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Mesophotic sponge assemblages in a region undergoing climate change stressors

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The biogeography of marine benthic assemblages worldwide is shifting to higher latitudes in response to climate change. Concurrently, extreme weather events are exacerbating environmental stressors. As is typical globally for temperate regions, sponge communities dominate the mesophotic reefs of the Motiti archipelago in the Bay of Plenty (east coast, North Island New Zealand). Although recently classified as a marine reserve for its importance as a refuge for fish and targeted invertebrates (crayfish, abalone/pāua, and sea urchins), the benthos was largely unexplored prior to this research. A series of recent cyclonically associated sedimentation and concurrent marine heatwave events provided an opportunity to examine responses of this benthic-pelagic assemblage important in trophic connectivity. Biogeographic affinities of Motiti's mesophotic reef benthos were established using remotely operated vehicles (ROVs). Fifty-three sponge species were conservatively identified: 22% representing the southernmost (highest latitude) geographic range recorded to date. Simultaneously, this community may be under threat by the changing marine climate that supported its establishment. Widespread sponge tissue necrosis (especially of Choristid sponges) and sediment smothering of encrusting benthos coincided with the sudden decline of a 'tumbleweed sponge' (species unknown). These observations co-occurred with a marine heat wave and major cyclonic event delivering fine sediments to these offshore reefs. This research provides a more nuanced understanding of short- and possibly long-term effects of multiple stressors on mesophotic benthic ecosystems. This newly identified biodiversity hotspot supporting southernmost ranges of Australasian species and its seemingly rapid deterioration, signals a warning for the stability of temperate mesophotic ecosystems.

KEYWORDS

mesophotic sponges, biogeography, marine heatwave, sedimentation stress, community ecology, climate change, foundation species, rocky reef

1 Introduction

Sponge-dominated rocky Temperate Mesophotic Ecosystems (TMEs) (30–150 m depth) are under-researched yet widely distributed and highly valued due to the vast array of ecosystem services they provide, most notably benthic-pelagic coupling and provision of habitat complexity (Battershill et al., 2010; Maldonado et al., 2017; Bart et al., 2021; Bell et al., 2022). In light of the mounting pressures of global warming, understanding these precious ecosystems has become a priority. Rapid ecological changes can occur in response to shifting environmental pressures such as alterations in oceanic currents (van Gennip et al., 2017), temperature fluctuations (Bell et al., 2023) or changes in sedimentation regimes (Beets, 2017). A significant consequence of this is an extension polewards of marine species biogeographic ranges (Ramos et al., 2018; Wolfe et al., 2025).

Sponge assemblages accurately reflect prevailing environmental regimes and therefore provide an opportunity to track any shifting ecosystem conditions, e.g., the composition of species within an assemblage, their abundance and their morphological adaptations provides information about the conditions of their habitat (Battershill and Bergquist, 1990; Bell et al., 2015; Schönberg, 2021). In addition, sponge communities are generally stable over time and dominated by slow-growing organisms (Ayling, 1983; Teixidó et al., 2009; Bell et al., 2014), making them ideal candidates for long-term monitoring. Although we do note that there are fast growing and ephemeral species (Ayling, 1983; Duckworth and Battershill, 2003; Page et al., 2005a, b; Perkins et al., 2025).

In New Zealand, all of these environmental pressures are either currently being observed (e.g., increasing temperature and sedimentation (Behrens et al., 2022; Cornwall et al., 2023; Noll and Andrews, 2023; Salinger et al., 2023) or are anticipated to occur in the near future (e.g., oceanic currents shifting spatially or in intensity, Boyd and Law, 2011). However, biogeographic shifts in encrusting marine benthic species have not been examined or reported to date in New Zealand. There are observations of range extensions of fish (Middleton et al., 2023) and mobile invertebrates, specifically the urchin *Centrostephanus rodgersii* to higher latitudes (Thomas et al., 2021), with the southernmost population identified by the authors at Lottin Point, New Zealand (-37.548357, 178.165978). Other pressures that can influence sponge assemblages include food limitation, ocean acidification (for calcareous sponges, e.g., Bell et al., 2018), damage from fishing gear and chemical waste, eutrophication, invasive species, and bottom-contact fishing methods (see Bell et al., 2022). When stressors such as those outlined above are experienced in combination, they can have a compounding effect, multiplying the stress from each individual physical and/or ecological pressure and causing more damage than these stressors would have done in isolation (Strand et al., 2017; Scanes et al., 2018; Bell et al., 2022).

The shifting dynamics of marine environments in response to global warming have spurred a re-evaluation of the biogeography and diversity of sponge assemblages in deeper waters (IPCC, 2023). By tracking any changes in the biogeographic distributions of sponge species, shifts in oceanic currents can be detected based on known sponge distributions and thus affinities to warm or cold water (Maldonado and Uriz, 1995; Mc Cormack, 2021). The biogeography of New Zealand's marine system is influenced by the mixing of major oceanic currents. Warm subtropical currents flow down from the north on the East Auckland Current (EAUC) while cold subantarctic currents flow up from the south, splitting and forming eddies around the irregular coastline. In the Bay of Plenty (study area of this study), Mc Cormack (2015) suggested that the mixing of warm northern and cold southern oceanic currents contributes to the high level of biodiversity found on the reefs here. A recent preliminary survey by Donald (2021) provided additional evidence to support this, showcasing the resulting unique assemblage with both subtropical and subantarctic affinities. If the EAUC shifts spatially or in magnitude (van Gennip et al., 2017), the impacts of this will likely be able to be seen by monitoring the sponge reefs in this region.

Following exploratory surveys in 2021 that uncovered vibrant and biodiverse sponge communities characterizing the mesophotic reefs of the Motiti Island archipelago, Bay of Plenty (BoP), a need to understand the system's ecology became apparent (Donald, 2021). Many of the species observed were representative of more tropical/warm temperate marine climates and represented the southernmost extensions of their biogeographic range (Donald, 2021). Furthermore, recent severe weather events in this region, such as marine heatwaves (Salinger et al., 2023) and Cyclone Gabrielle, have brought to light the catastrophic impacts of extreme weather events, with evidence of significant sediment plumes extending to offshore island and subtidal reef systems (Harrington et al., 2023; Noll and Andrews, 2023; Supplementary Figure 1). Hence, concern was raised that these newly discovered reef systems with species that appeared to be at the edges of, or beyond, their known biogeographic ranges were under immediate threat. Prior to this investigation, we have been blind to any biogeographic or ecological shifts on these reefs. Indeed, little is known of the speed at which biodiversity may change, especially in a situation where species ranges are shifting to previously colder latitudes (Poloczanska et al., 2016; Pinsky et al., 2020; Perkins et al., 2025) at the same time that coastal sedimentary stress (Crawshaw, 2022; Park et al., 2022) combined with marine heatwave events (Bell et al., 2023) are affecting benthic communities. The urgency of this research is driven by a need to establish a baseline for these communities in order to understand the speed and nature of any future biogeographic change in deeper reef benthic ecosystems at the edges of their range extensions, and to identify additional stressors that may be manageable, as these coastal benthic communities respond to long term climatic events.

Sedimentation and fallout of 'marine snow' (sinking particles of decaying organic material) is a natural marine process and as such marine sponges will usually be exposed to some level of suspended and settling sediment (Alldredge and Silver, 1988; Airoldi, 2003; Turner, 2015). However, when sedimentation levels increase above natural levels as they have in the BoP (Crawshaw, 2022; Park et al., 2022), and increasingly around coastal regions globally (Herbert-Read et al., 2022; Cornwall et al., 2023), it can become a significant stressor for sponges and can have negative effects on sponge pumping activities, respiration, feeding, reproduction, growth and symbiotic relationships (Reiswig, 1971; Gerrodette and Flechsig, 1979; Cheshire et al., 1995; Leys et al., 1999; Abdo et al., 2008; Lohrer et al., 2006; Whalan et al., 2007; Bannister et al., 2012; Tjensvoll et al., 2013; Kutti et al., 2015; Beets, 2017; Biggerstaff et al., 2017). In response, sponges exhibit species-specific active and passive responses. Active responses can include changes in respiration and pumping rates (Tompkins-Macdonald and Leys, 2008; Grant et al., 2018), 'sneezing' responses (Kornder et al., 2022), and mucus production (Biggerstaff et al., 2017; Pineda et al., 2017), amongst others, while the main passive responses over longer time periods include changes in functional morphology (Schönberg, 2021) and structural adaptations (Bell et al., 2002; Bell, 2004; Bannister et al., 2012; Bell et al., 2015). With the increasing frequency and severity of weather events amplifying coastal sedimentation concerns (IPCC, 2023; Noll and Andrews, 2023), sponges present an excellent avenue for ongoing monitoring to inform management strategies aimed at reducing the effects of a changing marine climate and enhancing resilience of important subtidal reef systems.

Sponges, as a diverse group of organisms, exhibit varying degrees of resilience to temperature fluctuations. While ocean temperatures have been rising slowly but surely (IPCC, 2023), the increasing frequency and intensity of marine heatwaves poses an immediate and severe threat to TME sponges (Frölicher et al., 2018; Bell et al., 2023). Sponge assemblages worldwide have been recorded exhibiting signs of heat stress (López-Legentil et al., 2008; Garrabou et al., 2022). With the predicted tropicalization of temperate mesophotic reefs (Marzloff et al., 2018) and the Motiti archipelago being directly influenced by the warming East Australian Current (Bull et al., 2020), it is likely that these benthic assemblages will shift toward warmer-water species in the coming decades (Wernberg et al., 2016; Holbrook et al., 2020; Wernberg et al., 2021).

Bell et al. (2023) notably provided the first published record in New Zealand of large-scale necrosis and bleaching of temperate marine sponges in response to a marine heatwave, suggesting those effects only represented a fraction of the true extent of damage caused (Bell et al., 2023). Ayling (1981) reported necrosis of similar species to those examined in this study, and Perkins et al. (2022) focused purely on one cup morphospecies. In all recent articles (Perkins et al., 2022; Bell et al., 2023, 2024), causality was assumed to be heat stress due to correlation of necrosis and bleaching with marine heat waves. Ayling (1981) reported sponge necrosis as outbreaks of bacterial/fungal disease, but she did note that these outbreaks occurred during summer months when water temperature was warmer than 17°C. Of concern is the fact that these effects have been recorded from sponges in the mesophotic zone (Perkins et al., 2022), which means that heat stress is reaching deeper than just the surface water. Their research collectively highlights the unseen damage that heat stress has, and likely will, inflict on sponge assemblages not only in New Zealand but globally. The advent of other simultaneous stressors occurring during increasingly severe and frequent storm events, i.e., coastal land runoff sedimentary inundation, emphasizes the urgency of this research.

This study aims to establish a preliminary baseline understanding of the sponge species diversity and extend Porifera species known biogeographic ranges, as well as examine the current condition of the Motiti Island archipelago mesophotic reefs, an exemplar of temperate coastal mesophotic reef systems in the South Pacific Ocean. Furthermore, it will investigate the importance of selected escalating environmental stressors in shaping sponge assemblages inhabiting this representative southern hemisphere TME, namely sedimentation and heat stress. We expect these factors to be significant drivers of any variation present in assemblage composition between depths and reefs within the Motiti archipelago.

2 Materials and methods

2.1 Field collection methods

2.1.1 Survey sites

Survey sites were situated within the Motiti archipelago (Figure 1), much of which was placed under no-take marine protection in August 2021 by local government. Multibeam Echosounder (MBES) depth data from the 2012/2013 LINZ HS39 Bay of Plenty Hydrographic Survey were used to select ROV survey sites and plan transect locations, as it was the highest quality hydrographic information available for the study region. Mesophotic reef sites (30–150 m) were identified based on steep topography changes and rocky reef structures confirmed using rugosity datasets. Te Poroiti Reef (Brewis Shoal), Nukutai Reef and Motuhaku Reef (Schooner Rocks) were chosen as survey sites based on the criteria that they must be deeper than 30 m and over biogenic habitat (i.e., rocky reef) (Figure 1). The Motiti reefs are all highly heterogeneous pinnacles of rock rising from depths of around 80 m and support an abundance of marine life (for detailed descriptions and current knowledge of these reefs, refer to Donald, 2021). The three reefs surveyed constitute highly complex habitats ranging from bedrock platforms to steep cliffs, from cobble and boulder fields to caves and overhangs (Donald, 2021; Ross et al., 2018; Boffa Miskell Ltd, 2021). The nearshore reefs around Motiti Island itself are more prone to sediment inputs (higher average concentration of total suspended solids) compared to the offshore reefs, Te Poroiti and Motuhaku (Crawshaw, 2022), hence a cline in exposure to sedimentation was investigated. Preliminary research by Donald (2021) used a rudimentary drop camera to explore a small area of Nukutai Reef but no research has been published to date on the mesophotic zones of Te Poroiti or Motuhaku reefs.

2.1.2 Remotely operated vehicle

Image collection was carried out from 4th – 6th August 2022. Discovery Marine Limited (DML) carried out the ROV fieldwork along with the author, using their survey vessel Tupaia. Weather

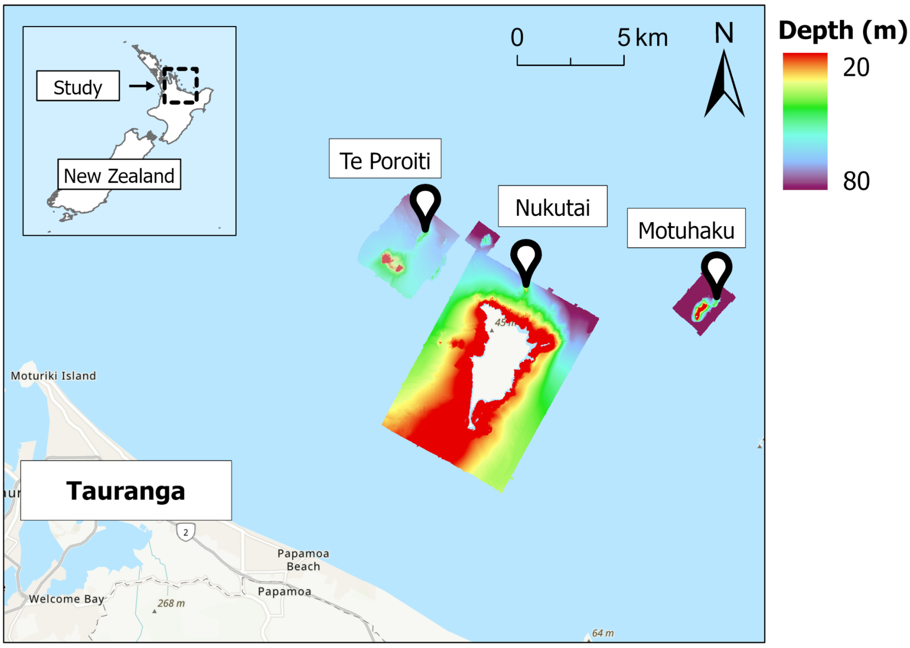

FIGURE 1
The three ROV survey sites marked by pin drops at Te Poroiti Reef, Nukutai Reef and the northern end of Motuhaku Reef.

conditions were largely fine, varying between 5–12 knot southerly winds, 0.5-1.2 meter swell and 0.2-0.5 meter chop.

Transect locations were pre-determined and selected to provide coverage on all sides (i.e., compass faces) of each reef location, starting at the deep sandy seabed and travelling up the rocky reef slope to 30 m depth, at the upper limit of the mesophotic zone. The purpose of spreading transects around the different sides of the reefs was to take into account any effect of predominant ocean currents on sponge community characteristics, as communities may be influenced by reef topography, reef position, or reef aspect. Five video transects were carried out at both Te Poroiti Reef and Motuhaku Reef, while four were completed at Nukutai Reef (Figure 2). The underwater position of the ROV was estimated with 2–5 m accuracy using a combination of the vessel's onboard GNSS positioning system and underwater features that were identified in the MBES data, such as prominent rocks, crevices and the known depth.

An observation class Chasing M2 Pro ROV (Supplementary Figure 2) was used to collect all footage, with a 200 m tether cable connecting the ROV to the topside control equipment on the vessel. Two visual data collection methods were utilized in this survey. Firstly, the inbuilt ROV camera (4K/12M pixel camera, 1/2.3 SONY CMOS, EIS stabilization feature) to collect a live video feed and, secondly, a GoPro Hero 9 Black was mounted atop the ROV facing 15° down from the horizontal line of the ROV, to take benthic photographs every 2 seconds along each transect. The addition of the GoPro as an auxiliary camera provided a more perpendicular angle than the ROV inbuilt camera could, which ensured parallax error was minimized as much as possible (Harris et al., 2021; Lesser and Slattery, 2021). The addition of a second camera also allowed the analyst to combine the more vertical GoPro images with oblique ROV video footage to make identification easier in the resulting footage. A two-point laser scale spaced 10 cm apart provided a scale of reference. Digital settings used for both cameras can be seen in Supplementary Table 1. There is one exception in transect S04 metadata, where depth data was estimated from location and time metadata due to failure of the ROV camera to record the whole transect. The GoPro still captured images but could not record depth.

2.1.3 Transect methodology

The survey vessel was positioned at the start of each transect using the GNSS positioning system combined with the onboard navigation software (QINSy) and an overlaid map of the historical MBES depth data. The ROV was deployed and first dove to the seabed then navigated on a fixed heading along the transect. Vessel position coordinates were logged as it followed above the ROV with a person on deck managing the length and direction of the tether. The ROV was flown approximately 1 m above the sea floor, facing (pitching) down by approximately 20° to be as perpendicular to the benthos as possible. With the addition of the GoPro, the camera to substrate angle was approximately 55° (oblique) throughout each transect (perpendicular being 0°). This angle fluctuated due to the nature of navigating over highly complex reef structure, so images had varying fields of view. Flying deep to shallow up the reef was the only feasible option for transects, due to the highly complex nature of reef bathymetry. Transect details can be seen in Supplementary Table 2.

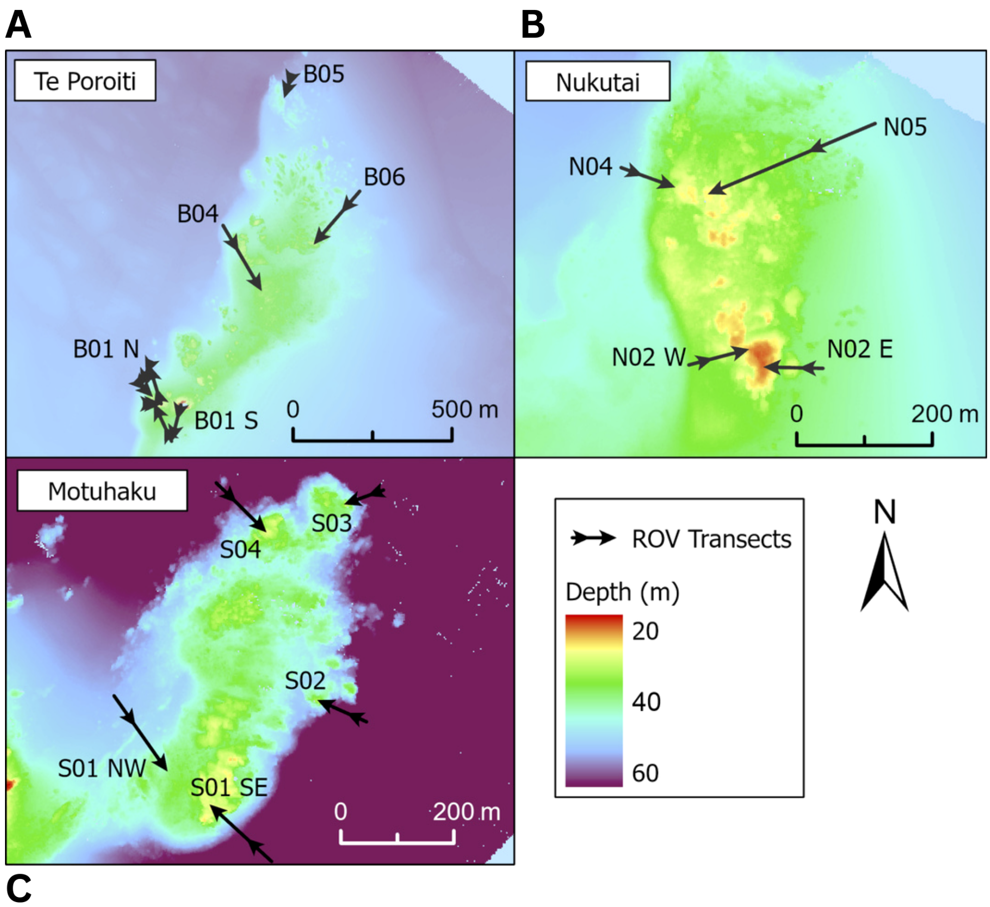

FIGURE 2
Labelled ROV transect locations at **(A)** Te Poroiti Reef, **(B)** Nukutai Reef and **(C)** Motuhaku Reef are shown by the black lines, with overlaid arrows indicating the direction of ROV travel.

2.2 Image analysis

2.2.1 Image post-processing

A total of 6,320 images were captured across all transects. All near-duplicate (photos taken too close together) and low-quality images (blurry, over-exposed, under-exposed, mid-water column, or <30 m deep) were deleted to retain only the high-quality images appropriate for carrying out taxonomic identification of sponges. Some transects were combined, where reasonable geographically, so that each transect had an adequate number of high-quality images (Supplementary Table 3). From the remaining high-quality images, 30 were selected from each transect for analysis, using a random number generator. The total number of images analyzed from 12 transects across all three reefs was 360 images.

2.2.2 Web-based annotation platform

Web-based annotation platforms offer a range of advantages over traditional image or video annotation software installed on individual computers. They enable remote collaboration and supervision by experts involved in a project, facilitate online storage of data for easy access from any computer, provide a contemporary and user-friendly interface equipped with helpful tools, and often incorporate AI capabilities to assist in annotation and analysis. After trialing multiple platforms, BIIGLE was chosen primarily because it has a free-form annotation method. Free-form annotation allows users to identify and annotate any objects of interest (OOI) in an image and not be limited to fixed- or random-point intercept methods, which often miss rare or small sponges in small sets of images. Other key features of note in BIIGLE include the ability to store images and footage online, the option to collaborate with experts or guests on your project and have their labels attach additionally to your OOI rather than replace your label, the Largo tool (Label Review Grid Overview) which allows you to review all OOI with the same label and quickly change, attach new labels or delete them, and the user-friendly, easy to navigate layout of the platform (Zurowietz and Nattkemper, 2021). BIIGLE is also constantly being updated with new features at the request of users.

2.2.3 Image annotation

The freeform annotation method available in BIIGLE was used to outline and label each individual sponge to the highest taxonomic level possible, generating count abundance data. Sponges that looked like they were joined together were counted as one. Where signs of tissue necrosis, bleaching or general stress were evident, that individual was given a second label to record the proportion of sponges in poor condition. Analysis was restricted to only the immediate field of view where sponges were considered discernible in high enough detail for taxonomic identification.

The whole image set was reviewed twice by the author in the interests of quality assurance and consistency. Battershill supervised identifications by collaborating online via BIIGLE, with the video footage playing alongside on a separate screen to give an additional 3D view for better perspective of each image. Identifications were backed up in most cases with taxonomic assignments based on spicule/skeletal morphologies of collected material (Battershill et al., 2010; Donald, 2021; Kelly, 2022, see also Table 1).

Although all identifications were made to the highest taxonomic level possible, there was invariably some level of uncertainty in identifying a number of sponges (not able to be collected) through images without analyzing a sample and examining spicules to confirm. To account for this, some species and morphotypes were aggregated to a higher level, usually genus, to ensure that each identification category certainly represents at least one species that is different, which is what is important for diversity measures. Consequently, this allowed measurements of diversity at the species level, where some species were represented by 'sp.', some similar looking groups of species within the same genus represented by 'spp.', and some distinctive morphotypes represented by Operational Taxonomic Units (OTUs) – for example, the commonly seen 'thin encrusting red Poecilosclerid' and 'fluffy cluster sponge'. Kelly (2022) was thoroughly reviewed to confirm which species recorded in this study are their first records this far south.

2.2.4 Sponge necrosis

Recent research in New Zealand has highlighted the stress sponges are facing from rising temperatures, in particular marine heat waves (Bell et al., 2023). The Motiti Island archipelago is no exception in this regard. Throughout the ROV footage, stressed sponges were evident by white necrotic patches of tissue, exposed by pinacoderm shedding/regrowth (Figure 3). Sponge necrosis data was recorded as the presence or absence of a visibly necrotic sponge in an image.

2.2.5 Percentage cover for assessing sediment smothered area

Sediment deposition has a greater impact on flat spaces, whereas sloping areas can have completely different communities and be less influenced by increased sediment level as gravity naturally allows sediment to drift down the slope (Figure 4) (Battershill, 1987). To assess the sediment smothered area (SSA) and thus get an indication of the sedimentation stress imposed on the Motiti mesophotic reef communities, image sampling was stratified by habitat type. Only flat reef areas were examined, such as boulder tops and relatively flat reef platforms, where sediment settles out of the water column and can smother benthic organisms. The number of 'flat reef' images analyzed from each transect can be seen in Supplementary Table 4. Percentage cover was analyzed using photoQuad (Trygonis and Sini, 2012). The broad categories identified were sponge, crustose coralline algae (CCA), sediment smothered area and other organisms. Sediment smothered area was used as a proxy for levels of sediment deposition.

Due to the fluctuating camera angle discussed earlier, analysis was restricted to only the immediate field of view. To achieve this, photo quadrats were manually drawn in photoQuad to only include reef area in the immediate field of view where organisms were most clearly discernible, ensuring that random points only fell within the target (Supplementary Figure 3). One-hundred points were sampled per quadrat using the stratified random sampling method to reduce clustering and under-sampling, while still minimizing problems associated with parallax error as the whole area was not sampled (Harris et al., 2021). In photoQuad, stratified random sampling creates a grid over the quadrat area and distributes points randomly within each grid cell (Supplementary Figure 3).

2.3 Statistical analysis

Data analysis was carried out in R Studio (R Core Team, 2025). Rarefied sampling curves used the R package "iNEXT" (Chao et al., 2016). All Generalized Linear Mixed Models (GLMMs) and Generalized Linear Models (GLMs) used the R package "lme4" (Bates et al., 2015), while *post-hoc* Tukey's tests for these models used the R package "emmeans" (Lenth, 2023). Aspect was not detected to have any correlation with dependant variables, likely due to the prevailing ocean current swinging in opposite directions between summer and winter (Montaño et al., 2023), and was therefore removed from statistical analyses.

2.3.1 Does the probability of seeing sponge necrosis vary amongst reefs or depths?

To test for the effects of reef and depth on the probability of seeing sponge necrosis in a photo quadrat, a GLMM with a binomial error distribution and logit link was used. 'Transect' was included as a random effect to account for possible spatial dependency between photo quadrats within each transect. Diagnostic plots using the R package "DHARMa" (Hartig, 2022) showed no overdispersion in the model and assumptions were satisfied (Supplementary Figure 4). Since the reefs do not all extend to the same depth (deepest photo quadrat on Nukutai Reef was 49.3 m), comparisons between reefs were made to a maximum of 50 m depth in order to interpret the data correctly, i.e., interpret the output only where model is predicting a pattern in a range where there's real data.

2.3.2 Is variation in flat reef area smothered by sediment explained by depth or reef?

To test for variation in flat reef area smothered by sediment amongst reefs and depths, a GLMM with binomial distribution and logit link was used to fit the maximal model. 'Transect' was included as a random effect to account for possible spatial dependency between photo quadrats within each transect. The response

TABLE 1 Total list of all species and OTUs from Te Poroiti, Nukutai and Motuhaku reef, ordered alphabetically.

Class	Order	Family	Genus	Species/OTU	Geographic affinity
Calcarea	Clathrinida	Clathrinidae	*Clathrina*	*Clathrina* spp.	–
		Leucettidae	*Rowella*	*Rowella* spp.	S
	Leucosolenida	Leucosoleniidae	*Leucosolenia*	*Leucosolenia rosea*	S
Demospongiae	Axinellida	Axinellida	*Pararhaphoxya*	*Pararhaphoxya sinclairi*	N
		Raspailiidae	*Raspailia*	*Raspailia* (*Raspaxilla*) *topsenti*	T
	Biemnida	Biemnidae	*Biemna*	*Biemna rufescens*	N
	Bubarida	Desmanthidae	*Petromica*	*Petromica* sp.	N
	Clionaida	Clionaidae	*Cliona*	*Cliona* sp.	G
	Dendroceratida	Darwinellidae	*Darwinella*	*Darwinella* cf. *gardineri*	G
				Darwinella oxeata	G
			Dendrilla	*Dendrilla* cf. *rosea*	G
	Dictyoceratida	Irciniidae	*Psammocinia*	*Psammocinia* spp.	G
		Thorectidae	*Taonura*	*Taonura* cf. *marginalis*	N
			Thorecta	*Thorecta* cf. *reticulatus*	S
	Haplosclerida	Callyspongiidae	*Callyspongia*	*Callyspongia* (*Callyspongia*) *nuda*	G
			Unknown	Callyspongiidae n. sp. 1	G
		Chalinidae	*Haliclona*	*Haliclona* sp.	G
			Petrosia	*Petrosia* (*Petrosia*) *hebes*	N
			Xestospongia	*Xestospongia* spp.	G
	Poecilosclerida	Acarnidae	*Iophon*	*Iophon laevistylus*	S
		Chondropsidae	*Chondropsis*	cf. *Chondropsis* sp.	G
		Desmacididae	*Desmacidon*	*Desmacidon mamillatum*	T
		Unknown		Thin encrusting red Poecilosclerid	–
				^Yellow thick encrusting Poecilosclerid	–
	Polymastiida	Polymastiidae	*Polymastia*	*Polymastia* cf. *massalis*	T

(*Continued*)

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TABLE 1 Continued

Class	Order	Family	Genus	Species/OTU	Geographic affinity
				Polymastia crocea	T
				Polymastia hirsuta	T
	Suberitida	Halichondriidae	*Ciocalypta*	*Ciocalypta* cf. *penicillus*	G
			Halichondria	*Halichondria* (*Halichondria*) *moorei*	T
			Hymeniacidon	*Hymeniacidon* cf. *perlevis*	T
		Suberitidae	*Aaptos*	*Aaptos* spp.	G
			Homaxinella	*Homaxinella* cf. *erecta*	T
			Suberites	*Suberites* spp.	G
	Tethyida	Tethyidae	*Tethya*	*Tethya* cf. *bergquistae*	G
				Tethya spp.	N
	Tetractinellida	Ancorinidae	*Ecionemia*	*Ecionemia alata*	T
			Stelletta	*Stelletta conulosa*	T
				Stelletta crater	S
				Stelletta maori	S
				Stelletta sandalinum	T
		Geodiidae	*Geodia*	*Geodia regina*	G
		Scleritodermidae	*Aciculites*	*Aciculites pulchra*	N
		Tetillidae	*Cinachyrella*	*Cinachyrella* spp.	N
	Trachycladida	Trachycladidae	*Trachycladus*	*Trachycladus stylifer*	N
	Desmacellida	Desmacellidae	*Desmacella*	*Desmacella dendyi*	G
Demospongiae (Subclass Heterosclero-morpha)	Unknown			Heteroscleromorpha n. sp. 1	–
Unknown				^Black and orange cup	–
				Dark encrusting sponge	–
				^Fluffy cluster sponge	–
				^Orange meandering sponge	–

(Continued)

TABLE 1 Continued

Class	Order	Family	Genus	Species/OTU	Geographic affinity
				^Oyster mushroom sponge	–
				^Possibly tumbleweed sponge	–
				Yellow smooth massive sponge	–

^New or undescribed species (full assignment of 'Unknown' OTUs pending a sample and workshop with Prof. Michelle Kelly, NIWA).
Geographic affinities are southern (S), northern (N), temperate (T), and generalist (G). For images of example OTUs, see Supplementary Figure 3.

variable was combined (two columns) from the number of successes and failures (SSA: Other) to prevent information loss of sample size.

The residual deviance was >1.5 times the residual degrees of freedom, so the maximal model was updated to a GLM with a quasibinomial distribution to account for overdispersion and the random effect removed. The maximal model was then simplified with backward selection using *p*-values to identify the minimum adequate model. The two models were compared using a likelihood ratio test based on the Chi-squared distribution, which confirmed that the minimum adequate model best explained the variance in SSA amongst reefs and depths. The assumption of multicollinearity was satisfied as general variance inflection factors were low (<3) for all predictor variables (Supplementary Table 5). Similar to the sponge necrosis analysis, comparisons between reefs were made to a maximum of 45 m depth in order to interpret the data correctly (deepest photo quadrat of flat reef area on Nukutai Reef was 45.4 m).

2.4 Limitations in data collection

The Chasing M2 Pro ROV did succeed in collecting sufficient footage for an extensive analysis of the targeted reefs, but it seemed that the vehicle was at the limit of its suitability for this type of project. The power supply and internal sensors failed while it was underwater, which led to repeat visits to the reefs and wear and tear on the vehicle. Another difficulty was encountered with the recording of positioning data. A small ultra-short baseline (USBL) acoustic positioning system was investigated to enable more accurate positioning of the ROV underwater but unfortunately, this equipment did not cooperate well with DML's other hardware and was not deemed suitable for the project. Despite these difficulties, the Chasing M2 Pro ROV was a cost-effective alternative to the larger, more robust commercial ROVs (not available for this study) which increase substantially in cost and complexity.

Varying camera to substrate angles resulted in most images being at oblique angles. The issue this raises is that oblique angle images introduce parallax error, geometric distortion and scaling error, making any measurement taken from a laser scale inaccurate whether that be measurement of sponges or quadrat area (Lesser and Slattery, 2021). Therefore, no measurements could be made using the laser scale which ruled out the use of some common measurements for abundance and species density data, such as biomass. This also affects percentage cover estimation, as features closer to the camera will be over-represented while features further away are under-represented. However, the level of parallax error was limited by restricting the photoquadrat to the immediate field of view and was appropriate for the purposes of identifying coarse categories and analyzing SSA.

3 Results

3.1 Diversity and biogeography

Analysis of ROV footage revealed highly diverse sponge communities inhabiting all three of the surveyed mesophotic reefs.

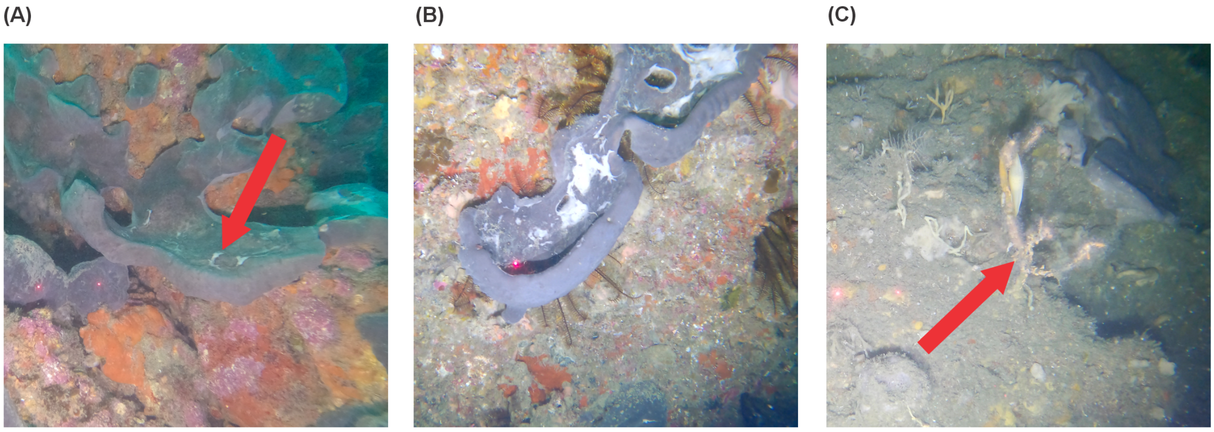

FIGURE 3
(A-C) Sponges with visible necrotic tissue. **(A)** Recovering *Ecionemia alata* sponge at 26.6 m depth on Te Poroiti Reef, transect B01 South; **(B)** Deteriorating *E. alata* at 38.8 m depth on Motuhaku Reef, transect S02; **(C)** Deteriorating erect-branching sponge at 83.3 m depth on Motuhaku Reef, transect S02. Red laser points are 10 cm apart.

Species richness was relatively similar amongst reefs, with 47 species recorded at Te Poroiti, 40 at Nukutai, and 46 at Motuhaku. Rarefied sampling curves show that species richness was still increasing in the last photoquadrats analyzed on Nukutai and Te Poroiti Reef but had plateaued at Motuhaku Reef (Figure 5). This suggests that further sampling in future would capture greater species richness at Nukutai and Te Poroiti reefs (Figure 5). Hence, findings presented in this study represent a conservative estimate of diversity.

A total of 53 different sponge species were identified from ROV footage (Table 1), this being a conservative number to ensure certainty of classifications as discussed earlier. Sponges were predominantly from the class Demospongiae, but some calcareous sponges were also seen (Table 1). Of those identified, six (11% of all species recorded) were possibly new or undescribed species (Figure 5, Table 1).

This study has updated the current biogeographic knowledge of the Bay of Plenty. Fifteen sponge species identified (22%) presented

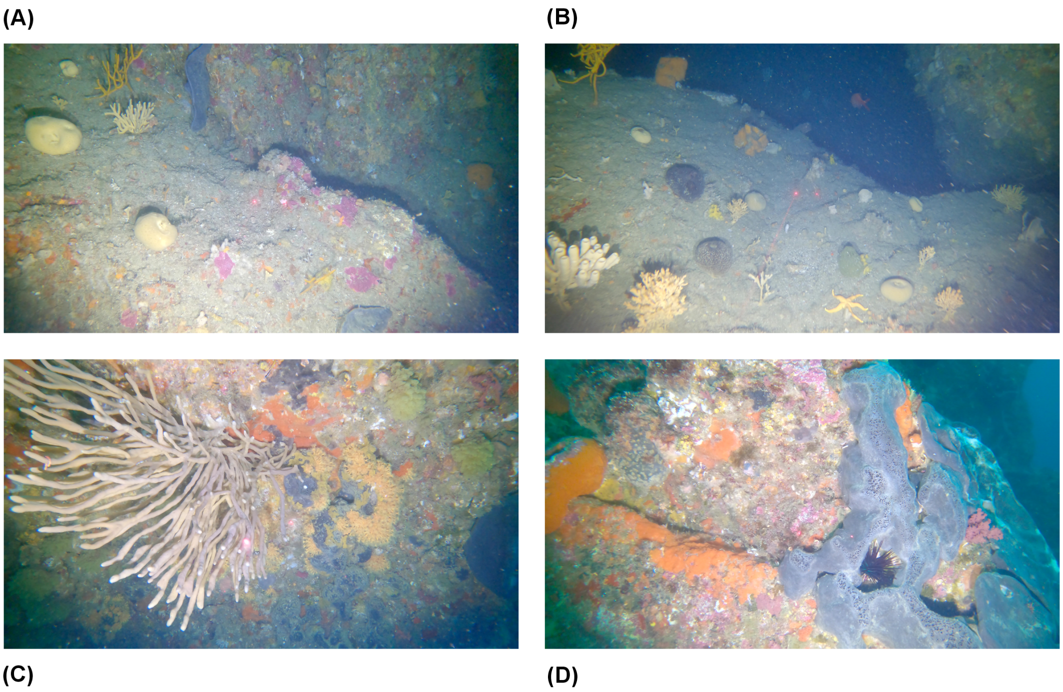

FIGURE 4
Example photos from Motuhaku Reef illustrating how sedimentation levels and communities can differ between flat **(A, B)** and sloping **(C, D)** habitats. In **(A, B)**, a thick sediment layer (i.e., sand) can be seen covering the flat rock surface. In contrast, in **(C, D)** sponges and coralline algae are spread over most of the wall **(C)** and sloping **(D)** rock surface. Red laser points are 10 cm apart.

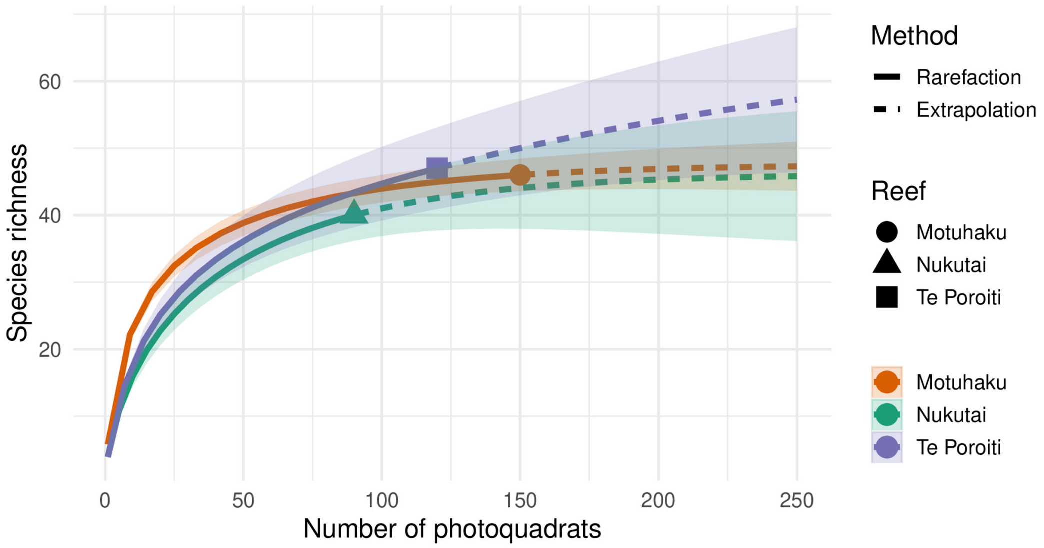

FIGURE 5
Sample-size-based rarefaction and extrapolation sampling curve for species richness per ROV photoquadrat on Motuhaku, Nukutai and Te Poroiti reefs.

new occurrence records for the region and some species' known depth ranges were extended (Table 2). The sponges identified in this study represent a highly mixed community made up of multiple well connected and diverse assemblages (Figure 6, Table 1). The total list of 53 species comprised of species with northern warm-water and southern cold-water affinities relative to the BoP (22% and 12%, respectively), as well as a range of temperate (27%) and generalist species (39%) (Figure 6, Table 1). Temperate represents species found only in temperate waters, both to the North and to the South of the BoP. Generalist represents species found from the tropics or subtropics all the way through to cold-temperate waters.

3.2 Sponge necrosis

The main species seen to have necrotic tissue were all large, 'tough' sponges with robust, dense spicular skeletons (subclass Heteroscleromorpha, orders Haplosclerida and Tetractinellida). The species that commonly had visible necrotic tissue on Motiti's mesophotic reefs were *Ecionemia alata*, *Petrosia* (*Petrosia*) cf. *hebes*, *Stelletta conulosa*, *Stelletta crater*, *Stelletta maori*, *Geodia regina*, as well as two unidentified morphotypes; 'orange meandering sponge', and 'black and orange cup'.

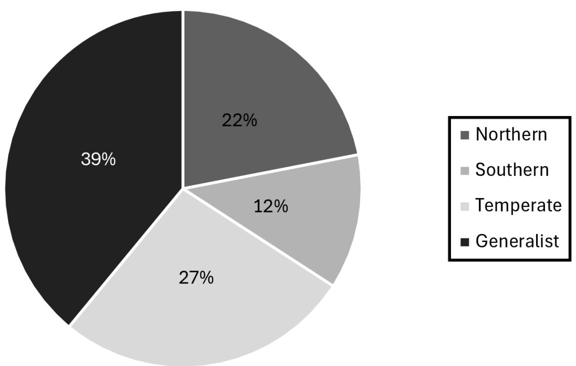

FIGURE 6
Compositional makeup of the sponge communities identified in this study according to their recorded geographical affinities.

Depth alone did not appear to have an effect on the probability of seeing sponge necrosis across all reefs (p >0.05, z = -1.03) (Figure 7B), but Nukutai Reef and its interaction with depth were significant predictors of sponge necrosis (p < 0.01, z = 2.76, and p < 0.01, z = -2.87, respectively) (Figure 7A) (Supplementary Table 6). Tukey-adjusted pairwise comparisons of the means revealed that the probability of seeing necrosis at Nukutai Reef was significantly lower at deeper depths compared to Motuhaku and Te Poroiti (Figure 7A) (Supplementary Table 7). For example, the GLMM model predicts that at 50 m depth, there is a 0.38% probability of seeing sponge necrosis at Nukutai Reef with an uncertainty (SE) of 0.54% (Supplementary Table 7). In contrast, the predicted probability of seeing sponge necrosis at 50m depth at Motuhaku Reef is 17% (SE ± 4%), and 14% (SE ± 5%) at Te Poroiti Reef (Supplementary Table 7).

This means that overall, the probability of seeing sponge necrosis in the mesophotic zones of the Motiti reefs was the same regardless of depth (Figure 7B). However, whatever is driving sponge necrosis on these reefs (e.g., environmental stressors) has a weaker influence in the deeper waters on Nukutai Reef (Figure 7A), as evidenced in the interaction term (Supplementary Table 6).

3.3 Sediment smothered area

Overall, SSA increased with depth (t = 8.24, p < 0.01), and was significantly greater on Nukutai Reef compared to Motuhaku

TABLE 2 Species occurrence records for ROV footage from the Motiti archipelago with new geographic and depth ranges.

Species	Previously known distribution	New record of range extension
Black & orange cup	Unidentified.	Possibly new species.
Cinachyrella sp.	Undescribed *Cinachyrella* sp. (golden hemisphere sponge) previously known from the eastern coast of Far North NZ, south to Great Barrier Island (Kelly, 2022). *Cinachyrella* genus generally distributed through circumtropical to warm temperate regions (WoRMS Editorial Board, 2025); Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Fluffy cluster sponge	Unidentified.	Possibly new species.
Halichondria (*Halichondria*) *moorei*	Down to 15 m, distributed around NZ (Mc Cormack, 2015).	New depth range extension to approximately 40 m.
Homaxinella cf. *erecta*	West coast of the North Island; east coast from Northland to Auckland; East Cape; and Chatham Islands (Kelly, 2022; WoRMS Editorial Board, 2025); Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Hymeniacidon cf. *perlevis*	Mainly temperate (WoRMS Editorial Board, 2025). In NZ: only intertidal on the eastern coast from the far north to the Hauraki Gulf; around Wellington; Nelson, and the west coast of Auckland (Kelly, 2022).	Yes. Also new depth range extension for NZ to approximately 50 m.
Leucosolenia rosea	Down to 30 m and only from the South Island, of NZ (Kelly, 2022; WoRMS Editorial Board, 2025).	Yes. Also new depth range extension – to approximately 70 m.
Orange meandering sponge	Unidentified.	Possibly new species.
Oyster mushroom sponge	Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Petromica sp.	Undescribed *Petromica* sp. ('witchy' finger sponge) known in NZ from Rodney Coast, Poor Knights Islands (Kelly, 2022); Nukutai Reef (Donald, 2021). *Petromica* genus is known to occur in tropical and temperate waters (WoRMS Editorial Board, 2025).	No, but only record in BoP is from unpublished study (Donald, 2021).
Possibly tumbleweed sponge	Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Taonura cf. *marginalis*	Known from northern and southern Australia; North Cape in NZ; Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Thorecta cf. *reticulatus*	South Island of NZ (Kelly, 2022).	Yes. Similar specimen was recorded in Donald (2021), so may not be a completely new record.
Trachycladus stylifer	Recorded in subtropical New Caledonia and the Far North and Bay of Islands in NZ (Kelly, 2022; WoRMS Editorial Board, 2025). Potentially Donald (2021) but ID uncertain.	Yes.
Yellow thick encrusting Poecilosclerid	Recorded on Nukutai Reef as a 'possibly new species' by Donald (2021).	No, but only record in BoP is from unpublished study (Donald, 2021).

Previously known distributions informed by Mc Cormack (2015); Donald (2021); Kelly (2022); Kelly and Sim-Smith (2023) and WoRMS Editorial Board (2025).

(*z*ratio = -3.35, $p < 0.01$) (Supplementary Tables 8, 9). This means that as the reef gets deeper, larger areas of the reef are smothered with deposited sediment (Figure 8B). However, although this trend holds true for all reefs sampled, the baseline level of SSA was greater at Nukutai Reef than Motuhaku (Figure 8A). In addition, many of the cup sponges photographed had layers of fine sediment covering their surfaces, showing the recent occurrence of a heavy sedimentation event (Figure 9). Sediment deposition was determined to be recent because fine sediment was sitting in a layer on top of many *Ecionemia alata* purple cup sponges (Figure 9B). This species does not tolerate high levels of sedimentation and will shed mucus to clear sediment that is sitting on it's surface (Ayling, 1983; Battershill and Bergquist, 1990; Bell et al., 2015; Schönberg, 2021). In Figure 9B stringy/webbed mucus that the sponge is producing to get rid of sediment that has deposited on top of it is evident.

3.4 Marine heatwave

From November 2021 to December 2022, the BoP experienced a marine heatwave which lasted for 381 days (Figure 10). The heatwave varied from strong to moderate intensity throughout the event, with a maximum sea surface temperature deviation of 2.5°C above the historic average (Figure 10). Since surveys for this study took place in early August of 2022, this means that the Motiti reefs had been continuously experiencing a marine heatwave for the past eight months at the time ROV surveys were carried out.

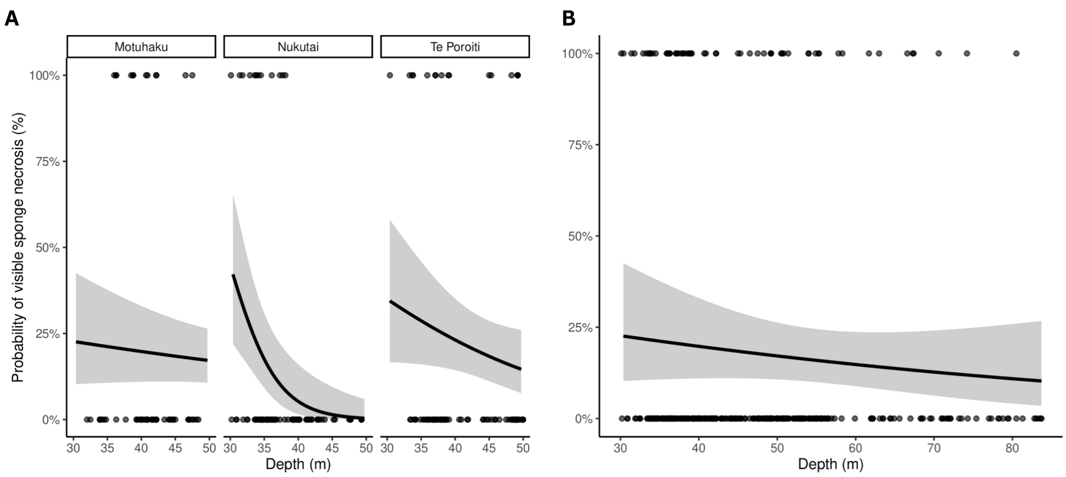

FIGURE 7
(A) The significant effect of Nukutai Reef and its interaction with depth (m) on the probability of visible sponge necrosis (%) ($p < 0.01$, $z = 2.76$, and $p < 0.01$, $z = -2.87$, respectively). **(B)** The overall insignificant effect of depth (m) on the probability of visible sponge necrosis (%), across the three surveyed reefs ($p > 0.05$, $z = -1.03$). Shaded area shows 95% confidence interval.

4 Discussion

4.1 Diversity and biogeography

Mesophotic rocky reefs are known to be biodiversity hotspots and the Motiti mesophotic archipelago has proven to be no exception (Bo et al., 2012; Donald, 2021; Rossi, 2013; Bart et al., 2021; Bell et al., 2022). Through a comprehensive examination of sponge biodiversity on Motiti's mesophotic reefs, this study conservatively identified fifty-three sponge species from ROV footage. The still-increasing rarefied sampling curves indicate that this study has only partially captured the true diversity of these mesophotic sponge communities. Greater sampling effort using equipment capable of finer-scale surveys would enable a more comprehensive record of species richness in future monitoring. Although species richness is difficult to compare between studies (Clarke and Warwick, 1998) it remains valuable information, providing a benchmark in an area with limited existing knowledge.

Over a quarter (28%) of the sponge species recorded in this study constitute novel occurrence records in terms of either their geographical distribution or depth range. Some of these newly documented occurrences, such as *Homaxinella erecta*, bridge previously known distributions both to the north and south of the BoP (Kelly, 2022; WoRMS Editorial Board, 2025). The diversity in sponge taxa found in this study provides valuable insights into the influence of currents within the BoP's mesophotic zone. The

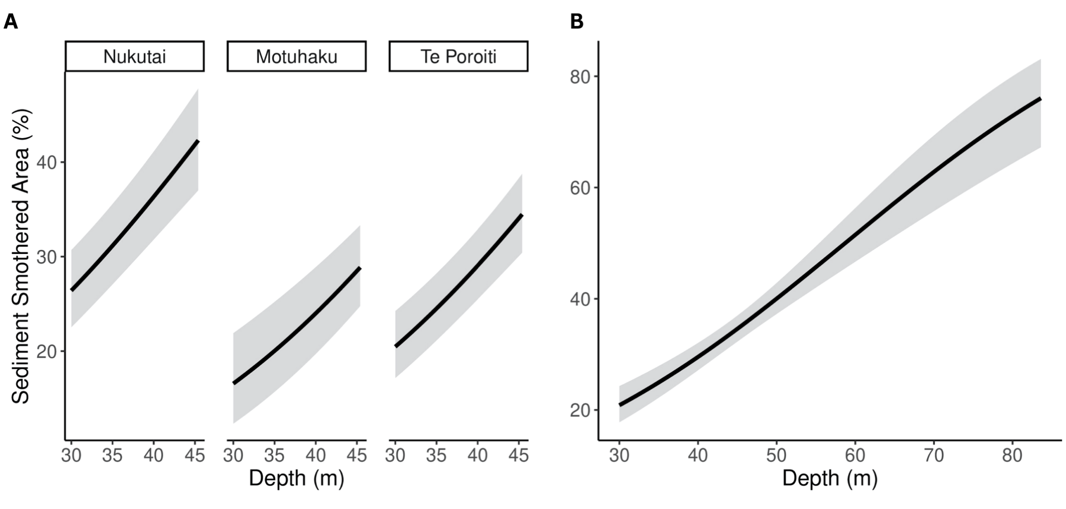

FIGURE 8
(A) The significantly greater sediment smothered area (%) on Nukutai Reef compared to Motuhaku (z ratio = -3.35, $p < 0.01$). **(B)** The overall significant positive relationship between depth (m) and sediment smothered area (%) across the three surveyed reefs ($t = 8.24$, $p < 0.01$). Shaded area shows 95% confidence interval.

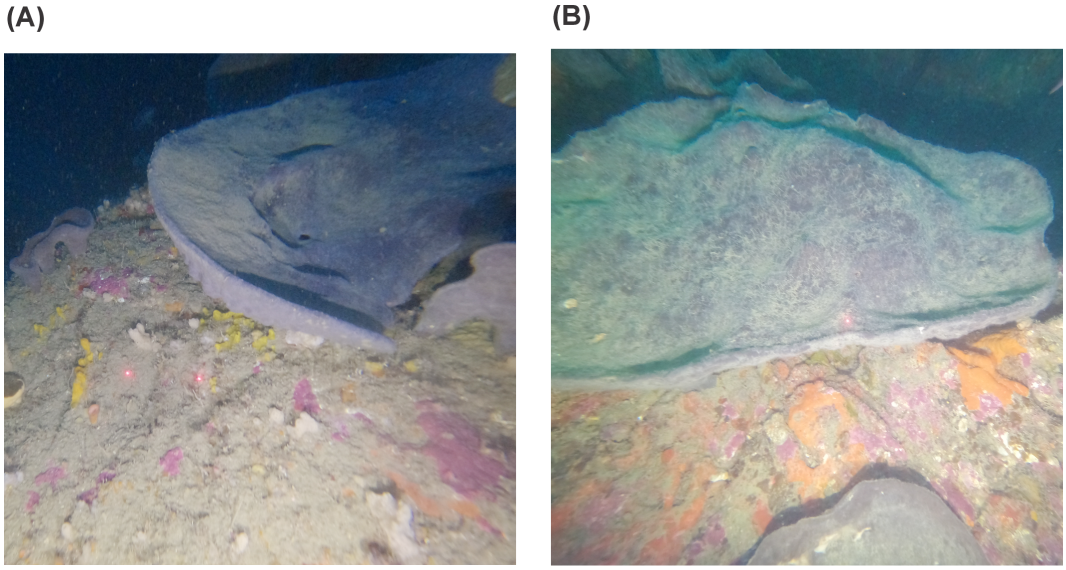

FIGURE 9
Layer of fine deposited sediment in massive cup sponges, both *Ecionemia alata*. **(A)** Photo captured on Motuhaku Reef at 62.2 m depth, transect S04; **(B)** Photo captured on Te Poroiti Reef at 38.8 m depth, transect B06. Red laser points are 10 cm apart.

composition of sponge communities in the Motiti mesophotic reefs and the broader BoP region reflects an amalgamation of warm-water (northern) and cold-water (southern) affinities, indicating the complex interplay of oceanic currents within this area. Notably, the proportion of species with demonstrated warm-water preferences (22%) was nearly double that of the species extending into colder regions further south (12%), indicating the pronounced influence of the warmer East Auckland Current (EAUC) in the BoP. Considering the significant influence of the EAUC in the BoP, as indicated by this study and supported by Donald (2021), an important question arises: how will the increasing frequency and intensity of marine heat waves transported from the tropics to New Zealand (Behrens et al., 2022) affect precious mesophotic ecosystems within the Bay of Plenty? These discoveries highlight the existence of a highly mixed sponge assemblage characterized by taxonomically diverse and interconnected communities. Their associations with oceanic currents make them a crucial area for further investigation and conservation efforts.

Among the 11% of new or undescribed species identified from ROV footage, the tumbleweed sponge emerged as an intriguing subject of investigation. Donald (2021) identified the tumbleweed sponge as a 'probably new species' due to its highly unusual morphology for a branching sponge in New Zealand, with no comparable species previously observed. It is most likely a *Callyspongia* species (Battershill, personal communication, June 2025). Its abundant presence was noted on Nukutai Reef between 40–50 m depth, in February 2021 (see https://youtu.be/7jfiwkn_W8M for original video transect footage from Donald, 2021). However, this study in the same region and including the same reef, conducted only a year and a half later, revealed a starkly contrasting scenario. The tumbleweed sponge was seldom encountered and when it was, specimen appeared markedly degraded (see Supplementary Figures 5T-U). In fact, they were only recorded as 'possibly tumbleweed sponge', due the obscurity and rarity of sightings in the ROV footage, the absence of physical samples, and limited prior records. There were only a few sightings of it and a full identification has not been possible (it has not been collected), hence confirmation of the taxonomy and ecology of this species remains to be carried out. There is however a possibility that the tumbleweed sponge originally identified by Donald (2021) has completely disappeared from these reefs. It is noted, however, that there are many sponge species that can have a rather ephemeral life history (Perkins et al., 2025) and we do acknowledge that the repeat surveys were not carried out along exactly the same transects, though they covered a much greater area of the Nukutai Reef than the preliminary survey in Donald (2021). Nonetheless, mesophotic sponge reefs are renowned as long-lived communities (Teixidó et al., 2009; Bell et al., 2014; Micaroni, 2022) and combined with the degree of sponge necrosis in other species, it would appear that these reef systems have been under significant stress. The size of the sponges alone, for example the large patches of encrusting sponges seen in ROV footage, indicates that the individuals observed in this study are likely to be decades old (Ayling, 1983). Consequently, this rapid shift in the tumbleweed sponge population, whether they have completely disappeared or there is still a remnant population, is a matter of considerable ecological significance.

The precise cause behind this shift is yet unknown, but a key initial observation was that all sightings except one, were exclusively at the deepest depths exceeding 80 m. Heat stress may be contributing factor to consider, as it is possible that the remnant population of the tumbleweed sponge persists only in deeper, cooler areas on these reefs (Idan et al., 2018). In addition, we observe that this community change coincides with a large marine heatwave

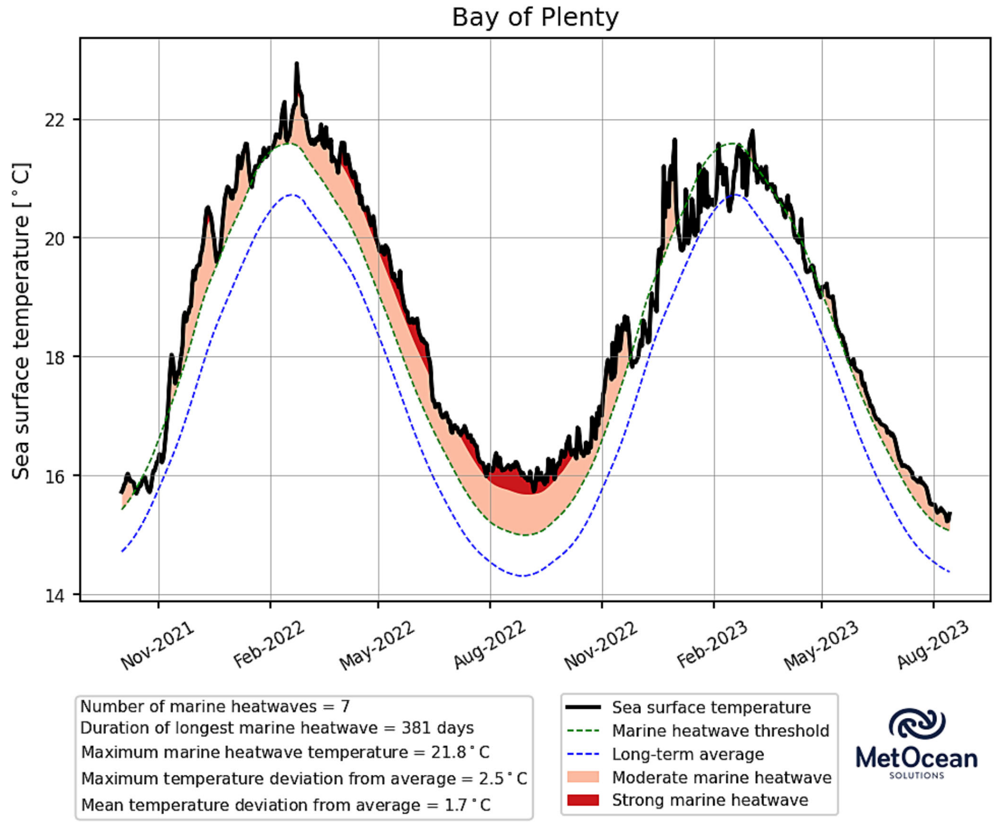

FIGURE 10
Historical sea surface temperatures (°C) in the BoP from October 2021 – October 2023, provided by Moana Project, MetOcean Solutions (2023).

event together with sedimentation effects caused by a major cyclonic event, Cyclone Gabriel (Harrington et al., 2023). It cannot be assumed that this combination of climatic events was the cause, nor that rapid fluctuations in these benthic species abundance are abnormal. However, it is important to note that these community shifts are happening elsewhere in this region, for example along shallow coastal reefs (Schiel et al., 2024), and predicted tropicalization of temperate waters (Wernberg et al., 2016). We propose that there is an opportunity for further monitoring at this site to examine longer term trends.

4.2 Heat stress

The widespread necrosis of sponges seen in this study provides evidence for sponge disintegration, morphology disruption and mortality under heat stress, which has been described as sponge rot by Ayling (1981), as sponges "melting" off the reef by Bell et al. (2023), and observed also as growth abnormalities in response to storm stress by Battershill and Bergquist (1990). New Zealand's coastal waters have experienced unprecedented marine heat waves in recent years (Bell et al., 2023; Salinger et al., 2023). As previously mentioned, the BoP experienced a prolonged and intense marine heatwave from November 2021 to December 2022. The timing of this marine heatwave, in line with the consistent presence of necrotic sponges seen in this study across all reefs and depths, supports recent studies in pointing towards heat stress as the cause of large-scale sponge necrosis (Perkins et al., 2022; Botté et al., 2023; Bell et al., 2023, 2024).

A key observation is that sponges exhibited visible signs of necrosis across all surveyed depths, from 30 to 80.5 m. The importance of this ecologically is the permeation of heat stress down to at least 80.5 m deep, despite a possible thermocline, likely to occur during severe and prolonged cyclonic storm events. Depth is therefore not acting as a thermal refuge for these mesophotic sponge communities in times of increasingly severe weather events. Perkins et al. (2022) came to the same conclusion for a mesophotic cup sponge morphospecies on the east coast of Tasmania, which they surveyed at depths down to 83 m. This finding is important in the context of other studies that have recorded temperate sponge necrosis as, except for Perkins et al. (2022), most have only surveyed shallow ecosystems down to 20 or 25 m (Ayling, 1981; Bell et al., 2023, 2024).

Observations of healing sponges suggest that, despite the marine heatwave continuing from summer into winter 2022, recovery was facilitated by cooler winter sea temperatures. Healing sponges showed an estimated 2–3 months of recovery, which can be seen in photos where hard lines are present between white tissue and pigmented tissue as evidence of pinacoderm regrowth over scarred or lost sponge matrix (Figure 3A), as opposed to fuzzy, sloughing white tissue indicative of deterioration (Figure 3B) (Ayling, 1981; Cerrano et al., 2001).

Rapid sponge death may have occurred earlier in the marine heat wave and therefore the full impacts on benthic communities were missed by the time ROV surveys were undertaken. Images from ROV footage show tissue regression on extremely degraded sponges which are not included in the aforementioned list of common, 'tough' species (e.g., Figure 3C). The difference in tumbleweed sponge population between this footage and Donald (2021) also provides evidence that some sponges had died off rapidly before ROV footage was captured on our revisitation to these reefs. Because of this, the full extent of marine heatwave damage to benthic marine diversity and TME function is yet unseen for the Motiti reefs.

4.3 Sedimentation stress

An often-overlooked factor is the compounding, or synergistic, effect that sedimentation (from land run-off) and heat stress can have on marine sponges (Strand et al., 2017; Scanes et al., 2018). Sedimentation and heat stress both significantly shape the Motiti mesophotic sponge assemblages, as evidenced by the widespread necrosis and sediment smothered rocky substrate. The greater SSA on Nukutai Reef is understandable as it is the northern side of Motiti Island, part of the same reef shelf that the island sits on, and therefore exposed to sediment run-off from Motiti Island itself (Crawshaw, 2022). By contrast, Te Poroiti and Motuhaku are both rocky pinnacles situated further away from Motiti Island. SSA increased with depth across all reefs, which is a natural trend that aligns with oceanic physical processes. Sediment gets lifted into suspension by wind-driven mixing in shallow waters, but falls out of suspension and smothers greater extents of benthic substrate on deeper reef areas, especially where it accumulates on flat areas (Airoldi, 2003). The resilience of sponges on these deeper reefs with high sedimentation levels largely depends on their species-specific ability to shed or tolerate sediments while under additional (heat) stress. This species-specific response invokes consideration of sponge morphology, physiology, the ability to 'back-flush' or 'sneeze' (Kornder et al., 2022), and elements of the sponge metabolism and biochemistry in response to increased energy demand coupled with less food and heightened pathogenic attack (Bannister et al., 2010, 2012).

Sedimentation also impacts the survival of sponges disintegrating under heat stress, by inhibiting the recruitment process of sponge propagules. Deposited sediment smothers benthic communities and as little as 10 mg cm^{-2} can exclude sponge larval recruitment (Battershill, 1987; Abdul Wahab et al., 2019). The ability for a number of species of sponge to rapidly re-organize cellular integrity such that the morphology becomes more 'fluid' (melts), appears to be associated with a response to unfavorable conditions, such as heat stress, and is a mechanism that results in fragmentation (Ayling, 1981) and generation of asexual propagules (Battershill and Bergquist, 1990). This latter phenomenon heightens chances of survival of the fragmenting sponge, as the relatively large size of propagules can re-settle into available space, re-attach and grow (Battershill and Bergquist, 1990). However, if sediment is settling and smothering vacated reef space faster than sponges can re-attach, recruit and grow, for example following fragmentation and generation of asexual propagules from sponge rot, recovery of sponge assemblages after a die-off or disturbance event like a marine heatwave would be severely hindered. This compounding stress of marine heatwaves and heavy sedimentation could cause recruitment of new individuals to become limited to niches and slopes where minimal sediment deposition occurs.

Given the projected increase in the intensity and severity of future weather events (IPCC, 2023; Noll and Andrews, 2023), although heavy sedimentation may not currently constitute the prevailing conditions, it is likely a frequent and escalating stressor for Motiti Island reef communities. The compounding effect of these stressors is likely to play a role in the impacts of the marine heatwaves and will significantly alter the species composition of benthic communities, as we are starting to see in this study.

5 Conclusion

This study has captured a snapshot of Motiti's mesophotic reef system during an unstable time marked by the identification of new extensions to sponge species' biogeographic ranges, widespread sponge necrosis and rapid changes in benthic community composition under the combined pressures of escalating heat and sedimentation stress. Our conservative identification of fifty-three species serves as a benchmark for future research and monitoring, yet it is clear we have only begun to characterize these vibrant sponge communities. The wider implications of these findings must be considered for management of coastal zones. For instance, this may indicate a shifting contribution to coastal productivity, as different taxonomic groups vary in their contributions to carbon flux (Maldonado et al., 2012; Snelgrove et al., 2018). Further research at these GPS-recorded survey sites is urgently needed to determine how, and to what extent, the benthic community is changing over time. This study has importance not only for New Zealand, but also globally and at all trophic levels as a signal of mesophotic reefs under substantial environmental stress. It is our hope that this research will facilitate the preservation and sustainable management of these ecologically invaluable mesophotic reefs, and stimulate similar actions for TMEs worldwide.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

ED: Formal analysis, Data curation, Visualization, Project administration, Validation, Investigation, Writing – review & editing, Methodology, Funding acquisition, Writing – original draft, Conceptualization. CB: Supervision, Conceptualization, Funding acquisition, Resources, Writing – review & editing.

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Conflict of interest

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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.2025.1668859/full#supplementary-material

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