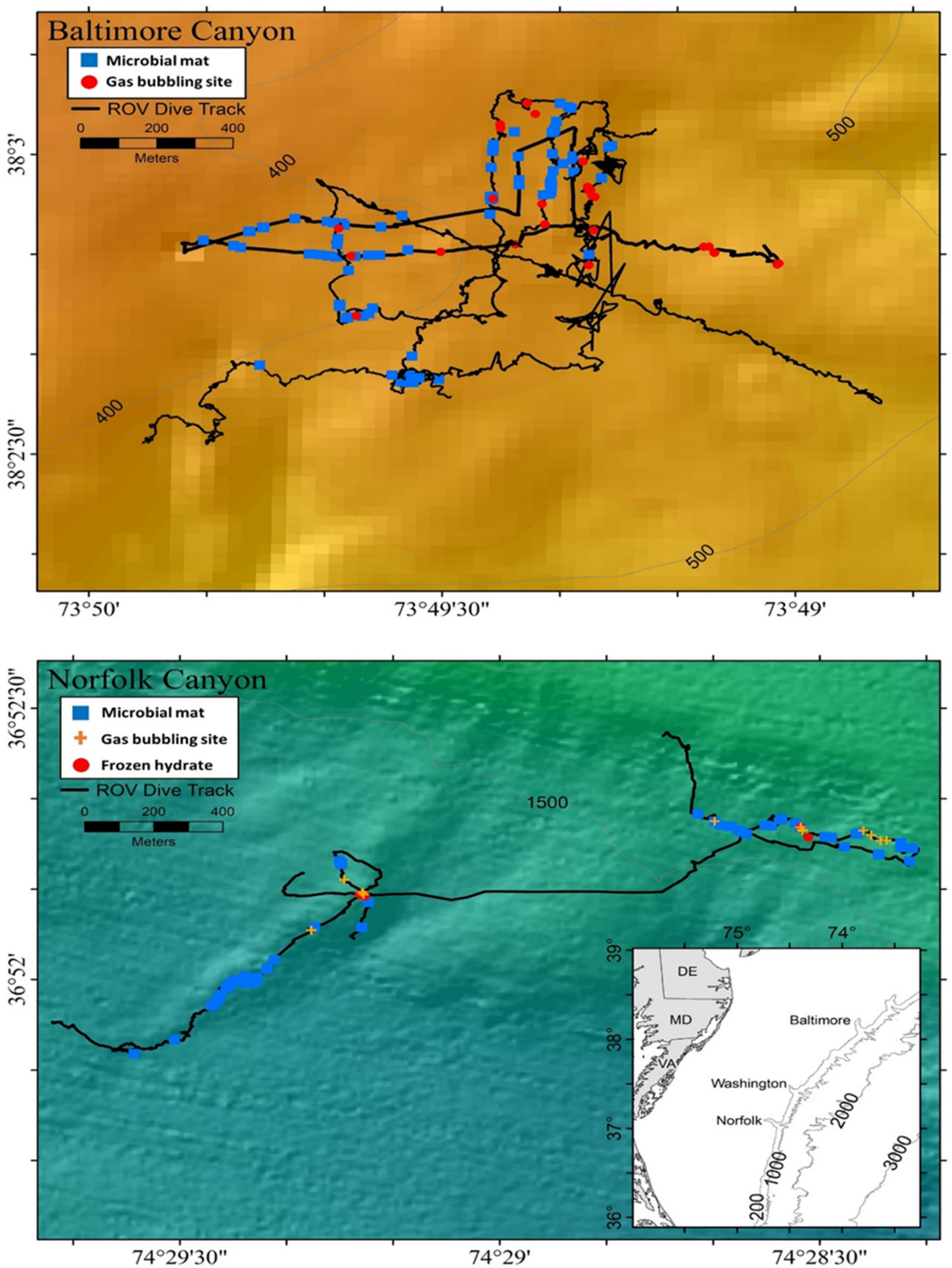


FIGURE 1 | Bathymetric maps (depth in meters) derived from multibeam sonar of Baltimore Canyon and Norfolk Canyon off the northeast United States coast, showing ROV (black lines) dives done in 2012 and 2013.

between 14.7 ± 0.6 ka and 15.7 ± 1.6 ka and at the Norfolk field between 1.0 ± 0.7 ka and 3.3 ± 1.3 ka (Prouty et al., 2016).

Both sites contained extensive living mussel communities within the *Bathymodiolus childressi*-complex (Olu-Le Roy et al., 2007; Coykendall et al., 2019). Mussel patch sizes were more variable at NC sites, ranging from a few individuals to several hundred per km-squared (Demopoulos et al., 2019). The lineage *B. childressi* forms a monophyletic group with species in the genus *Gigantidas*, as reclassified by Thubaut et al. (2013). Since recent studies for this area used *B. childressi*

(CSA Ocean Sciences Inc. et al., 2017; Coykendall et al., 2019; Demopoulos et al., 2019), we will continue with that name for consistency. It should be clarified though that the species name *Bathymodiolus childressi* is not accepted anymore at the World Register of Marine Species[1]; the valid species name is *Gigantidas childressi*[2]. Both BC and NC sites contained microbial mats, authigenic carbonate rocks, and methane bubble activity (Bourque et al., 2017). NC showed high seep activity along two well-defined ridge features separated by about 1 km and contained stable methane hydrates. In contrast, the BC sites were more concentrated in a single area of relatively flat sandy bottom (Skarke et al., 2014; CSA Ocean Sciences Inc. et al., 2017).

Collection of Underwater Video Material and Data Analysis

Remotely Operated Vehicles (ROV) Dives

During the 2012 NOAA research vessel *Nancy Foster* expedition (17/08/2012–14/09/2012), 20 dives were conducted using the *Kraken II* ROV (University of Connecticut), and three of them took place at the BC site (412–434 m). During the 2013 NOAA research vessel *Ronald H. Brown* expedition (02/05/2013–18/05/2013), 13 dives were conducted using the *Jason II* ROV (Woods Hole Oceanographic Institution) – one dive was at the BC (353–441 m) and two at the NC (1,421–1,612 m) sites (CSA Ocean Sciences Inc. et al., 2017; **Figure 1**). The dives began at the deepest location and moved upslope (navigation and video facilitated by multibeam sonar bathymetry obtained in 2011), and the ROV position was recorded continuously with an ultra-short baseline tracking system, with position data synchronized to video data (Ross et al., 2015). A SeaBird SBE 911+ conductivity-temperature-depth (CTD) logger attached to the ROV recorded density ($\sigma\theta$, kg m^{-3}), depth (m), dissolved oxygen (DO, ml/l), pH, salinity, turbidity (formazin turbidity units), and temperature (°C), once per second throughout each dive (**Table 1**). To standardize operations as much as possible, ROVs ran near the bottom along video transects at speeds of <0.93 km/h, with color video cameras tilted slightly downward and set to wide angle. Two laser pointers spaced 10 cm apart were positioned directly in line with the video camera and were switched on during most dives (Ross et al., 2015). The video recorded continuously and across varied transect lengths within each ROV dive, covering all habitat types. Transects (i.e., anytime the ROV was moving) were interspersed with the ROV stopping to collect regular grab/suction samples of megafauna (to confirm species identifications). Erroneous bottom position track data (e.g., cases where the actual distance traveled by the ROV was greater than the theoretical maximum distance) were removed, following Partyka et al. (2007); Quattrini et al. (2012), and Ross et al. (2015).

Classification of Habitats

Seven cold seep habitat types were defined following Ross et al. (2015) and CSA Ocean Sciences Inc. et al. (2017). The habitats were: (i) sand-mud (S), (ii) sand mixed with dead mussels (SDM), (iii) sand with dead and live mussels (SDM + LM), (iv) mixed hard-soft (Mix), (v) mixed hard-soft with dead mussels (MixDM), (vi) mixed hard-soft with live mussels (MixLM), (vii) mixed hard-soft with dead and live mussels (MixDM + LM) (**Figure 2**). The habitats sand-mud and sand mixed with dead mussels were regarded as soft habitats. The latter was regarded as a soft habitat as it was mainly composed from soft sediments and dead mussels were a minority. The other five habitats, i.e., sand with dead and live mussels, mixed hard-soft, mixed hard-soft with dead mussels, mixed hard-soft with live mussels, and mixed hard-soft with dead and live mussels were regarded as hard habitats.

Annotations of Megafauna

In total, ∼ 57 h of videos were recorded, which were viewed in QuickTime Player (version 10.5) on Apple ProRes 422 HD in resolution 1920 × 1080 at 29.7 frames per second (FPS). The videos were paused in "frame grabs" to enumerate and identify

[1]http://www.marinespecies.org/aphia.php?p=taxdetails&id=420692

[2]http://www.marinespecies.org/aphia.php?p=taxdetails&id=1346725

TABLE 1 | Environmental parameters for water depth (m), water temperature (°C), salinity (psu), dissolved oxygen (DO; ml/l), density ($\sigma\theta$, kg m^{-3}), and pH for each of the ROV dives at the Baltimore Canyon (BC) and the Norfolk Canyon (NC).

ROV Dives – environmental parameters	Depth (m)	T (°C)	Salinity (psu)	DO (ml/l)	Density (kg m^{-3})	pH	Turbidity (formazin turbidity units)
BC (NF-07)	424 ± 0.62 (409–449)	7.35 ± 0.01 (7.17–7.68)	35.08 ± 0.00 (35.07–35.11)	3.84 ± 0.00 (3.67–3.93)	27.44 ± 0.00 (27.40–27.46)	7.96 ± 0.00 (7.95–7.97)	43.91 ± 3.74 (35.33–917.48)
BC (NF-08)	414 ± 0.18 (391–455)	7.33 ± 0.01 (6.90–7.89)	35.08 ± 0.00 (35.03–35.15)	3.84 ± 0.01 (3.55–4.08)	27.44 ± 0.00 (27.38–27.52)	7.98 ± 0.00 (7.96–7.99)	47.31 ± 2.35 (35.48–806.74)
BC (NF-14)	409 ± 1.51 (361–507)	7.09 ± 0.02 (6.12–7.93)	35.06 ± 0.00 (35.02–35.11)	3.95 ± 0.01 (3.52–4.55)	27.46 ± 0.00 (27.37–27.56)	8.02 ± 0.00 (8.01–8.06)	45.74 ± 3.65 (32.92–1769.38)
BC (J2-689)	393 ± 1.25 (359–439)	8.75 ± 0.03 (7.36–9.40)	35.18 ± 0.00 (35.00–35.34)	2.68 ± 0.01 (1.79–3.51)	27.31 ± 0.00 (27.23–27.59)	8.02 ± 0.00 (7.99–8.04)	14.30 ± 0.46 (7.78–77.21)
NC (J2-682)	1575 ± 2.46 (1532–1610)	3.97 ± 0.00 (3.89–4.02)	34.95 ± 0.00 (34.94–34.96)	4.48 ± 0.03 (3.41–5.16)	27.76 ± 0.00 (27.75–27.77)	8.12 ± 0.00 (8.08–8.13)	7.77 ± 1.59 (2.48–141.79)
NC (J2-683)	1496 ± 2.65 (1446–1564)	4.02 ± 0.00 (3.96–4.12)	34.95 ± 0.00 (34.94–34.96)	4.61 ± 0.03 (3.37–5.14)	27.76 ± 0.00 (27.75–27.77)	8.12 ± 0.00 (8.08–8.13)	5.34 ± 0.45 (2.56–58.98)

Data are mean ± standard error with ranges in parentheses for the environmental data recorded at the time points when high quality image frames were extracted.

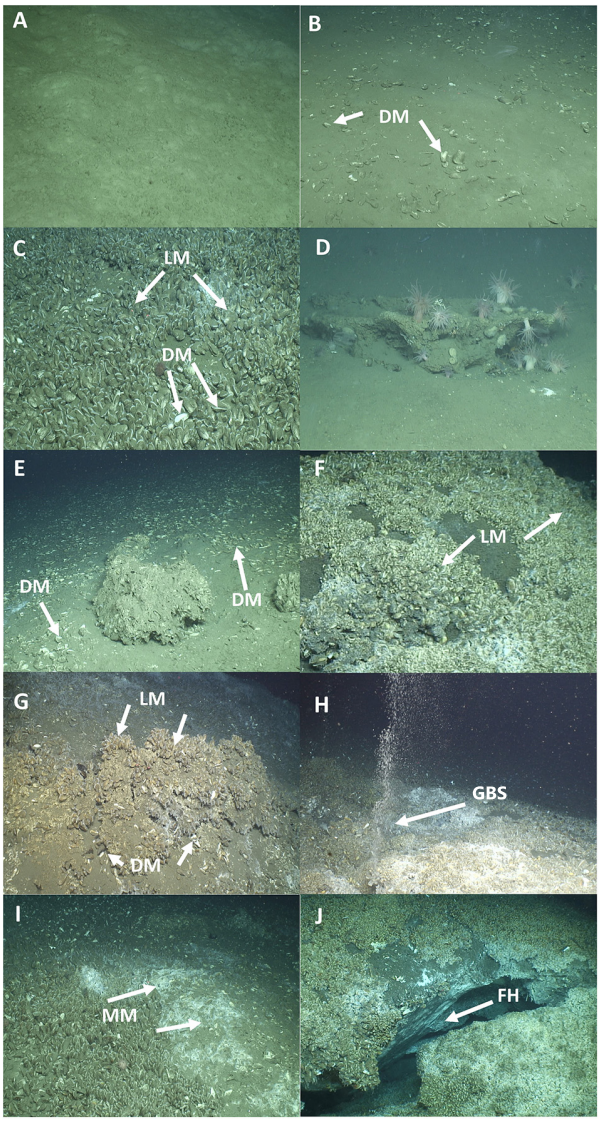


FIGURE 2 | Types of habitats, gas bubbling sites, and microbial mats. **(A)** Sand-mud; **(B)** sand with dead mussels (DM); **(C)** sand with dead and live mussels (LM); **(D)** mixed hard-soft; **(E)** mixed hard-soft with dead mussels; **(F)** mixed hard-soft with live mussels; **(G)** mixed hard-soft with dead and live mussels; **(H)** presence of gas bubbling site (GBS); **(I)** presence of microbial mat (MM); **(J)** frozen hydrate (FH).

benthic invertebrate megafauna to the lowest possible taxonomic level. Each frame was given an Eastern Daylight Time (EDT) stamp following Ross et al. (2015). The initial number of extracted frames was 2858. From these we excluded those frames with either low image quality or frames having no fauna (n = 514). We also excluded those frames where the ROV was stationary (n = 269). This resulted in 2075 high-quality frames that we analyzed in the present study.

Taxonomic identifications were based on the best available literature (CSA Ocean Sciences Inc. et al., 2017; Turner et al., 2020) and guidance from world-class taxonomic specialists. The number of megabenthic individuals was counted in each image. Counting was conservative to avoid misidentifications and was carried out for almost all megafauna seen in the images. Presence/absence data were recorded for colonial species (e.g., encrusting sponges) and for four solitary species (the polychaete *Hyalinoecia* sp., the planktonic tunicates Salpidae sp., the red shrimps, and the comb jellies) because their massive numbers made counting unreliable. When it was too challenging to identify individuals to species-level, they were combined and reported as a higher taxonomic rank, following Quattrini et al. (2012). Those individuals which could not be identified as a group due to the lack of taxonomic identification, were grouped as morphotypes, e.g., sponges were grouped into two morphotype categories (1, encrusting, cushion; 2, massive, papillate), following Kazanidis et al. (2019).

Depth measurements from the SeaBird SBE 911+ data logger, latitude/longitude (universal transverse mercator; UTM), temperature, density, salinity, pH, oxygen concentration, and turbidity were time synchronized to each annotated frame. This synchronization was based on the time stamps (Hours: Minutes: Seconds) of each image frame and collected environmental data. The presence of gas bubbling sites, microbial mats, and frozen hydrates were also noted (**Figure 1** and **Supplementary Tables 1–3**) and the distances between gas bubbling sites, microbial mats, frozen hydrates and the points that high quality images were extracted, were calculated in QGIS v.3.16.2 using the Analysis Tool "Distance Matrix" (QGIS Development Team, 2019). Fish trap lines, potential trawl marks and litter were also noted, including their depth, latitude and longitude values.

Data Analysis

Each high-quality image extracted from the ROV videos was set as the sampling unit. Samples where no faunal records were made were excluded from further analysis. In addition, three taxa (the bubblegum coral *Paragorgia arborea*, the soft coral *Parazoanthus* sp. and unidentified hydrozoans) were excluded from data analysis as they were absent in >90% of the samples (Ross and Quattrini, 2007; Ross et al., 2015).

In each high-quality image we measured the number of species/morphotypes (SR), total number of individuals (N) and the biodiversity indices Margalef (d), Pielou's evenness (J′), and Shannon (H′). The calculation of d, J′, and H′ was carried out in the software Primer v.7 (Clarke and Gorley, 2015). Statistically significant differences across habitats in terms of SR, N, d, J′, and H′ were examined using analysis of variance in R, following Kazanidis et al. (2018). In the case of one-way ANOVA, multiple comparisons were carried out through the Tukey's test. In the case of one-way analysis of means the comparisons were carried out through the Games Howell test (Burk, 2018). When the Kruskal–Wallis test was used, the pairwise comparisons were carried out through the Dunn test (Dinno, 2017). Accounting for the multiple comparisons, the p values were adjusted using the Bonferroni correction (Armstrong, 2014).

Analyses on the faunal composition and structure of megabenthic associations were also completed using Primer. Data on the abundance of megabenthos were square-root transformed and were used in the calculation of Bray–Curtis

similarities and similarity matrices. Based on these matrices, non-metric multi-dimensional scaling (nMDS) 2-dimensional (2D) plots were constructed. Analysis of similarities (ANOSIM) was used to identify the existence of statistically significant differences in community composition between BC and NC as well as across habitats for each seep system. In addition, SIMPER analysis was used to identify species responsible for the average dissimilarity between (a) BC and NC, (b) pairs of habitats within BC and NC.

Finally, the roles of environmental parameters (i.e., depth, latitude, longitude, type of habitat, temperature, salinity, density, oxygen concentration, pH, turbidity, presence of microbial mats, presence of frozen hydrates, and presence of gas bubbling sites) in shaping megabenthic associations within each of the six ROV dives, were analyzed. The role of microbial mats, frozen hydrates and gas bubbling sites in shaping megabenthos was examined by measuring their numbers within a 20 m radius for each single image frame. This radius was set noting that bacterial mats and gas bubbling sites affect megafauna communities on a scale of tens of meters (Levin et al., 2016; Sen et al., 2019). The role of environmental parameters in shaping megabenthos was examined considering megafauna and environmental data recorded in each image frame (see section "Annotations of Megafauna" for details). The role of environmental variability in shaping megabenthic communities was examined in Primer using distance-based linear modeling ("Dist-LM" routine) (Anderson et al., 2008). This routine quantifies the relative contribution of environmental variables in shaping the variability of biological communities (Anderson et al., 2008). To avoid Type I error inflation, explanatory variables were checked for correlation (using Draftsman plots in Primer) and variables with significant correlation scores (Pearson's $r > 0.7$ or < -0.7) were discarded (Wei and Simko, 2017). A stepwise selection was applied to retain the statistically significant explanatory variables and the Akaike information criterion (AIC) was used as a selection criterion (Anderson et al., 2008).

RESULTS

Distribution of Habitat Types

The distribution of the seven types of habitats differed between the six ROV dives (**Figure 3**). In NF-07, NF-08, NF-14, and J2-689 dives there was a strong presence of sand-mud habitat while sand with dead and live mussels was dominant in dives J2-682 and J2-683.

Community Composition and Structure

In total 40 discrete taxa or morphotypes were recorded across the two seeps, and 37 of these were included in the analyses. The three that were excluded -as they were seen only in 13 images in total- were *Paragorgia arborea*, *Parazoanthus* sp., and hydrozoans. The 37 taxa/morphotypes were distributed as follows: 24 (∼65%) were exclusively found at BC, nine (∼24%) were exclusively found in NC and four (∼11%) were found in both areas (**Table 2**). The distribution of the total number of taxa was as follows: 11 arthropods (∼30%), ten echinoderms (∼27%), seven anthozoans (∼19%), five mollusks (∼14%), two sponges (∼5%), one polychaete (∼3%), and one tunicate (∼3%) (**Figure 4** and **Table 2**).

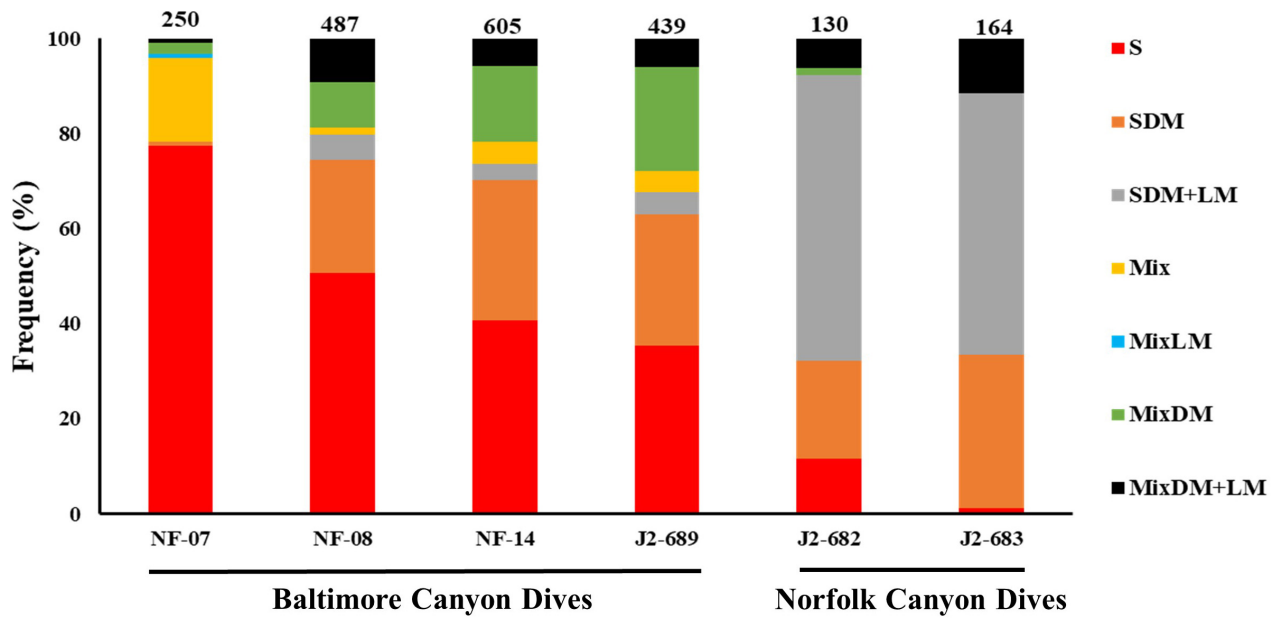


FIGURE 3 | Distribution (%) of the types of habitats across the six remotely operated vehicle (ROV) dives in Baltimore (NF-07, NF-08, NF-14, and J2-689) and Norfolk canyons (J2-682 and J2-683). The number of video frames processed from each ROV dive is shown above each bar. Habitat types: sand-mud (S), sand mixed with dead mussels (SDM), sand with dead and live mussels (SDM+LM), mixed hard-soft (Mix), mixed hard-soft with dead mussels (MixDM), mixed hard-soft with live mussels (MixLM), mixed hard-soft with dead and live mussels (MixDM+LM).

TABLE 2 | Megafaunal categories included in the still image analysis, with cross-references to the example images in **Figure 4**.

Major group	Taxon/Morphotype	Description, canyon found and image reference	*n*
Cnidaria	*Actinoscyphia* sp.	Solitary anemone ("venus flytrap") (Actinoscyphiidae). BC and NC. **Figure 4.1**	198
	Comb jellies	Gelatinous ctenophores. BC. **Figure 4.2**	242
	Hormathia sp. (red morphotype)	Solitary anemone (Hormathiidae). BC. **Figure 4.3**	36
	Hormathia sp. (white morphotype)	Solitary anemone (Hormathiidae). BC. **Figure 4.4**	670
	Cerianthus sp. (white morphotype)	Tube-dwelling anemone (Cerianthidae). BC and NC. **Figure 4.5**	70
	Cerianthus sp. (red/brown morphotype)	Tube-dwelling anemone (Cerianthidae). BC. **Figure 4.6**	16
	Bolocera tuediae (Johnston, 1832)	Solitary anemone ("deeplet sea anemone") (Actiniidae). BC. **Figure 4.7**	1087
Arthropoda	*Alvinocaris markensis* (Williams, 1988)	Decapod predator found in chemosynthetic environments (Alvinocarididae). NC. **Figure 4.8**	2
	Red shrimp	Uncategorized decapods. BC and NC. **Figure 4.9**	689
	Chaceon quinquedens (Smith, 1879)	Brachyuran ("Atlantic deep-sea red crab") (Geryonidae). BC. **Figure 4.10**	649
	Cancer sp.	Brachyuran (Cancridae). BC. **Figure 4.11**	124
	Eumunida picta (Smith, 1883)	Decapods ("deep-sea squat lobster") (Eumunididae). BC. **Figure 4.12**	7
	Galathea sp.	Decapods (Galatheidae). BC.	12
	White spider crab	Decapods, probably in the genus *Lithodes*. BC. **Figure 4.13**	88
	Lithodes sp.	Decapods (Lithodidae). BC and NC. **Figure 4.14**	6
	Penaeidae	Decapods. BC. **Figure 4.15**	74
	Tomopaguropsis sp.	Deep-sea hermit crab (Paguridae). BC. **Figure 4.16**	438
	Pantopoda	Deep-sea spiders. NC. **Figure 4.17**	5
Annelida	*Hyalinoecia* sp.	Tube dwelling polychaete (Onuphidae). BC. **Figure 4.18**	921
Echinodermata	White starfish	Uncategorized sea star. BC. **Figure 4.19**	36
	Unidentified echinoid	Uncategorized sea urchin (Echinidae). BC. **Figure 4.20**	5
	Brisingida	Deep-sea dwelling starfish (Brisingidae). NC. **Figure 4.21**	1
	Porania sp.	Seastar (Poranidae). BC. **Figure 4.22**	3
	White echinoid	Uncategorized echinoid, probably *Gracilechinus* sp. NC. **Figure 4.23**	65
	Red echinoid	Uncategorized echinoid, probably *Echinus* sp. NC. **Figure 4.24**	40
	Ophiuroidea	Uncategorized ophiuroids. NC. **Figure 4.25**	148
	Hygrosoma sp.	Echinoid, probably *H. petersii* (Echinothuriidae). NC. **Figure 4.26**	3
	Phormosoma sp.	Echinoid, probably *P. placenta* ("pancake sea urchins") (Phormosomatidae). NC. **Figure 4.27**	10
	Chiridota heheva (Pawson and Vance, 2004)	Mobile deposit feeding holothurian (Chiridotidae). NC. **Figure 4.28**	22
Molluska	*Muusoctopus johnsonianus* (Allcock et al., 2006)	Deep-sea octopus (Enteroctopodidae). NC. **Figure 4.29**	7
	Graneledone verrucosa (Verrill, 1881)	Deep-sea octopus (Megaleledonidae). NC. **Figure 4.30**	4
	Illex sp.	Shortfin squid (Ommastrephidae). BC. **Figure 4.31**	51
	Bathypolypus sp.	Deep-sea octopus, probably *B. bairdii.* (Bathypolypodidae). BC. **Figure 4.32**	5
	Neogastropoda	Uncategorized neogastropods. BC. **Figure 4.33**	12
Porifera	*Polymastia* sp.	Filter-feeding sponge (Polymastiidae). BC. **Figure 4.34**	161
	Encrusting sponge	Sheet-forming sponge. BC. **Figure 4.35**	21
Chordata	Salpidae sp.	Salpa (barrel-shaped planktic tunicates). BC. **Figure 4.36**	160

BC, Baltimore Canyon; NC, Norfolk Canyon. n, number of images in which each taxon/morphotype was observed.

The nMDS analyses revealed clear differences in the fauna composition and density of taxa and morphotypes between BC and NC (**Figure 5A**). ANOSIM analysis between BC and NC showed an R value of 0.746 ($p < 0.01\%$). Due to this sharp difference in faunal composition between BC and NC, further analyses (e.g., on the role of habitat complexity in shaping megabenthos) were carried out separately for each of the seep areas. SIMPER analysis showed the taxonomic groups with the higher contribution in dissimilarity between NC and BC were the Ophiuroidea (19.29% contribution in the total dissimilarity), the anthozoans *Bolocera tuediae* (16.71%) and *Hormathia* sp. white morphotype (7.82%), the polychaete *Hyalinoecia* sp. (9.16%), and the red crab *Chaceon quinquedens* (7.59%).

At BC, habitat complexity had a prominent role in shaping megafaunal composition (**Figure 5B**). There was a clear clustering of communities found in soft habitats (sand-mud, sand mixed with dead mussels) versus those found in hard habitats (e.g., mixed hard-soft, mixed hard-soft with dead mussels). ANOSIM analysis revealed statistically significant differences for 14 out of the 21 groups examined (**Supplementary Table 4**).

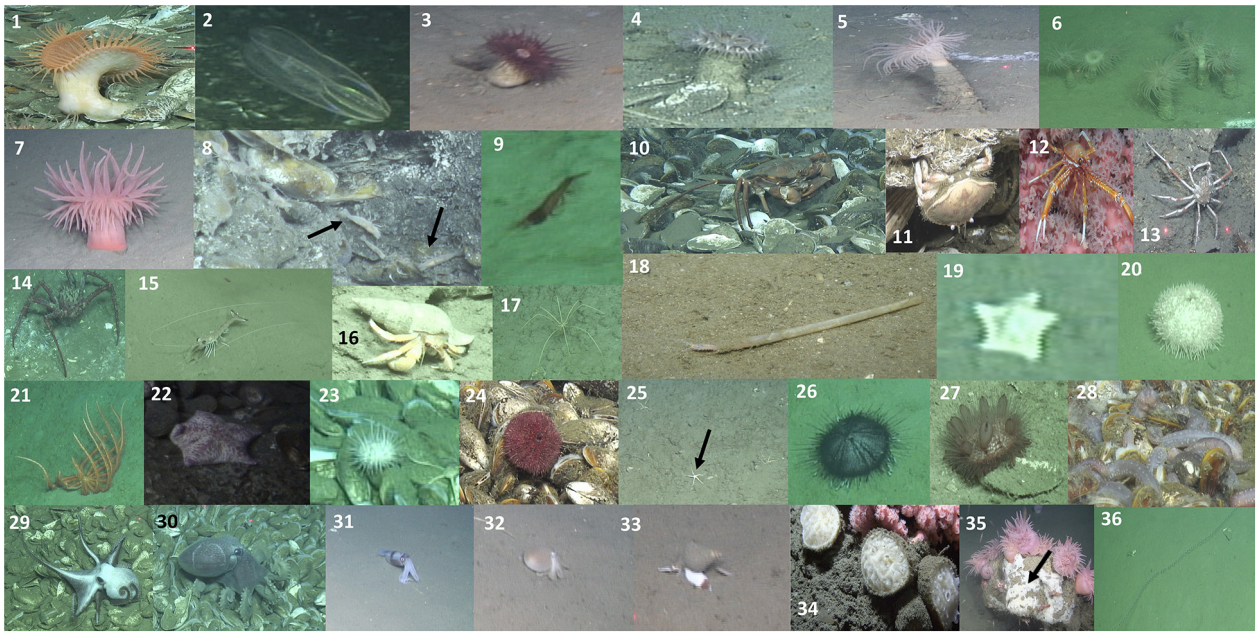


FIGURE 4 | Photographs illustrating the megafaunal categories listed in **Table 2**. See **Table 2** for description of each image. Black arrows in panel **8** highlight the specimens of *Alvinocaris markensis*, in panel **25** the ophiuroid specimens, and in panel **35** highlights encrusting sponge.

Overall, the differences between the BC groups were mainly driven by the sponge *Polymastia* sp., the anthozoans *Actinoscyphia* sp., *Hormathia* sp. (white morphotype), and *Bolocera tuediae*, the arthropod *Chaceon quinquedens*, "red shrimp," "white spider crab," *Tomopaguropsis* sp., and the polychaete *Hyalinoecia* sp. (**Supplementary Table 6**). For example, the dissimilarity in the pair sand-mud vs. mixed hard-soft with dead and live mussels (the pair with the highest level of dissimilarity) was driven by the anthozoans *B. tuediae* (16.15% contribution in dissimilarity) and *Hormathia* sp. white morphotype (15.33%), and the sponge *Polymastia* sp. (11.47%). *Hormathia* and *Polymastia* had higher average densities in mixed hard-soft with dead and live mussels than sand-mud, while *B. tuediae* had higher average density in sand-mud than mixed hard-soft with dead and live mussels (**Supplementary Table 6**).

The type of habitat also had a major contribution in shaping megabenthic communities in NC (**Figure 5C**). ANOSIM analyses showed significant differences for sand-mud vs. sand with dead mussels (R = 0.197, p = 0.019), sand-mud vs. mixed hard-soft with dead and live mussels (R = 0.255, p = 0.001), sand with dead mussels vs. sand with dead and live mussels (R = 0.076, p = 0.001), sand with dead mussels vs. mixed hard-soft with dead and live mussels (R = 0.632, p = 0.001) and sand with dead and live mussels vs. mixed hard-soft with dead and live mussels (R = 0.057, p = 0.049) (**Supplementary Table 5**). The dissimilarity in the pair sand with dead mussels vs. mixed hard soft with dead and live mussels (the pair with the highest level of dissimilarity) was driven by Ophiuroidea (43.20% contribution in the average dissimilarity) and Echinoidea 1 white morphotype (28.52%). Ophiuroids had higher average density at sand mixed with dead mussels while Echinoidea 1 white morphotype had higher average density at habitat mixed hard-soft with dead and live mussels (**Supplementary Table 7**).

Values of SR, N, d, J′, and H′ showed statistically significant differences across the types of habitats, especially at BC dives. Overall, higher values of megafaunal density and biodiversity were found in hard (e.g., mixed hard-soft with dead mussels, mixed hard-soft with dead, and live mussels) than soft (sand-mud, sand mixed with dead mussels) habitats (**Figure 6** and **Table 3**).

Role of Environmental Parameters in Shaping Seep Community Structure

Dist-LM analyses showed that the amount of biological variability explained by certain key environmental factors ranged from 17.31% (J2-682 dive) to 31.41% (NF-07 dive). In five out of the six ROV dives, habitat was the leading parameter explaining biological variability (**Table 4**). At NC (J2-682 and J2-683 dives), the type of habitat, microbial mats, pH, and gas bubbling sites were the parameters that had a statistically significant contribution in explaining variability, while at BC (i.e., NF-07, NF-08, NF-14, and J2-689 dives) there was a larger number of variables shaping megabenthic communities (**Table 4**).

The presence of microbial mats and gas bubbling sites had a minor but statistically significant contribution toward explaining community structure at all four BC dives. In contrast, the NC microbial mats and gas bubbling sites had a statistically significant contribution only in J2-683 dive (**Table 4**). SIMPER analysis revealed the species with the higher contribution to megafaunal dissimilarities between locations with and without microbial mats/gas bubbling sites (**Supplementary Tables 8, 9**).

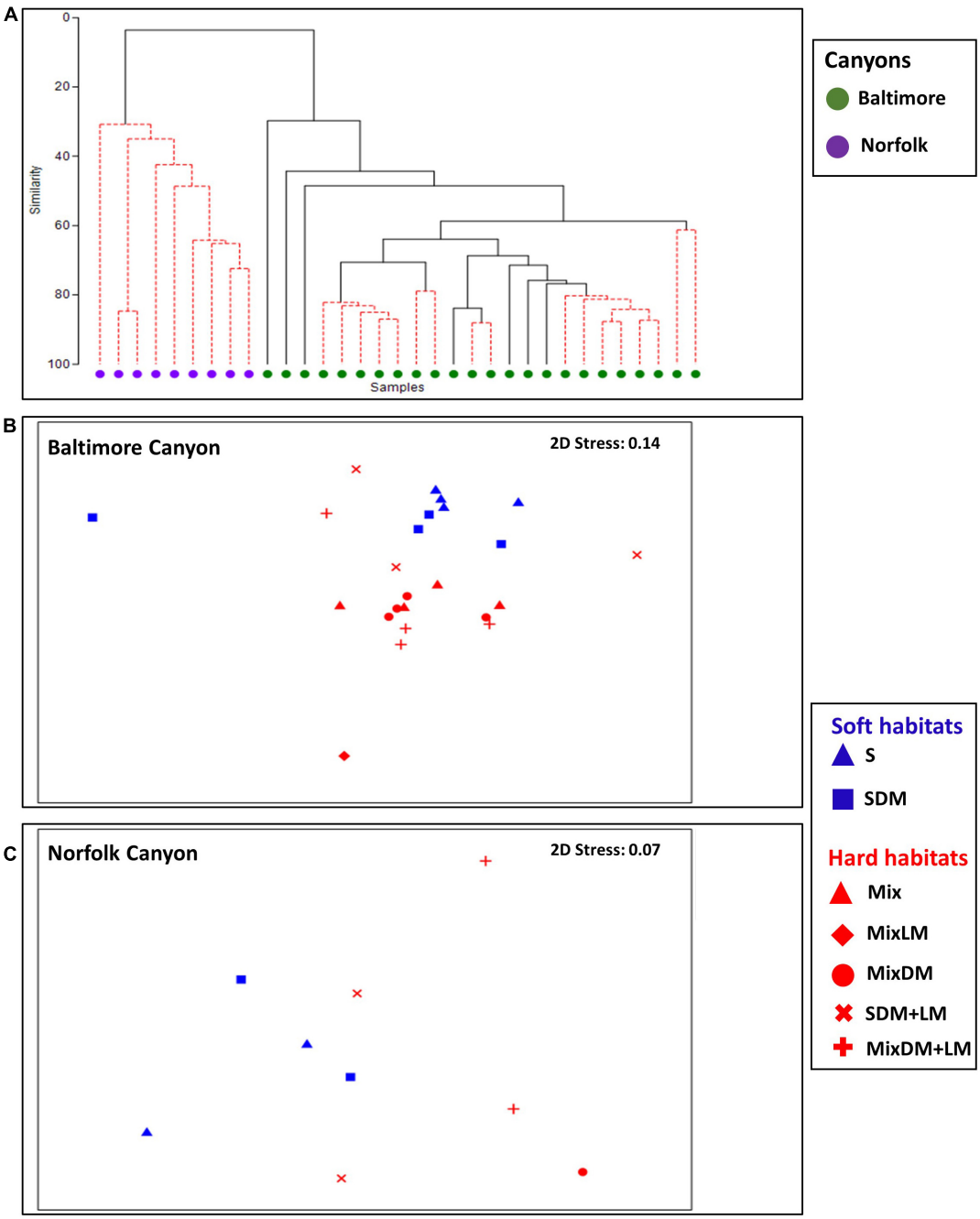


FIGURE 5 | Non-metric multidimensional scaling showing the grouping of samples **(A)** at Baltimore Canyon (BC) and Norfolk Canyon (NC), **(B)** across habitats at BC, and **(C)** across habitats at NC.

At BC the species with higher average density in locations with microbial mats were mainly the hermit crab *Tomopaguropsis* sp. and the anthozoan *Hormathia* sp. white morphotype (**Supplementary Table 8**). SIMPER showed the species with higher average density at BC locations with gas bubbling sites were mainly *Hormathia* sp. white morphotype, the red crab *Chaceon quinquedens* and the polychaete *Hyalinoecia* sp. (**Supplementary Table 9**). At NC, the species with higher average density in locations with microbial mats and gas bubbling sites were the "Echinoid red morph" and "Echinoid white morph" (**Supplementary Tables 8, 9**).

Records of Marine Litter in the Baltimore and Norfolk Canyons

The presence of marine litter in the two seeps was limited to fifteen images containing litter items: two images in NF-07, two

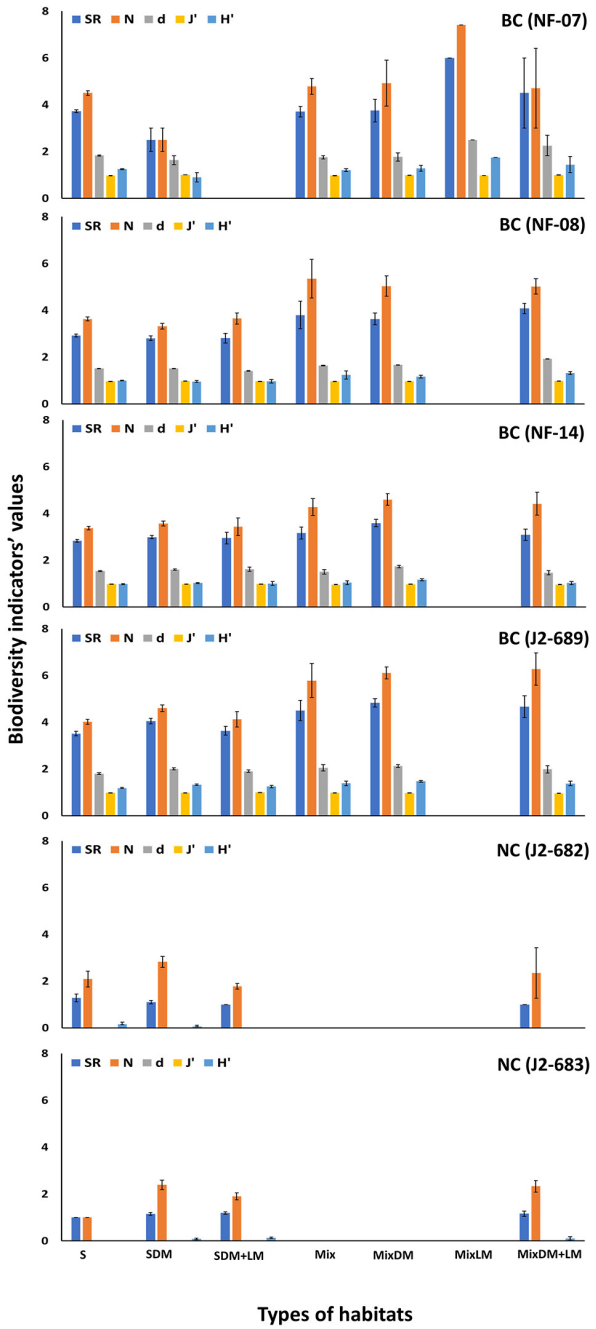


FIGURE 6 | Mean values and standard error of number of species (S), number of individuals (N), Margalef index (d), Pielou's evenness (J′), and Shannon index (H′) across the types of habitats for each of the six ROV dives at Baltimore (BC) and Norfolk (NC) canyons. Habitat types: sand-mud (S), sand mixed with dead mussels (SDM), sand with dead and live mussels (SDM + LM), mixed hard-soft (Mix), mixed hard-soft with dead mussels (MixDM), mixed hard-soft with live mussels (MixLM), mixed hard-soft with dead and live mussels (MixDM + LM).

in NF-08, four in NF-14, four in J2-683, one in J2-682, and two in J2-689. Most of these items were plastic bags and lost/abandoned fishing gear (e.g., fishery trap lines) (**Figure 7**).

DISCUSSION

Changes in Megabenthic Associations Across Depth

Differences in depth played a major role in structuring the megafaunal communities between the shallower Baltimore Canyon (340–496 m) and deeper Norfolk Canyon (1,444–1,611 m) seep sites. There were only four common taxa/morphotypes (e.g., *Lithodes* sp., *Actinoscyphia* sp., "red shrimps," *Cerianthus* sp.) shared between BC and NC seeps and overall, densities of such species were higher at BC than NC. Two of the relatively common faunal components that were found solely at BC were comb jellies and salps. Cacchione et al. (1978) observed salp carcasses close to the seabed in the Hudson Canyon at ∼3,400 m water depth; salp carcasses might supply more than half of the daily energy requirements of benthic microfauna in that area (Wiebe et al., 1979). On top of northwest Atlantic canyons, jellyfish have been shown to play an important role in pelagic carbon cycling (Condon et al., 2011; Fuentes et al., 2018) and can also form a substantial food input for benthic communities (Luo et al., 2020) including those in the deep sea (Billett et al., 2006; Lebrato et al., 2012; Sweetman et al., 2014). Our findings about sharp differences in megafaunal composition between BC and NC agree with previous work from Brooke et al. (2017) showing differences in the densities of hexacorals and octocorals between BC and NC. Our findings are also in line with those from Turner et al. (2020) reporting almost no overlap between BC and NC megabenthos. Studies on BC and NC demersal fishes showed depth was the key factor separating communities in two zones with a boundary around 1,400 m (Ross et al., 2015). Studies at BC and NC macroinfauna (∼180–1200 m water depth) showed a departure from the expected depth-density relationship, driven by higher faunal abundance at 800 and 900 m which was a deposition zone for organic matter (Robertson et al., 2020). Studies by Robertson et al. (2020) have also shown that NC and adjacent slope were more organically enriched than BC and slope. Furthermore, in Robertson et al. (2020) it was shown that upper slopes in both areas contained macrofaunal communities that were more disturbed than those communities in deeper areas; it was speculated that this disturbance may be due to impacts from fishing activities or interactions of the shelf with hydrography (CSA Ocean Sciences Inc. et al., 2017).

Our results agree with findings in the deep northwestern Atlantic and with findings about zonation of deep-sea biota on continental margins (Rowe et al., 1982; Carney, 2005 and references therein). Specifically, evidence has been provided for the occupation of different bathymetric zones between mussels: in the Gulf of Mexico *Bathymodiolus childressi* was found in shallower waters than *Bathymodiolus heckerae* (1,005–2,284 and 2,180–2,745 m, respectively), with the two species never found together (Cordes et al., 2010a). In the Gulf of Mexico's seeps little or no overlap was found between upper and lower slope macro- or megafaunal communities. A striking difference between the two zones was the dominance of the ophiuroid *Ophioctenella acies* in the deeper communities; the shift in faunal composition

seems to take place between 1,300 and 1,700 m (Cordes et al., 2007). Thus, there is further reinforcement for a widespread, faunal bathymetric transition zone in the region near 1,400–1,500 m as suggested by Ross et al. (2015).

The examination of biodiversity gradients across depth in the North Atlantic have revealed different patterns. Firstly, studies in northwestern Atlantic have shown the presence of a unimodal distribution for macrofauna (gastropods, polychaetes, protobranchs, and cumaceans) as well as for invertebrate and fish megafauna (e.g., Rex, 1981; Pineda and Caswell, 1998; Stuart and Rex, 2009). In this pattern, relatively low values of species diversity are seen in the continental shelf, followed by an increase and a peak at mid to lower bathyal zone and then decreases toward the abyssal plains (Rex, 1981). Comparisons among recorded unimodal distributions have revealed variability regarding the depth of the peak (Rex, 1981; Etter and Grassle, 1992; Allen and Sanders, 1996; Levin et al., 2001). The unimodal distribution of diversity is possibly explained by the dynamic equilibrium model predictions (Huston, 1979) where species interactions have an important role in shaping patterns of diversity (Rex, 1981; Stuart et al., 2003). Furthermore, studies on benthic megafauna on the continental margin south of New England (242–2,394 m depth) defined four megafaunal slope zones: upper, upper-middle, transition on the lower- middle, and a lower slope zone (Hecker, 1990). Faunal density was high in the upper and lower slope and low in the two middle slope zones; density and species composition patterns across depth were similar at three of the locations but they were significantly different at the eastern edge of Georges Bank, an area characterized by steep topography, glacial erratics, and outcrops (Hecker, 1990). Furthermore, studies on megafaunal assemblages off Cape Hatteras (157–1,924 m) showed that populations in the upper and lower slope were similar in terms of density and species composition, to those found at other locations; in contrast, megafaunal abundances were elevated in mid slope, mainly reflecting dense populations of fish, eels and anemones, probably related to enhanced food availability (Hecker, 1994). In the Rockall Trough (northeast Atlantic), Paterson and Lambshead (1995) have shown a parabolic distribution in polychaetes' species richness with a peak located at about 1,800 m water depth. The authors mentioned that disturbance, in terms of the frequency of high energy currents, and intrataxocene predation was important on the Hebridean Slope. Gage et al. (2000) have shown reduced macrobenthic species diversity at ∼400 m depth in the continental slope off Scotland, probably due to hydrodynamic disturbance, but no clear mid-slope peak in species diversity was found. The examination of macrobenthic communities in the Goban Spur region (northeast Atlantic continental slope) showed an increase in species diversity from ∼200 down to 4,500 m water depth; species richness, however, had a parabolic pattern with a peak in the upper slope (1425 m). Differences in life-history characteristics and food supply could explain to some extent the diversity patterns found across the depth gradient (Flach and De Bruin, 1999). Finally, in the Porcupine Seabight and adjacent Abyssal Plain, Olabarria (2005) recorded a pattern of increasing bivalve diversity from ∼500 to 1,600 m followed by a decrease to minimum at about 2,700 m, followed by an increase up to maximum at ∼4,100 and then a drop to ∼4,900 m. The low values of diversity between 2,100 and 2,700 m were associated to an extent to the high abundance of the bivalve *Kelliella atlantica* while high values of diversity in the abyssal depths were associated in part with the source-sink hypothesis (Rex et al., 2005), low predation (Allen and Sanders, 1996), and strong fluxes of organic matter (Billett et al., 2001).

Changes in Megabenthic Associations Across Habitats

Habitat type played an important role in shaping the composition of the seep megabenthic communities. At both BC and NC, the communities found in soft habitats were clearly separated from those communities on hard habitats. At BC the sponge *Polymastia* sp. was among the species with the highest contribution in the dissimilarities found between soft and hard habitats. The close association of *Polymastia* sp. with hard habitats in coastal southern Brazil (Bumbeer et al., 2016) and northern Norway (Dunlop et al., 2020) facilitates the successful settlement of larvae and survival of juveniles. Soft sediments may not be ideal for the proliferation of *Polymastia* sp. due to the negative impacts caused by sedimentation on filtering and oxygenation in sponges (Kutti et al., 2015). *Hormathia* sp. anthozoans had higher densities in hard habitats than soft habitats which agrees with findings on *Hormathia pacifica* recorded living upon manganese encrusted basalt and dead sponge tissue in the Taney Seamounts (Sanamyan et al., 2015). Our results fit well with previous studies on Belgica Province carbonate mounds where on-mound habitat had higher biodiversity than off-mound (Henry and Roberts, 2007).

Contrary to *Polymasti*a sp. and *Hormathia* sp., the red shrimps had stronger presence in soft than hard habitats. Due to low taxonomic resolution it is challenging to define the drivers that shape the recorded patterns. Some Penaeidae living in deep waters (e.g., *Parapenaeus longirostris* found in the eastern Atlantic from 20 to 750 m water depth) inhabit sand-mud bottoms and feed on a large variety of bathypelagic, benthic and endobenthic prey (Kapiris, 2004). The *Hyalinoecia* sp. polychaetes also had stronger presence in habitats composed of soft sediments and dead mussels than those containing a mix of hard and soft sediments and live and dead mussels. Our data agree with studies on the ecology of *Hyalinoecia artifex* from the United States Continental Margin, noting this species is a predator/scavenger found mainly on soft sediments and is negatively associated with authigenic carbonates (Meyer et al., 2016). *Bolocera tuediae* anemones in our study were found both in hard and soft sediments; in previous studies they have been recorded in high abundance in bioturbated soft sediments in the Franken Carbonate Mound (Wienberg et al., 2008). In NC, SIMPER analysis provided evidence that "Echinoid white morphotype" had higher densities in hard than soft habitats. The drivers behind this pattern are not known, but we propose this is related to feeding. Studies on the carbon stable isotope values of *Echinus* sp. in deep-sea cold seeps in the Mediterranean provided some preliminary indication of reliance on chemosynthesis originated carbon (Olu-Le Roy et al., 2004). Further work is needed to

TABLE 3 | Analysis of variance for number of species (SR), number of individuals (N), Margalef index (d), Pielou's evenness (J′), and Shannon index (H′) across the types of habitats for each of the six ROV dives at Baltimore Canyon (BC) and Norfolk Canyon (NC).

	SR	N	d	J′	H′
BC (NF-07)	KW = 6.96, ns	KW = 6.47, ns	KW = 6.69, ns	KW = 6.27, ns	KW = 6.27, ns
BC (NF-08)	KW = 39.02*** S vs. MixDM + LM*** SDM vs. MixDM** SDM vs. MixDM + LM*** SDM + LM vs. MixDM + LM**	KW = 37.23*** S vs. Mix + DM* S vs. MixDM + LM*** SDM vs. MixDM** SDM vs. MixDM + LM***	KW = 30.45*** S vs. MixDM + LM*** SDM vs. MixDM + LM*** SDM + LM vs. MixDM + LM**	KW = 5.55 ns	KW = 36.16*** SM vs. MixDM + LM*** SDM vs. MixDM* SDM vs. MixDM + LM*** SDM + LM vs. MixDM + LM**
BC (NF-14)	KW = 17.79*** S vs. MixDM***	KW = 24.66*** S vs. MixDM** SDM vs. MixDM*	KW = 12.31* S vs. MixDM*	KW = 12.57*	KW = 15.89** S vs. MixDM***
BC (J2-689)	KW = 44.58*** S vs. SDM** S vs. MixDM*** SDM vs. MixDM* SDM + LM vs. MixLM*	KW = 60.76*** S vs. MixLM*** S vs. MixDM + LM*** SDM vs. MixDM*** SDM + LM vs. MixDM**	*F* = 4.89*** S vs. SDM** S vs. MixDM**	KW = 25.00*** S vs. MixDM + LM* SDM vs. MixDM** SDM vs. MixDM + LM** SDM + LM vs. MixLM* SDM + LM vs. MixDM + LM**	KW = 36.77*** S vs. SDM** S vs. MixDM***
NC (J2-682)	KW = 10.91* S vs. SDM + LM**	KW = 13.65** SDM vs. SDM + LM***	–	–	KW = 10.72* S vs. SDM + LM**
NC (J2-683)	KW = 0.70, ns	KW = 9.62*	–	–	KW = 1.06, ns

*KW, Kruskal–Wallis rank sum test; F, oneway test not assuming equal variances. p values are given (*0.01 < p < 0.05, **p < 0.01, ***p < 0.001, "ns" non-significant). Types of habitats: sand-mud (S), sand mixed with dead mussels (SDM), sand with dead and live mussels (SDM + LM), mixed hard-soft (Mix), mixed hard-soft with dead mussels (MixDM), mixed hard-soft with live mussels (MixLM), mixed hard-soft with dead and live mussels (MixDM + LM).*

determine whether echinoids in NC contain symbiotic bacteria assimilating chemical compounds, graze on bacteria or feed on mussel tissues.

Apart from differences between soft and hard habitats, differences were also recorded between other habitats. The red crab *Chaceon quinquedens* had higher density in habitats with live *Bathymodiolus* mussels than habitats without live mussels, suggesting an affiliation between the two. During this project, *C. quinquedens* was observed in dense live mussel beds at BC, apparently feeding upon mussel tissue (S. W. Ross, pers. obs.). Stable isotope analysis from the United States Continental Margin showed the proportion of methane-derived carbon within crab tissue is highly variable (∼0% to ∼30–50% of nutrition), depending on location (Turner et al., 2020); they also suggested that some seep mussel beds may act as a nursery ground for *C. quinquedens*.

A relatively small number of species (mainly echinoids and ophiuroids) were responsible for the dissimilarities found between habitats at NC, in contrast to BC. Although direct evidence is lacking, we hypothesize this observation is related to the life-history characteristics of species recorded at NC. Most of them were mobile (e.g., decapods, sea spiders, echinoids, ophiuroids, and holothurians) and apparently do not have equally strong affiliations with a specific type of substrate as seen at BC (e.g., *Polymastia* and *Hormathia*). The holothurian *Chiridota heheva* seen at NC is a cosmopolitan chemosynthetic ecosystem species (Thomas et al., 2020) feeding on various food sources (Carney, 2010). Pantopoda and *Lithodes* crabs in chemosynthetic environments (e.g., *Lithodes longispina*) have been characterized as predators/scavengers (Bowden et al., 2013; Wang et al., 2016; Dietz et al., 2018) moving across habitats and searching for prey.

The existence of clear differences among habitats both at BC and NC agrees with previous studies. At BC there were higher mean densities of macroinfauna in microbial mats (∼80,000 ind/m^2) than background sediments (∼15,000 ind/m^2) (Bourque et al., 2017). At NC, Bourque et al. (2021) recorded similar macroinfaunal densities among habitats sampled at comparable depths, but diversity was higher near the hard substrate environments, likely due to their increased habitat heterogeneity and enhanced food supply. Differences in demersal fish communities among BC habitats were also reported with assemblages in sandy habitats being significantly different from the most complex habitats, e.g., mixed hard substrates with soft sediments (Ross et al., 2015). In the Barents Sea taxonomic richness and abundance of megabenthos were much higher at the Svanefjell seep site compared with a non-seep site; crusts of seep carbonates drove the higher diversity of the seep site (Sen et al., 2019). Ross et al. (2015) reported a decrease in the role of habitat complexity in shaping demersal fish communities from the shallower BC to the deeper NC. They suggested the decreased availability of complex habitat (seamounts excluded) and limited food supply as depth increases argue against strong habitat association in deep environments, where flexibility and opportunism might be more advantageous. Our findings do not support a decrease in the importance of habitat complexity for megabenthos with depth; similarly, in Bourque et al. (2017) the type of habitat had a statistically significant contribution in explaining the structure of macroinfaunal communities both at BC and NC. The apparent explanation about this

TABLE 4 | Outcome of distance-based linear modeling on the role of environmental parameters in explaining the variation of benthic megafauna in each of the six ROV dives at the Baltimore (BC) and Norfolk (NC) canyons.

BC (NF-07)

Marginal tests

Group	*P*	Prop. (%)
Habitat	0.001	18.83
Depth	0.001	15.20
MM	0.001	13.68
Temperature	0.001	3.89
Turbidity	0.015	1.80

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Habitat	1728.1	0.001	18.83	18.83
+Depth	1714.4	0.001	5.06	23.88
+Temperature	1704.3	0.001	3.69	27.57
+MM	1697.8	0.001	2.47	30.05
+Turbidity	1695	0.01	1.37	**31.42**

BC (NF-08)

Marginal tests

Group	*P*	Prop. (%)
Habitat	0.001	8.34
Depth	0.001	6.05
Temperature	0.001	5.73
UTMEast	0.001	3.31
MM	0.001	2.84
GBS	0.001	2.18
UTMNorth	0.001	1.52
pH	0.008	0.76
Turbidity	0.706	0.12

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Habitat	3630.2	0.001	8.34	8.34
+Depth	3596.1	0.001	6.79	15.13
+Temperature	3587.1	0.001	1.96	17.10
+MM	3583.2	0.001	1.03	18.13
+UTMEast	3579.8	0.001	0.95	19.08
+GBS	3575.9	0.001	1.01	20.09
+UTMNorth	3572.6	0.003	0.89	20.98
+pH	3572.1	0.051	0.42	**21.40**

BC (NF-14)

Marginal tests

Group	*P*	Prop. (%)
Depth	0.001	9.36
Habitat	0.001	7.33
MM	0.001	6.09
UTMNorth	0.001	4.22
GBS	0.001	1.09
Turbidity	0.003	0.62

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Depth	4480.9	0.001	9.36	9.36
+Habitat	4449.7	0.001	6.25	15.61
+MM	4430.2	0.001	3.09	18.70
+UTMNorth	4419.2	0.001	1.81	20.51
+Turbidity	4417.2	0.006	0.55	21.06
+GBS	4416.2	0.032	0.40	**21.46**

NC (J2-682)

Marginal tests

Group	*P*	Prop. (%)
Habitat	0.001	12.73
MM	0.019	3.53
Salinity	0.091	2.20
FH	0.016	2.19
Depth	0.105	1.95
GBS	0.146	1.92
Turbidity	0.569	0.77
DO	0.83	0.46

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Habitat	733.66	0.001	12.73	12.73
+MM	733.15	0.059	2.37	15.11
+Salinity	732.75	0.064	2.21	**17.32**

NC (J2-683)

Marginal tests

Group	*P*	Prop. (%)
Habitat	0.001	16.17
Depth	0.001	9.74
MM	0.001	6.04
FH	0.002	4.13
pH	0.002	2.57
Turbidity	0.005	2.20
Salinity	0.014	2.12
GBS	0.023	2.05
DO	0.811	0.34

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Habitat	1112.3	0.001	16.17	16.17
+MM	1111.5	0.017	1.73	17.89
+FH	1111.2	0.057	1.33	19.23
+pH	1110.9	0.046	1.33	20.55
+GBS	1110.5	0.035	1.37	**21.92**

BC (J2-689)

Marginal tests

Group	*P*	Prop. (%)
Habitat	0.001	13.58
Depth	0.001	9.98
pH	0.001	4.97
DO	0.001	4.32
MM	0.001	4.15
UTMNorth	0.001	3.92
GBS	0.001	2.23
Turbidity	0.001	2.17

Sequential tests

Group	AIC	*P*	Prop. (%)	Cumul. (%)
+Habitat	3129.9	0.001	13.58	13.58
+Depth	3106.7	0.001	5.19	18.77
+MM	3099.4	0.001	1.84	20.61
+UTMNorth	3092.3	0.001	1.76	22.37
+pH	3086.2	0.001	1.51	23.89
+GBS	3083.7	0.001	0.84	24.73
+Turbidity	3081.8	0.002	0.72	**25.44**

MM, microbial mats; GBS, gas bubbling sites; FH, frozen hydrates; DO, dissolved oxygen; P, p-values; Prop., proportion of biological variability explained; Cumul., cumulative proportion of biological variability explained (values in bold show the total amount of biological variability explained by the environmental variables); AIC, Akaike information criterion.

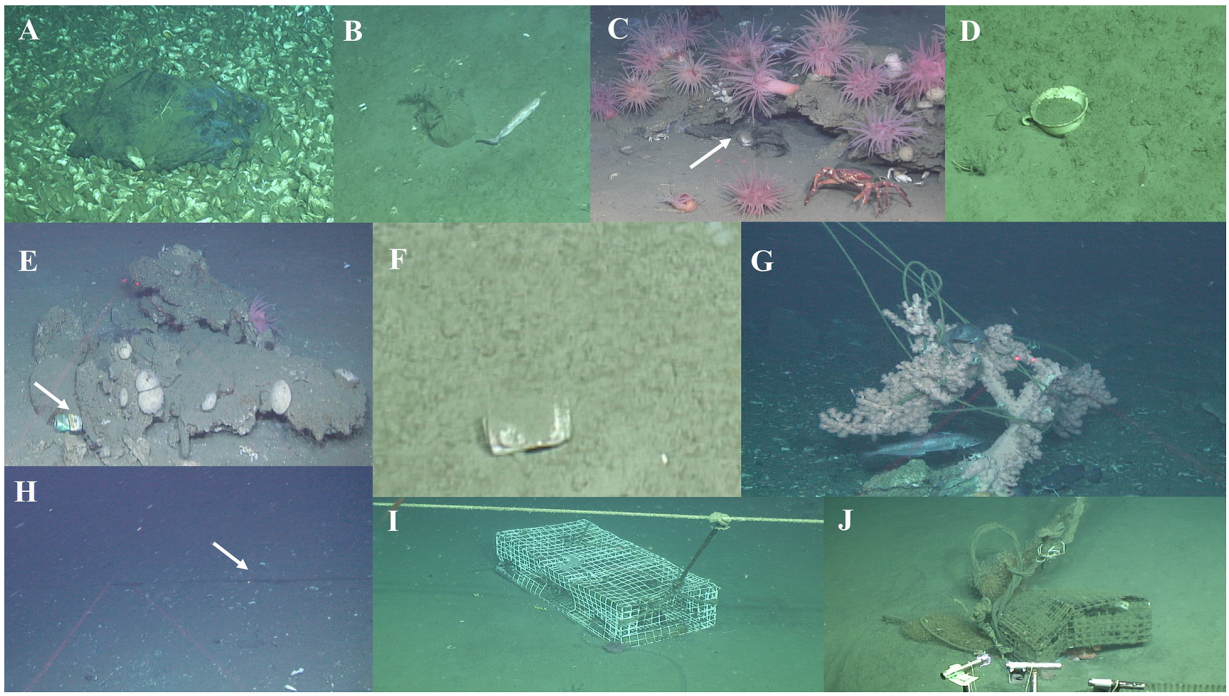


FIGURE 7 | Marine litter items at Baltimore (BC) and the Norfolk (NC) canyon seeps. Plastic bags **(A,B)** and teacup **(D)** at NC; plastic bag at BC **(C)**. Tin cans at BC **(E)** and NC **(F)**. Lost/abandoned fishing gear at the BC **(G–J)**; note at **(G)** the large colony of *Paragorgia arborea* tangled in the abandoned gear.

discrepancy between benthic and benthopelagic ecosystem components may be that macroinfaunal and megabenthic communities have a higher dependency on the seafloor compared to pelagic organisms, and this is reflected in the type of environmental variables explaining faunal distribution across space (Gallucci et al., 2020).

Role of Microbial Mats and Gas Bubbling Sites in Shaping Megabenthic Associations

The presence of microbial mats and gas bubbling sites had a minor but statistically significant contribution in the explanation of variability in megabenthos. Microbial mats are formed where methane flux and anaerobic oxidation of methane rates are high, and therefore the upper layer (∼1 cm) of sediment is rich with sulfide (Foucher et al., 2009). At BC, the hermit crab *Tomopaguropsis* sp. was among the species with a higher contribution in explaining dissimilarities between locations with and without microbial mats (**Supplementary Table 8**). Without access to biological samples it is impossible to draw conclusions on the type (if any) of association between these hermit crabs and microbial mats. However, investigation of carbon sources on *Paralomis* sp. crabs in cold seeps in Costa Rica revealed microbial mat-derived carbon provided an important contribution to the crab's nutrition. Lipid analyses showed *Paralomis* were feeding on other ^{13}C-depleted organic matter, probably symbiont-bearing megafauna as well as sedimentary detritus (Niemann et al., 2013). Hermit crabs have also been reported feeding on *Beggiatoa* mats at the Gullfaks seeps in the North Sea (Hovland, 2007). Apart from the hermit crab *Tomopaguropsis* sp., the anthozoans *Hormathia* sp., and *Actinoscyphia* sp. had higher average density in locations closer to mats and gas bubbling sites, respectively. *Hormathia* in Concepción Methane Seep Area, Chile was characterized as a non-endemic seep species (Sellanes et al., 2008). Although direct evidence for the BC anthozoans is lacking, it is likely these species can assimilate, through their microbial symbionts, chemical compounds released to the water column (Rodríguez and Daly, 2010; Goffredi et al., 2021). Macroinfaunal densities at BC and NC microbial mats were four times greater than those at mussel beds and slope sediments, dominated by polychaete families; multivariate analysis showed specific sediment properties shaped macrofaunal communities, including larger grain sizes at NC microbial mats (Bourque et al., 2017).

In contrast to BC, the presence of microbial mats and gas bubbling sites at NC had a statistically significant contribution in shaping megabenthic associations only in one dive, i.e., J2-683. SIMPER analysis showed that echinoids (white and red morphs) had higher densities in samples with, than those without, microbial mats/gas bubbling sites. Again, without access to biological samples it is impossible to draw firm conclusions on the associations, if any, between these echinoids and the microbial mats/gas bubbling sites. It should be mentioned though that studies analyzing gonad fatty acids have suggested that the urchin *Spatangus purpureus* feeds on phytodetritus, faunal detritus, microbial mats or a combination of all three sources (Barberá et al., 2011). The possible discrepancy regarding the role of microbial mats and gas bubbling sites between BC and

NC is an intriguing finding considering that the numbers of microbial mats recorded at NC were comparable to those at BC (**Figure 1** and **Supplementary Table 2**). The reasons behind this discrepancy are not known. Possibly they are related to spatial variability in the distribution, intensity and/or composition of chemical fluxes and/or the mat microbial species composition. The mapping of 570 seeps in the United States Atlantic Margin showed approximately 440 of them lie on the upper continental slope between ∼180 m (shelf break) and 600 m water depth (Skarke et al., 2014). Furthermore, studies have shown the role of sulfide fluxes in shaping macrofaunal community structure at gas hydrates deposits with flux being highest in *Beggiatoa*, slightly less in *Calyptogena* clams, and low in areas with *Acharax* bivalves (Sahling et al., 2002). Horizontal and vertical distribution of sulfide also shaped the fine-scale distribution, structure, and composition of macrofaunal associations in Pacific methane seeps off California (Levin et al., 2003), while studies in the Gulf of Mexico revealed significant differences in the structure of infaunal communities across the *Arcobacter*, *Thioploca*, and *Beggiatoa* microbial mats (Robinson et al., 2004). The concentric zonation of mussels, clams and Siboglinidae polychaetes around pockmarks in the Blake Ridge Diapir seep field and Congo-Angola Margin suggested the influence of chemical gradients on megafaunal distribution (Olu-Le Roy et al., 2007). The relatively limited role of microbial mats in shaping megabenthic associations at NC could be due to the most abundant species recorded at NC (e.g., ophiuroids, the sea cucumber *Chiridota heheva*, two morphotypes of sea urchins) not relying heavily on microbial mats as a food source. Studies from Gulf of Mexico cold seeps showed asteroids and ophiuroids had tissue isotope values reflecting the input of free-living microbial detritus in their diet or predation (Carney, 2010); *C. heheva* can feed on various sources (Carney, 2010) and partially preys on bivalve tissues (Olu et al., 2009); sea urchins on the Oregon and California Margin seem to have photosynthesis-based diets (Levin and Michener, 2002). Stable isotope analysis of BC and NC megafauna will provide an insight to their diets and dependency on microbial mats (Demopoulos et al., 2019).

Marine Litter at the BC and NC Sites

Image analysis revealed a relatively small number of marine litter items at BC and NC sites. Some of them were clearly related to commercial fishing activities (e.g., abandoned nets) such as for the red crab *C. quinquedens* and fishes (Ross et al., 2015; Turner et al., 2020). We note here that both seep sites were outside the main axes of the two major canyons. Since canyons, including BC and NC, are known to accumulate, concentrate and transport debris and litter (Van den Beld et al., 2017; Dominguez-Carrió et al., 2020; S. W. Ross, unpubl. data), we might expect less density of anthropogenic debris on the open slope outside the main canyon axes than within. Despite the small number of items observed, their negative impacts can be long-lasting, particularly in the case where long-lived ecosystem engineers are affected (e.g., see the damaged bubblegum coral, **Figure 7G**; Williams et al., 2010). In addition to the direct impacts on deep-sea fauna, bottom trawling can further affect the health status of canyon fauna through the alteration of physical properties of surface sediments (Martin et al., 2014), sediment resuspension (Paradis et al., 2017), downslope deposition and smothering (Puig et al., 2012); close monitoring of health status and the establishment of area-based management tools (e.g., marine protected areas) will serve the conservation of rich seep biodiversity and associated ecosystem services for the future.

CONCLUSION

The present study advanced our understanding about the key role that environmental parameters (e.g., depth, type of habitat, and microbial mats) play in shaping the distribution of cold seep megabenthos. This information is crucial for improving model predictions on the spatial distribution of seep fauna and for the successful protection of deep-sea habitats, e.g., through the designation of networks of ecologically coherent marine protected areas. In 2016 the Northeast Canyons and Seamounts Marine National Monument was designated aiming to protect an area of high diversity and ecological connectivity across depths and along the United States Atlantic continental margin (Auster et al., 2020 and references therein; see also links below for the Frank R. Lautenberg Deep-Sea Coral Protection Area which took effect in early 2017)[3]. In addition to its high diversity, the Monument is relatively undisturbed and could serve as a reference point, which is vital for the assessment of deep-sea environmental status (Orejas et al., 2020). Deep-sea ecosystems are currently threatened by multiple anthropogenic stressors. Development of basin-scale strategic research and establishment of interdisciplinary collaborations are keys for the efficient protection and conservation of fragile deep-sea ecosystems for the future.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SWR designed and co-led the ship and ROV surveys. SWR, JMR, and JC coordinated the data collection. JC analyzed the video material and completed the megafauna annotations. GK and JC carried out the statistical analysis and wrote the manuscript with editorial assistance from SWR and JMR. All authors contributed to the article and approved the submitted version.

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[3]https://www.fisheries.noaa.gov/resource/map/frank-r-lautenberg-deep-sea-coral-protection-areas-map-gis

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Exceptional 20th Century Shifts in Deep-Sea Ecosystems Are Spatially Heterogeneous and Associated With Local Surface Ocean Variability

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Traditionally, deep-sea ecosystems have been considered to be insulated from the effects of modern climate change, but with the recognition of the importance of food supply from the surface ocean and deep-sea currents to sustaining these systems, the potential for rapid response of benthic systems to climate change is gaining increasing attention. However, very few ecological time-series exist for the deep ocean covering the twentieth century. Benthic responses to past climate change have been well-documented using marine sediment cores on glacial-interglacial timescales, and ocean sediments have also begun to reveal that planktic species assemblages are already being influenced by global warming. Here, we use benthic foraminifera found in mid-latitude and subpolar North Atlantic sediment cores to show that, in locations beneath areas of major surface water change, benthic ecosystems have also changed significantly over the last ∼150 years. The maximum benthic response occurs in areas which have seen large changes in surface circulation, temperature, and/or productivity. We infer that the observed surface-deep ocean coupling is due to changes in the supply of organic matter exported from the surface ocean and delivered to the seafloor. The local-to-regional scale nature of these changes highlights that accurate projections of changes in deep-sea ecosystems will require (1) increased spatial coverage of deep-sea proxy records, and (2) models capable of adequately resolving these relatively small-scale oceanographic features.

Keywords: foraminifera, benthic, Atlantic, climate change, circulation, ecosystem, deep-sea

INTRODUCTION

The deep-sea benthic habitat is one of the most extensive on Earth. It spans continental slopes, seamounts, deep-ocean trenches, and the abyssal plains. Habitat types range from soft sediment environments to rocky slopes, boulder fields, and hydrothermal vents. Habitat forming species such as cold-water corals and sponges add additional three-dimensional structure and provide nursery and shelter for many other species (Roberts et al., 2006; Howell et al., 2016). New species are frequently discovered during scientific expeditions.

When compared with the surface ocean environment, the deep ocean is relatively isolated from the habitat changes most typically associated with anthropogenic greenhouse gas emissions, i.e., temperature change, ocean acidification and changes in mixed layer depth. However, direct and rapid links between the surface and deep ocean are increasingly being recognized. The main source of food to organisms living in the deep ocean is organic matter sinking as a result of surface productivity, and the amount and type of this export productivity is a driver of the abundance and diversity of benthic species (Sun et al., 2006; Corliss et al., 2009; Gooday et al., 2012; Diz and Barker, 2016). The volume of this export productivity is controlled by numerous factors (temperature, positions of fronts, nutrient supply, mixed layer depth, size, and type of matter), which are all affected by climate change. In addition, the presence or absence, and strength, of deep-sea currents plays an active role in determining the bottom habitat, and in stimulating food supply for suspension feeders. The strength of such currents can respond quickly to wind and buoyancy forcing of the surface ocean. The deep ocean is therefore not immune to the effects of anthropogenic climate change.

However, deep-ocean ecosystems are difficult to monitor at spatial scales beyond the light penetration limit of submersibles, or over long time periods. With the exception of a few dedicated monitoring stations (Gooday et al., 2010) and rare high resolution sedimentary records (Dijkstra et al., 2015, 2017), observations of deep-sea ecosystems are made from research expeditions that rarely return to exactly the same locations. It has therefore been difficult to demonstrate that modern climate change is affecting deep-sea ecosystems beyond the range of natural variability.

Over much longer timescales, deep-sea sedimentary records containing benthic foraminifera, as well as collections of ancient coral skeletons, have revealed that both types of organism have responded rapidly to climatic change during the last 100,000 years. For example, cold-water coral mounds expanded northward in the North Atlantic and species changed their ranges in the Drake Passage during the last deglaciation, keeping pace with deglacial climate change (Henry et al., 2014; Margolin et al., 2014). Benthic foraminifera inhabit a number of niches in deep-sea sediments, including epifaunal species sensitive to the presence of a bottom layer of detritus derived from surface productivity, and infaunal species sensitive to pore water oxygen concentration, itself a function of the concentration of organic matter within the sediment. Previous work has shown that benthic foraminifera responded to past rapid climate changes, such as abrupt events during the last glacial period (Thomas et al., 1995; Ohkushi et al., 2013; Moffitt et al., 2014, 2015), and to more modest climatic change during the Holocene (Ohkushi et al., 2013; Moffitt et al., 2014, 2015; Perner et al., 2015; Smart et al., 2019; Palmer et al., 2020).

Now, with a growing collection of high-resolution sediment archives that capture recent climate variability, we are able to explore changes in benthic ecosystems during the twentieth century and place them in the context of thousands of years of prior ocean history. Here, we present data on benthic foraminifera populations over the Holocene period from the North Atlantic, a region of the ocean that has been responding to industrial-era (∼1850 CE onward) climate change in a variety of ways, mainly via changes in the strength and positions of surface and deep ocean currents and associated changes in temperature and productivity (Thornalley et al., 2018; Osman et al., 2019; Spooner et al., 2020). The primary aim of this research is to undertake an initial investigation into whether the anomalous changes in the oceanography of the 20th century North Atlantic have altered benthic ecosystems, and if so, where. Building on the work of Spooner et al. (2020), which investigated 20th century changes in ecology and hydrology in the northeast Atlantic surface ocean, we examine benthic and planktic records from across the North Atlantic basin. We supplement the (mostly planktic) data of Spooner et al. (2020) with new planktic and/or benthic data from the northeast Atlantic (shallow Iceland Basin, the Reykjanes Ridge, and the Eirik Drift) and present new data from the northwest Atlantic (the Scotian Slope and the Laurentian Slope). In this basin-wide overview, we focus on the common features and relationships observed across our sites for the Holocene and the industrial era (past ∼10 kyr). We show that, in areas most affected by surface ocean changes (i.e., the northeast and western margin of the Atlantic close to major water mass transitions), benthic foraminifera underwent large 20th century changes. In some cases, and in line with certain surface ocean data, these changes appear exceptional in the last 10,000 years.

MATERIALS AND METHODS

Benthic foraminifera assemblages were analyzed from six locations spanning the North Atlantic between 35°N and 60°N. With the exception of Reykjanes Ridge, two cores were analyzed from each location: a gravity or piston core spanning thousands of years, and a companion multi- or box-core containing the sediment-water interface (**Table 1** and **Figure 1**).

RAPiD-17-5P/EN539-MC16-A/B are three cores from within 100 m of one another from the Iceland Basin, within the path of the Iceland Scotland overflow water (ISOW; Moffá-Sanchez et al., 2015; Spooner et al., 2020). We shall refer to these cores as "IB deep." EW9302-29GGC and EN539-MC25-A are also from the Iceland Basin, but lie in shallower water closer to Iceland and are bathed by Eastern Mode Water (Hátún et al., 2016). We shall refer to these cores as "IB shallow." The core RAPiD-21-3K, "Reyk R," is from the eastern Reykjanes Ridge and lies in downstream ISOW, where flow speed is modulated by Labrador Sea Water (Boessenkool et al., 2007). The cores RAPiD-35-14P/RAPiD-35-25B (Moffa-Sánchez et al., 2014; Moffá-Sanchez et al., 2015), "Eirik D," are from the Eirik Drift, located in the central subpolar gyre within the path of Denmark Straits overflow water (DSOW). These cores have been spliced together in previous studies (RAPiD-35-COM; Moffá-Sanchez et al., 2015), although in our present study a separate sub-core of RAPiD-35-25B has been used: a slab taken at the time of the box-core retrieval, obtained by pressing a plastic tray used for kasten core sampling into the side of the box-core. The "slab" sub-core has a more highly resolved top few centimeters compared to the Moffa-Sánchez et al. (2014) and Moffá-Sanchez et al. (2015) sub-core whose uppermost portion underwent significant compaction during sub-coring and

TABLE 1 | Locations and details of sediment cores used in this study.

Location	Abbreviation	Core	Latitude (°N)	Longitude (°W)	Depth (m)	Gear type*	References
Northeast Atlantic	IB deep	EN539-MC16-A	61.4831	19.5361	2311	MC	Spooner et al., 2020
		EN539-MC16-B	61.4831	19.5361	2311	MC	Spooner et al., 2020
		RAPiD-17-5P	61.4817	19.5360	2303	P	Moffá-Sanchez et al., 2015; Spooner et al., 2020
	IB shallow	EN539-MC25-A	62.6125	20.6358	1310	MC	Spooner et al., 2020
		EW9302-29GGC	62.6123	20.6375	1299	GGC	Thornalley et al., 2013
	Reyk R	RAPiD-21-3K	57.2715	27.5488	2630	K	Boessenkool et al., 2007; Sicre et al., 2011; Miettinen et al., 2012; Spooner et al., 2020
Labrador Sea	Eirik D	RAPiD-35-25B	57.51	48.72	3486	B	Moffa-Sánchez et al., 2014
		RAPiD-35-14P	57.50	48.72	3484	P	Moffá-Sanchez et al., 2015
Northwest Atlantic	Laurent S	KNR158-4-10MC	44.50	54.54	1854	MC	Marchitto and de Menocal, 2003; Thornalley et al., 2018
		KNR158-4-9GGC	44.50	54.54	1854	GGC	Marchitto and de Menocal, 2003
	Scot S	KNR197-10-MC45-C	43.35	60.21	966	MC	This study
		KNR197-10-44GGC	43.35	60.21	966	GGC	This study

**MC, multi-core; B, box-core; K, Kasten core; P, piston core; GGC, giant gravity core.*
IB, Iceland basin; Reyk R, Reykjanes Ridge; Eirik D, Eirik Drift; Laurent S, Laurentian Slope; Scot S, Scotian Slope.

its storage in an upright vertical position for several years prior to sampling. The remaining cores are from the Scotian Slope and Laurentian Slope in the western North Atlantic, a region which has undergone significant change in upper ocean temperature and inferred circulation (Thornalley et al., 2018). KNR197-10-MC45-C and KNR197-10-44GGC, "Scot S," are within the path of upper Labrador Sea Water (LSW) and KNR158-4-9GGC and KNR158-4-10MC, "Laurent S," are within the path of LSW.

Age models for IB deep, IB shallow, Eirik D, and Laurent S were taken from the literature cited in **Table 1** (most notably, see Extended Data **Figure 2** of Thornalley et al., 2018, and **Supplementary Figure 7** of Spooner et al., 2020). Given the uncompacted core top of our subcore for RAPiD-35-25B, and that the box-core sediment-water interface was collected intact, we assume a modern age for the sediment-water interface, and then apply the age constraints of Moffa-Sánchez et al. (2014) by transferring the age-depth tie points onto our subcore depths via the alignment of the common features in their percent coarse fraction records (**Supplementary Figure 1**). A new age model for Reyk R was constructed using ^{210}Pb and ^{14}C data from Boessenkool et al. (2007) and Sicre et al. (2011). ^{210}Pb data was taken from the companion core RAPiD-21-12B (Boessenkool et al., 2007). The percent coarse fraction records of both cores suggest that these data can be applied to Reyk R (**Supplementary Figure 2**; Miettinen et al., 2012; Moffa-Sánchez and Hall, 2017). ^{14}C data were calibrated using the MARINE13 calibration curve (Reimer et al., 2013), individually using Calib7.1 (Stuiver et al., 2021), and by using a Bayesian framework in OxCal with a Poisson distribution model (Ramsey, 2008). One date at 206–207 cm was excluded from the age model due to poor agreement. A new age model for KNR197-10-MC45-C was constructed using ^{210}Pb data measured on bulk sediment at University College London (**Supplementary Figure 3**). The age model for KNR197-10-44GGC was constructed using δ^{18}O measurements measured on *Neogloboquadrina pachyderma* at the University of Cambridge and ^{210}Pb data measured on bulk sediment at University College London. *N. pachyderma* δ^{18}O measurements were tuned to published *N. pachyderma* δ^{18}O data from the previously radiocarbon-dated cores OCE326 14GGC and OCE326 26GGC (**Supplementary Figure 4**; Keigwin et al., 2005). The core top of KNR197-10-44GGC was shown to overlap with the base of KNR197-10-MC45-C using a combination of planktic foraminifera species counts and grain size data (**Supplementary Figure 5**).

Benthic foraminifera were typically counted in the >150 μm fraction (rather than >63 μm) because the cores sites are located at drift sites where the relatively fast flowing bottom currents have the potential to transport smaller benthic foraminifera. Counts on the >63 μm fraction were conducted at Reyk R, where sediment grain size analysis indicates the presence of only relatively fine silts (**Supplementary Figure 6**; Boessenkool et al., 2007). In EN539-MC25-A, higher resolution counts were also made in the >212 μm size fraction (**Supplementary Figure 7**). Choice of size fraction can impact the relative abundance of species found at different sites. For example, the epifaunal foraminifera *Epistominella exigua* is generally smaller than >150 μm, but is abundant in the 63–150 μm size fraction. Therefore, we compare general trends across core sites rather than comparing species assemblages, and our main arguments rely on the total accumulation of benthic foraminifera.

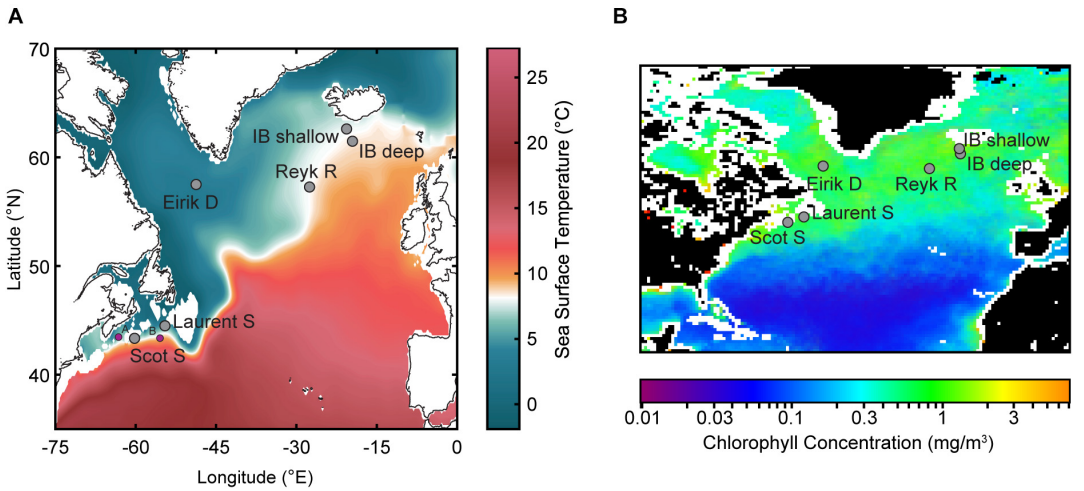


FIGURE 1 | The subpolar North Atlantic with locations of core sites used in this study (see **Table 1**). **(A)** Colors indicate the mean annual climatological sea-surface temperature (SST; °C) from the World Ocean Atlas (Locarnini et al., 2013). Purple circles indicate A, OCE-326-30GGC/MC29 (Emerald Basin; Keigwin et al., 2003), and B, OCE-326-14GGC/MC13 (Laurentian Fan; Keigwin and Pickart, 1999). **(B)** Ocean color data of average annual chlorophyll in 2010 (mg/m^3) from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Ocean Color Data (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, and Ocean Biology Processing Group, 2018 Reprocessing).

Furthermore, at site IB shallow, and more limited data at site Reyk R, we note that similar trends are observed for the total benthic abundance obtained from >63, >150, and >212 μm (**Supplementary Figures 6–8**), suggesting the robustness of these trends regardless of specific size fraction. Benthic foraminifera counts included calcifying species, and excluded agglutinating forms due to their typical poor preservation downcore, with the exception of the well-preserved Miliolida *Sigmoilopsis schlumbergeri*. We include planktic foraminifera counts from the literature or newly counted on the >150 μm size fraction to discern changes in the surface ocean. We provide new, unpublished counts in EW9302-29GGC, RAPiD-35-14P and 25B, Laurent S and Scot S.

Accumulation rates (AR) of benthic and planktic foraminifera were calculated according to the formula:

$$AR = \#/g \times \rho \times sedimentation\ rate$$

where #/g is the number per wet gram of sediment, and ρ is the density of the wet sediment, calculated from the dry mass and mass of water assuming an average grain density of 2.65 g/cm^3, and water density of 1.027 g/cm^3. Water content data were not collected for EW9302-29GGC or KNR158-4-10MC, and we therefore estimated the water content in these cores from the base of EN539-MC25-A (50%) and the whole of KNR158-4-9GGC (50%), respectively. Water content for the samples taken from RAPID-35-25B was estimated using the samples in Moffa-Sánchez et al. (2014). The sedimentation rate at the top of EW9302-29GGC is complicated by a ∼5 cm thick ash layer between 6 and 11 cm. Therefore, despite the radiocarbon dates suggesting a very high sedimentation rate of 84 cm/kyr, we assign a sedimentation rate to the top sample (0–1 cm) of 27 cm/kyr, the mean sedimentation rate of the Holocene section of the core (±4.3 cm/kyr 2 SD).

Accumulation rates and % abundance data were plotted on linear time-series to examine temporal trends and were accompanied by density plots to more clearly evaluate the distribution of Holocene (10 kyr b2k to 1750 CE) versus industrial era (1900 CE onward) values in each dataset.

RESULTS AND DISCUSSION

Our results demonstrate that benthic foraminifera have been responding to ongoing climate change during the industrial era, and that the state reached by the benthic fluxes can be unusual for the Holocene. In addition, the regions that show the largest magnitude changes in the benthic accumulation rates are also subject to significant surface ocean changes involving the shifting properties/locations of major ocean currents (**Figures 1**, **2**). Thus, the benthic response to climate change is not an *en masse* basin-wide response, but is dependent on local surface ocean conditions and can therefore differ depending on location.

Northeast Atlantic

In the northeast Atlantic close to Iceland, we find a range of 20th century benthic responses. At IB deep, the abundance of benthic foraminifera declined during the 20th century and reached a Holocene low (0.2 cm^{-2} yr^{-1}) during the last few decades (this study; Spooner et al., 2020). This result is compared to a Holocene maximum of up to 4 cm^{-2} yr^{-1} (**Figures 3A,B**). Epifaunal and infaunal genera show the same trends in constant relative abundance (**Supplementary Figure 9**), so the decline in accumulation rate cannot be explained by a core top expression of habitat zoning. The decline in abundance is not accompanied

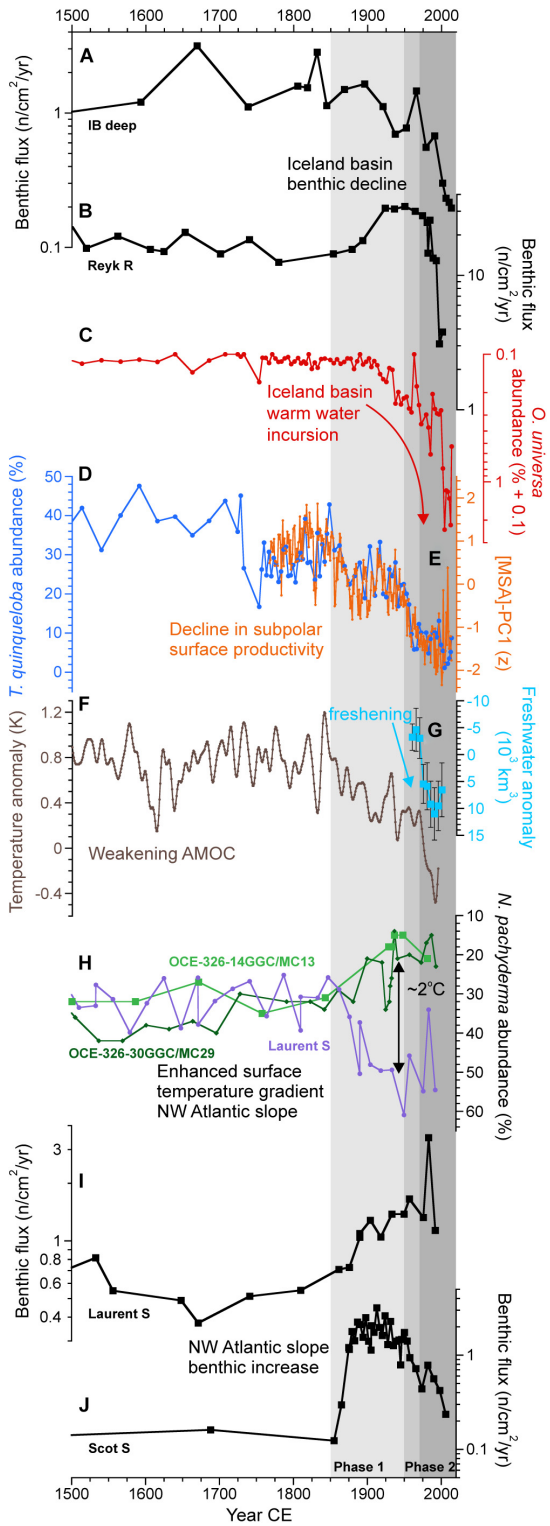


FIGURE 2 | Five hundred-year North Atlantic benthic foraminifera accumulation rates in relation to key oceanographic changes. **(A)** Benthic foraminifera flux in IB deep* (Spooner et al., 2020; this study); **(B)** Benthic foraminifera flux in Reyk R (this study); **(C)** % abundance of warm water *O. universa* in IB deep* (Spooner et al., 2020); **(D,E)** Indicators of Iceland *(Continued)*

FIGURE 2 | (Continued)
basin and subpolar surface productivity; **(D)** Subpolar, high productivity species *T. quinqueloba* % abundance in IB deep* (Spooner et al., 2020), blue; **(E)** Greenland ice core methanesulfonic acid (MSA) record of subpolar surface ocean productivity, orange (Osman et al., 2019); **(F)** AMOC index of Rahmstorf et al. (2015); **(G)** 5-year averaged subarctic Atlantic freshwater storage anomalies (±2σ; anomalies relative to 1955) from Curry and Mauritzen (2005); **(H)** Surface ocean temperature changes in the northwest Atlantic slope region based on % abundance of the polar species *N. pachyderma* in cores OCE-326-14GGC/MC13 [Laurentian Fan; (Keigwin and Pickart, 1999); age model updated to include a tie at 4.5 cm for the 1929 Grand Banks turbidite which deposited a red clay layer at this site], OCE-326-30GGC/MC29 [Emerald Basin; (Keigwin et al., 2003); using the published ^{14}C and ^{210}Pb data for the age model], and Laurent S (Laurentian Slope; Thornalley et al., 2018; and this study), for visualization of the relative temperature changes OCE-326-14GGC/MC13 has been offset by +10%; **(I)** Benthic foraminifera flux in Laurent S (this study); **(J)** Benthic foraminifera flux in Scot S (this study). Vertical gray-shaded bands indicate post-1850, 1950, and 1970 periods. *Note, for this figure an additional age tie was included for IB deep (20.75 cm = 1848 CE, decreasing the core age by 28 years, well within the age model uncertainty) based on alignment of the % *T. quinqueloba* record with the remarkably similar MSA subpolar productivity record, the latter benefiting from a more precise age model.

by significant changes in the percentages of any major group of benthic foraminifera [e.g., high food group (Smart et al., 2019), phytodetritus group, epifaunal, infaunal, Miliolida] at either core site (**Supplementary Figure 9**), suggesting that selective taphonomic bias also does not affect our results (Stefanoudis et al., 2017). The abundance trend is similar to the collapse in planktic foraminifera abundance in the northern Iceland Basin over the 20th century (**Figures 3F,G**), as well as a change in the dominant planktic species (**Figures 3K,L**), suggesting declining export productivity at the eastern edge of the subpolar gyre (SPG). It has previously been argued that this change in productivity was caused by a shift in local frontal activity associated with the retreat of subpolar water and its replacement by transitional water with its origins in the subtropical gyre, as evidenced by the steep decline in the abundance of the subpolar and high productivity-associated planktic foraminifer *Turborotalita quinqueloba* (**Figures 3K,L**), and the increase in transitional-subtropical *Orbulina universa* (**Figures 3P,Q**) (Spooner et al., 2020).

Slightly further north at site IB shallow, there is some evidence for a higher recent accumulation rate of benthic foraminifera, but this is not beyond other events seen in the Holocene (**Figures 3C,D**). In addition, the number of benthic foraminifera per gram of sediment does not show such a prominent late 20th increase as seen in IB deep (**Supplementary Figure 16**). Moreover, the observed slight increase in benthic foraminiferal accumulation rate at IB shallow does not exceed our uncertainty estimates. Overall, the evidence for a significant 20th century shift in benthic foraminifera at this site is not very robust. This finding reflects our earlier results that showed little change in the planktic foraminifera assemblage and abundance (most notably *T. quinqueloba*) over this time interval (**Figures 3H,I,M,N,R,S**; Spooner et al., 2020).

Approximately 500 km to the southwest, at Reyk R, the 20th century is characterized by an increase and then a decrease in

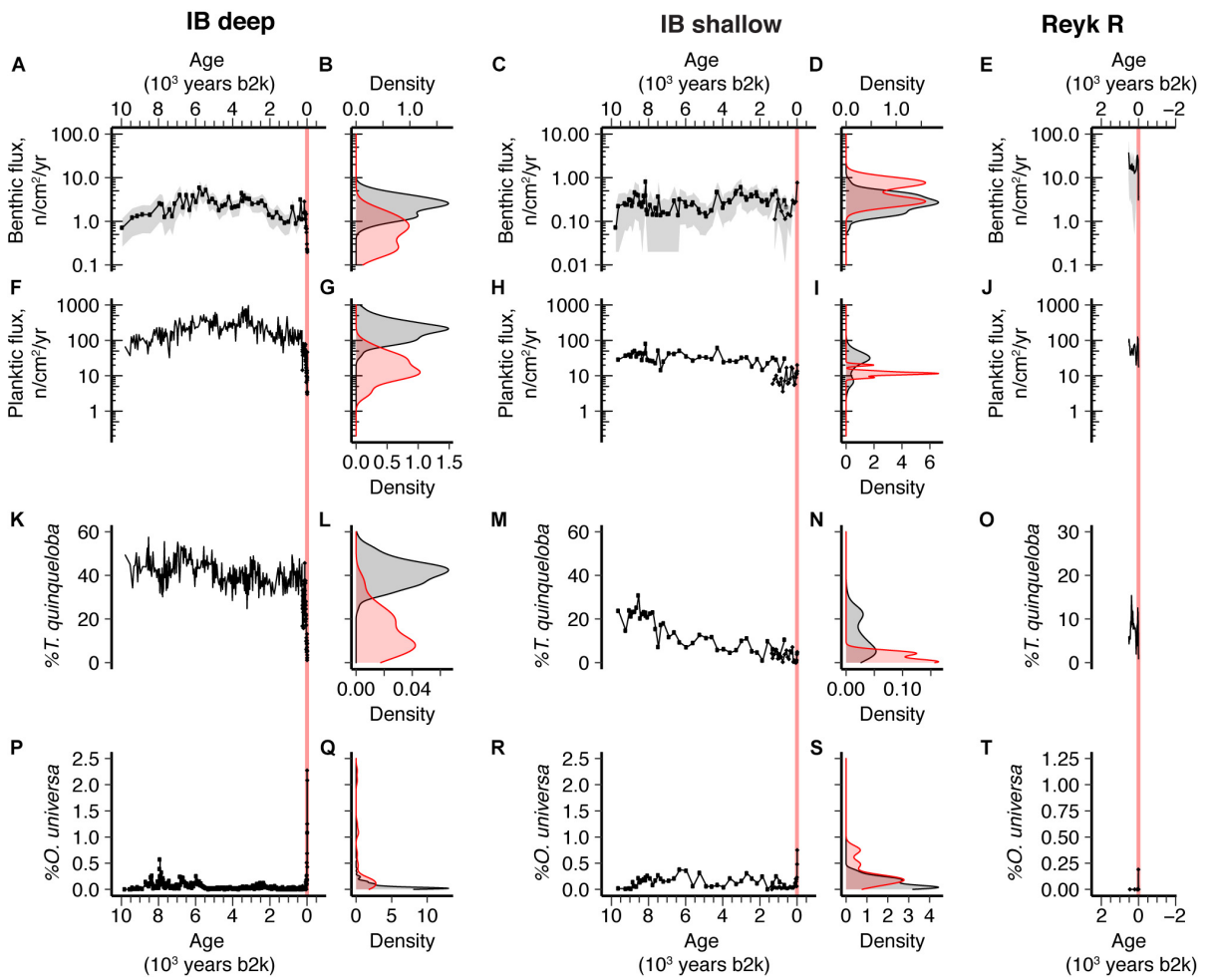


FIGURE 3 | Ten thousand-year northeast Atlantic sediment records and density distribution plots comparing the distribution of Holocene (black) versus industrial era (red) data from IB deep **(A,B,F,G,K,L,P,Q)**, IB shallow **(C,D,H,I,M,N,R,S)**, and Reyk R **(E,J,O,T)**. **(A–E)** Benthic foraminifer flux; **(F–J)** planktic foraminifer flux; **(K–O)** *Turborotalita quinqueloba* % abundance; *Orbulina universa* % abundance **(P–T)**. *Turborotalita quinqueloba* % abundance in IB deep and Reyk R, and *Orbulina universa* % abundance data in IB deep, are from Spooner et al. (2020). Benthic abundance data (benthics g^{-1}) for IB deep and planktic abundance data (planktics g^{-1}) for IB deep and Reyk R were previously published (Spooner et al., 2020) and have been converted to benthic and planktic fluxes, respectively (this study). Vertical red-shaded band indicates industrial era. Gray-shading in the benthic flux time series plots represents 2σ error.

both the benthic and planktic accumulation rates (**Figures 3E,J**). The benthic decline after around 1980 leads to the lowest benthic accumulation rate in the record (spanning 1500 years). The most abundant benthic foraminifera at Reyk R (>63 μm) was *Epistominella exigua*, an opportunistic species that dwells in the phytodetritus layer; however, the recent decline in benthic foraminifera is seen in infaunal and epifaunal species, and photodetritus and non-photodetritus associated species (**Supplementary Figure 12**). Although more muted than the surface ocean changes recorded at our sites closer to Iceland, after ∼1980, Reyk R also records a decline in the high-productivity, subpolar planktic species *T. quinqueloba* (**Figure 3O**) (Spooner et al., 2020) and an increase in the warm, more-oligotrophic associated *O. universa* (**Figure 3T**), suggesting a moderate decrease in the local surface ocean productivity. Additionally, Reyk R lies downstream of IB deep in the Iceland-Scotland overflow water (ISOW), so it is possible that the effects of changes in surface oceanography and export in the northern Iceland Basin were propagated by deep-sea currents to the deep ecosystems of the Reykjanes Ridge, compounding any local decrease in the surface-to-deep food supply.

The Labrador Sea

In the central SPG (Eirik D, **Figures 1,4**), the range of variability in benthic foraminifera abundance over the last 500 years is not significantly different to that of the whole Holocene. There is also no difference in the mean benthic flux for the 20th century compared with the Holocene (**Figure 4B**). The cores from this location are not as exceptionally high sedimentation rate as those from the eastern north Atlantic, so it is possible

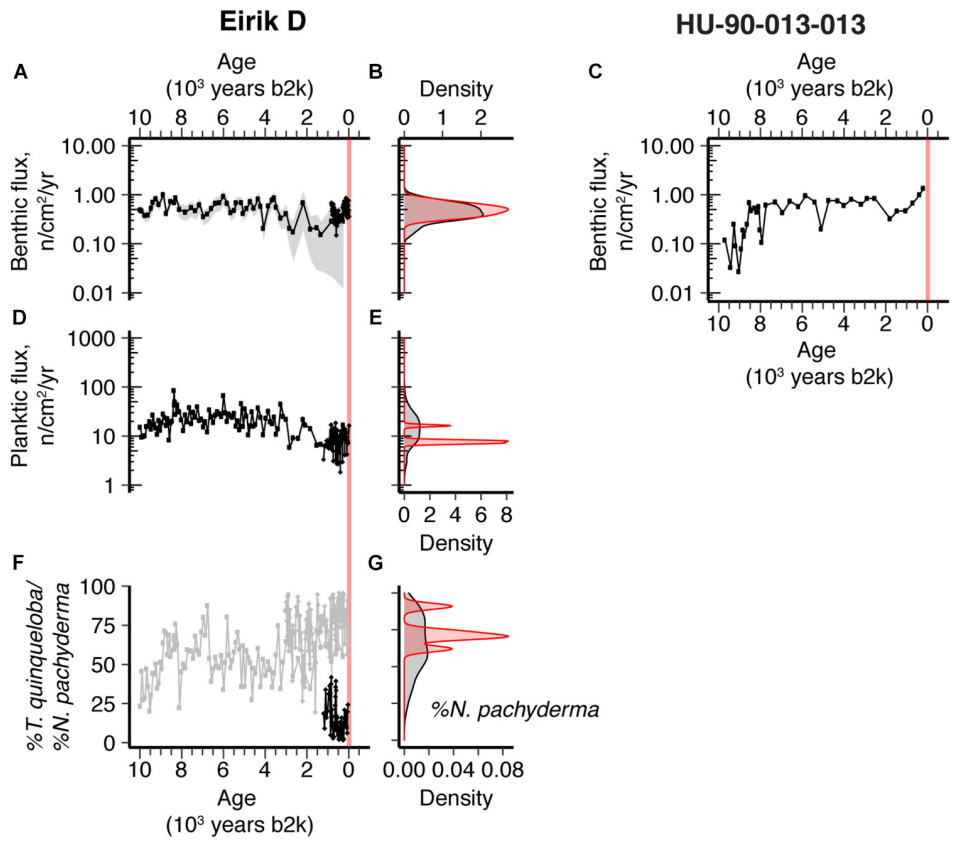


FIGURE 4 | Ten thousand–year Labrador Sea sediment records and density distribution plots comparing the distribution of Holocene (black) versus industrial era (red) data from Eirik D **(A,C,E)** and HU-90-013-013 (Bilodeau et al., 1994). **(A–C)** Benthic foraminifera flux; **(D,E)** planktic foraminifera flux; **(F,G)** *Turborotalita quinqueloba* % abundance (black, panel **F** only) and *Neogloboquadrina pachyderma* % abundance (gray). Vertical red-shaded band indicates industrial era. Gray-shading in the benthic flux time series plots represents 2σ error.

that some shorter term climate signals have been smoothed by bioturbation; however, the presence and exponential decline of excess ^{210}Pb in the top 5 cm and bomb radiocarbon in the core-top sample in the lower resolution subcore used by Moffa-Sánchez et al. (2014) suggest bioturbation was not too extensive; we estimate that the top 4 cm of our subcore captures the 20th century (**Supplementary Figure 1**). Holocene benthic foraminifera abundances at Eirik D are similar in magnitude and variability to benthic fluxes reported for nearby core HU-90-013-013 from the Greenland Rise (Bilodeau et al., 1994). The two youngest samples (∼1550 and 1750 C.E.) from HU-90-013-013 show unexpectedly high values compared with Eirik D, but this could be due to disturbance of the core top. Overall, the null hypothesis that benthic foraminifera have not significantly changed during the industrial era is consistent with the existing data.

Eirik D planktic foraminifera abundance (**Figures 4C,D**) and the relative abundances of key indicator species such as *N. pachyderma* (**Figures 4E,F**) show a slight decrease and increase, respectively, in the industrial era relative to the Holocene. The increase in % *N. pachyderma* began well before the onset of the industrial era, around 3000 years b2k (**Figure 4E**). Overall, however, planktic foraminifera do not show significant industrial era shifts in these cores, suggesting only small changes in surface ocean conditions. In the northeast central Labrador Sea, the core site is not in a position where significant changes in water mass might be expected, being influenced by subpolar waters and the topographically constrained extension of the East Greenland Current. The site is located close to the so-called "warming hole" – the subpolar region where there has been an absence of recent warming (a relative cooling compared to the global mean SST) and which has been related to an industrial-era weakening of AMOC (Caesar et al., 2018); the lack of any recent warming is consistent with our observation of no major industrial-era changes in the planktic foraminifera assemblages. Furthermore, recent observational results indicate that the Labrador Sea contributes minimally to basin-wide overturning (Lozier et al., 2019; Petit et al., 2020), and convection in the Labrador Sea is not closely related to the basin meridional overturning circulation due to density compensation (Zou et al., 2020). Therefore changes in AMOC can be achieved without major shifts in the circulation and overturning of the Labrador

Sea. Overall, we conclude that Eirik D has likely experienced relatively similar surface productivity conditions throughout the Holocene and industrial era.

Northwest Atlantic Slope

In the northwest Atlantic, at the Laurentian Slope site Laurent S, benthic foraminifera accumulation was quite stable for the last 8.5 ka at around 0.5 cm^{-2} yr^{-1}, but an increase in abundance up to typically 1–2 cm^{-2} yr^{-1} emerged during the late 19th century and 20th century (**Figures 5A,B**). This increase in overall abundance of benthic foraminifera is not associated with any clear change in the relative or absolute abundance of different species groups (**Supplementary Figure 14**), suggesting that the change is a broad response to increased food supply but remaining within the same type of benthic environment. Notably, a rapid increase in the relative abundance of the planktic foraminifera *N. pachyderma* from 25 to 50% occurred over the same time interval (**Figures 5I,J**).

Just slightly further south, at site Scot S on the Scotian Slope, benthic fluxes were low in the Holocene, ∼0.01–0.1 cm^{-2} yr^{-1} and then increased from the late 19th century to typical values of 1–2 cm^{-2} yr^{-1} for the 20th century (**Figures 5C,D**). Unlike Laurent S, planktic accumulation rates were higher in the 20th century, 2 cm^{-2} yr^{-1}, compared with the Holocene, <0.1 cm^{-2} yr^{-1} (**Figures 5G,H**). Also, % *N. pachyderma* abundances were variable in the Holocene and decreased in the 20th century (**Figures 5K,L**).

The elevated 20th century benthic foraminifera accumulation rates at both the Laurentian and Scotian Slope sites (**Figures 5A–D**), which experienced contrasting surface ocean changes (**Figures 5E–L**), may be related to inferred changes in ocean frontal gradients/activity. In general, the northwest Atlantic slope region is characterized by northeastward flowing warm slope water influenced by the Gulf Stream, and southwestward flowing cold Labrador slope water. The confluence of these two water masses results in sharp surface ocean thermal gradients and strong frontal activity – in the region of our sites termed the Slope Water jet/front (Pickart et al., 1999) – resulting in highly productive waters and enhanced food supply to the benthos (Belkin et al., 2009). Evidence presented here, and in previous work (Thornalley et al., 2018, Extended Data Figure 5), reveals that after the late 1800s, there was a greater proportion of cold Labrador slope water on the Laurentian Slope at site Laurent S (**Figures 5I,J**, **2H**), while sites located further south and west [Laurentian Fan sites, site Scot S (**Figures 5K,L**), and Emerald Basin (**Figure 2H**)], where there is greater dominance of warm Gulf Stream derived waters, show warmer waters – the opposite signal. This pattern implies that in comparison to earlier centuries, the 20th century is associated with increased temperature gradients across the region, which will have resulted in enhanced surface ocean frontal activity. Here, we suggest that this inferred frontal activity likely promoted increased export productivity from the surface ocean to the deep sea and thus the observed greater benthic productivity at our slope sites.

Although the northwest Atlantic shelf and slope region is an area with complex ocean circulation, we suggest that the broad regional oceanographic changes described above may be related to previously reported weakening of both the AMOC (Thornalley et al., 2018) and the SPG (Spooner et al., 2020). AMOC weakening since ca. 1850 (**Figure 2F**) is thought to cause a northward shift of the Gulf Stream, causing warming at the southwest sites and cooling at the Laurentian Slope site (Thornalley et al., 2018). Furthermore, weakening of the SPG has also been associated with greater penetration of cold subpolar water into the Newfoundland basin, which may also help explain the cooling observed at our open-ocean Laurentian Slope site (Bersch, 2002; Hátún et al., 2005). Earlier work by Pickart et al. (1999) identified a similar mode of variability operating on shorter timescales (interannual-decadal) at the Scotian Slope, characterized by a northward shift of the Slope Water front at the same time as a strengthening of the off-shelf, southwestward flowing, cold Labrador Current and the offshore, northeastward flowing, warm Slope Water jet.

It is important to note that the benthic ecosystem changes we observe at our offshore, open-ocean, relatively deep slope sites (∼1 and 1.8 km water depth) should be considered distinct from reported changes occurring on the shallow continental shelf, including the Gulf of Maine, where there are different ocean currents and dynamics [notably the inshore shelf branch(es) of the Labrador Current]. Moreover, on the shelf, benthic ecosystems can be controlled directly by changes in the upper ocean circulation that bathes the seafloor at the shallow water depths, with a reported recent warming of the shelf causing substantial changes in shallow marine ecosystems (Pershing et al., 2015; Kavanaugh et al., 2017).

Timing and Cause of the Benthic Responses to Industrial Era Climate Change

Our results demonstrate that North Atlantic benthic foraminifera exhibited regional responses to changes in climate and ocean circulation during the industrial era. However, for locations where benthic fluxes show significant shifts in the industrial era compared to the Holocene, the timing of these changes are not always synchronous between sites (**Figure 2**). Our ability to link the timing of benthic foraminifera changes to specific changes in North Atlantic ocean circulation is hindered by limitations in our knowledge of when, what and how circulation changed during the industrial era. Notwithstanding these limitations, and by greatly simplifying the evidence, existing proxy data suggest that there have been two major industrial era shifts, the first (Phase 1) occurring at ∼1850–1900, and then a series of shifts occurring through the mid-late 20th century (Phase 2) with evidence for more marked changes at ∼1970 onward in some datasets, which may be linked to increased freshwater in the subarctic Atlantic (**Figure 2**; Rahmstorf et al., 2015; Moore et al., 2017; Caesar et al., 2018, 2021; Thornalley et al., 2018; Osman et al., 2019; Lower-Spies et al., 2020; Spooner et al., 2020). There has also been large amplitude recent decadal variability through the 1990s and early 21st century (Robson et al., 2016; Holliday et al., 2020). The first shift (Phase 1) has been associated with weakening of LSW flow in the Deep Western Boundary Current [$DWBC_{LSW}$ (Thornalley et al., 2018); please note that

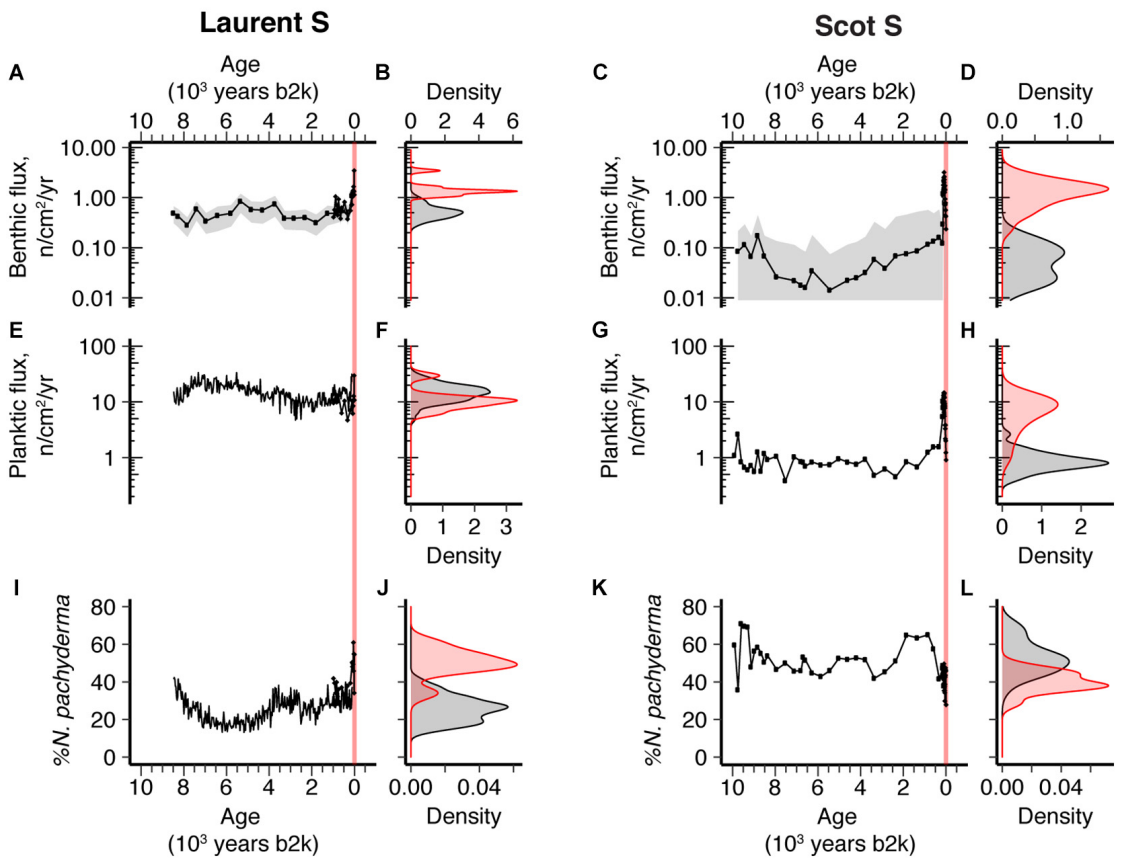


FIGURE 5 | Ten thousand-year northwest Atlantic sediment records and density distribution plots comparing the distribution of Holocene (black) versus industrial era (red) data from Laurent S **(A,B,E,F,I,J)** and Scot S **(C,D,G,H,K,L)**. **(A–D)** Benthic foraminifer flux; **(E–H)** planktic foraminifer flux; **(I–L)** *Neogloboquadrina pachyderma* % abundance. Vertical red-shaded band indicates industrial era. Gray-shading in the benthic flux time series plots represents 2σ error.

recent work has suggested that density changes in the Labrador Sea may be governed by "upstream" processes occurring in the subpolar NE Atlantic (Lozier et al., 2019; Zou et al., 2020)], a weakening of the AMOC, a westward contraction and weakening of the SPG, and exceptional shifts in the surface circulation of the northwest Atlantic slope and shelf. The late 20th century changes (Phase 2) appear most pronounced in records linked to the upper ocean subpolar gyre, while little-to-no change is recorded in the $DWBC_{LSW}$ data, the off-shelf surface temperature records of the northwest Atlantic or the Zhang subsurface AMOC temperature fingerprint index (Thornalley et al., 2018; **Figure 2**). Similarly, previous work has also noted that the spatial pattern of temperature change in the subpolar North Atlantic over recent decades differs from the longer-term, century trend (Spooner et al., 2020). Therefore, there are likely different underlying mechanisms and circulation patterns associated with the two major industrial era shifts as well as recent decadal variability, that are not yet fully resolved or understood.

Figure 2A shows that at IB deep in the northeast Atlantic, there was only a modest decrease in benthic foraminifera flux during the early stage of the industrial era, but a steeper decline occurred after 1950 (Phase 2), which has been linked to changes in SPG circulation (Spooner et al., 2020). At Reyk R, also in the northeast Atlantic, benthic fluxes increased slightly during the second half of the 19th century (Phase 1), remained stable for most of the 20th century, before declining sharply during Phase 2 from the 1980s onward (**Figure 2B**). The recent decline coincides with the more extreme changes observed at IB deep and the enhanced incursion of warm oligotrophic waters into the Iceland Basin (**Figure 2C**). This may be interpreted as a threshold response at Reyk R, such that only the more extreme recent conditions led to a significant change at this site. The contrasting benthic shifts at Reyk R between Phase 1 (increase) and late Phase 2 (decrease) may also be related to the underlying circulation differences between these two phases, noting specifically that the 1980s through to the early 2000s was associated with strong basin-wide warming, whereas Phase 1 had eastern subpolar surface warming but central subpolar cooling (Spooner et al., 2020). Labrador Sea (Eirik D) and the Iceland Slope (IB shallow) north of the SPG show no clear signal during the recent most decades. Taken together, this suggests that the major changes in the central Iceland Basin (IB deep) and along the eastern flank

of the Reykjanes Ridge (Reyk R) are not due to broad changes in the SPG water masses, nor in the subpolar mode waters around the eastern periphery of this gyre, but instead reflect shifts in a major frontal system.

Both northwest Atlantic slope sites (Scot S and Laurent S) record a sharp rise in benthic foraminifera abundance during Phase 1 (∼1850–1900; **Figures 2I,J**), which we have linked to the concomitant exceptional regional surface ocean changes that resulted in enhanced thermal gradients and inferred frontal activity. It is hypothesized that the underlying driver for this regional circulation shift was weakening of the AMOC and/or SPG, although continued work is required to elucidate the details of circulation changes in this region and their link to basin-wide circulation features. At Scotian Slope site Scot S there is a decline in benthic foraminifera abundance from ∼1930 onward (Phase 2), the cause of which remains uncertain, although it may relate to the documented increasing dominance of warm slope water in the region and its impact on the regional ecosystem (Sherwood et al., 2011). At Laurentian Slope site Laurent S there is no major trend or shift in benthic foraminifera abundance during Phase 2 (**Figure 2I**), mirroring the surface ocean records (**Figure 2H**), although the core does not span the most recent decades.

Assumptions in the Interpretation of Benthic Foraminifera Abundance Data

Our main findings are based on the assumption that benthic foraminifera accumulation rates are primarily controlled by food supply from the surface ocean, and covary with surface export productivity (Sun et al., 2006; Jorissen et al., 2007; Corliss et al., 2009; Gooday et al., 2012; Diz and Barker, 2016). However, the amount of organic material reaching the seafloor also depends upon the efficiency of the surface-to-deep organic matter flux, which can vary according to the size of organic matter and its packaging into larger aggregates. Benthic foraminifera may also respond more strongly to seasonal blooms of export of food to the seafloor, as opposed to the integrated annual flux, and certain species feed heavily on food supplied by lateral advection in deep sea currents. Yet, the prevailing picture at all our sites is that there are only minor changes in the species assemblage and, instead, the changes in total foraminiferal accumulation rates are reflected across all the major groups of benthic foraminifera (notwithstanding a small change in Reyk R; see **Supplementary Figure 12**). We suggest this may indicate that there has been no overall change in the style and type of food delivery (and other environmental conditions) at our sites, rather, there has just been a change (increase or decrease, depending on site) in the overall amount of food. This finding may partly be a limitation of typically only counting from the >150 μm fraction, and greater % relative abundance changes, for example in smaller phytodetritus species, may have been obtained with examination of the >63 μm fraction (avoided due to concerns that smaller foraminifera could be transported by strong bottom currents). Yet at site Reyk R, which lies in the path of downstream ISOW controlled by LSW (Boessenkool et al., 2007) and where we counted the >63 μm fraction, we also saw no major shifts in the relative abundance of species. Further investigation of new cores throughout the North Atlantic can test if there are deep ocean sites where major shifts in species assemblage have occurred. Available published datasets and newly generated grain size records from this study (**Supplementary Figures 17–20**) also suggest that changes in the strength of the deep sea currents associated with our different sites, which could have altered the supply of organic matter to our sites by variability in lateral advection, were not a strong control on benthic foraminifera accumulation rates. This is further supported by our observation of no major shifts in the species assemblage, which likely would be expected if there was a significant shift in the proportion of food delivered by lateral advection rather vertical sinking.

CONCLUSION

This study has analyzed benthic foraminifera abundances in high accumulation rate sediment cores from the North Atlantic to investigate if the previously documented anomalous ocean circulation changes of the industrial era have impacted benthic ecosystems. Our results reveal that there are spatially variable changes in benthic foraminiferal abundances during the industrial era, with abundance levels in the 20th century at many sites emerging as exceptional compared to anything seen throughout the prior several thousand years of the Holocene. The most substantial changes have occurred in regions where there have been concomitant anomalous shifts in surface ocean conditions such as temperature and surface productivity. We infer that shifts in surface ocean frontal activity altered the food supply to the benthos, such that areas with decreased (increased) surface frontal activity saw a decrease (increase) in benthic abundance and sites where little surface ocean variability occurred also recorded little-to-no change in benthic foraminiferal abundance.

FUTURE WORK AND IMPLICATIONS

This study represents a preliminary investigation into industrial era changes in North Atlantic deep-sea benthic ecosystems, specifically benthic foraminifera. The obvious next step is to better map out the recent and ongoing shifts in benthic foraminifera reported here, and test the hypothesis that anomalous benthic shifts occur at sites where there have been large magnitude surface ocean changes, particularly ocean fronts. Prior work has been limited by the availability of sufficiently high-resolution sediment records, and future work will rely upon obtaining and examining cores from many more high sedimentation rate sites, with obvious benefits from gathering new cores that can capture some of the large magnitude ocean changes that have occurred in the most recent decades. However, this information will inherently be biased since it depends on selecting sites with high accumulation rates, likely placing restrictions on the types of benthic community that can be examined. Therefore, as far as possible, a wide range of benthic environments should be investigated for marine sediment core work, and this information should be combined with evidence of

deep sea environment and ecosystem change from other archives, such as deep sea corals. As greater time overlap builds between our proxy archives and time series of observed ecological changes, robust testing of the relationships between these two types of data will be possible. Finally, in addition to ecological investigation, additional work is also needed to better constrain and understand the physical oceanographic changes that occurred during the industrial era, for example examining the regional expressions of changes in the AMOC and SPG circulation, and how they may vary in the future.

Our results have broad implications for marine ecosystem management and planning. The impact of changes in large scale circulation features like the AMOC have been modeled previously, for example, a weakening AMOC has been linked to a broad decline in marine productivity (Schmittner, 2005; Whitt and Jansen, 2020). Simple predictive theory suggests that under global warming, reduction in northward nutrient transport is the primary suppressor of Subarctic Atlantic Ocean productivity, while local reductions in vertical mixing have an important, but secondary, effect (Whitt and Jansen, 2020). The spatial heterogeneity that we observe in 20th century shifts in deep sea benthos, linked to surface ocean variability, cautions that accurate projection of future deep sea benthic ecosystems will require models that can capture the local-to-regional scale features of surface ocean circulation – well-illustrated by the complexity of the northwest Atlantic shelf and slope region (Saba et al., 2016; Claret et al., 2018). Marine ecosystem projections based on CMIP5 climate models, which do not adequately resolve many of these features (e.g., Saba et al., 2016), are probably missing likely hotspots of future benthic ecological change. Based on the results of our study, improved modeling capability will be of particular value where deep sea benthic sites of special importance for ecological reasons or socio-economic reasons coincide with regions expected to undergo large shifts in surface ocean properties and frontal migration.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

DT conceived and designed the project. PS, JW, EP, ND, DF, RG, TL, FS, FP, and DT collected the data. CO'B, PS, and JW conducted the data analysis. PS, CO'B, and DT produced the figures and wrote the manuscript. All authors contributed to initial data interpretation.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.663009/full#supplementary-material

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