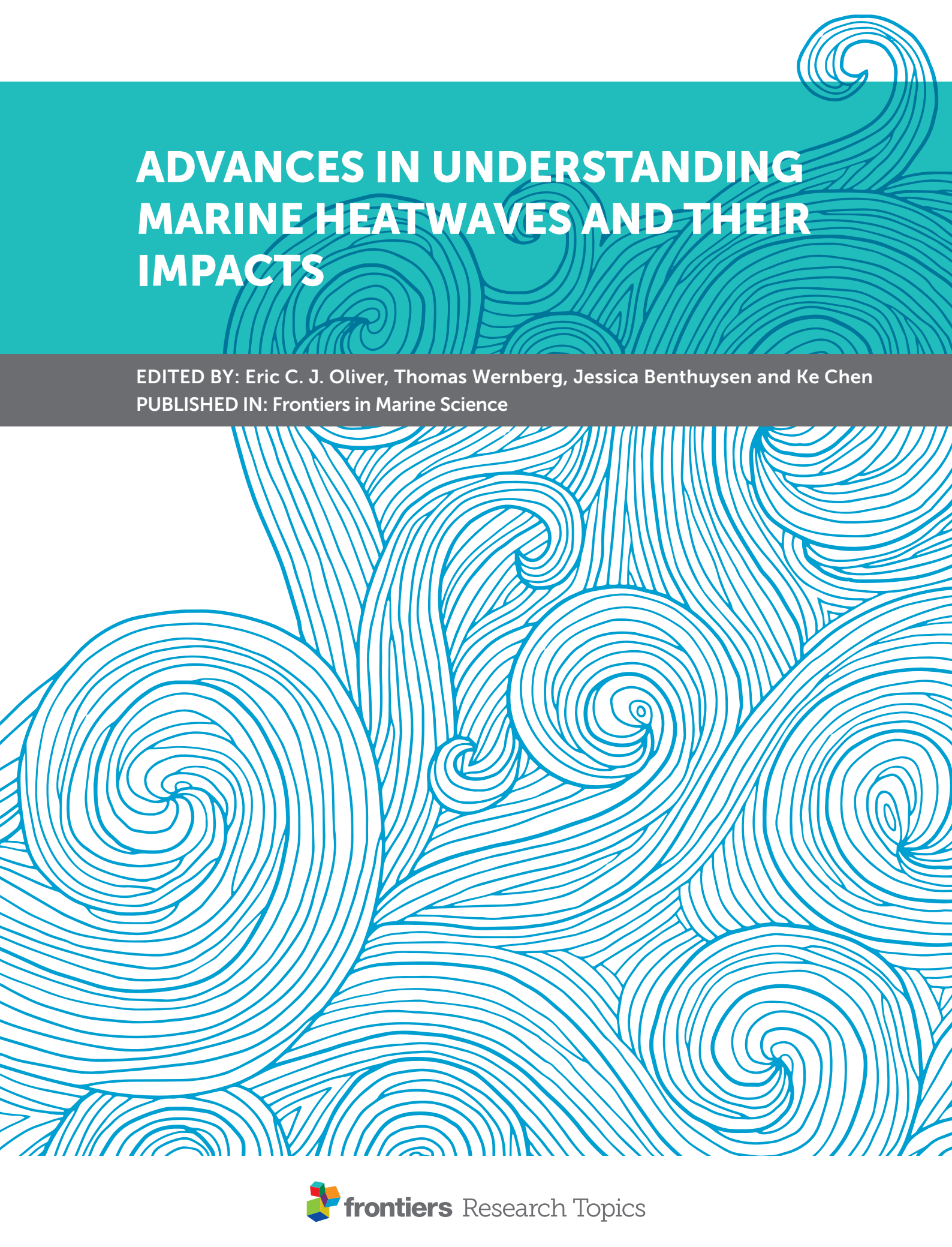




ADVANCES IN UNDERSTANDING MARINE HEATWAVES AND THEIR IMPACTS

EDITED BY: Eric C. J. Oliver, Thomas Wernberg, Jessica Benthuisen and Ke Chen
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ADVANCES IN UNDERSTANDING MARINE HEATWAVES AND THEIR IMPACTS

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Editorial: Advances in Understanding Marine Heatwaves and Their Impacts

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Editorial on the Research Topic

Advances in Understanding Marine Heatwaves and Their Impacts

In recent years, prolonged, extremely warm water events, known as marine heatwaves, have featured prominently around the globe with their disruptive consequences for marine ecosystems. Over the past decade, marine heatwaves have occurred from the open ocean to marginal seas and coastal regions, including the unprecedented 2011 Western Australia marine heatwave (Ningaloo Niño) in the eastern Indian Ocean (e.g., Pearce et al., 2011), the 2012 northwest Atlantic marine heatwave (Chen et al., 2014), the 2012 and 2015 Mediterranean Sea marine heatwaves (Darmaraki et al., 2019), the 2013/14 western South Atlantic (Rodrigues et al., 2019) and 2017 southwestern Atlantic marine heatwave (Manta et al., 2018), the persistent 2014–2016 “Blob” in the North Pacific (Bond et al., 2015; Di Lorenzo and Mantua, 2016), the 2015/16 marine heatwave spanning the southeastern tropical Indian Ocean to the Coral Sea (Benthuisen et al., 2018), and the Tasman Sea marine heatwaves in 2015/16 (Oliver et al., 2017) and 2017/18 (Salinger et al., 2019). These events have set new records for marine heatwave intensity, the temperature anomaly exceeding a climatology, and duration, the sustained period of extreme temperatures. We have witnessed the profound consequences of these thermal disturbances from acute changes to marine life to enduring impacts on species, populations, and communities (Smale et al., 2019).

These marine heatwaves have spurred a diversity of research spanning the methodology of identifying and quantifying the events (e.g., Hobday et al., 2016) and their historical trends (Oliver et al., 2018), understanding their physical mechanisms and relationships with climate modes (e.g., Holbrook et al., 2019), climate projections (Frölicher et al., 2018), and understanding the biological impacts for organisms and ecosystem function and services (e.g., Smale et al., 2019). By using sea surface temperature percentiles, temperature anomalies can be quantified based on their local variability and account for the broad range of temperature regimes in different marine environments. For temperatures exceeding a 90th-percentile threshold beyond a period of 5-days, marine heatwaves can be classified into categories based on their intensity (Hobday et al., 2018). While these recent advances have provided the framework for understanding key aspects of marine heatwaves, a challenge lies ahead for effective integration of physical and biological knowledge for prediction of marine heatwaves and their ecological impacts.

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This Research Topic is motivated by the need to understand the mechanisms for how marine heatwaves develop and the biological responses to thermal stress events. This Research Topic is a collection of 18 research articles and three review articles aimed at advancing our knowledge of marine heatwaves within four themes. These themes include methods for detecting marine heatwaves, understanding their physical mechanisms, seasonal forecasting and climate projections, and ecological impacts.

DETECTION METHODS

Defining and identifying extreme warm water events require historical temperature records for quantifying climatological means and variance. Schlegel et al. investigate the results of using sub-optimal temperature time series. They determine how time series shorter than 30 years or with missing data affect marine heatwave statistics and offer best practices for improving the accuracy of marine heatwave detection. Identifying marine heatwaves with depth has the challenge of data sparsity and with instruments that may change position over time. Elzahaby and Schaeffer present new ways of identifying and comparing sub-surface marine heatwaves, using observations in the Tasman Sea. They find that surface characteristics of marine heatwaves do not necessarily reflect characteristics with depth and meso-scale eddies influence the deeper structure.

PHYSICAL MECHANISMS

Documenting marine heatwaves, through observations and ocean models, and developing the physical understanding of why they occur are essential for building the tools for prediction and mitigating their impacts. The articles document a diversity of marine heatwaves arising from changes in the atmospheric circulation and air-sea heat fluxes, ocean heat advection, and ocean heat content preconditioning.

Off southeast Queensland, Australia, Heidemann and Ribbe show that marine heatwave days tend to correlate with El Niño years in biodiverse, ecologically important marine sub-regions. They find that the time-lagged relationship with El Niño was strongest in the Southeast Queensland Marine Coastal Zone. Hervey Bay had the longest and most intense marine heatwave events and was likely more influenced by air-sea heat flux in its shallow and sheltered environment.

In the Tasman Sea, Behrens et al. demonstrate how wind stress curl and meridional heat transport are important for setting the ocean heat content. Enhanced ocean heat content preconditions waters to marine heatwaves. Ocean heat content has a predictive skill on timescales of weeks, thus acting as an indicator for marine heatwave likelihood.

In the southeast Indian Ocean, Feng and Shinoda analyze air-sea heat flux variability during Ningaloo Niño events off Western Australia. They determine that major sources of uncertainties owe to bulk flux algorithms based on six air-sea flux products. In the development phase, large uncertainties occur primarily related to sea surface temperature anomaly differences. However,

during the decay phase, anomalous latent heat flux is consistently important in all datasets.

In the North Pacific Ocean, Fewings and Brown examine the 2014–2016 marine heatwave and its dipole structure in sea surface temperature anomalies. They find that the 2015 split in spatial structure was caused a dipole-wind pattern configured by the coastline. The regional winds experienced longer than usual relaxations and were consistent with a large-scale, persistent mid-level atmospheric ridging pattern.

In the northwest Atlantic Ocean, Gawarkiewicz et al. describe an extensive, advective marine heatwave in the coastal waters off the northeastern USA in early 2017. The warm, salty water anomalies reached +6°C and were associated with a warm core ring, which impinged on the shelf south of Nantucket Shoals, with warm waters transiting southward along the Middle Atlantic Bight. They suggest that increasing occurrences of warm core rings combined with trapping processes may be an important contributor to marine heatwave events along shelf waters.

SEASONAL FORECASTS AND CLIMATE PROJECTIONS

Seasonal forecast models and climate model projections provide a path toward informing strategies for proactive marine ecosystem management given marine heatwave conditions months to years into the future. Using a multi-model ensemble of seasonal forecasts, Jacox et al. assess the predictability of the 2014–2016 northeast Pacific Ocean marine heatwave. For the California Current System, skillful predictions of warming periods in 2014 coincided with offshore warm anomalies and in 2016 with an oceanic response to the strong El Niño. Reduced forecast skill occurred during late-2014 consistent with the lack of skill for wind-driven sea surface temperature anomalies during a neutral El Niño Southern Oscillation.

Over longer timescales, climate projections are used to measure the change in likelihood of marine heatwaves under greenhouse gas emission scenarios. Based on global climate simulations, Oliver et al. consider the future changes in marine heatwaves based on their category and potential ecological impact. A “permanent marine heatwave state” arises in many parts of the ocean by the late 21st Century. Based on these projections and known ecological responses from exposure time and temperature anomalies, impacts on marine ecosystems are expected to be widespread, significant, and persistent through this century.

ECOLOGICAL IMPACTS

There has been a shift toward not only understanding how gradual global and regional warming trends affect marine ecosystems but also how marine species, populations, and communities respond to acute thermal stress during marine heatwaves. Here, articles document marine heatwave impacts on foundation species, including coral, seagrass, and kelp, invertebrate species, fishes, and also micronekton and microzooplankton. For coral reef environments, the review

by Fordyce et al. provides a framework describing how compounding factors, including extreme thermal anomalies and light penetration, affect the coral photo-endosymbiotic organism causing coral tissue loss and skeletal decay. Summer marine heatwave “hotspots” are proposed as a distinct class of thermal stress events with particular coral physiological responses. Marine heatwave metrics identified coral bleaching events when degree heating week estimates did not indicate a bleaching alert, and hence such metrics may improve ecological response predictability.

The review by Straub et al. provides an overview of how seaweeds have responded to past marine heatwaves with consequences varying from no detectable effects to local extinction. Marine heatwaves negatively affected canopy-forming seaweeds while promoting turf-forming seaweeds. They highlight the challenges associated with monitoring how marine heatwaves impact seaweeds based on extreme thermal stress compared with co-occurring stressors and interacting processes.

The systematic review by Kendrick et al. examines how the 2011 Ningaloo Niño and concurrent flooding affected the Shark Bay (Western Australia) seagrass ecosystem. Extensive temperate seagrass meadows perished, paving the way for small tropical seagrasses. These changes had flow-on effects to consumers, including sea snakes and dugongs, who rely on seagrass for food and habitat. They synthesize the conditions, feedbacks, and responses affecting seagrass structure and composition during the event's timeline.

Following southern New Zealand's strongest recorded marine heatwave in 2017/18, Thomsen et al. document the local extinction of bull kelp, a habitat-forming seaweed, in low intertidal zones. Losses were attributed to extremely warm ocean temperatures, given an assessment of potential stressors. These events were followed by a bloom of invasive kelp *Undaria* and colonization of other fast-growing seaweeds.

Giant kelp forests are fundamental habitats that were affected by the 2014–2016 marine heatwave in the California Current System. Using satellite imagery from southern California to Baja California, Cavanaugh et al. found that canopy biomass loss and recovery had latitudinal variations. Kelp loss was found to occur when the warmest month's mean sea surface temperatures exceeded 24°C. At sites in the Baja California Pacific Islands, Arafeh-Dalmau et al. document losses in giant kelp density and coverage, sessile invertebrates, sea stars, and cold water species and the appearance of invasive seaweed species. Both studies indicate that kelp forests at the equatorial edge are vulnerable to marine heatwaves and future increases in their likelihood.

Burdett et al. experimentally simulated sub-lethal, acute heat stress in two common, habitat forming kelp species from the northeast Atlantic. The shallow water species *Laminaria digitata*, from populations near their upper thermal limit, had higher sensitivity in terms of photosynthesis compared to *Laminaria hyperborea*, which displayed no apparent change in net photosynthesis. While the kelp species displayed some resilience to short term heat stress, further studies are important for assessing photo-physiological responses with greater duration heat stress.

Following the 2011 Ningaloo Niño, Caputi et al. synthesize the recovery status of Western Australia's invertebrate fisheries

and develops a framework for managing fish stocks during and post marine heatwaves. The recovery rate was affected by factors including the species' distribution and sensitivity to increased water temperatures, level of recruitment and spawning stock impairment, life-cycle characteristics, habitat loss, and if management interventions occurred. Prior to a fishing season, fisheries pre-recruit surveys provide early detection of marine heatwave impacts on the stock and potential early management strategies. Furthermore, Chandrapavan et al. examine how the marine heatwave caused recruitment failure and subsequent stock decline of the commercially important blue swimmer crab fishery in Shark Bay. Stock partially recovered within 18 months. By 3 years, full recovery occurred largely owing to water temperatures and fishery closure to aid spawning stock recovery. The studies demonstrate how the rebuilding of impacted stocks can occur through increased monitoring of stock abundance and the environment and timely management actions combined with industry cooperation.

Off Western Australia, Smith et al. discuss a longer-term poleward shift in *Sillago schomburgkii*, a temperate fish known as yellowfin whiting that is commercially fished. They propose that self-recruitment at higher latitudes is important. After the 2011 Ningaloo Niño, whiting abundance was found shifted markedly poleward. This shift was associated with the unusually strong poleward flow and larval dispersal combined with an extended spawning period from warmer waters at higher latitudes.

In the California Current System, Brodeur et al. examine the pelagic micronekton (crustaceans, small fish, and squid) and macrozooplankton communities prior to and during the 2014–2016 marine heatwave. Using multi-year trawl catch data, they find a major structural shift in species assemblages, from a crustacean to a gelatinous dominated system, in relation to environmental conditions.

For Australia's coastal ecosystems, Babcock et al. synthesize the impacts of recent extreme climate events, including marine heatwaves, on habitat forming species such as coral reefs, kelp forests, seagrasses and mangroves. They use ecosystem models to contrast the long-term implications of simulated pulse, episodic, or step-change disturbances. From multiple model types, the longest recovery times were associated with delays in habitat recovery, with longer recovery timescales for tropical systems compared to temperate systems.

ADVANCING OUR UNDERSTANDING OF MARINE HEATWAVES

In summary, this Research Topic contributes toward progress in understanding the detection, mechanisms, and prediction of marine heatwaves and their ecological consequences. In this emerging research field on ocean temperature extremes, rapid dissemination of knowledge is crucial for meeting the challenges of the increasing frequency of marine heatwaves. This collection has brought together research aimed at closing the gap in our understanding of the physical mechanisms for marine heatwaves, the ecological impacts and risks for marine ecosystems and timescales of recovery. In doing so, this Research Topic supports a framework for disseminating new, multidisciplinary knowledge

so scientists, marine resource managers, and marine industries can develop proactive responses through monitoring, prediction, and solution-oriented approaches to marine heatwaves.

AUTHOR CONTRIBUTIONS

JB led the writing with all other authors contributing in summarizing the literature and editing. All authors listed have contributed to this work and approved the manuscript for publication.

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Marine Heat Waves and the Influence of El Niño off Southeast Queensland, Australia

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In this paper, we investigate the occurrence and spatial variability of marine heat waves (MHWs) off the southeast coast of Queensland, Australia. The focus is on identifying sea surface temperature (SST) variability in two key ecological hotspots located south of the Australian Great Barrier Reef. This coastal region is bordered in the east by the intensification zone of the East Australian Current (EAC). It includes Hervey Bay, which is part of a UNESCO declared marine biosphere and the Southeast Fraser Island Upwelling System. The analysis of remotely sensed SST for the period 1993 to 2016 identifies the largest number of MHW days for Hervey Bay with a mean length of 12 days. The maximum length of 64 days occurred during the austral summer 2005/2006. The years with the largest number of MHW days was found to occur following the El Niño events in 1998, 2010, and 2016. A cross-correlation and Empirical Orthogonal Function analysis identified a significant correlation with a time lag of 7 months between SST anomalies in the Niño 3.4 region and the southeast Queensland coast. 78% of variance in SST anomalies is explained by the first mode of variability. The strength of the relationship with El Niño was spatially variable and the weakest in Hervey Bay. Due to its sheltered location and shallowness, it is argued that local weather patterns and air-sea fluxes influence this area more than the other two regions, where remotely forced changes in oceanic heat advection may have a stronger impact on generating MHWs. Biodiverse coastal shelf ecosystems are already under tremendous pressure due to human activities. This is likely to be compounded by continued climatic change and an increasing number of MHWs. Thus, similar studies are encouraged for other regional shelves and smaller scale coastal systems.

Keywords: marine heat wave, El Niño Southern Oscillation, sea surface temperature, Hervey Bay, climate variability

INTRODUCTION

Climatic extreme events such as marine heat waves (MHWs), cold spells, floods, and storms can strongly effect marine ecosystems (Hobday et al., 2016). These events alter species distributions as well as ecosystem structures and functioning (Wernberg et al., 2013). Due to a changing climate, terrestrial heat waves and severe rainfall events are likely to increase in intensity and frequency

in the future (Coumou and Rahmstorf, 2012). The same has been found for MHWs (Frölicher et al., 2018). Marine ecological impacts of extreme events are much less well understood than on land, but MHWs have shown to significantly affect marine communities (Frölicher and Laufkötter, 2018) and can have severe economic consequences for fisheries (Mills et al., 2017). The El Niño Southern Oscillation (ENSO), which is the most significant global climate anomaly on an inter-annual time scale (Timmermann et al., 2018), is one of the drivers of sea surface temperature (SST) extremes such as MHWs (Oliver et al., 2018a) and cold spells (Salinger et al., 2016). SST variability due to ENSO has been shown to globally impact on ecosystem structures on various spatial scales. This includes the oceans surrounding Australia (Pearce and Feng, 2013; Sprogis et al., 2017; Arias-Ortiz et al., 2018; Benthuisen et al., 2018; Stuart-Smith et al., 2018), the Peruvian Upwelling Ecosystem (Quispe-Ccalluari et al., 2018), the Gulf of California (García-Morales et al., 2017) and the northeastern Arabian Sea (Vidya and Kurian, 2018).

Large scale anomalous warming of the Australian coastal ocean has been observed as a consequence of ENSO influenced SST variability for the World Heritage Great Barrier Reef (GBR, Redondo-Rodriguez et al., 2012; Hughes et al., 2017; McGowan and Theobald, 2017; Benthuisen et al., 2018; Stuart-Smith et al., 2018), the Leeuwin Current (Holbrook et al., 2009; Feng et al., 2013), the East Australian Current (EAC) (Holbrook et al., 2009), and the Tasman Sea (Oliver et al., 2017). In regards to the GBR, the relation between El Niño/La Niña and summer SST anomalies is spatially variable and the strongest in the south of the reef over a 60 years study period (Redondo-Rodriguez et al., 2012). It appears that ENSO generally has a larger impact on SST variability along the west than the east coast of Australia, however, this impact increases toward the Coral Sea in the northeast (Holbrook et al., 2009). In the GBR region, coral bleaching was enhanced by specific local El Niño associated weather patterns. These were dominated by reduced cloud coverage during most previously reported bleaching events in 1983, 1987, 1992, 1993, 1998, 2010, and 2016 (McGowan and Theobald, 2017). The 1997/1998 El Niño caused global coral bleaching (Hoegh-Guldberg, 1999). This was followed by GBR mass coral bleaching events during 2002 and again in 2016 due to a MHW influenced by the 2015/2016 El Niño. The bleaching event had the largest spatial extent (Hughes et al., 2017), leading to severe ecosystem disturbances (Stuart-Smith et al., 2018). The last event occurred in 2017 (Great Barrier Reef Marine Park Authority, 2016). In this study, we refer to ENSO as detected in SST variability through advective processes, but discuss the role of changes in local air-sea heat fluxes as potential MHW drivers too, with both processes being the drivers of MHWs (Oliver et al., 2017).

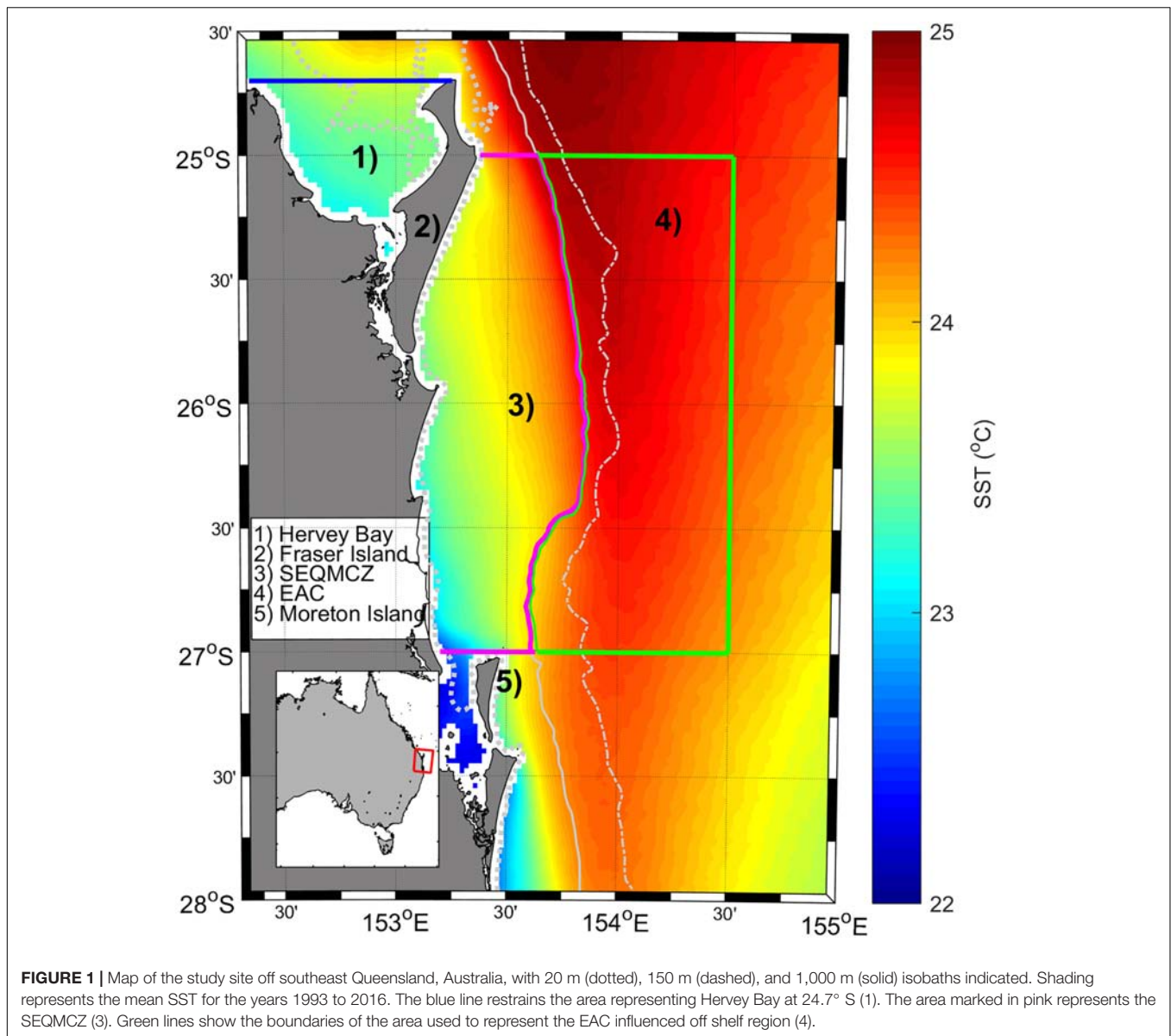
Extreme SST anomalies (SSTa) occurred off Western Australia in 2011 and were found to be driven by a moderate to strong 2010–2011 La Niña event. This was associated with a strengthening of the Leeuwin Current transporting anomalous warm waters southwards (Feng et al., 2013). Local atmospheric heating enhanced the current driven warming resulting in maximum SSTa of more than 3°C (Rose et al., 2012). The event had severe ecological impacts by increasing fish and invertebrate

mortality, triggering a southward shift of tropical species (Pearce and Feng, 2013) and coral bleaching (Feng et al., 2013). Kelp forests north of 29°S, which have a temperature threshold of 2.5°C above the summer climatology, have not recovered from this event and have instead been replaced by turf forming seaweeds (Wernberg et al., 2016).

Along Tasmania's coast, the strongest MHW occurred in 2015/2016. It lasted for 251 days and reached 2.9°C above average, taking place during the strongest El Niño on record (Oliver et al., 2017). Its cause was mainly oceanic heat advection through the anomalous intense poleward flow of the EAC (Oliver et al., 2018b), on which ENSO had a weak impact and which very likely was only possible due to climate change driven ocean warming (Oliver et al., 2017). The EAC is the western boundary current of the South Pacific subtropical gyre. MHWs linked to ENSO are superimposed on the documented long-term warming trend, which for the EAC region is estimated by Shears and Bowen (2017) to be in the order of 0.1–0.2°C per decade. Anomalous ocean currents and anomalous warm air temperatures are the main triggers of MHWs (Schlegel et al., 2017).

Recent studies identify and examine MHWs in different parts of Australia. However, no study focuses on the area just south of the GBR, where two key ecological hotspots are located. Hervey Bay is one of the most biodiverse marine environments in Australia and a UNESCO world heritage designated biosphere (Ribbe, 2014). Further south, the Southeast Queensland Marine Coastal Zone (SEQMCZ) is a key area for biodiversity as well as for fisheries which is driven by the Southeast Fraser Upwelling System (Ward et al., 2003; Brieva et al., 2015). Therefore, we aim to identify the occurrence and timing of MHWs in these small scale ecological hotspots and discuss potential physical drivers and their ecological impacts. To do so, we analyze remotely sensed SST and the relationship with El Niño events in our study area off southeast Queensland, Australia (**Figure 1**), between 1993 and 2016. The region is located between about 24° and 28° S, and the eastern border is located at 155° E. It comprises Hervey Bay (Ribbe, 2014), the SEQMCZ (Brieva et al., 2015), and the intensification zone of the EAC (Ridgway and Dunn, 2003). We contrast MHW occurrences and ENSO influences in Hervey Bay to those in the other two key regions. The study expands on Gräwe et al. (2010), who focused on the link between ENSO and local rainfall and flooding events in Hervey Bay. We identify MHWs from SSTa, calculate their metrics and statistics according to Hobday et al. (2016) and apply the Hobday et al. (2018) categorization to identify and discuss key events for each of the regions. In addition, we conduct an Empirical Orthogonal Function analysis and cross-correlation analysis to investigate the influence of ENSO on MHWs.

Hervey Bay covers an area of about 4000 km² and is located south of the GBR (**Figure 1**). The climate of the region is subtropical with a mean near surface air temperature between about 17 and 26°C, high evaporation and low rainfall (Ribbe, 2014). Terrestrial runoff is generally low (Ribbe, 2014) but large inflow can occur due to local weather extremes and as result of strong ENSO (La Niña) driven floods (e.g., Gräwe et al., 2010).



Hervey Bay is recognized for its marine biodiversity and is part of a UNESCO listed biosphere. The largest sea grass meadows at the east Australian coast are found here (Sheppard et al., 2007), which are home to significant populations of dugongs and marine turtles (e.g., Brodie and Pearson, 2016). The dominant seagrass is *Halodule uninervis*, which covers 81% of the seagrass pasture (Sheppard et al., 2007). Hervey Bay is also a resting place for thousands of humpback whales that annually migrate between the tropical Pacific Ocean and the Southern Ocean (Forestell et al., 2011; Franklin et al., 2018).

The SEQMCZ covers the continental shelf south off Fraser Island (Figure 1). It is one of eight key ecological hotspots along the east Australian coast and known for its marine biodiversity. It is important to fisheries and as spawning area for many temperate fish species and has a high diversity of pelagic fish (Ward et al., 2003; Young et al., 2011; Dambacher

et al., 2012). Important physical oceanographic processes that drive the marine biodiversity of the region include the SEQMCZ spanning wind-driven Fraser Gyre (Azis Ismail et al., 2017), the Southeast Fraser Island Upwelling System (Brieva et al., 2015), and cyclonic frontal eddies (Ribbe et al., 2018). The SEQMCZ's eastern boundary is the intensification zone of the EAC (Ridgway and Dunn, 2003), which is the region of the EAC we identified and examined in this study (Figure 1). The EAC transports warm Coral Sea water southward along Australia's east coast (Suthers et al., 2011) and approaches the continental shelf just to the south of Fraser Island. The shape of the continental shelf influences its flow direction. In the area off southeast Queensland, the EAC intensifies (Suthers et al., 2011) and shows maxima in surface current velocities and water volume transported (Ridgway and Dunn, 2003). The interaction of the EAC with the shelf-break drives seasonal upwelling onto the shelf (Brieva et al., 2015) and

constitutes the eastern branch of the shelf-occupying Fraser Gyre (Azis Ismail et al., 2017).

In this study, we document that the largest number of MHW days occurred following medium to strong El Niño events. In addition, we identify a significant, time-lagged relationship between ENSO, as detected in ocean temperature variability, and inter-annual SST variability, which is the strongest in the SEQMCZ and the weakest in Hervey Bay. In Hervey Bay, the total number of MHW days between 1993 and 2016 was the largest. MHWs lasted up to 64 days and reached the highest mean (1.3°C) and maximum intensities (4.2°C) in comparison to the other two areas.

DATA AND METHODS

Sea Surface Temperature (SST)

Daily sea surface temperatures (SST) were obtained from the Advanced Very High Resolution Radiometer (AVHRR) on a spatial resolution of $0.02^{\circ} \times 0.02^{\circ}$ for the period January 1993 to December 2016. The data are day and night composites that show a 24 h average SST for every grid cell (IMOS, 2017) and were used previously in studies of the Southeast Fraser Upwelling System (Brieva et al., 2015) and the Fraser Gyre (Azis Ismail et al., 2017).

The climatology and the threshold values (90th percentile) were calculated for each day of the year, using an 11-day window centered on each specific date. A 30-day moving average was then applied to generate a smooth climatology and threshold time series, following the methodology of Hobday et al. (2016) to detect MHWs.

Daily SSTa were computed by subtracting the climatology from the corresponding daily SST. This was performed for the whole region as well as each individual region of interest, which are displayed in **Figure 1**. Daily SSTa were averaged to monthly SSTa as well. The data were spatially averaged over each single region (Hervey Bay, SEQMCZ, EAC, shown in **Figure 1**) to generate a time series of monthly SST for each separate region. A 3-months moving average of monthly SSTa was computed for the study region to remove short-term variability. This data are used to examine interannual SSTa variability between 1993 and 2016 (**Figure 2**).

A linear regression was applied to monthly SSTa of the entire area using a least-squares fit to determine the SST warming trend over the entire period.

Marine Heat Waves (MHW)

Marine Heat Waves (MHWs) were defined as prolonged, discrete and anomalous warm water events, following the approach by Hobday et al. (2016). The metrics to characterize each event were calculated from daily SST data, using the criteria and methodology introduced by Hobday et al. (2016). The climatology was calculated as an 11-day centered average for each day of the year for 24 years of remotely sensed data (1993–2016). For a smooth climatology, a 30-day moving average was applied, as recommended by Hobday et al. (2016). Leap years in the climatology were accounted for by interpolating the climatological value for the 29th February when calculating

SST anomalies during a leap year. Using the same methods, the seasonally varying 90th percentiles were computed. These were the threshold values that defined MHWs. Subtracting the climatology from the daily SST an anomaly time series was obtained. Following Hobday et al. (2016), a MHW event had a specific start and end time and took place, when the seasonally varying threshold was exceeded for at least 5 consecutive days. Two events, which had a gap of less than 3 days were counted as one MHW event. To examine the properties of each MHW, the duration, maximum, mean and cumulative intensity for each event were calculated. In addition, yearly statistics were calculated including number of MHW, mean intensity, mean duration and total number of MHW days per year. The metrics were obtained for all three regions of interest (Hervey Bay, SEQMCZ, and EAC region) separately to compare spatial differences. Trends in frequency, MHW intensity, MHW days per year and average MHW duration from 1993 to 2016 were calculated as well, however, have to be interpreted with moderation due to the short time series. The MHW analysis was implemented in Matlab.

Empirical Orthogonal Function Analysis

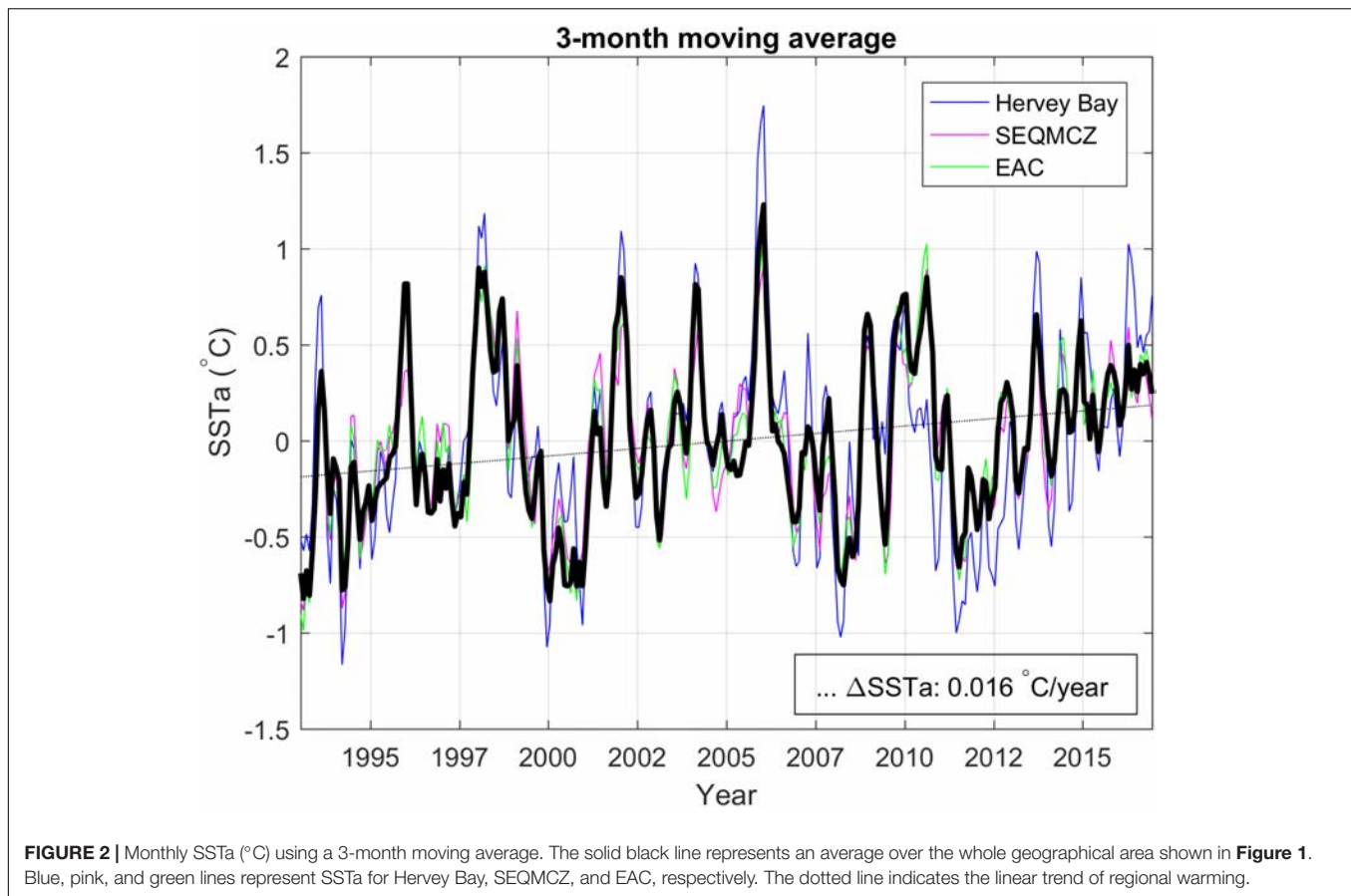
Using detrended and deseasoned SSTa, Empirical Orthogonal Function (EOF) Analysis was conducted. This gives an indication of the spatial and temporal SSTa variability (Redondo-Rodriguez et al., 2012). To examine temporal patterns, principal components were computed, while the maps of EOFs provided information about spatial patterns (Oliver et al., 2018b). The amount of variance, which could be explained by each mode of variability, was determined. The three first modes of variability and its principal components (pc1, pc2, and pc3) were considered.

Oceanic Niño Index (ONI) and ENSO Classification

The Oceanic Niño Index (ONI)¹ is used as a measure for ENSO variability (NOAA, 2017). The ONI is a 3-month running mean of the monthly Extended Reconstructed Sea Surface Temperature (ERSSTv4) anomalies for the Niño 3.4 region located at the equatorial Pacific Ocean (5°N to 5°S and 120° to 170°W) with a base period of 1986–2015 (NOAA, 2017). Monthly SSTa for Hervey Bay, the SEQMCZ and the EAC were used for a comparison to the ONI.

The ONI indicates periods of El Niño and La Niña events and their strength with SSTa above or below a threshold of $+0.8$ or -0.8°C . The equatorial SSTa is compared with SSTa along the Australian east coast to examine the influence of ENSO events in our regions of interest. In this study, we use the Australian Bureau of Meteorology's El Niño and La Niña categorization (BOM, 2017a,b). The strongest El Niño events according to the BOM criteria occurred in 1997 to 1998, 2009 to 2010 and 2015 to 2016, while the strongest La Niña events were recorded during the periods 1998 to 2001, 2007 to 2008, and 2010 to 2012.

¹<http://www.cpc.ncep.noaa.gov/data/indices/>



Monthly ERSSTv5 anomalies² for the Niño 3 region (5° N to 5° S and 90° to 150°W), located east of and overlapping with the Niño 3.4 region and for the Niño 4 region (5° N to 5° S and 150°E to 150°W), which overlaps with the Niño 3.4 region toward the west (NOAA, 2018), were considered as well. Their base period was 1981–2010 (NOAA, 2018) and a 3-months running mean was taken to make them comparable to the ONI. These data aid our discussion of the spatial relationship of SSTa in the study region to El Niño.

Air Temperature

Daily maximum air temperature data from the Maryborough weather station were provided by the Australian Bureau of Meteorology from 1993 to 2016 (BOM, 2018; station number: 040126). Monthly averages and temperature anomalies were calculated as a deviation from the monthly mean air temperature. Data are not shown but inform the discussion of local processes contributing to SST variations.

Correlations

Pearson's correlation coefficients (R) between SSTa and the ONI, as well as 3 months running averaged SSTa from the Niño 3 and the Niño 4 region, were determined. Cross-correlating monthly SSTa and these Indices determined the maximum lag between

the variables. The maximum lag was used to align both datasets before performing the lag correlation. The resulting correlation coefficient represents a time-lagged correlation of both variables. P -values were applied as a measure of statistical significance to the results and a correlation defined as significant when $p < 0.05$. In addition, cross-correlation has been conducted for the first principal component, determined by EOF analysis, and the most widely used Index (ONI).

RESULTS

SST at the Southeast Queensland Coast

The climatological SST averaged for the period 1993–2016 shows spatial differences off the southeast Queensland coast (**Figure 1**) which characterizes the three distinct regions considered further in this analysis. The off shelf region of the EAC intensification zone is warmer than the on shelf regions of the SEQMCZ and Hervey Bay, since the EAC advects warm subtropical Coral Sea surface water southward. Highest SST are found in the north with about 25°C. Further south, surface water is cooler and the maximum SST distribution appears to align with the 150 m isobaths reflecting the shelf-hugging intensification zone of the EAC. On-shelf SST within Hervey Bay and the SEQMCZ is much lower than within the EAC, which is consistent with findings by Wijffels et al. (2018), and lowest (~22.18°C) in the southern

²<http://www.cpc.ncep.noaa.gov/data/indices/>

region of the SEQMCZ. The climatology was used to compute all anomalies discussed further.

The time series of the 3-months running spatially averaged SSTa shows distinct interannual variability for all three regions as well as the underlying warming trend computed across the whole domain (**Figure 2**). This underlying warming trend is 0.016°C per year, which agrees with the warming trend for the EAC region, as previously found by Shears and Bowen (2017). Anomalous SST, negative as well as positive, were the strongest in Hervey Bay (**Figure 2**).

MHWs Characteristics

Hervey Bay was the region impacted the most by MHWs. A total of 746 MHW days were identified during the 24 years period (**Table 1**). This compares to 673 and 655 days in the SEQMCZ and EAC region, respectively. On average, a MHW lasted longer in Hervey Bay than in the other areas, and had a mean duration of 12 days, in contrast to 10 days in the SEQMCZ and the EAC. As a consequence, Hervey Bay had the smallest number of MHW (61 MHWs), however, the largest number of MHW days. The mean intensity of a MHW was with 1.3°C the largest in Hervey Bay as well. In the SEQMCZ, 65 MHWs and in the EAC 63 MHWs were detected and a mean MHW intensity of 1.1°C . The maximum intensities during a MHW reached SSTa of 4.15°C in Hervey Bay on the 26.10.2001, 2.88°C in the SEQMCZ (3.10.1999) and 3.87°C in the EAC (26.10.2001).

The longest MHW lasted for 64 days (24.11.2005–27.01.2006) in Hervey Bay, 37 days (24.11.2005–31.12.2005) in the SEQMCZ and 45 days (21.7.2010–5.09.2010) in the EAC. The maximum cumulative intensity occurred in Hervey Bay as well and was with 120°C days (24.11.2005–27.1.2006) at least double as high as in the other areas. In comparison, the maximum was 43°C days (20.07.2010–23.08.2010) in the SEQMCZ and 61°C days (21.07.2010–5.09.2010) in the EAC.

Yearly statistics, as displayed in **Figure 3** and **Table 1**, show that in Hervey Bay, the largest number of MHWs per year occurred in 1998 with 8 MHWs, followed by 2007 and 2016 (6 MHWs) and 5 MHWs in 2005 and 2014. In the SEQMCZ the maximum amount took place in 1998 (10 MHWs), 2014 (8 MHWs) and 2010 (7 MHWs). In the EAC there were 10 MHWs in 2016, followed by 8 MHWs in 2010 and 7 in 1998. In Hervey Bay, the maximum number of MHW days per year were 111 days in 2016, 97 days in 2005 and 65 days in 1998. In the SEQMCZ, the largest number of MHW days per year were 137 days in 1998, 99 days in 2010 and 57 days in 2016. In the EAC, the maximum was 109 days in 2010, 93 days in 1998 and 70 days in 2016. The years, in which on average MHWs lasted the longest in Hervey Bay were 1993 (20 days), 2005 and 2016 (19 days). In the SEQMCZ, the year with the longest average duration was 2005 (16 days), followed by 2010 (14 days). In the EAC, the maximum average duration occurred in 2006 (16 days) and 2010 (14 days). Between 1993 and 2016, the average frequency of MHWs was 3 MHW per year in all three regions (**Table 1** and **Figure 3**). In Hervey Bay, there were 3 years, in which no MHWs occurred. These years were 1994, 2000, and 2012. In the SEQMCZ, no MHWs occurred in 2 years, 2000 and 2012. In the EAC region, there were no MHWs in 1993, 1994, 2000, and 2007 (**Figure 3**).

To summarize, Hervey Bay was the region with the largest amount of MHW days, the maximum SST anomalies, longest duration of MHWs and maximum cumulative intensity. Therefore, MHWs were the most intense, persisted the longest and occurred the most frequently in Hervey Bay and consequently, we expect the largest impact of MHWs on ecosystems in this area. For that reason we focused further analysis on Hervey Bay.

We identified the 3 years with the largest amount of MHW days for Hervey Bay. The year with the maximum MHW days, which were 111 days, was 2016. In spring, the maximum intensity during a MHW occurred, which was a $+3.3^{\circ}\text{C}$ SST anomaly on the 12.11.2016. During 2016, 6 MHWs occurred in total, with an average duration of 19 days per MHW. The longest MHW during this year lasted for 5 weeks (36 days) and took place in autumn (18.3.2016–23.4.2016). The mean MHW intensity was 1.13°C . The second most MHW days occurred in 2005, which were 97 days in total and 5 MHWs. In summer 2005/2006, the longest MHW from 1993 to 2016 occurred, which lasted for 9 weeks (64 days) from 24.11.2005 to 27.01.2006. It had the maximum cumulative intensity of the study period, which were 120°C days. Therefore, this particular MHW has possibly caused the largest negative ecological impact and its intensity was more than twice as large as the maximum cumulative intensity in the SEQMCZ and the EAC. The year with the third most MHW days (65), and 8 MHWs in total, was 1998. The mean MHW intensity was 1.29°C and the average duration was 8 days.

ENSO Influence

The magnitude of the ONI is used to classify persisting equatorial SSTa as El Niño and La Niña events (NOAA, 2017). To explore the influence of El Niño influenced advective oceanic processes on the study area at the east Australian coast, this index is compared with SSTa for Hervey Bay, SEQMCZ, and the EAC in **Figure 4** for the period 1993–2016. To explore the spatial relationship to El Niño, two additional indices from the Niño 3 and Niño 4 region are considered as well. During the study period, the largest ENSO warm events occurred in 1997/98, 2009/2010, and 2015/16 with equatorial warming exceeding the $+0.8^{\circ}\text{C}$ El Niño threshold.

At the southeast QLD coast, the largest number of MHW days occurred during El Niño years. In Hervey Bay, 2 out of 3 years with the maximum amount of MHW days in total occurred during El Niño influenced years, which were 1998 and 2016. 111 MHW days occurred in 2016, followed by 97 days in 2005, which was ENSO neutral, and 65 days in 1998. In the remaining two areas, the SEQMCZ and the EAC, all 3 years with the maximum number of MHW days took place during El Niño years, which were 1998, 2010, and 2016. Therefore, El Niño events seem to be a key driver for MHWs.

To validate this assumption, we conducted a cross-correlation between the ONI and monthly SSTa along the southeast Queensland coast. Results show a time lagged response of approximately 7 months. Aligned correlation coefficients were positive and the relationship between ONI and regional SSTa was significant. Therefore, positive ONI (El Niño) appeared to have an influence on time-lagged positive SSTa and negative

TABLE 1 | Summary of MHW event properties and metrics, divided into Hervey Bay, SEQMCZ and EAC.

Region	Hervey Bay	SEQMCZ	EAC
Total MHW days (1993–2016)	746	673	655
MHW counts (1993–2016)	61	65	63
Maximum intensity (°C) (date)	4.153 (26.10.2001) 3.422 (9.10.2007) 3.287 (12.11.2016)	2.876 (3.10.1999) 2.445 (22.02.2004) 2.348 (12.02.2002)	3.872 (26.10.2001) 3.286 (30.07.1997) 2.625 (15.1.1999)
Mean intensity (°C)	1.339	1.048	1.097
Maximum duration (date)	64 days (24.11.2005–27.01.2006) 36 days (20.08.2009–24.9.2009), (18.3.2016–23.4.2016)	37 days (24.11.2005–31.12.2005) 34 days (20.07.2010–23.08.2010) 26 days (17.4.1998–14.5.1998), (25.09.1998–20.10.1998)	45 days (21.7.2010–5.09.2010) 31 days (24.12.2005–26.01.2006) 24 days (9.12.2008–2.1.2009)
Mean duration (days)	12.03 days	10.35 days	10.23 days
Max. cum intensity (date)	119.81°C days (24.11.2005–27.01.2006) 51.65°C days (11.09.2013–14.10.2013) 48.80°C days (2.05.2016–5.06.2016)	42.47°C days (20.07.2010–23.08.2010) 41.93°C days (24.11.2005–31.12.2005) 27.16°C days (17.04.1998–14.05.1998)	60.53°C days (21.07.2010–5.09.2010) 40.99°C days (24.12.2005–26.01.2006) 36.47°C days (9.12.2008–2.1.2009)
Yearly statistics			
Maximum MHW count	8 (1998) 6 (2016,2007) 5 (2005,2014)	10 (1998) 8 (2014) 7 (2010)	10 (2016) 8 (2010) 7 (1998)
Mean intensity (°C)	2.28 (1996) 1.66 (2006) 1.58 (2002)	1.63 (2002) 1.54 (1999) 1.53 (1996)	1.74 (1997) 1.73 (2002) 1.63 (1996)
Maximum MHW days per year	111 days (2016) 97 days (2005) 65 days (1998)	137 days (1998) 99 days (2010) 57 days (2016)	109 days (2010) 93 days (1998) 70 days (2016)
Average duration	20 days (1993) 19 days (2016) 19 days (2005)	16 days (2005) 14 days (2010) 13 days (2009)	16 days (2006) 14 days (2010) 13 days (1998)
Average MHW frequency per year	2.71	2.71	2.75
Yearly trends between 1993 and 2016			
Counts MHW per year	+0.06 MHW (Ø of 2 in 1993 to 3.4 in 2016)	+0.13 MHW (Ø of 1.25 in 1993 to 4.16 in 2016)	+0.16 MHW (Ø of 0.89 in 1993 to 4.52 in 2016)
Mean intensity (°C)	+0.003°C (Ø 1.17°C in 1993 – 1.23°C in 2016)	–0.005°C (Ø 1–3°C in 1993 to 0.91°C in 2016)	+0.01°C (Ø 0.89°C in 1993 to 1.12°C in 2016)
MHW days per year	+1.19 days (Ø 17 days in 1993 to 45 days in 2016)	+0.75 days (Ø 19 days in 1993 to 37 days in 2016)	+1.13 days (Ø 14 days in 1993 to 40 days in 2016)
Average duration	+0.16 days (Ø 8.05 days in 1993 to 11.68 days in 2016)	–0.16 days (Ø 10.75 days in 1993 to 7.11 days in 2016)	+0.09 days (Ø 7.73 days in 1993 to 9.85 days in 2016)

Highlighted values indicate the criteria used to identify the three case studies shown in **Figure 5**: Case 1: marked in red; Case 2: marked in green; Case 3: marked in yellow. MHW properties include the total number of MHWs and MHW days, the maximum and mean intensity, the maximum and mean duration as well as the maximum cumulative intensity. Yearly statistics follow, as well as yearly MHW trends between 1993 and 2016.

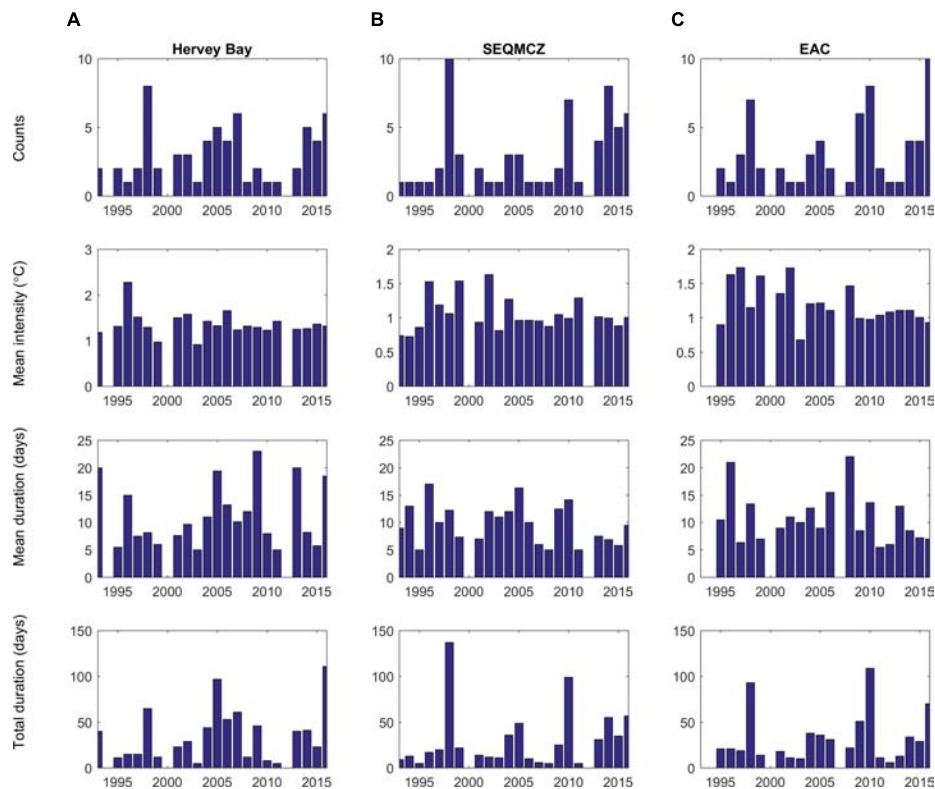


FIGURE 3 | Yearly MHW statistics for (A) Hervey Bay, (B) the SEQMCZ, and (C) the EAC. Top row: number of MHWs per year; second row: mean MHW intensity (°C); third row: mean MHW duration (days) and bottom row: total number of MHW days per year.

ONI (La Niña) on negative SSTa in the region of interest. The spatial differences in cross correlation coefficients can be seen in **Figure 4**. The lowest correlation was found for Hervey Bay. The highest cross correlation coefficient appeared in the SEQMCZ and eastward. The regionally averaged correlations were significant ($p < 0.05$) and coefficients $R = 0.30$ for Hervey Bay, $R = 0.36$ for the EAC and $R = 0.37$ for the SEQMCZ. The same process was conducted using the Niño 3 and Niño 4 indices. These reveal very similar relationship with the lowest correlation for Hervey Bay, followed by the EAC and the strongest one for the SEQMCZ. Correlations are the lowest in the most westerly located Niño 4 region, followed by the Niño 3.4 region, represented as the ONI, and were the strongest in the most easterly located Niño 3 region. Correlations are significant and the coefficients for the Niño 4 region were $R = 0.28$ for Hervey Bay, $R = 0.34$ for the EAC and $R = 0.35$ for the SEQMCZ. For the Niño 3 region coefficients were $R = 0.31$ for Hervey Bay, $R = 0.38$ for the EAC and $R = 0.40$ for the SEQMCZ. As the differences in correlations were very small, we focus on the widely used Niño 3.4 region (ONI) in the following discussion.

The first mode of variability of the EOF analysis explained 78.2% of the variance in SSTa, and cross-correlating its eigenvectors with the ONI resulted in a maximum lag of 7 months as well. Consequently, this first principal component showed the ONI influence on SST anomalies at the southeast Queensland coast. The second and third EOF mode explained 7.6 and 6.7%

of variance, respectively. Therefore, equatorial SSTa were the most important influence on interannual variability of SST at the southeast Queensland coast and ENSO events contributed to triggering MHWs.

MHW Trends

The MHW frequency was on average three events per year. However, between 1993 and 2016 the MHW frequency increased with a trend of +0.06 events per year in Hervey Bay, +0.13 events in SEQMCZ and +0.16 events in the EAC, which exceeded the global average of +0.045 events per year (Oliver et al., 2018a). In Hervey Bay, the trend of the mean intensity, MHW days per year and average MHW duration was increasing as well (**Table 1**). The number of MHW days per year increased in all regions. The largest rise occurred in Hervey Bay (+1.19 days per year), where the average number of MHW days increased from 17 days in 1993 to 45 days in 2016. In the SEQMCZ, MHWs increased by +0.75 days per year and in the EAC, by +1.13 days per year (**Table 1**).

DISCUSSION AND CONCLUSION

This study provides insight into the occurrence of MHWs along the southeast coast of Queensland and the influence of ENSO warm events. In this area, ENSO appears to be the primary driver

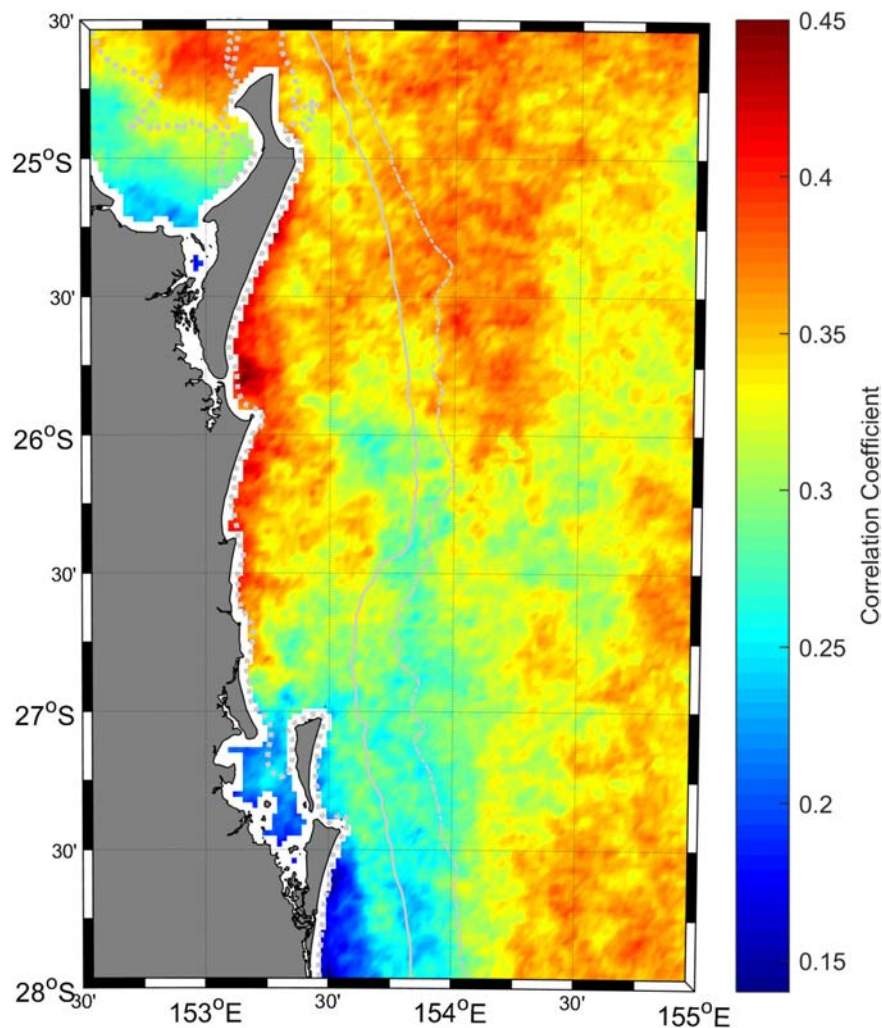


FIGURE 4 | Map of Correlation Coefficients between ONI and SSTa.

for inter-annual SST variability possibly through heat advection (78% of variance explained using EOFs) between 1993 and 2016. Hervey Bay is the region with the lowest cross correlation to the ONI ($R = 0.30$) and the SEQMCZ the region with the highest cross correlation ($R = 0.37$). The strongest response of SSTa to ENSO occurred with a time lag of 7 months. The spatial relationship between equatorial SSTa and SSTa in the study region became slightly stronger toward the eastern Pacific (Niño 3 region). In addition, the largest number of MHW days per year occurred during the 3 years following strong El Niño events in all regions with one exception found for Hervey Bay in the ENSO neutral summer 2005 to 2006. The largest number of total MHW days, the largest maximum as well as mean intensity, duration and cumulative intensity were found in Hervey Bay, which is the most shallow environment and possibly stronger influenced by air-sea fluxes. Therefore, this region may see large ecological impacts due to MHWs in the future as well. A relation between strong and moderate El Niño events and MHW frequency and intensity was evident on a global scale. In a previous analysis,

it was found to be the strongest in the eastern tropical Pacific by Oliver et al. (2018a). Possible explanations for these spatial differences and different drivers for MHWs in the study area will be discussed in the following.

MHWs and ENSO

Redondo-Rodriguez et al. (2012) found that inter-annual SSTa were partially associated with ENSO in the GBR region located to the north of our study site. Redondo-Rodriguez et al. (2012) also identified spatial differences in the correlation between the ONI and SSTa. Both these previous results are consistent with findings presented in this study. El Niño events were identified to affect SSTa and contributed in triggering MHWs. However, it appears that atmospheric drivers impact on MHW occurrence in particular in Hervey Bay as well, as it is the region with the lowest correlation to the ONI. These atmospheric processes may be caused by El Niño events and induce positive air-sea heat fluxes due to changes in, for example, cloud coverage. ENSO driven advective ocean processes have a larger influence on the

more exposed coastlines south of Hervey Bay. Furthermore, Redondo-Rodriguez et al. (2012) showed a time lag between the ONI and SSTa for the GBR and a significant correlation between the ONI in spring and summer as well as SSTa during the subsequent winter. This is in good agreement with the identified time lagged response to the ONI of about 7 months at the southeast Queensland coast to the south of the GBR. It is unclear, if atmospheric or oceanic patterns cause the longest and most extreme MHWs (Schlegel et al., 2017).

A very strong El Niño took place from 1997 to 1998. It coincided with, in 1998, the third highest number of MHW days per year in Hervey Bay (64 days), the highest amount of MHW days per year in the SEQMCZ (137 days) and the second highest number of MHW days per year in the EAC (93 days). Air temperatures in the area, near Hervey Bay (Maryborough) were above average in summer 1997/1998 as well and reached anomalies of $+2.1^{\circ}\text{C}$ in December 1997. In February 1998, SSTa were the largest with $+1.9^{\circ}\text{C}$ higher than usual. This occurred at the same time as on southern and central parts of the GBR, where a MHW was up to 2°C larger than average, and was followed by a mass coral bleaching event in January and February 1998 (Salinger et al., 2016).

At the southeast Queensland coast, many years with a particularly low number of MHW days per year coincide with moderate and strong La Niña events (2000, 2011, and 2012). La Niña events, as the 2011 event, can be associated with strong rainfall in southeast Queensland (Cai and Van Rensch, 2012). While El Niño events drive warm water anomalies at Australia's north and east coast, La Niña events can induce these at the coast of Western Australia. The 2011 La Niña event had extreme consequences at the coast of Western Australia, where it drove a MHW with significant ecological impacts on a variety of different marine species (Feng et al., 2013; Pearce and Feng, 2013; Wernberg et al., 2013), damaging more than a third of the seagrass meadows in a key site for seagrass ecosystems and carbon stocks in Western Australia (Arias-Ortiz et al., 2018). In addition, the same MHW event caused an extreme loss of kelp forests by 43% on the Great Southern Reef and its complete dieback north of 29°S . Temperate species replaced subtropical and tropical species along the west coast (Wernberg et al., 2016).

In 2016, the largest number of MHW days occurred in Hervey Bay. These events occurred during and followed the strong 2015/2016 El Niño, which caused a large number of strong MHWs in northern Australian waters, lead to mass coral bleaching events (Benthuyssen et al., 2018) and total structural ecosystem changes (Stuart-Smith et al., 2018). The maximum warming during MHWs in 2016 in Hervey Bay (3.29°C) was even larger than the maximum intensity reached in the areas further north, e.g., around the Torres Strait, the northern GBR and the western Coral Sea (2.05°C) (Benthuyssen et al., 2018), possibly due to its shallow environment. There were more MHW days in this tropical and much larger area (200 MHW days in 2016 in contrast to 111 MHW days in Hervey Bay). Starting in the austral summer 2015/2016, large areas of tropical Australia were exposed to MHWs for 3–4 months in a row (Benthuyssen et al., 2018). During February, March, and April 2016, SSTs were the highest on record on the GBR and this heat stress did not only induce mass

coral bleaching, but also caused complete irreversible mortality of corals especially in the northern parts of the reef, where the threshold of $3\text{--}4^{\circ}\text{C}$ weeks were exceeded (Hughes et al., 2017). It is assumed that these MHWs caused ecological disturbances in Hervey Bay as well, which may have been less extreme than those for the GBR. MHWs did not persist as long as they did in tropical Australian waters (maximum duration was 36 days). MHWs started occurring in March and lasted for a maximum of 5°C weeks. The south of Hervey Bay is habituated by corals (Zann et al., 2012), which may have been disturbed by this event. It is possible that the extensive seaweed meadows have not been damaged as the dominant species (*H. uninervis*) is adapted to tropical temperatures. In a recent study, which exposed the same species to temperatures of up to 33°C , Collier et al. (2012) found that its' growth and biomass even increased with rising temperatures. During the same year, at the southeast coast of Australia, a strong MHW, which lasted for 251 days, occurred due to an anomalous southward extension of the EAC, and had dramatic impacts on biodiversity, fisheries and aquaculture. In this case, the maximum intensity reached off coastal Tasmania was 2.9°C above the climatology (Oliver et al., 2017). Due to the very long duration of this MHW, ecological impacts are expected to be much larger than at the southeast Queensland coast, where the peak intensity was higher, however, the duration of the MHWs in 2016 lower.

Case Studies

To further discuss specific MHW events, their spatial SSTa signatures and their potential physical drivers, three case studies were identified based on their duration (see **Table 1**) and intensity (see **Figure 2**) and were classified according to Hobday et al. (2018). These include Case 1 for the whole region, Case 2 for the SEQMCZ, and Case 3 for Hervey Bay. The two main drivers of MHWs are advective ocean processes and air-sea fluxes, and we discuss the most likely in causing these MHWs. For each case, a sequence of averaged SSTa distributions covering periods of onset, maximum intensity and termination as well as a time series of daily mean SSTa averaged for each region are shown in **Figures 5A–C**. Maps show an average over the time period indicated above each panel, which are weekly in all cases but the last panel (end of the MHW, 4th panel from the left), which shows an average over the remaining period of the MHW. These are 9 days in Case 1 (**Figure 5A**, 4th panel from the left), 5 days in Case 2 (**Figure 5B**, 4th panel from the left) and 7 days in Case 3 (**Figure 5C**, 4th panel from the left).

Case 1: Broader Region (Figure 5A)

Using the Hobday et al. (2018) heat wave classification scheme, we find that the most significant MHW over the broader region occurred during the austral summer 2005–2006. It was characterized by the highest SSTa (**Figure 2**) during this ENSO neutral summer. It also coincided with longest and most intense MHW found in Hervey Bay (see below) and lasted for 9 weeks (65 days) from the 24.11.2005 to 27.02.2006. It peaked as a Strong MHW (Category II) for 26% of that period and reached a maximum SSTa of 2.77°C (**Figure 5A**, bottom row). For the remainder of that period (74%), it was categorized as a Moderate

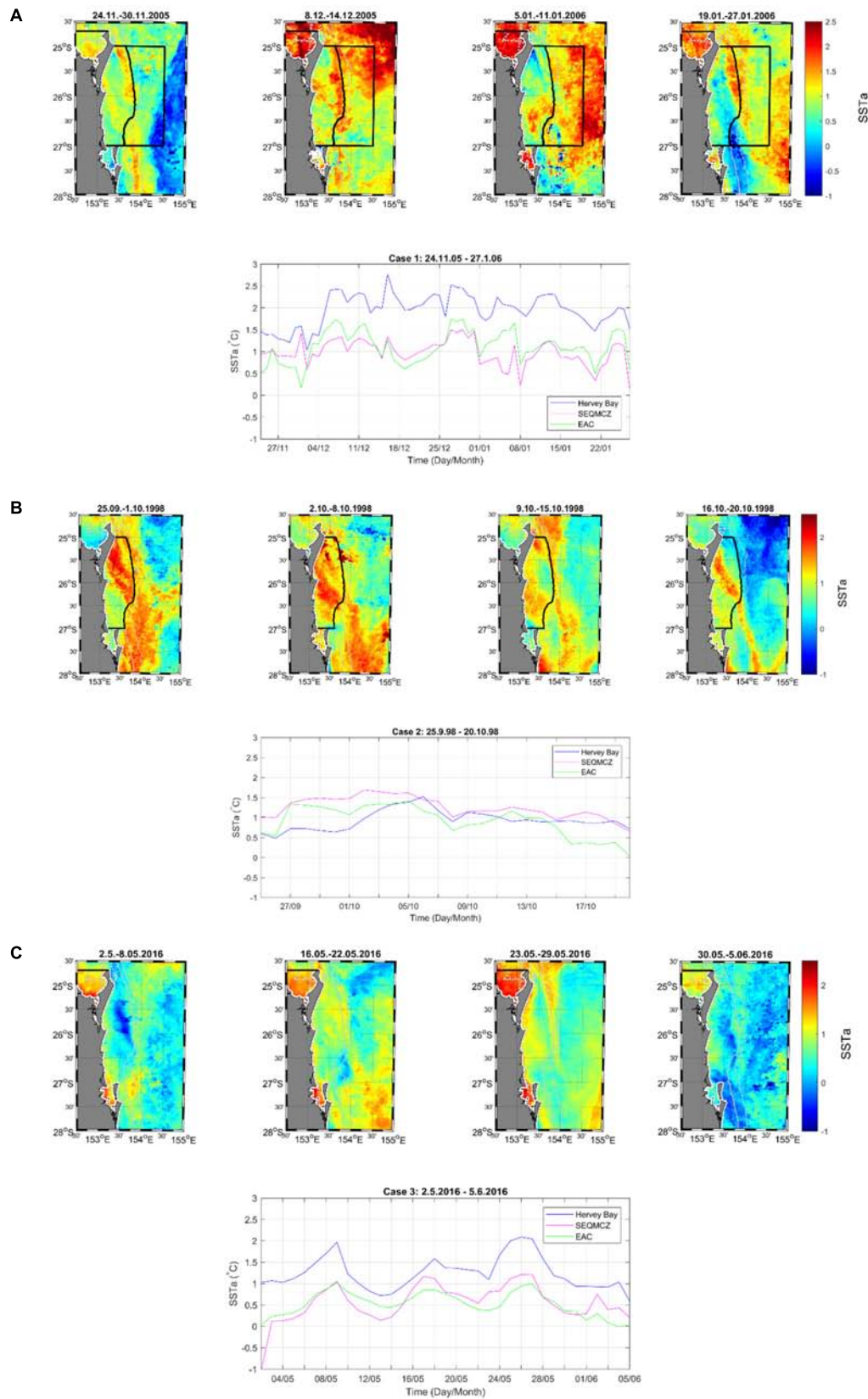


FIGURE 5 | Summary of three Case Studies. **(A)** Case 1 (24.11.2005–27.1.2006). Top row: weekly averaged SSTa maps in all cases but the last panel (end of the MHW, 4th panel from the left), which shows an average over the remaining period of the MHW. The time period averaged for each map is indicated above each panel. Maps include the most relevant weeks during this MHW. Black lines indicate the location of three study regions Hervey Bay, SEQMCZ and the EAC region. Bottom row: time series of daily SSTa for the examined time period, divided into three study regions. **(B)** Case 2 (25.09.1998–20.10.1998). Top row: weekly averaged SSTa maps in all cases but the last panel (end of the MHW, 4th panel from the left), which shows an average over the remaining period of the MHW. Maps include all weeks during this MHW. The time period averaged for each map is indicated above each panel. Black lines indicate the location of the SEQMCZ. Bottom row: time series of daily SSTa for the examined time period, divided into three study regions. **(C)** Case 3 (2.05.2016–5.05.2016). Top row: weekly averaged SSTa maps including the most relevant weeks during this MHW. The time period averaged for each map is indicated above each panel. Black lines indicate the location of Hervey Bay. Bottom row: time series of daily SSTa for the examined time period, divided into three study regions.

MHW (Category I). In the SEQMCZ and the EAC region, MHWs developed as well (see **Table 1**, marked in red). The 38 days lasting MHW in the SEQMCZ (24.11.2005–31.12.2005) was classified as Moderate (Category I) for 92% and Strong (Category II) for 5% of the time. It peaked with a maximum intensity of 1.5°C (**Figure 5A**, bottom panel). In the EAC region, the 31 days MHW (24.12.2005–26.1.2006) peaked with 1.7°C (**Figure 5A**, bottom panel) and remained a Moderate MHW (Category I) throughout this time.

Figure 5A shows the spatial distribution of SSTa during this prolonged MHW. These maps represent the onset period of the MHW (24.11.2005–30.11.2005), followed by the period with maximum SSTa in Hervey Bay (8.12.2005–14.12.2005), a period with high SSTa (5.01.2006–11.01.2006) and the termination period (19.01.2006–27.01.2006). The event started to develop at the end of November 2005 (**Figure 5A**, left panel) and intensified early December. During 8–14th December (**Figure 5A**, 2nd panel from the left), strong SSTa had developed in Hervey Bay, the EAC and eastern parts of the SEQMCZ along the shelf break. From 15th–29th, a narrow band of cooler water appeared along the shelf break and the eastern border of the SEQMCZ most likely due to upwelling of cooler subsurface waters, keeping parts of the SEQMCZ comparably cooler than Hervey Bay and the EAC by separating the shelf from the EAC waters.

For the majority of the heat wave (1.12.2005–27.01.2006), SSTa stayed constantly high in Hervey Bay, while more variations in SSTa were observed in the remaining study area and especially in the by upwelling influenced SEQMCZ (**Figure 5A**, 2nd–4th panel from the left). Analysis of ERA-Interim ECMWF wind data³ shows that the wind direction was northeasterly during the 1st week of the MHW (24.11.2005–30.11.2005) and veered to northerly during the 2nd week (1.12.2005–7.12.2005) of the MHW. Winds stayed northerly and with a small easterly component from the 1.12.2005–11.01.2006. Winds veered to easterly from the 12.01.2006–27.01.2006, when the MHW ends. An analysis of local air temperatures (data not shown, BOM, 2018; station number: 040126) in Maryborough shows positive anomalies as well, with a monthly average of 1.89°C above average in December 2005.

This broad scale event is possibly driven by oceanic heat advection due to an anomalous warm southwest Pacific Ocean. It likely lead to an increased heat transport by the EAC. The northerly winds from the beginning of December 2005 to the beginning of January 2006 may have contributed to the enhanced

transport of warm water from the Great Barrier Reef region into our study region (**Figure 5A**, 2nd panel from the left). Due to continuous north and northeasterly winds, warm surface water is advected into and retained in Hervey Bay, which possibly lead to intense and more persistent warming in Hervey Bay. In addition, air temperatures near Hervey Bay were anomalous high. This may have enhanced the MHW due to Hervey Bay's shallowness and protected environment. The SEQMCZ and the EAC region, in contrast, are strongly influenced by current driven transport, dispersing the anomalous warm water masses over a large area and leading to more variable SSTa in this region. Easterly winds toward the end of the MHW possibly contributed to dissipate the MHW by inducing a transport of cool water masses from the east into the study region.

Case 2: SEQMCZ (Figure 5B)

Case 2 is one of the longest lasting MHWs in the SEQMCZ. It occurred following the very strong 1997/1998 El Niño event. The MHW lasted for 26 days, from 25.09.1998 to 20.10.1998 (**Table 1**, marked in green; **Figures 2, 5B** bottom panel shows daily SSTa during this period) and peaked with a SSTa of 1.7°C . It was classified as a Strong MHW (Category II) for 42% of its duration and as Moderate (Category I) for 48% of days.

The spatial SSTa signature during this MHW is shown in **Figure 5B**. The event is characterized by a rapid onset and evolved to an intense MHW within the 1st week (25.09.1998–1.10.1998). It continued to weaken for the remainder of the event (**Figure 5B**). A wide region with above average SSTa covered the SEQMCZ during the 1st week, which was also the period of maximum intensity (25.09.1998–1.10.1998), extending south eastward and across the southern half of the EAC region. The maximum SSTa was found to the southeast of Fraser Island. In Hervey Bay, SST were average in the south and SSTa increased toward the north (**Figure 5B**, left panel). During the following week (2.10.1998–8.10.1998) the band of warm SST shifted slightly southward. Small regions with high SSTa occurred off the Fraser Island Coast. A small area of warm SSTa extended through the southern end of the EAC region (**Figure 5B**, 2nd panel from the left) as the area of warm waters moved further south. In the 3rd week of this MHW (9.10.1998–15.10.1998) a narrow strip of warm SSTa followed the shelf break south (**Figure 5B**, 3rd panel from the left), as warm waters were transported southwards. The warm patch in the SEQMCZ had slightly weakened and moved further south. During the termination of the MHW, from the 16.10.1998–20.10.1998, anomalous cool waters appear in the north of the EAC and therefore anomalies in the EAC region were mostly negative (**Figure 5B**, 4th panel from the left; bottom row).

³<https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/browse-reanalysis-datasets>

A region of warm SSTa remained on the shelf in the SEQMCZ, which extended southwards.

During the whole time period, SSTa were low in Hervey Bay. The wind direction was south-easterly during the onset (25.09.1998–1.10.1998), veering to northerly winds in from the 2.10.1998–15.10.1998, and north-easterly winds in from the 16.10.1998–20.10.1998 (ECMWF wind data, see above for source, not shown). The air temperatures for Maryborough (BOM weather data, see above for source, not shown) during September (-1.01°C) and October 1998 (-0.48°C) were colder than usual.

This event is likely driven by large scale heat advection due to the 1998 El Niño event. The lowest warming occurred in the region with the lowest correlation to the ONI (Hervey Bay), where also air temperatures were below average. The largest warming occurred in the region with the highest correlation to the ONI, the SEQMCZ. The lag correlation of 7 months shows the shelves' connection with the Pacific Ocean through the advective pathway. These observed above average SSTa occurred during spring 1998 and were time lagged following the El Niño event, which peaked in summer 1997/1998. There is no indication that the Indian Ocean Dipole has influence on atmospheric conditions through an atmospheric bridge in the study region (Risbey et al., 2009).

Case 3: Hervey Bay (Figure 5C)

Case 3 shows the third longest and intense MHW in Hervey Bay. This is one of the MHWs, which occurred following the 2016 El Niño event and lasted for 5 weeks from 2.05.2016 to 5.6.2016 (Table 1, marked in yellow; Figure 5C, bottom row). It is characterized by a slow onset, peaking in the 4th week and terminating afterwards.

The MHW peaked briefly for 3 days (9% of days) as a Severe MHW (Category III) with a maximum intensity of 2.09°C and stayed a Strong MHW (Category II) for 29% of days. During the onset (2.05.2016–8.05.2016), SSTa were the highest in the south of Hervey Bay, where it is the shallowest, and were above average in the whole bay. In contrast, average to below average conditions were found in most of the SEQMCZ and the EAC region (Figure 5C, left panel). The pathway of the EAC shows a slight positive anomaly, which is low compared to Hervey Bay.

In the east of the SEQMCZ toward the shelf break, an area of cool below average SSTa occurred due to upwelling of cool subsurface waters. This upwelling is visible in the following week as well, however, has weakened. The positive anomaly in Hervey Bay remained. In the 3rd week of the MHW (16.05.2016–22.05.2016), SSTa rose in Hervey Bay, showing a constant positive SSTa of up to 2°C extending beyond the 20 m Isobath (Figure 5C, second panel). SSTa in the EAC region and in the SEQMCZ were low. No upwelling was apparent during this time. The 4th week (23.05.2016–29.05.2016) was the period of maximum intensity, which showed on average, the highest SSTa in Hervey Bay. In the northern part of the study area, positive SSTa hugged the 150 m Isobath. SSTa of the same strength were observed off Fraser Island. The remaining areas of the SEQMCZ and the EAC region showed small positive SSTa (Figure 5C, 3rd panel from the left). During the termination (30.05.2016–5.06.2016) week, the anomaly weakened in the entire study area. Hervey Bay

remained warmer than usual, while average to below average SSTa occurred in the other regions (Figure 5C, 4th panel from the left). Winds were south-easterly during the first 3 weeks (2.05.2016–22.05.2016), veered to westerly winds in week of maximum SSTa (23.05.2016–29.05.2016) and to easterlies in the termination period (30.05.2016–5.06.2016; ECMWF wind data, not shown). During May, air temperature from Maryborough (BOM weather station air temperature, data not shown) reached an average anomaly of 3.2°C . This was the largest monthly average air temperature anomaly recorded between 1993 and 2016.

This regional MHW event in Hervey Bay is most likely not driven by oceanic heat convection, but by air-sea heat fluxes into the ocean. El Niño related atmospheric conditions potentially reduce cloud coverage, thus leading to increase heat flux into the ocean. As previously documented by Benthuyssen et al. (2018), these weather patterns induced a long lasting MHW on the Northern Great Barrier Reef starting in mid-May 2016, which overlaps with the time of this analyzed MHW in Hervey Bay. This is consistent with our findings that Hervey Bay showed the weakest correlation with SSTa in the tropical Pacific (ONI) and thus is likely to be more influenced changes in air-sea fluxes.

MHW Trends

Marine heat waves have often a more extreme negative impact on ecosystems than the gradual ocean warming trend (Oliver et al., 2018a) and many ecosystems may not be resilient to these abrupt disturbances (Wernberg et al., 2016). In a world of 2°C warmer than at present time, MHWs as in 2016 in north eastern Australia would, with high confidence, happen double as often. This would have severe effects on the GBR (King et al., 2017). Due to warming temperatures the probability of heat waves, in the ocean and on land, is increasing. However, knowledge of MHWs and their evolution is limited as is the ability to predict the severity of future events (Frölicher and Laufkötter, 2018), which is why more small scale studies will be a valuable tool in understanding future challenges. Adopting a consistent methodology such as that proposed by Hobday et al. (2016) and used in this study will make studies more comparable. Currently, there is only a small number of studies using the same definition and metrics (Frölicher and Laufkötter, 2018), which is increasing. It is known that the MHW frequency has risen globally (Oliver et al., 2018a) and may become more frequent as global warming continues (Frölicher et al., 2018). The rate of change along the southeast Queensland coast ($+0.06$ MHW events per year in Hervey Bay, $+0.13$ MHW events per year in the SEQMCZ and $+0.16$ MHW events per year in the EAC) is exceeding the global average of 0.045 events per year (Oliver et al., 2018a). However, these trends need to be considered with caution due to our relatively short length (1993–2016) of the dataset.

Limitations

Potential limitations of this study include the length of the time series in regards to the discussion of trends. In addition, the choice of data (Day/Night composite SST) may introduce a bias in the shallow areas due to diurnal heating and cooling. This may have a small to insignificant impact in the deeper regions of the

shelf and the EAC region. In future research, this analysis is to be revisited using additional data and the time frame expanded. Why the sensitivity of the correlation coefficient to the chosen equatorial SST regions shifts and the correlation becomes slightly stronger toward the eastern Pacific, requires further analysis as well.

In summary, this study finds that ENSO driven heat advection is likely to influence interannual variability of SSTa along the southeast Queensland coast and drives MHWs. This influence is the strongest at the exposed coastline and the weakest in the enclosed region of Hervey Bay. The analysis of SSTa variability finds the strongest signal to the ONI with a time lag of 7 months. Furthermore, SSTa in Hervey Bay are the most extreme, revealing the strongest MHWs within the study area. Large anomalies occur much more frequently in this than in the other areas, possibly due to the bay's shallowness and enclosed location leading to more rapid heating. North to northeasterly winds may enhance this by retaining warm water masses in this environment. Therefore, we suggest that ENSO in terms of heat advection, but also strongly through air-sea fluxes and local atmospheric and site specific conditions impact on generating these large MHWs. As Hervey Bay and the SEQMCZ are key ecological and biodiverse marine sites along the east Australian coast, investigating and understanding drivers for MHWs and examining ecological impacts of them through field studies is an important task for further investigations. MHWs, and their rising probability with continuously warming oceans, will continue to cause thermal stress and have already shown severe consequences on the GBR, just north of the study area, and all over Australia. This study stands in contrast to many other studies that investigate MHWs for

larger scale systems such as the Tasman Sea, the GBR and the Great Southern Reef. It is one of very few studies, that investigate ENSO-driven MHWs in small scale biodiverse coastal and shelf systems. Similar studies for other shelf and coastal regions globally should be inspired. Coastal shelf regions are already under increasing pressure and highly impacted by processes detrimental to biodiversity, which will compound in the future with proceeding climatic change and increasing numbers of MHWs.

DATA AVAILABILITY STATEMENT

The datasets analyzed for this study are publically available through IMOS (2017), as referenced in the methods section.

AUTHOR CONTRIBUTIONS

HH and JR designed the study. HH processed and analyzed the datasets and worked on interpretations of the results with JR. HH wrote the draft. JR contributed to the text by reviewing and writing.

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Local Extinction of Bull Kelp (*Durvillaea* spp.) Due to a Marine Heatwave

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Detailed research has documented gradual changes to biological communities attributed to increases in global average temperatures. However, localized and abrupt temperature anomalies associated with heatwaves may cause more rapid biological changes. We analyzed temperature data from the South Island of New Zealand and investigated whether the hot summer of 2017/18 affected species of bull kelp, *Durvillaea antarctica*, *D. poha*, and *D. willana*. *Durvillaea* spp. are large iconic seaweeds that inhabit the low intertidal zone of exposed coastlines, where they underpin biodiversity and ecosystem functioning. Sea surface temperatures (SST) during the summer of 2017/18 included the strongest marine heatwaves recorded in 38 years of existing oceanic satellite data for this region. Air temperatures were also high, and, coupled with small wave heights, resulted in strong desiccation stress during daytime low tides. Before-After analysis of drone images of four reef platforms (42, 42, 44, and 45°S) was used to evaluate changes to bull kelp over the hot summer. Bull kelp loss varied among species and reefs, with the greatest (100%) loss of *D. poha* at Pile Bay in Lyttelton Harbor (44°S). In Pile Bay, SST exceeded 23°C and air temperatures exceeded 30°C, while *Durvillaea* was exposed for up to 3 h per day during low tide. Follow-up surveys showed that all bull kelps were eliminated from Pile Bay, and from all reefs within and immediately outside of Lyttelton Harbor. Following the localized extinction of bull kelp in Pile Bay, the invasive kelp *Undaria pinnatifida* recruited in high densities (average of 120 m⁻²). We conclude that bull kelps are likely to experience additional mortalities in the future because heatwaves are predicted to increase in magnitude and durations. Losses of the endemic *D. poha* are particularly concerning due to its narrow distributional range.

Keywords: canopy forming seaweed, temperature anomaly, marine heatwave, extinction, endemic species, foundation species

INTRODUCTION

Between 1950 and 2009, mean sea surface temperature (SST) of the Atlantic, Indian, and Pacific Oceans increased by 0.41, 0.65, and 0.31°C, respectively (Hoegh-Guldberg et al., 2014). This increase has brought creeping changes to species distributions around the world (Hoegh-Guldberg and Bruno, 2005; Wernberg et al., 2011; Poloczanska et al., 2013). Superimposed on slow and

gradual temperature increases are discrete heating events covering smaller regions (1–1000 km) and occurring over shorter durations (days–months). These events are referred to as “heatwaves” (Perkins and Alexander, 2013; Hobday et al., 2016; Oliver et al., 2018) and can have more instantaneous and conspicuous effects (Wernberg et al., 2016; Le Nohaïc et al., 2017; Hobday et al., 2018; Smale et al., 2019). For example, in 2011 an extensive heat wave in Western Australia caused large scale southward range contraction of the canopy-forming fucoid *Scytothalia dorycarpa* (Smale and Wernberg, 2013) and kelp *Ecklonia radiata* (Wernberg et al., 2016). During the heatwave, temperatures exceeded the physiological tolerance of these species (Wernberg et al., 2010; Smale and Wernberg, 2013). Similarly, in northern Spain, range contractions have been reported for several canopy-forming seaweeds, including *Fucus serratus* and *Himanthalia elongata* (Duarte et al., 2013).

New Zealand recently experienced an exceptionally hot summer with unusually high sea water temperatures in coastal regions of the South Island (Megan, 2018). However, nearshore rocky intertidal marine species on the South Island of New Zealand are embedded within a wide temperate biogeographical region, are not near a convergence with warm subtropical waters, and are therefore expected to be relatively robust to short-term temperature anomalies (Schiel, 2004, 2011; Ayers and Waters, 2005; Schiel et al., 2016).

In southern New Zealand waters, the largest seaweeds over most of the coastline are southern bull kelps (*Durvillaea* spp.), the world’s largest fucoid algae. Because of their occurrence at the intertidal-subtidal margin they can experience both elevated air and sea temperatures during periods of emersion and immersion. On the South Island there are three co-occurring bull kelp species with either narrow endemic (*Durvillaea willana*, *Durvillaea poha*) or wide (*Durvillaea antarctica*) latitudinal ranges (Fraser et al., 2009, 2012). Individuals of these species can reach up to 10 m long, weigh up to 70 kg, and live for up to 10 years (Hurd, 2003). *D. poha* and *D. antarctica* are exposed during low-water on spring tides and *D. willana* is mostly subtidal with only some individuals being exposed on the biggest spring tides. Together, they form dense stands with extensive canopy cover. These bull kelps are important foundation species which control local community structure, affect biodiversity and provide food and habitat to culturally and economically important species, including lobsters and abalone (Smith and Simpson, 1995; Taylor and Schiel, 2005; Schiel et al., 2018b).

The objective of this study was to quantify changes in the abundance of *Durvillaea* spp. and associated short-term ecological changes following the hot summer of 2017/18 in New Zealand. To address the objective, we first quantified temperature changes in New Zealand, focusing on 42.5–45.4°S on the east coast of the South Island. Second, we quantified changes in abundances of bull kelp on reefs from the same regions before and after the 2017/18 summer. We hypothesized that bull kelp generally would decrease in abundance and that *D. poha*, with the most southern northern range limit, would be most severely affected (Smale and Wernberg, 2013; Bennett et al., 2015; Thomson et al., 2015; Wernberg et al., 2016; Arias-Ortiz et al., 2018). Finally, we quantified effects of bull kelp loss, by

comparing changes in abundances of key organisms before and after the hot summer in Pile Bay, to changes that followed from a manipulative bull kelp removal experiment. We hypothesized that bull kelp loss would be followed by rapid colonization of weedy macroalgae, irrespective of whether the loss of bull kelp occurred through high temperatures or experimental removals, and that abundances of weedy macroalgae are correlated negatively with abundances of juvenile bull kelp (Wernberg and Connell, 2008; Flukes et al., 2014; Benes and Carpenter, 2015; Wernberg et al., 2016).

MATERIALS AND METHODS

Study Sites

This study was done in the rocky intertidal zone on the east coast of the South Island of New Zealand. Surveys were conducted before and after the heatwave on reefs at Oaro (−42.516396, 173.510030), Pile Bay in the semi-protected Lyttelton Harbor (−43.615418, 172.765899) and two reefs in Moeraki (Kaik, −45.356039, 170.861386 and Point, −45.363833, 170.863349). These reefs extend 40–150 m from the upper intertidal to the subtidal zones, are generally protected from severe wave action by offshore reefs, and have a coastal topography that deflects swells. Following this survey (which showed bull kelp elimination from Pile Bay; see Results), other nearby reefs within and outside Lyttelton Harbor were surveyed to identify the wider area of bull kelp loss. Finally, we also used data from a canopy-loss experiment at Oaro and the two Moeraki reefs to estimate wider ecological impacts from the heatwave.

Changes in Temperature

First we used offshore sea-surface temperature (SST) to characterize heatwaves at the three main study sites using the R marine heatwave package (Smit et al., 2018). A heatwave was defined as a period of 5 or more consecutive days where the SST was greater than the 90th percentile calculated from > 30 years of data (Hobday et al., 2016). This analysis was based on NOAA high resolution blended analysis of daily SST data in 1/4 degree grids derived from satellites and *in situ* data¹ (Reynolds et al., 2007). Data were used from 30 August 1980 to 20 April 2018 from Oaro (grid centered on 42.625°S, 173.625°E), Pile Bay (43.375°S, 173.125°E) and Moeraki (45.375°S, 171.125°E). The distance from the reef sites to the grid center was < 25 km. To compare the summer of 2017/18 with past temperature anomalies we calculated (1) duration (in days), (2) maximum intensity (temperatures above the 90% threshold) and (3) cumulative intensity (duration × intensity) of all heatwaves, as defined by Smit et al. (2018) during the 38 years of available satellite SST. This analysis was based on daily mean temperatures from offshore waters and was carried out for each of the three sites separately. However, Pile Bay is located within the outer reaches of a harbor so this location may experience higher temperature fluctuations.

¹<https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html#detail>

We therefore also analyzed hourly SST from 4 nearby inshore buoys within the harbor from August 2016 to April 2018 (all sites were less than 4 km from Pile Bay²). The offshore and Lyttelton Harbor temperature data were analyzed graphically. Finally, we provide additional analyses and data in online **Supplementary Material** to better understand the environmental context and impacts of the hot summer. We analyzed the large-scale extent of the temperature anomaly **Supplementary Figure S1**, visualized marine heatwaves at the three main sites with different graphs (**Supplementary Figures S2, S3**) plotted 38 years of maximum air temperature for the same regions (recorded at the nearest airport, **Supplementary Figure S4**) and corresponding atmospheric heatwaves (**Supplementary Figure S5**), measured rocky shore intertidal high-resolution temperature from Hobo-pendant loggers at Oaro over the summer of 17/18 (**Supplementary Figure S6**), and plotted high resolution wave data from January 2014 to July 2018 from an offshore buoy near Lyttelton harbor (**Supplementary Figure S7**).

Changes in Abundances of Bull Kelp; Regional Survey

Four reef platforms from Oaro to Moeraki were sampled before the summer of 2017/18 with an Advanced Phantom 3 drone equipped with a 12 MP HD camera. Geo-tagged images were taken at low tide 10 m above the reef, with each image covering c. 95 m² that was estimated from survey tapes and 1 m² fixed quadrats positioned on each reef (Murfit et al., 2017). Drone images were collected in 2017 before the hot summer, with 20 images collected from Oaro (5 April), 20 from Pile Bay (24 August), 20 from Kaik reef (29 April), and 31 from Point reef (29 May). These reefs were re-visited in April 2018, where each entire reef was photographed (“after” data). Note that these surveys of coastal platforms may have underestimated the abundance of *D. willana*, because it occurs mostly in the subtidal zone. In the laboratory, Orthorectified and georeferenced maps of the reefs were created and the exact locations of the 2017 images were identified using a combination of the geotagged coordinates and visual land markers (boulders, channels, etc.). Percent cover of the three bull kelp species was estimated visually for each image (with a super-imposed grid of 100 cells), differentiating among the three species based on color and width of the blades and stipe characteristics (Adams, 1994; Fraser et al., 2009, 2012; Nelson, 2013). Data contained many zeroes and could not be transformed to variance homogeneity. We therefore tested our hypotheses that bull kelp would decrease in abundance and that *D. poha* would be most severely affected by the hot summer, using Wilcoxon Signed Paired Rank Tests for each of the three species (pooling data across reefs). For this analysis we only included paired before-after images where bull kelps were observed in at least one of the two sampling events.

Changes in Abundances of Bull Kelp; Local Surveys

The regional drone survey showed that *Durvillaea* spp. had become locally extinct at Pile Bay. We therefore visited 19 reefs

in March–May 2018 around Pile Bay, where we had information about the existence of healthy bull kelp in the years prior to the hot summer, based on a combination of geotagged photos and personal observations (by co-authors and locals). At each reef we recorded whether bull kelp blades were present (i.e., *Durvillaea* were alive), only holdfasts remained (“ghost holdfasts,” i.e., *Durvillaea* were dying, see **Figure 1**), or if we could see fresh “rock scars” that are typically visible following the recent detachment of *Durvillaea* holdfasts (i.e., *Durvillaea* have recently died) (Schiel et al., 2018a). We classified each reef as having experienced 100 (not a single blade left), >90 (a few blades were left), 90–30 (patches of blades were left) or <30% (many blades remained, only a few ghost holdfasts were found) loss of bull kelp. In addition to visiting these 19 reefs, we also surveyed the entire Lyttelton Harbor for any traces of surviving bull kelp blades using a boat that was slowly driven along the coastline. These surveys were all done during low tides when emergent bull kelp blades and ghost holdfasts are easy to see. The results from these semi-quantitative surveys were analyzed by visually inspecting maps that showed spatial locations of reefs with surviving bull kelp vs. localized extinctions.

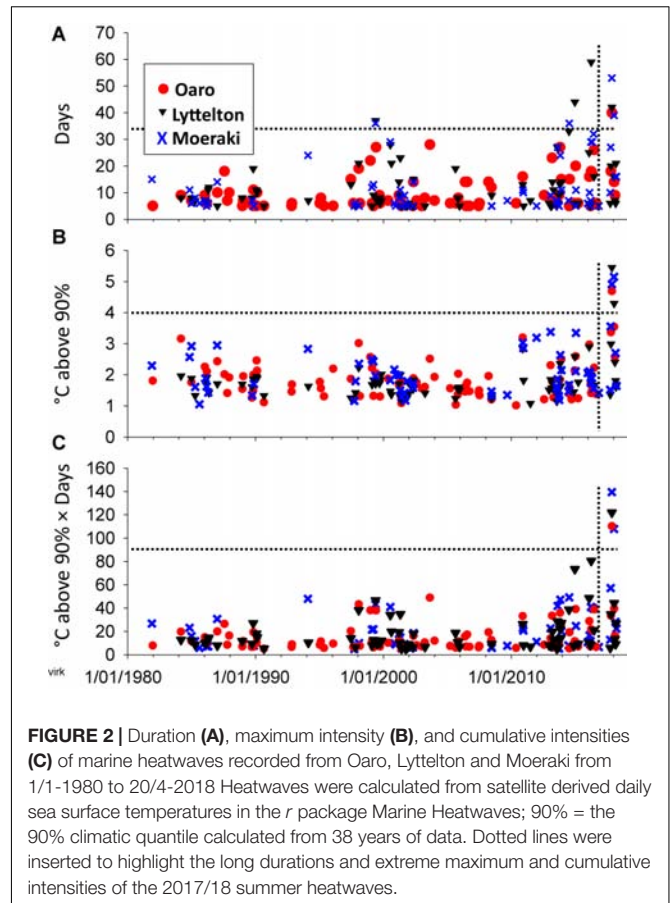
Effects of Bull Kelp Loss: Changes Following the Hot Summer

We photographed 10 0.25 m² plots with >90% bull kelp cover in Pile Bay (where the canopy was moved to make understory species visible) in August 2017 (“before” data). We then also photographed 13 0.25 m² plots at the same sites in March 2018 after bull kelp had been eliminated from the reef (“after” data). From these photos we estimated cover of conspicuous sessile organisms that were easy to identify. Data included many zeros and could not be transformed to variance homogeneity. We therefore used Mann–Whitney ranked *U*-tests on before-after data to test the hypothesis that weedy macroalgae would be more abundant after bull kelp were lost from the reef. We also tested whether mussels changed abundances because mussels were the most common and conspicuous understory species in these plots prior to the hot summer.

Effects of Bull Kelp Loss: Removal Experiment

Prior to the summer 2017/18 we had set up a bull kelp removal experiment at Oaro, Kaik and Point reefs, to simulate different intensities of bull kelp loss: no removals (control plots with 100% canopy-cover), removals of blades (cutting blades off 10 cm above the end of the stipe), removals of stipes (cutting the middle of the stipe), and removals of holdfasts (i.e., removing the entire plant, very small holdfasts with diameters less than 2 cm were left undisturbed in all plots). Each plot was 1 m² and each treatment was replicated four times. Kaik and Point reef plots were established in May 2017 and Oaro plots in June 2017, just prior to the reproductive period of bull kelp (Taylor and Schiel, 2003, 2005). After 4 months we counted the number of juvenile bull kelps and estimated the percent cover of weedy macroalgae (the green sheet-forming *Ulva* spp. and *U. pinnatifida*), two taxa that were absent in the plots prior to removals. Variances were

²<http://vmh18812.hosting24.com.au/public/?pid=20>



homogenous after arcsin-square root transformation (Cochran's C for the removal treatment and Reef factor; $p = 0.78$ and 0.51 , respectively). Nested Anova (3 reefs nested within 4 removal levels) was therefore used to test the hypothesis that the loss of fronds, stipes or holdfast would result in colonization of weedy macroalgae. A significant effect of removals was followed by SNK *post hoc* tests to identify differences among treatments. Note that the experimental and the before-after impact-analyses supplemented each other; colonization by macroalgae in Pile Bay following the hot summer could be caused by either loss of bull kelp and/or because of high summer temperature, whereas colonization following experimental removals could only be caused by loss of bull kelp. Finally, we were also interested in examining whether weedy macroalgae inhibited bull kelp recovery and vice versa, that is, if bull kelp recruits inhibit weedy macroalgae. These variables were not manipulated in the experiment so that causation cannot be inferred. We therefore tested the hypothesis that the cover of weedy macroalgae correlated negatively with density of juvenile bull kelp across the 48 plots using Spearman's rank correlation coefficient.

RESULTS

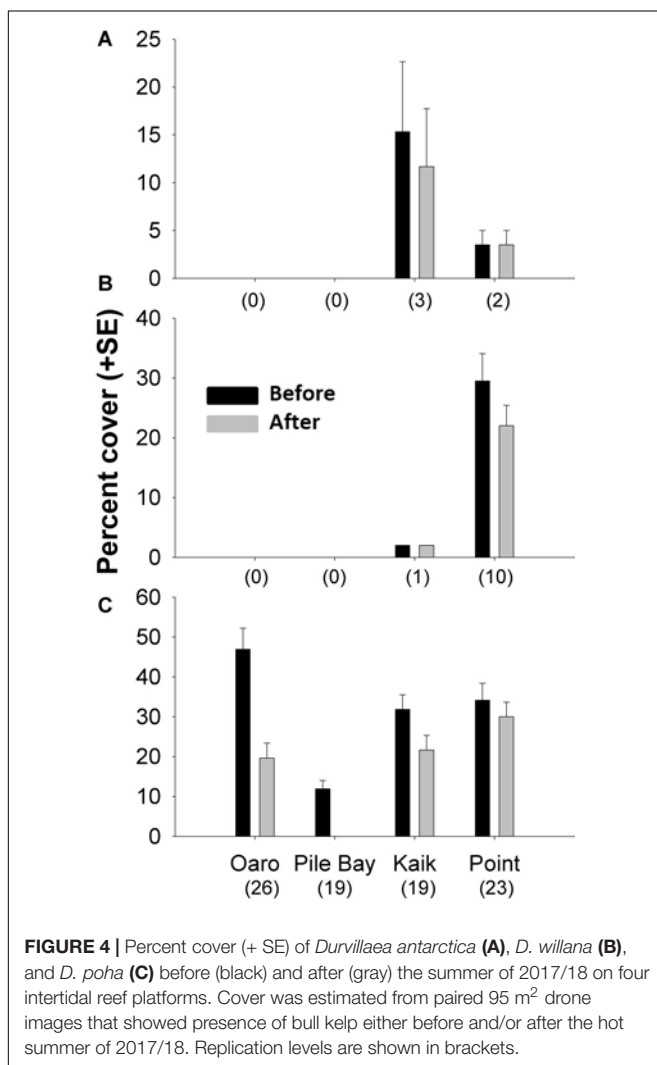
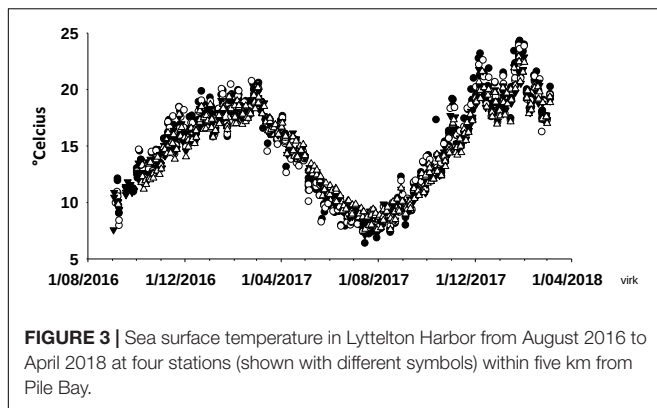
Changes in Temperature

Oaro, Lyttelton, and Moeraki have experienced many heatwaves since 1980, but with increasing durations and intensities since

2014 (Figure 2). The heatwaves over the 2017/18 summer were particular strong with maximum and cumulative intensities being approximately two times greater than any recorded event since 1980 (Figures 2B,C). Satellite-derived oceanic SSTs were generally lowest at the most southern site (Moeraki) and highest at the mid-latitude region (Lyttelton) (Supplementary Material), but because data were derived from offshore satellite images they may not have captured temperature extremes at inshore protected bays and inlets or intertidal rocky shores (see discussion in Smale and Wernberg, 2009). Analysis of SST data near Pile Bay within Lyttelton Harbor showed many days with water temperatures exceeding 23°C during the summer of 2017/18 (Figure 3) and intertidal *in situ* loggers at Oaro showed several days where atmospheric temperatures on the reef platforms exceeded $>45^{\circ}\text{C}$ (when cloudless days co-occurred with big, mid-day low tides, see Supplementary Figure S6).

Changes in Abundances of Bull Kelp; Regional Survey

Prior to the summer of 2017/18, the four intertidal platforms were dominated by *D. poha*, with smaller patches of *D. willana* and *D. antarctica* at the Point and Kaik reefs (Figure 4). We found a strong reduction in abundances of *D. poha* (Z-Statistic = 7.154, $p < 0.001$, $n = 87$), smaller reductions in *D. willana* (Z-Statistic = 2.032, $p = 0.042$, $n = 11$), and no change in abundance



of *D. antarctica* (Z-Statistic = 1.342, $p = 0.180$, $n = 5$). Importantly, *D. poha* from Pile Bay decreased from 12 to 0 percent cover (Figure 4), suggesting dramatic population-wide effects for this species on this particular reef.

Changes in Abundances of Bull Kelp; Local Survey

Detailed and targeted follow-up reef-surveys revealed total elimination of bull kelp on 12 out of 19 reefs, including the entire Pile Bay reef (see above, Figure 5). All 12 reefs that experienced total loss of bull kelp were within, or immediately north and south of, Lyttelton Harbor. We were assured that each of these reefs were inhabited by bull kelp before the hot summer of 2017/18 because abundant remnant and decaying ghost holdfasts (Figure 1) attested to very recent living bull kelp populations. It was not possible to distinguish *D. antarctica* and *D. poha* using ghost holdfasts, but our prior qualitative observations and collections from many of these reefs suggested they were mainly *D. poha*. A few surviving blades of *D. poha* were found at one site close to Lyttelton Harbor, and relatively abundant populations were found at reefs > 10 km north and south of the Harbor (Figure 5).

Effects of Bull Kelp Loss: Changes Following the Hot Summer

There were no *Undaria* under bull kelp canopies in Pile Bay in August 2017. However, in March 2018, after the elimination of bull kelp, densities increased from 0 (± 0) to 121 m⁻² (± 20 SE) juvenile *Undaria* in the area previously occupied by *Durvillaea*, whereas cover increased from 0 (± 0) to 20.9% (± 5.6 SE). Cover of other weedy macroalgae also increased, including *Colpomenia sinuosa* that increased from 0 (± 0) to 1.6% (± 0.5) and *Dictyota* sp. that increased from 0.02% (± 0.01) to 1.6% (± 0.6). Finally we also found that mussels (mainly *Perna canaliculus*) declined from 7.3% (± 2.0) to 0.7 (± 0.1)%. These changes in both cover and densities were all significant (all Z-scores > 1.98, all $p < 0.05$).

Effects of Bull Kelp Loss: Removal Experiment

There were no weedy macroalgae (*Undaria* or *Ulva*) under healthy bull kelp canopies in any of the 48 plots prior to removal treatments (data not shown). However, 4 months after the removals we found significant differences in cover of weedy macroalgae ($F_{\text{removal}} = 8.257$, $p < 0.001$) across the three reefs [$F_{\text{reef}(\text{removal})} = 0.760$, $p = 0.639$]. *Post hoc* SNK tests showed significantly more weedy macroalgae in the three removal treatments (which had similar cover) compared to the control plots (Figure 6). *Ulva* generally colonized removal plots at Oaro whereas *Undaria* colonized removal plots at Kaik and Point reefs in Moeraki (Figure 6). We also found a significant negative relationship between cover of weedy macroalgae and density of bull kelp recruits ($r = -0.414$, $p = 0.003$, Figure 7).

DISCUSSION

Who Died, Where, and Why?

We documented the loss of bull kelp following the unusually hot summer of 2017/18, characterized by high sea and air temperatures, low daytime tides, and reduced wave action (Figures 2,3 and Supplementary Figures S1–S6), so that

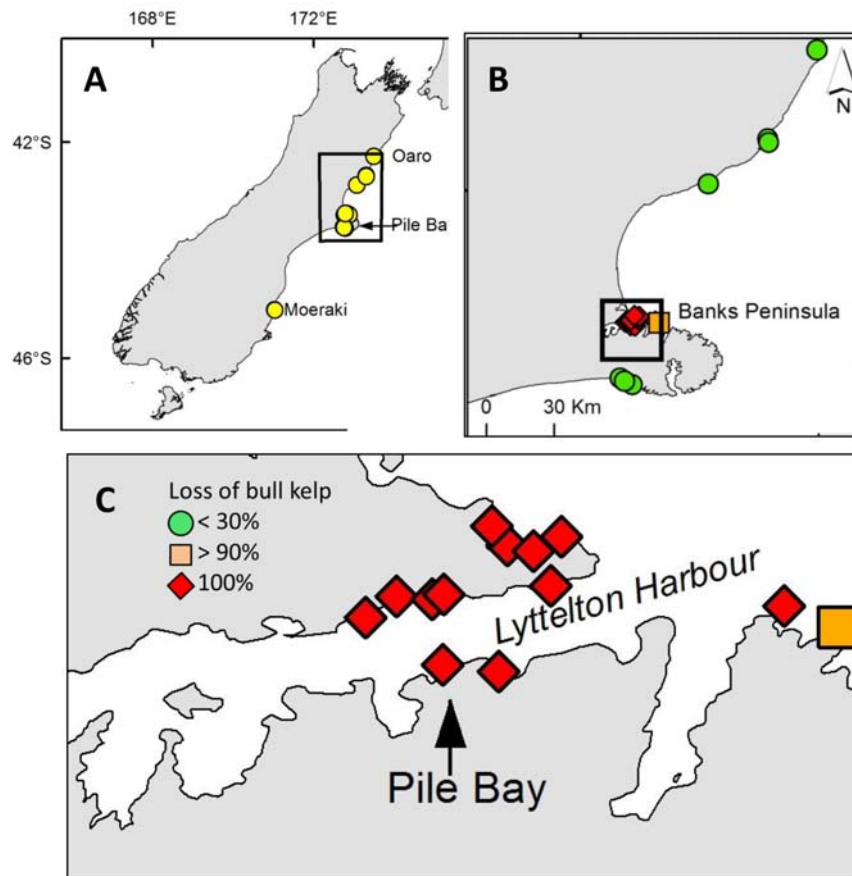


FIGURE 5 | (A) Surveyed bull kelp sites on the South Island of New Zealand; drone surveys were done at Oaro, Pile Bay and Point and Kaik reefs in Moeraki. **(B)** Close-up of reefs around Banks Peninsula where detailed searches for live bull kelp blades and dead “ghost holdfasts” were done. **(C)** Close-up of sites with reef-wide extinctions of bull kelp around Pile Bay in Lyttelton Harbor.

Durvillaea could have been stressed at both high and low tide. Elevated SST alone can cause similar losses, as has been shown for subtidal kelp and seagrasses around their northern range limits in Western Australia following the Ningaloo 2010/11 marine heatwave (Smale and Wernberg, 2013; Thomson et al., 2015; Wernberg et al., 2016; Arias-Ortiz et al., 2018). However, kelp and seagrasses are typically considered to be more robust to sea temperature anomalies within their range limits (Diaz-Almela et al., 2007; Reed et al., 2016; Wernberg et al., 2016). Our results differ because *D. poha* were eliminated from reefs more than 200 km south of its northern range limit (Fraser et al., 2012). This mid-range local extinction event (Bennett et al., 2015) occurred in inshore bay-waters, which were several degrees warmer than the coastal waters closer to the species northern range limit (Adams, 1994; Fraser et al., 2012). *Durvillaea* species are not tolerant to long periods of desiccation (Hay, 1979; Taylor and Schiel, 2005) and inhabit exposed coasts where wave splash keeps them moist. Typically, individuals have a bleached appearance as they deteriorate, which was observed in earthquake uplifted and exposed *Durvillaea* populations north of Oaro (Schiel et al., 2018a) and also in Lyttelton Harbor (this study). It seems likely that at least *D. poha* was near its ecophysiological limit. Indeed,

there appeared to be a relationship between maximum observed temperature and bull kelp loss (Pile Bay > Oaro > Moeraki), as seen for *Ecklonia radiata* in Western Australia following the Ningaloo 2010/11 heatwave (Wernberg et al., 2016).

The three *Durvillaea* species typically occupy the intertidal-subtidal fringe with their down-shore distributions shifting from *D. poha* that is exposed on all spring tides, to *D. antarctica* and then *D. willana* which is normally subtidal and exposed only on the largest spring tides (Adams, 1994; Fraser et al., 2012). The ocean temperatures analyzed in this study do not account for air-temperature stress occurring during emersion that can correlate with fucoid canopy-cover (Schiel et al., 2016). Coastal air and water temperature typically co-vary over larger and longer time-scales (Rayner et al., 2003; Schiel et al., 2016) and air temperature was also high during the 2017/18 summer (Supplementary Figures S4–S6). This almost certainly contributed to the die-off of *D. poha*, which is typically exposed to the air for longer than other species of *Durvillaea* (Fraser et al., 2012). It is likely that the die-off of bull kelp therefore reflects the net effects of duration and intensity of extreme water and air temperatures, their timing relative to diurnal and lunar cycles, but also the configuration of the landscape (e.g., slope, aspect). Finally, after

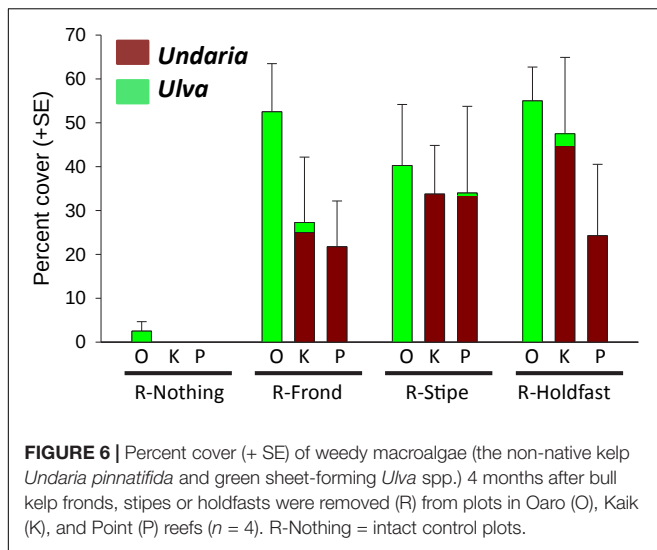


FIGURE 6 | Percent cover (+ SE) of weedy macroalgae (the non-native kelp *Undaria pinnatifida* and green sheet-forming *Ulva* spp.) 4 months after bull kelp fronds, stipes or holdfasts were removed (R) from plots in Oaro (O), Kaik (K), and Point (P) reefs ($n = 4$). R-Nothing = intact control plots.

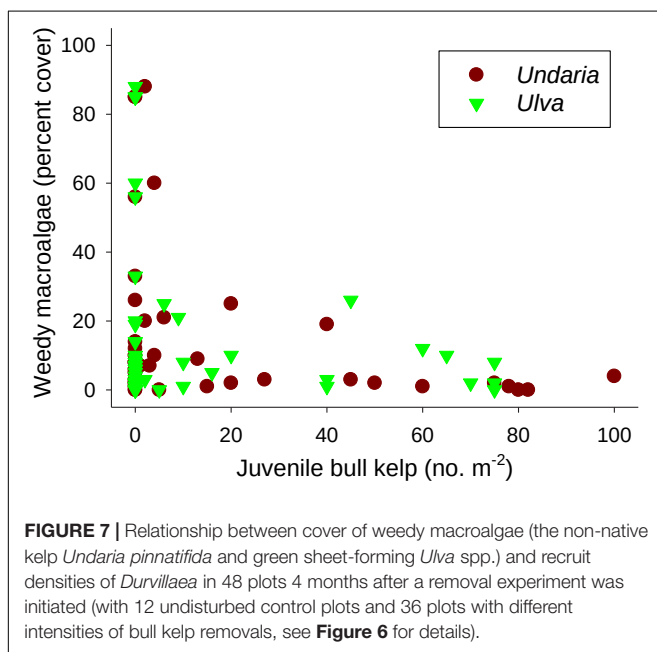


FIGURE 7 | Relationship between cover of weedy macroalgae (the non-native kelp *Undaria pinnatifida* and green sheet-forming *Ulva* spp.) and recruit densities of *Durvillaea* in 48 plots 4 months after a removal experiment was initiated (with 12 undisturbed control plots and 36 plots with different intensities of bull kelp removals, see **Figure 6** for details).

being exposed to desiccation and high air temperatures at low tides (exceeding 45°C, see **Supplementary Figure S6**), the elevated seawater temperature increased stress and offered little opportunity for recovery.

Our results suggest that *D. poha* was more affected than *D. willana* that again was more affected than *D. antarctica*, a pattern that co-varies with their northern range limits. *D. poha* inhabits only the South Island of New Zealand, *D. willana* is found on the South Island and in the southern North Island, whereas *D. antarctica* is common around the coast of New Zealand as well as in temperate Australia and Chile (Adams, 1994; Fraser et al., 2009, 2012). Similar relationships between poleward range limits and resistance to temperature stress have been shown for both terrestrial and aquatic organisms (Hickling et al., 2006; Wernberg et al., 2011; Poloczanska et al., 2013;

Smale et al., 2019). As previously noted, our drone survey prior to the heatwave was not designed to sample the more wave-exposed *D. antarctica* and more subtidal *D. willana* so their losses were calculated from fewer drone images and require further studies. However, qualitative observations support our quantitative analyses showing some loss of both species at Moeraki, and we observed unusually large wrack accumulations, particularly of *D. willana*, at many sites from Oaro to Moeraki (cf. **Figure 1**).

Possible Co-occurring Stressors

Our study was, in essence, a natural experiment (Hargrove and Pickering, 1992) like other marine heatwave impact studies (Garrabou et al., 2009; Short et al., 2015; Wernberg et al., 2016; Smale et al., 2019). Other factors could have contributed to the loss of bull kelp, but we argue that temperature effects were the most significant region-wide stressor. First, bull kelp are long-lived plants with relatively low seasonal variation in the cover of adult canopies that maintain consistent beds for long time periods (Hay, 1979; Santelices et al., 1980; Westermeier et al., 1994; Hurd, 2003; Taylor and Schiel, 2005). This implies that large scale die-offs are unusual events that previously only have been reported following dramatic seismic uplifts (Castilla, 1988; Schiel et al., 2018a). Second, there were no unusually large storms during the 2017/18 summer (**Supplementary Figure S7**). Given that storms rarely cover 600 km coastline and that bull kelp are adapted to high wave action and can survive massive storms, it seems unlikely to have caused the extensive large-scale mortalities recorded in this study (Taylor and Schiel, 2003, 2005; Thomsen and Wernberg, 2005; Taylor et al., 2010). Third, we did not observe any unusual turbidity or sedimentation events at any of our regular sampling sites during the summer of 2017/18. Fourth, bull kelps are typically not limited by grazers along the east coast of New Zealand, even though the odacid fish *Odax pullus* can affect juvenile recruitment at some sites and have characteristic bite marks (Taylor et al., 2010). Finally, we are not aware of any bull kelp pathogens, except for gall-forming parasites, which are relatively harmless and clearly visible and were not observed to occur (Goetze et al., 2012; Murúa et al., 2017). Nevertheless, it is plausible that temperature stressed bull kelp became more susceptible to infectious diseases and thereby accelerated the decay (Campbell et al., 2011, 2014; Case et al., 2011; Marzinelli et al., 2015). Similarly, temperature stressed and bacteria-coated bull kelp may also have experienced increased grazing from limpet, snails and herbivorous fish (Kristensen et al., 1992; Taylor et al., 2010; Campbell et al., 2014). However, these indirect effects are proximate stressors that would only effectuate after bull kelp were stressed by high temperatures.

Ecological Implications of Die-Off

The loss of an algal canopy can have positive and negative effects on sub-canopy species (Lilley and Schiel, 2006; Schiel, 2006; Wernberg and Connell, 2008; Wernberg et al., 2013; Flukes et al., 2014). At Pile Bay the dominant understory taxa, encrusting coralline algae, did not appear to be immediately affected but weedy macroalgae, including ephemeral (*Ulva*, *Colpomenia*), opportunistic (*Undaria*) or low-lying (*Dictyota*) species increased, probably due to competitive release from

Durvillaea (Taylor and Schiel, 2005; Arkema et al., 2009; Benes and Carpenter, 2015; Schiel et al., 2018b). Colonization by *Undaria pinnatifida* was also seen in the removal plots in Moeraki, supporting past studies done within stands of *Durvillaea* spp. and other canopy-forming algae in New Zealand (Thompson and Schiel, 2012; South et al., 2016; South and Thomsen, 2016; Schiel et al., 2018b), Australia (Valentine and Johnson, 2003, 2004), and the United Kingdom (De Leij et al., 2017). In places where *Undaria* was not present, other opportunistic fast-growing seaweeds, especially *Ulva*, colonized disturbed plots. This was also seen after the extensive canopy loss of *Durvillaea* and other fucoid algae after seismic uplift along 100 km of coastline (Schiel et al., 2018b). We also found that mussels decreased dramatically following bull kelp loss, possibly due to increased predation from shore birds, fish and crabs (Rilov and Schiel, 2006), or increased exposure to light and decreased humidity – stress-factors exaggerated by the high summer temperatures. It is likely that more complex effects will follow over time. For example, calcareous encrusting algae may be outcompeted by turf-forming taxa (Wernberg et al., 2013; Connell et al., 2014; Filbee-Dexter and Wernberg, 2018) with cascading negative effects on species that depend on these algae, such as abalone (*Haliotis* spp.) that cue in on this substrate for larval settlement (Morse and Morse, 1984; Daume et al., 1999; Roberts et al., 2004). It is also possible that expansion of weedy macroalgae creates an unfavorable habitat for *Durvillaea* to recolonize, should it be dispersed into the harbor by drifting individuals (Taylor and Schiel, 2003; Taylor et al., 2010; Fraser et al., 2011). Indeed, past studies, and our new correlation analysis, suggests that weedy macroalgae can inhibit recruitment of large and long-lived macroalgae, that instead require rocky substratum to attach firmly to – and thereby withstand years of strong hydrodynamic wave-forces (Taylor and Schiel, 2003; Taylor et al., 2010; Wernberg et al., 2013; Connell et al., 2014; Filbee-Dexter and Wernberg, 2018).

CONCLUSION

Extensive losses of bull kelp were recorded at many reefs along three degrees of latitude following an unusually warm summer with *Durvillaea* being eliminated from the warmest areas. Following the die-off, weedy macroalgae, especially the non-native kelp *Undaria pinnatifida* and sheet-forming *Ulva* spp. rapidly colonized empty spaces. The long-term implications are not yet clear, but if the trend of warming seas and increased intensities of marine heatwaves continues (Oliver et al., 2018), especially when coincident with hot air temperatures, there may be “press” effects that habitat-forming species such as *Durvillaea* cannot overcome (Martínez et al., 2018). Where

appropriate micro-habitats still exist, there may be a need to enhance connectivity between remaining populations by the use of novel techniques, such as transplantations, restoration, and strain selection, to ensure the long-term survival of these iconic foundation species in affected areas.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Drone surveys were done with high sensitivity to wildlife. In particular, sites and timing of surveys were chosen to avoid potential effects on seals and seabirds. If these species were present, flights were postponed to another day.

AUTHOR CONTRIBUTIONS

MT conceived the idea for the manuscript, collected some of the data, analyzed most of the data, and wrote the manuscript. LM, TA, SG, LT, and PS collected some of the data and commented on the manuscript. SL analyzed some data and commented on the manuscript. DS commented on 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.2019.00084/full#supplementary-material>

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Major Shifts in Pelagic Micronekton and Macrozooplankton Community Structure in an Upwelling Ecosystem Related to an Unprecedented Marine Heatwave

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The community structure of pelagic zooplankton and micronekton may be a sensitive indicator of changes in environmental conditions within the California Current ecosystem. Substantial oceanographic changes in 2015 and 2016, due to the anomalously warm ocean conditions associated with a large-scale marine heatwave perturbation, resulted in onshore and northward advection of warmer and more stratified surface waters resulting in reduced upwelling. Here we quantify changes in the macrozooplankton and micronekton community composition and structure based on five highly contrasting ocean conditions. Data from fine-mesh pelagic trawl surveys conducted off Oregon and Washington during early summer of 2011 and 2013–2016 were examined for interannual changes in spatial distribution and abundance of fish and invertebrate taxa. Overall species diversity was highest in 2015 and lowest in 2011, but 2016 was similar to the other years, although the evenness was somewhat lower. The community of taxa in both 2015 and 2016 was significantly different from the previously sampled years. Crustacean plankton densities (especially Euphausiidae) were extremely low in both of these years, and the invertebrate composition became dominated mostly by gelatinous zooplankton. Fishes and cephalopods showed mixed trends overall, but some species such as age-0 Pacific hake were found in relatively high abundances mainly along the shelf break in 2015 and 2016. These results suggest dramatically different pelagic communities were present during the recent warm years with a greater contribution from offshore taxa, especially gelatinous taxa, during 2015 and 2016. The substantial reorganization of the pelagic community has the potential to lead to major alterations in trophic functioning in this normally productive ecosystem.

Keywords: micronekton, Euphausiidae, fish, gelatinous, warm blob, El Niño, California current, Pacific Ocean

INTRODUCTION

Changes in global climate patterns are driving ecosystem responses in coastal and open oceans around the world. These systems are undergoing significant physical and chemical changes due to buildup of greenhouse gases, including increases in ocean temperature and acidification, decreases in dissolved oxygen concentrations, changes in circulation patterns, and alterations to freshwater inputs into the coastal ocean (Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012; Howard et al., 2013; Hewitt et al., 2016). These stressors have had a multitude of effects, including changes in productivity, phenology, and species distributions relative to the historical record (Poloczanska et al., 2016).

Among the stressors resulting from climate change in marine ecosystems, increases in ocean temperatures are likely to affect marine organisms the most, leading to poleward or deeper shifts in distribution, anomalous timing of life history events, and changes in physiology required to adapt to the warmer conditions (Doney et al., 2012; Hauser et al., 2016; Poloczanska et al., 2016). In addition to the long-term secular warming observed in many marine ecosystems, a more recent phenomenon has been the increased occurrence and severity of anomalous warming events, termed marine heat waves (MHWs, Hobday et al., 2016, 2018; Scannell et al., 2016; Oliver et al., 2018). To date, most of the impacts of these MHWs have been documented for demersal habitats and their effects of pelagic ecosystems are poorly known.

The northern California Current (NCC) is a highly productive upwelling region that stretches from Vancouver Island, Canada to Cape Mendocino in California. The high productivity can be attributed to intense seasonal upwelling, but also to retention on the shelf of nutrients from river runoff and other sources (Hickey and Banas, 2008). The NCC undergoes substantial variability in temperature related to local and remote forcing, and may fluctuate between warm and cold periods on a regular basis (Fiedler and Mantua, 2017) with apparent increasing frequency in the recent decades (Sydeman et al., 2013). Well beyond this normal variability, conditions since 2014 have been extraordinary due to the development of the so-called “warm blob” that covered much of the Subarctic North Pacific Ocean (Bond et al., 2015) followed by the northward progression of a major tropical El Niño (Jacox et al., 2016). The superposition of several anomalous atmospheric and oceanographic drivers resulted in a prolonged MHW, with temperature anomalies of 2–3°C affecting the entire California Current (Di Lorenzo and Mantua, 2016; Jacox et al., 2018). Profound ecosystem effects have been attributed to this anomaly including changes in species abundance and distribution patterns, spawning occurrence, feeding, and mass mortalities (Cavole et al., 2016; Di Lorenzo and Mantua, 2016; McClatchie et al., 2016; Daly et al., 2017; Peterson et al., 2017; Auth et al., 2018; Jacox et al., 2018). Among the MHWs recognized to have occurred in recent decades, this North Pacific event had the longest duration by far (711 days—almost three times longer than any other heatwave) and was classified as a Category III (Severe) event, among the strongest in terms of intensity (Hobday et al., 2018). These MHW events have had devastating biodiversity and economic consequences for both

temperate and tropical ecosystems in many parts of the world's oceans (Mills et al., 2013; Wernberg et al., 2013; Smale et al., 2019), and are predicted to be more intense and common under current climate projection scenarios (Frölicher et al., 2018).

Most of the climate-related changes documented so far in the NCC have been made for smaller planktonic and larger nektonic species which tend to be extensively sampled through time and therefore possess a well-established baseline of normal distribution and abundance patterns. Although sampled extensively during some periods (e.g., Brodeur et al., 2003; Phillips et al., 2009), the intermediate trophic level referred to as macrozooplankton (euphausiids and other large sized zooplankton) and micronekton (i.e., large crustaceans and small fish and squid) has been substantially less sampled and on an intermittent basis, such that the effects of major environmental perturbations are not as well known (Brodeur et al., 2006). Off California, the pronounced effects of the 2015 “warm blob” have recently been documented for this community (Sakuma et al., 2016; Santora et al., 2017), but to date there exists no similar studies of the effect of the recent anomalous marine heatwave on macrozooplankton and micronekton in the northern region of the California Current.

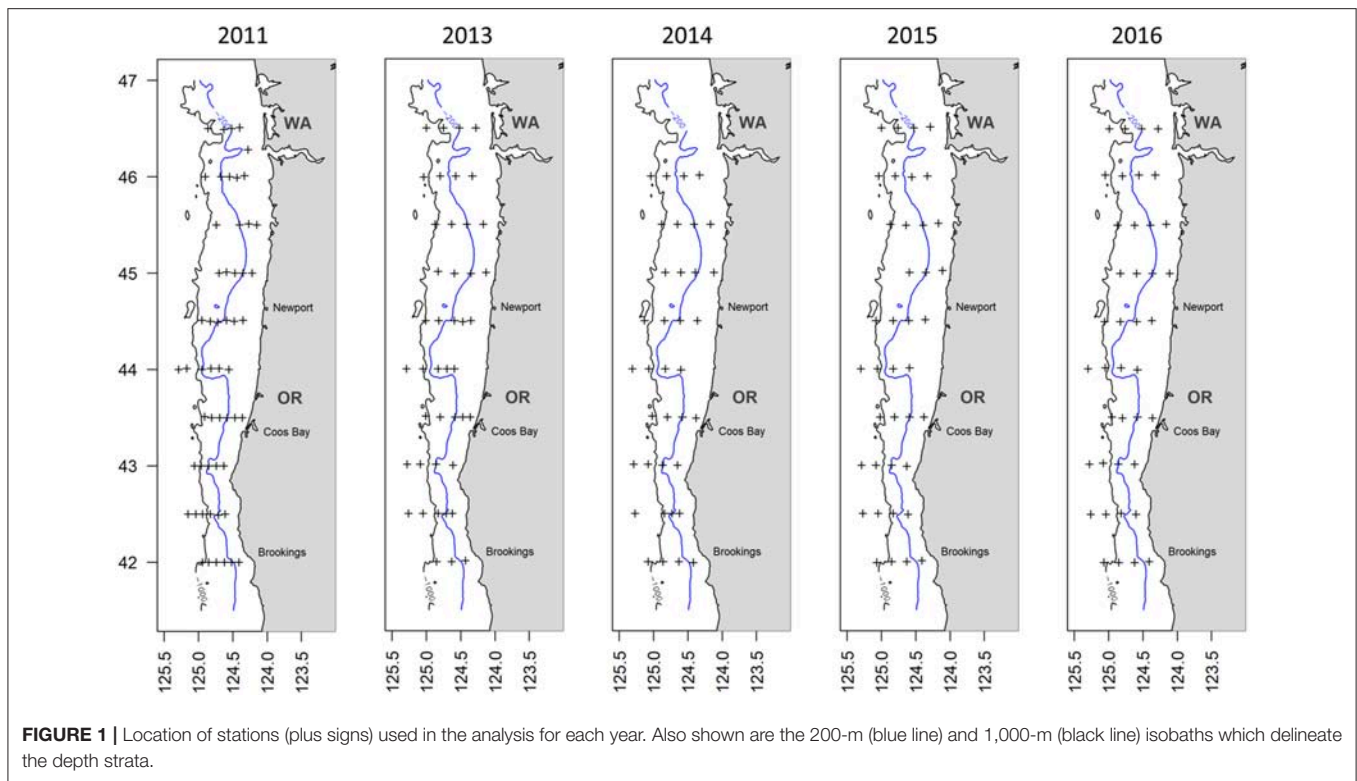
In this paper, we analyze environmental and trawl catch data from 5 years that were highly variable oceanographically based on early summer surveys of the NCC. We examine the trawl catches in terms of overall species richness, diversity, and evenness, and then analyze the community structure of the dominant taxa in relation to the varying ocean conditions, with special emphasis on the recent MHW. Our overarching hypothesis is that the recent extreme warming will affect locally-adapted taxa most heavily and introduce novel species to the system, resulting in major changes to ecosystem standing stocks and production.

MATERIALS AND METHODS

Sampling Procedures

Trawl samples from a total of 212 hauls were collected from five annual cruises between late-May and early-July 2011 and 2013–16: June 1–16, 2011; June 23–July 6, 2013; June 18–28, 2014; May 30–June 9, 2015; and June 13–25, 2016. Samples were collected at 3–5 predetermined stations (4–6 stations in 2011) extending ~7–92 km offshore at ~20 km intervals along each of 10 transects at 0.5°-latitude lines from 42 to 46.5°N off the Oregon and southern Washington coasts, for a total of ~40 stations per annual cruise (54 stations in 2011; **Figure 1**).

Samples were collected at night using a modified-Cobb midwater trawl (MWT) with a 26-m headrope towed for 15 min (~1 km) at an average ship speed of 3.7 km h⁻¹. The mouth opening was estimated to be ~144 m³ (Sakuma et al., 2016). The outside net mesh size (stretched) decreased from 152 mm in the wings and body to 38 mm in the codend but the net had a 9.5 mm liner. Target depth range of sampling was between 30 and 42 m for each tow. At two stations sampled in 2016, we conducted a series of three consecutive night time tows to examine the vertical distribution of our main species (see below). These tows were done at the normal target depth and also one tow shallower and another deeper in randomized order. Each tow started with



25–85 m of wire out with adjustments made if target depth was not obtained, as determined from depth recordings collected from time-depth recorders (TDRs) and the ship's acoustic trawl net monitoring sensors, which were attached to the net during each tow. Ship speed was adjusted while trawling to maintain target depth (using the acoustic trawl net monitoring system) while the amount of wire out remained fixed. Temperature ($^{\circ}\text{C}$), salinity, density (sigma theta, kg m^{-3}), chlorophyll *a* (mg m^{-3}), turbidity (mg m^{-3}), dissolved oxygen concentration (DO, ml L^{-1}), and DO saturation (%) were measured throughout the water column (to a maximum depth of 500 m) at each station during the day using a Seabird SBE 43 CTD (Sea-Bird Electronics Inc., Bellevue, WA, USA). Not all environmental parameters were measured at all stations due to periodic instrumentation malfunctions.

All organisms (except for *Cancer* spp. megalopae and zoeae, and smaller gelatinous taxa such as *Pleurobrachia* spp., Mitrocomidae, and Cymbuliidae) collected from each sample were sorted, measured, counted, and identified to the lowest taxonomic level possible at sea according to a standard sample processing protocol (see below). Certain appropriate fish species were separated into two stage categories and processed separately: adult and young (mostly age-0 fish that have not yet achieved adult characteristics). Other fish and all invertebrate taxa were categorized as undetermined stage (U). All pelagic juvenile *Sebastes* spp. were frozen for later identification to species or species groups in the laboratory. For the sample processing protocol, if the sample was small (i.e., there did not appear to be >30 individuals from any one taxon), then

all organisms of concern in the sample were sorted, identified, counted, and measured. If not, then we measured the smallest random subsample (based on volume; ml) that yielded at least 30 individuals from the most numerous taxon and processed completely as described above. We continued to measure out, and process completely, sequential subsamples (based on the smallest volume that yielded at least 30 individuals from the next numerous taxon total from the second, third, fourth, etc. subsamples combined) until at least 30 individuals or the entirety of individuals from all taxa had been processed. We then measured the total volume of the full sample, and scaled up the total counts of each taxon based on the proportion of the subsample volumes for each taxon to the total sample volume.

Data Analyses

The total number of individuals per taxon collected in each haul was used as the basic measure for all analyses, since the tow duration and mouth opening (and therefore volume of water filtered) was assumed to be uniform for all tows. Taxon richness, diversity, and evenness were analyzed based on all identifiable collected taxa except for Euphausiidae ($n = 141$), which when present were often disproportionately more numerous than any other taxon. Both adult and juvenile individuals were combined for taxa that had representatives of both stages. This resulted in a matrix of 111 taxa and 177 stations. Richness was defined as the number of different taxa present in a haul. The Shannon diversity index (H') was used to measure diversity, where higher H' values denote greater diversity. Evenness was

assessed using Pielou's evenness index (J'), which ranges from 0 to 1, with the maximum J' value indicating that all taxa are represented in the same relative concentrations. Both H' and J' were calculated according to the formulas found in Shannon and Weaver (1949) and Krebs (1989). Hauls where 0–1 individuals were collected were not included in the analyses because richness, J' , and H' cannot be calculated (although richness = 0 at $n = 1$ taxon). The software utilized to calculate the richness, diversity, and evenness indices was the PRIMER 7 statistical software package (Clarke and Gorley, 2015). Significant differences among years in these indices were tested using the non-parametric Kruskal-Wallis One Way ANOVA followed by a Dunn's Test.

We restricted our analysis of community structure to the common taxa by removing taxa not found in at least 10% of the collections. This resulted in a matrix of 38 taxa and 176 collections. To minimize the importance of the most abundant taxa, we fourth-root transformed the abundance data and conducted multivariate analyses on data grouping by year, area, and depth categories (Clarke and Gorley, 2015). For the depth categories, we grouped the data in depth-strata bins with bottom depth < 200 m (shelf), between 200 and 1,000 m (slope), and >1,000 m (offshore). To examine regional differences, we divided the entire sampling area into three latitudinal strata with stratum boundaries at 44.75 and 43.25°N, such that all strata contained 3–4 transects of sampling.

We used Principal Coordinate Analysis (PCoA) to resolve patterns in the communities in relation to our three factors. PCoA reduces the dimensionality of complex data matrices by transforming dissimilarities in sample compositions and uses rank transformation to describe non-linear distributions, as commonly found when examining the spatial distribution of organisms (McCune and Grace, 2002). Dissimilarities between sample units (trawls) were calculated using the Bray-Curtis (Sørensen) measure (McCune and Grace, 2002). Analysis of the stress statistic indicated that two axes were appropriate for this dataset. PCoA plots were rotated such that the greatest variation in the data was represented by axis 1. We overlaid vectors of the four main *in situ* environmental variables sampled (temperature, salinity, chlorophyll *a*, and dissolved oxygen at 30 m) on the first two axes to show their explanatory contributions to the ordination.

Community differences were explored using a non-parametric Multi-Response Permutation Procedure (MRPP) to test for significant annual, cross-shelf, and regional community changes. The MRPP generates an A-statistic ranging from 0 to 1 with the maximum value indicating complete agreement between groups (McCune and Grace, 2002). To determine which taxa contributed to significant annual, depth, or regional differences, Indicator Species Analysis (ISA) was also performed on fourth-root transformed abundance data using 5000 random restarts for each Monte Carlo simulation to test taxonomic fidelity within each group (Dufrêne and Legendre, 1997). All MRPP and ISA analyses were performed using PC-Ord Version 5 statistical software (McCune and Mefford, 2006).

Contour Maps were made in R [version 3.5.2, (R Core Team, 2015)] with the “akima” package using the function “interp.” The

function “interp” implements bivariate interpolation onto a grid for irregularly spaced input data (Akima, 1996). The function “interp” is meant for cases in which x, y values are scattered over a plane with a corresponding z value for each. The abundance data were transformed: $\ln(\text{number} + 1)$. To allow for better comparison of the plots, the contour plots are displayed on the same scale for all years.

RESULTS

Physical Environment

Although the warm blob first appeared in the Gulf of Alaska in the winter of 2013–2014, strong upwelling anomalies in the summer of 2014 kept the surface signature of the warm anomaly off the Oregon shelf until relaxation in mid-September of 2014 (Peterson et al., 2017). This delay can be seen in the sea surface temperature (SST) anomaly plot for the study area since 2011 (**Supplementary Figure 1**). The SST values exceeded the threshold for a MHW event throughout much of the following winter and spring before returning to near the 1983–2012 climatological mean in late spring of 2015. This was followed by another extended period of anomalous warm water from the fall of 2015 to the spring of 2016 (**Supplementary Figure 1**). There was another short but highly anomalous warm period in the fall of 2016, subsequently returning to near-normal conditions by that winter.

Temperatures at the depth of the trawl headrope (30 m) averaged over all stations showed that 2011 had cool but not extreme temperatures (median $\sim 9.5^\circ\text{C}$), but significantly lower temperatures were observed in 2013 indicative of new-upwelled water (Dunn's Multiple Comparison Test, all $p < 0.001$; **Figure 2**). Temperatures increased for the next 3 years, with 2015 and especially 2016 being exceptional as compared to normal June temperatures. Salinities at 30 m depth were similar overall, with 2011 being slightly lower than the other 4 years (**Figure 2**). Dissolved oxygen was more variable, with the highest value in 2015 and relatively low levels in 2013 and 2014, but all years were well above the level demarcating hypoxic conditions (1.4 mL l^{-1} , **Figure 2**). Chlorophyll *a* concentrations were more variable, with low levels in 2013 and 2014 and highly variable levels in 2011 and 2015, with only 2015 being significantly higher than the other years (all $p < 0.001$; **Figure 2**).

These interannual differences were also reflected in vertical profiles taken at the same location (station at 43.0°N, 124.5°W, 49.8 km off of Coos Bay, Oregon) all 5 years (**Figure 3**). The water column at this location in 2013 was well-mixed and relatively cool throughout, typical of upwelling conditions, whereas it was well stratified in 2015 and 2016, with a thermocline at or slightly above the sampling strata. Salinity showed a gradual increase with depth, with only 2011 showing the presence of fresher water at the surface above the trawl sampling depths (**Figure 3**). Dissolved oxygen showed a relatively slow decline with depth in all years, with 2015 exhibiting the highest oxygen levels at most depths (**Figure 3**). Finally, chlorophyll was most variable, with 2011, 2015, and 2016 having subsurface chlorophyll *a* maxima around the trawl depth, with a second maximum around 100 m in 2015 (**Figure 3**).

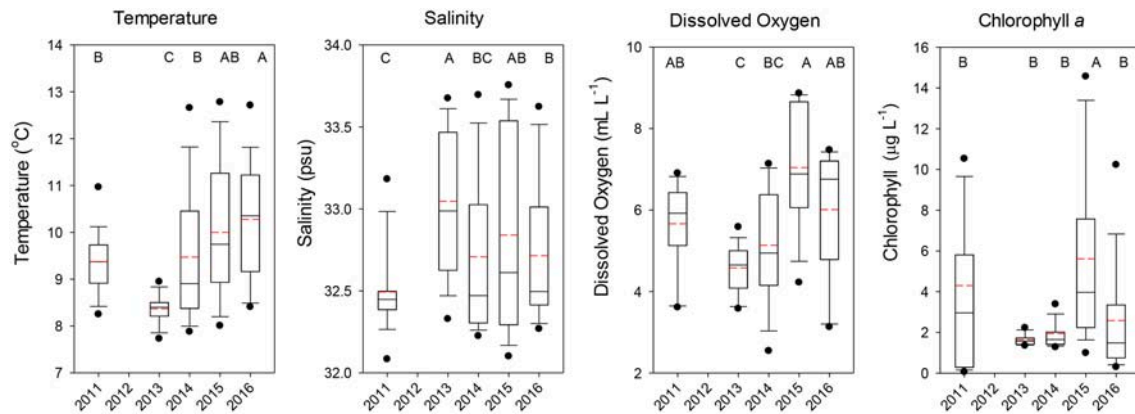


FIGURE 2 | Boxplots of the temperature, salinity, dissolved oxygen, and chlorophyll a observed at the depth of the top of the trawl (30 m) for all stations combined by year. The lower boundary of the box indicates the 25th percentile, a line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers (error bars) and data points above and below the box indicate the 90 and 10th percentiles and 95 and 5th percentiles, respectively. Dashed red line indicates the mean value. Years with significantly ($p < 0.05$) different values are designated with different letters on the top of each graph.

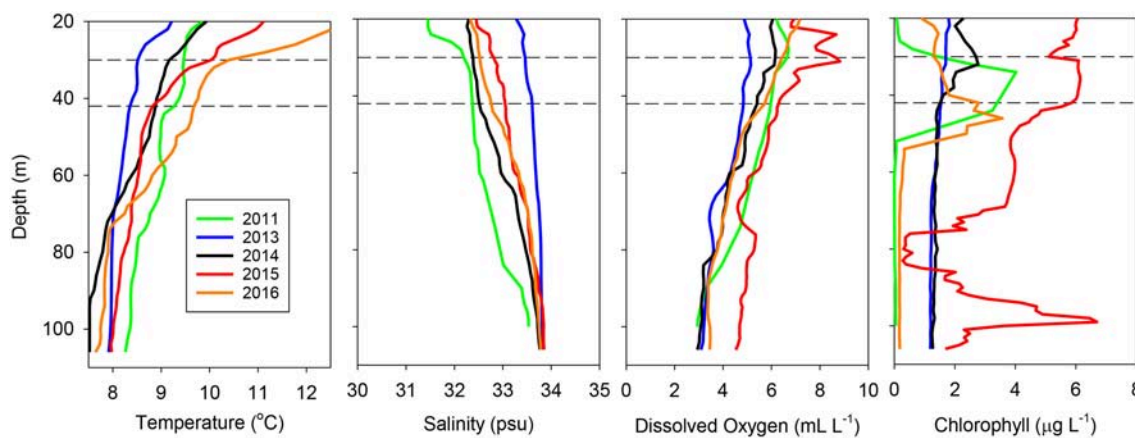


FIGURE 3 | Temperature, salinity, dissolved oxygen, and chlorophyll a profiles for the same station (43.0°N, 124.5°W) during each of the years examined. The horizontal dashed lines represent the approximate depth interval sampled by the trawl at all stations.

Catch and Diversity Patterns

A total of over a million individuals were caught representing ~142 taxa in the trawls examined. Of these, 43 taxa were represented by more than 100 individuals captured (**Table 1**). Euphausiids represented the bulk of the catch and were >95% of the total catch in this group. Two crustacean species, the pink shrimp (*Pandalus jordani*) and the glass shrimp (*Sergestes similis*), were also among the dominant taxa caught. Several gelatinous taxa (i.e., the pelagic tunicates *Salpa* spp., *Thetys vagina*, and *Pyrosoma atlanticum*, and the hydrozoan *Aequorea victoria*) were very abundant some years but were scarce in others (**Table 1**). Teleost fishes were the most diverse group among these dominant taxa (24 out of 43), but only three fell within the top ten by abundance ranking—two were mesopelagic lanternfish species (i.e., *Stenobrachius leucopsarus* and *Tarletonbeania crenularis*) and the other was age-0 Pacific hake (*Merluccius productus*). The last major taxonomic group, Cephalopoda, was dominated by the

black-tip squid (*Abraliopsis felis*) and the clawed armhook squid (*Gonatus onyx*) (**Table 1**).

The average number of species caught at each station was significantly lower (median = 7) for 2011 (Dunn's Multiple Comparison Tests, all $p < 0.001$), whereas the other years had similar mean numbers of species caught (median = 14–16; **Figure 4**). Similarly for Shannon diversity, 2011 and 2016 were the lowest years overall, but were only significantly lower than 2015, which had the highest value of the 5 years examined (**Figure 4**). Pielou's evenness was not significantly different among the first 4 years, but 2016 had a significantly lower evenness (median $J' = 0.364$; all $p < 0.035$; **Figure 4**) due to the dominance of a few taxa such as *Salpa* spp., *M. productus*, and *P. atlanticum* that were extremely abundant at a few stations (**Table 1**, **Supplementary Figure 2**).

The sum of the total annual abundances by the four major taxonomic groupings (i.e., cephalopods, crustaceans, gelatinous,

TABLE 1 | Yearly abundance of the dominant taxa collected in the trawls by year ranked by total catch for all years combined.

Taxon	2011	2013	2014	2015	2016	Total catch	Grouping
Euphausiidae	2,780,942	3,326,376	2,859,777	9,743	6,910	8,983,751	Crustacean
<i>Salpa</i> spp. ^a	34,549	32,042	4	3,857	9	70,461	Gelatinous
<i>Pandalus jordani</i>	47,675	5,987	15,711	109	23	69,505	Crustacean
<i>Sergestes similis</i>	21,955	17,977	19,017	1806	7,694	68,449	Crustacean
<i>Stenobranchius leucopsarus</i>	1,329	38,466	13,219	744	608	54,366	Teleost
<i>Merluccius productus</i>	335	27	4	5,496	43,674	49,536	Teleost
<i>Pyrosoma atlanticum</i>	0	0	42	359	13,797	14,198	Gelatinous
<i>Tarletonbeania crenularis</i>	3,068	1,172	1,702	606	2,539	9,087	Teleost
<i>Aequorea victoria</i>	83	65	120	6,441	2,048	8,757	Gelatinous
<i>Thetys vagina</i>	0	5,189	121	245	1,196	6,751	Gelatinous
<i>Aburropsis felis</i>	560	2,391	2,585	210	650	6,396	Cephalopod
<i>Gonatus onyx</i>	1,419	1,790	871	518	311	4,909	Cephalopod
<i>Engraulis mordax</i> ^b	119	1,070	305	1,048	1,570	4,112	Teleost
<i>Allosmerus elongatus</i>	373	1,469	63	97	0	2,002	Teleost
Osmeridae	370	1,313	73	0	0	1,756	Teleost
<i>Citharichthys sordidus</i>	382	88	191	666	73	1,400	Teleost
<i>Diaphus theta</i>	206	428	131	47	402	1,214	Teleost
<i>Praya</i> spp.	2	30	30	722	390	1,174	Gelatinous
<i>Thaleichthys pacificus</i>	0	7	596	451	1	1,055	Teleost
<i>Lipolagus ochotensis</i>	125	272	228	49	265	939	Teleost
<i>Lestidiops ringens</i>	194	301	65	77	59	696	Teleost
<i>Glyptocephalus zachirus</i>	59	128	187	223	18	615	Teleost
<i>Carinaria japonica</i>	26	434	65	62	26	613	Gelatinous
<i>Aurelia labiata</i>	600	0	1	1	10	612	Gelatinous
<i>Sebastes entomelas</i>	12	257	136	12	126	543	Teleost
<i>Phronima sedentaria</i>	314	50	4	152	22	542	Crustacean
<i>Crangon</i> spp.	469	13	3	0	3	488	Crustacean
<i>Citharichthys stigmatosus</i>	94	57	60	165	33	409	Teleost
<i>Ronquilus jordani</i>	4	385	2	0	0	391	Teleost
<i>Loligo opalescens</i>	12	3	13	260	101	389	Cephalopod
<i>Gonatopsis borealis</i>	217	47	31	13	51	359	Cephalopod
<i>Sebastes flavidus</i>	0	21	40	0	275	336	Teleost
<i>Psettichthys melanostictus</i>	41	74	52	113	26	306	Teleost
<i>Symbolophorus californiensis</i>	56	25	3	15	175	274	Teleost
<i>Sebastes pinniger</i>	95	42	31	20	80	268	Teleost
<i>Isopsetta isolepis</i>	158	15	51	3	0	227	Teleost
<i>Chiroteuthis calyx</i>	46	27	90	47	12	222	Cephalopod
<i>Lyopsetta exilis</i>	10	13	123	66	7	219	Teleost
<i>Phacellophora camtschatica</i>	2	14	2	114	30	162	Gelatinous
<i>Cavolinia tridentata</i>	161	0	0	0	0	161	Gelatinous
<i>Atheresthes stomias</i>	41	63	9	20	3	136	Teleost
<i>Sebastes crameri</i>	26	95	1	7	4	133	Teleost
<i>Sebastes melanops</i>	123	1	0	0	0	124	Teleost

^a Many salps were too damaged to get positive identifications but appeared to be mostly *Salpa fusiformis* or *S. aspera*.

^b Mostly age-0 fish but older age classes present.

and teleosts) showed significant shifts during the 5 years of sampling (Figure 5). The first 3 years were dominated by crustaceans (mainly euphausiids but also *P. jordani* and *S. similis*) which were located throughout the sampling region (Figure 5B). Crustaceans continued to be an important group,

but their abundances decreased by several orders of magnitude during 2015 and 2016. They were supplanted as the top group by gelatinous taxa during these 2 years, which were more evenly spread throughout the shelf (Figure 5C). Teleosts and cephalopods showed a mixed pattern but both were fairly

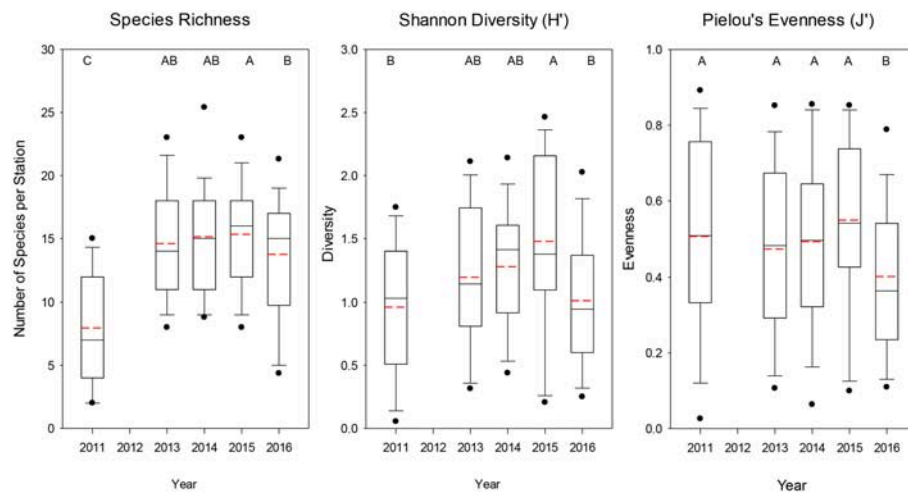


FIGURE 4 | Boxplots of overall species richness, Shannon diversity index, and Pielou's evenness index for all trawls included for each year. The lower boundary of the box indicates the 25th percentile, a line within the box marks the median, and the upper boundary of the box indicates the 75th percentile. Whiskers (error bars) and data points above and below the box indicate the 90 and 10th percentiles and 95 and 5th percentiles, respectively. Dashed red line indicates the mean value. Years with significantly ($p < 0.05$) different values are designated with different letters on the top of each graph.

important in 2013 and 2014 (Figure 5A and AD), whereas teleosts were equally important in 2016 mainly due to a high number of *M. productus* caught in the northern part of the survey area that year (Table 1, Supplementary Figure 2).

Community Analysis

The Principal Coordinate Ordination revealed some differences among the stations grouped by year (Figure 6). The first 3 years (2011, 2013, and 2014) overlapped somewhat in ordination space, and none of the years were significantly different from each other (MRPP, all $p > 0.05$). In contrast, 2015 and to a greater extent 2016 were more distinct in multivariate space, and were distinguished from the other years mainly along the second PCoA axis (Figure 6). These 2 years were significantly different (MRPP, $p < 0.05$) from each other and individually from all the other years. The taxa most influential in driving the first two ordination axes (vectors on Figure 6) were butter sole *Isopsetta isolepis* (indicative of cooler, inshore stations), *T. crenularis* (indicative of cooler, offshore stations), *A. victoria* (indicative of warmer, inshore stations), and *P. atlanticum* (indicative of warmer, offshore stations). The results of the ISA analysis (Figure 7) show that at least a third of the assemblages showed overlap among the first 3 years, although 2011 had substantially different indicator species compared to 2013 and 2014, which had two of their top three indicator species in common. In contrast, 2015 and 2016 shared many of the same dominant indicator species despite being significantly different in terms of their overall assemblages (Figure 7).

When the stations were displayed in terms of their bottom depth, a clear segregation was observed along the first axis between the inshore shelf stations (<200 m, mostly positive values on PCO1) and the other two depth strata (mostly negative values on PCO2; Figure 8). The shelf stratum (<200 m) was significantly different from both offshore strata (ANOSIM, $p <$

0.05), whereas the offshore two depth strata were not significantly different from each other ($p = 0.17$). Temperature was negatively and salinity was positively associated with axis 2, whereas chlorophyll *a* (higher inshore) and to a lesser extent dissolved oxygen (higher offshore) were associated with axis 1 (vectors on Figure 8).

In terms of indicator species, the shelf stations were represented by *A. victoria* and two age-0 flatfish species (i.e., *Citharichthys sordidus* and *Glyptocephalus zachirus*), while the slope and offshore groupings were characterized by two squid species and two myctophid fish species (Figure 9). When examined by latitudinal geographic areas, none of the three regions had significantly different overall taxonomic compositions from the others (ANOSIM, all $p > 0.05$), indicating that there was a general continuous distribution of these micronekton along the shelf in the study area for most of the taxa examined.

DISCUSSION

These results depict a major upwelling ecosystem that has undergone dramatic changes resulting from an extraordinary and unprecedented environmental perturbation lasting multiple years. Consistent sampling using standardized methodology makes it possible to capture differences in species diversity, distribution, and abundance patterns as they evolved in response to the dramatic physical changes. Similar changes have already been documented in the NCC for lower trophic levels such as zooplankton and ichthyoplankton (Peterson et al., 2017; Auth et al., 2018). This shift followed the neritic arrival of the “warm blob” water mass that came onto the Oregon shelf in September 2014 (Peterson et al., 2017), resulting in large positive SST anomalies that remained until at least September

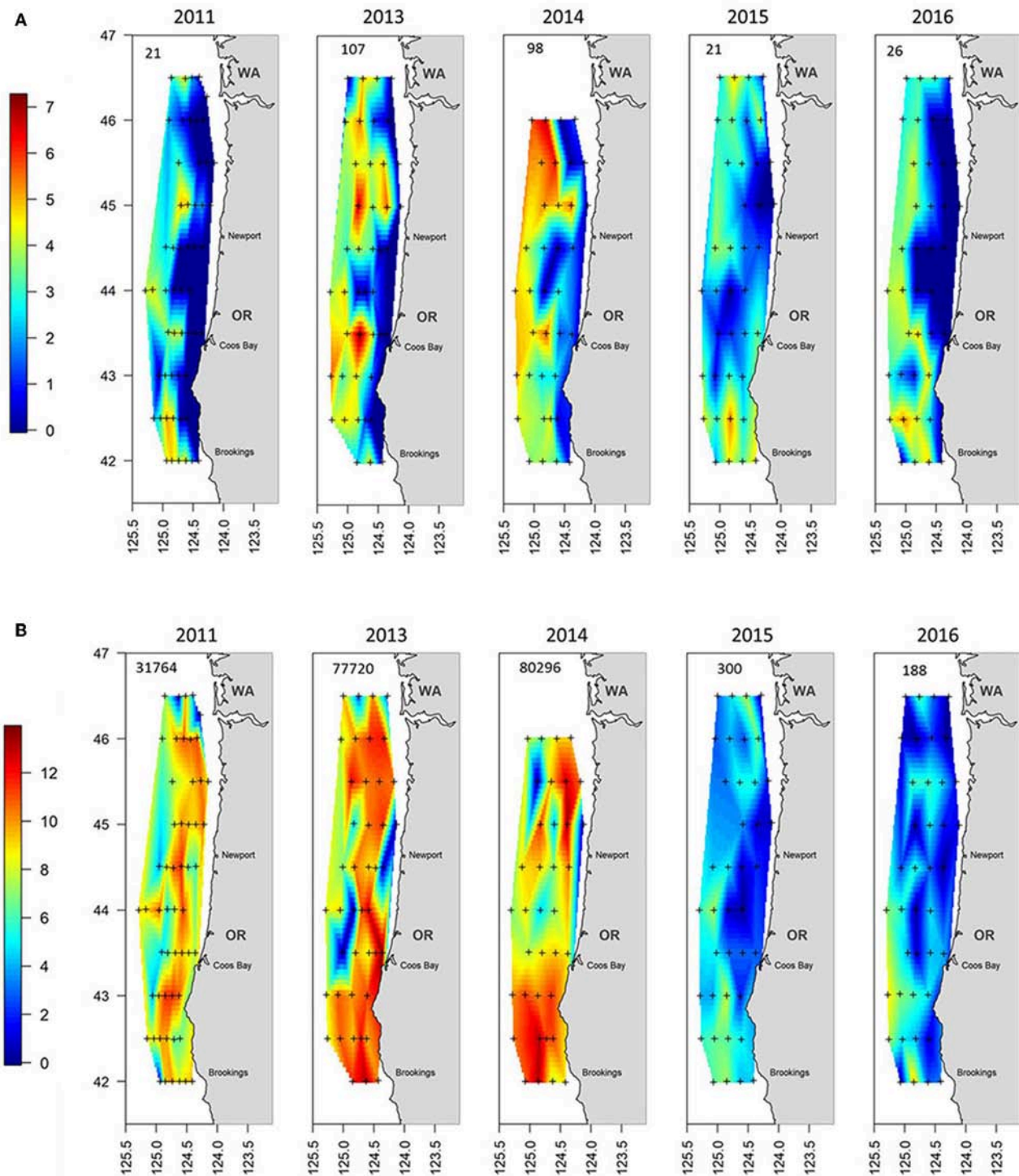


FIGURE 5 |

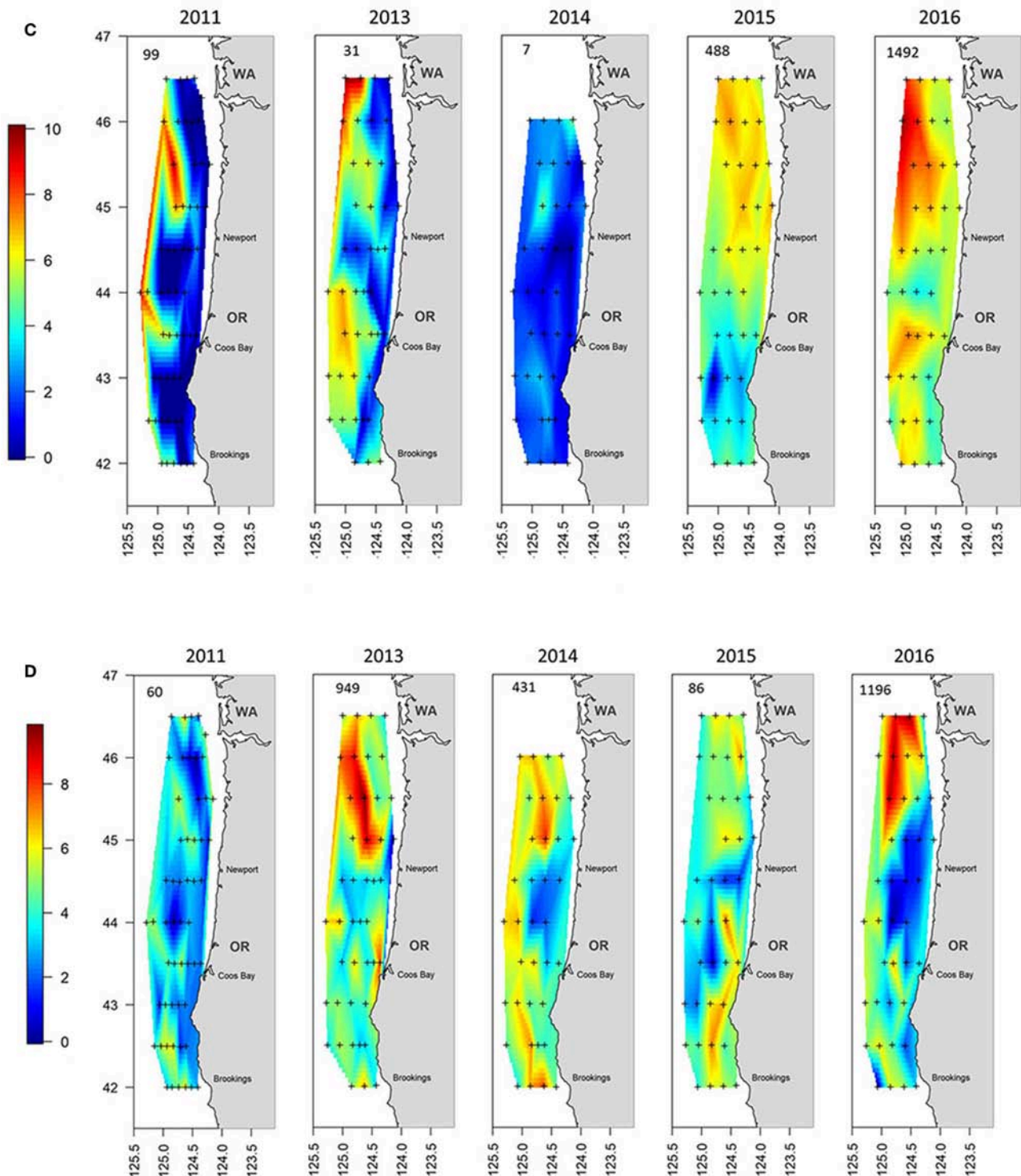


FIGURE 5 | Distribution maps of the catch by year for the aggregated groupings of **(A)** Cephalopods, **(B)** Crustacea, **(C)** Gelatinous, and **(D)** Teleosts. The number in the upper left of each panel indicates the geometric mean catch of that grouping per haul by year. Note that the scale bar is logarithmic. The plus signs indicate locations where trawling was conducted.

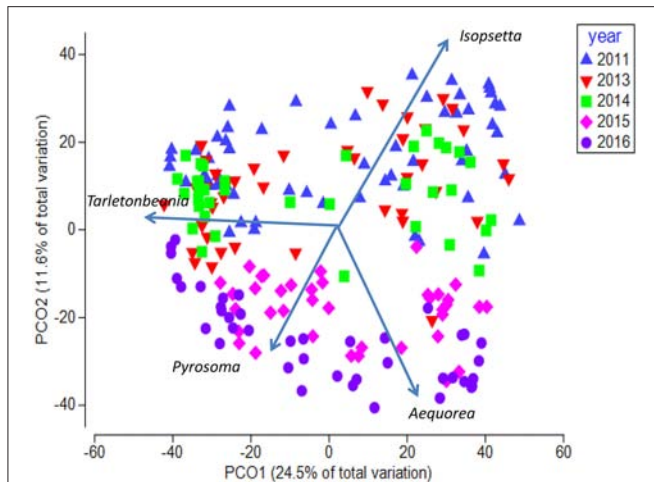


FIGURE 6 | Principal Coordinate Analysis biplot for first two axes showing yearly differences. Each symbol represents the catch of a single trawl. Overlaid are the vectors for the most influential species driving the observed differences in species composition. The amount of variance explained by each axis is shown on the axes labels.

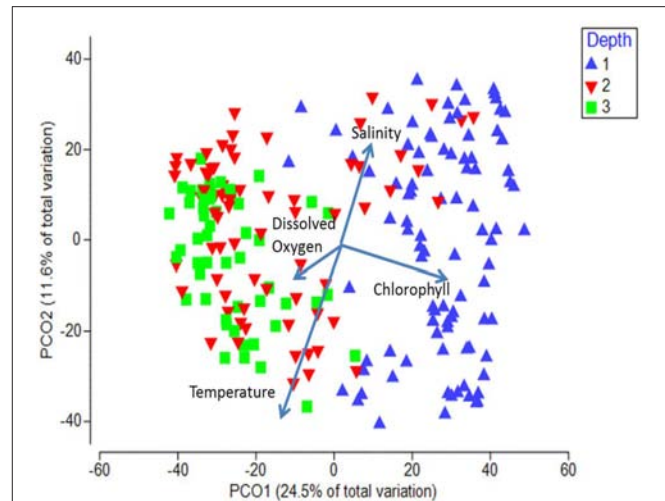


FIGURE 8 | Principal Coordinate Analysis biplot for first two axes showing depth differences. Each symbol represents the catch of a single trawl. Depth strata are as follows: 1 = <200 m, 2 = 200–1,000 m, 3 = >1,000 m. The amount of variance explained by each axis is shown on the axes labels. Overlaid are the vectors of the environmental parameters measured at each station.

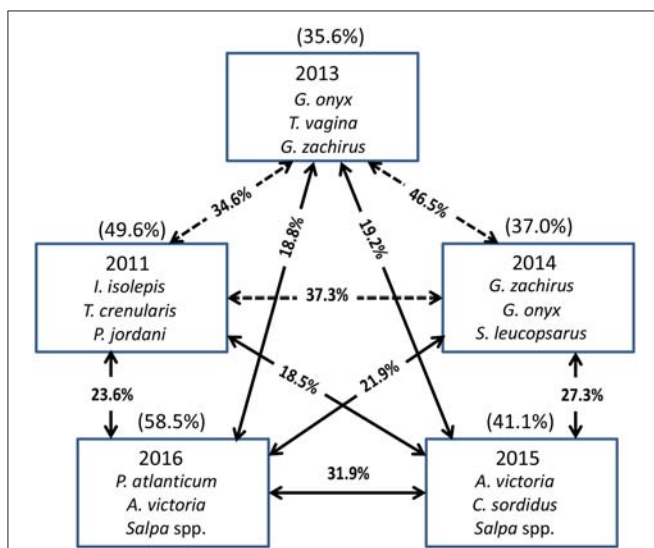


FIGURE 7 | The top three species contributing to the assemblages each year based on Indicator Species Analysis (ISA). Their cumulative percentage contribution to the total assemblage is given in parentheses above each box. The percentage similarity between year pairs is shown on the arrows between the boxes. The solid arrows connect years that are significantly different from each other (MRPP, $p < 0.05$), whereas the dashed arrows connect years that are not significantly different from each other.

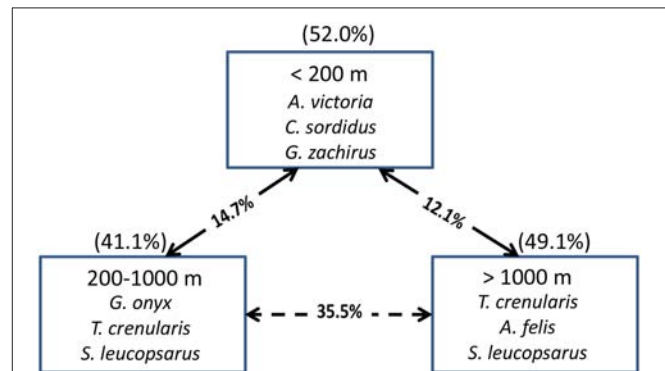


FIGURE 9 | The top three species contributing to the assemblages in each depth strata for all years combined based on Indicator Species Analysis (ISA). Their cumulative percentage contribution to the total assemblage is given in parentheses above each box. The percentage similarity between depth strata pairs is shown on the arrows between the boxes. The solid arrows connect depth strata that are significantly different from each other (MRPP, $p < 0.05$), whereas the dashed arrows connect depth strata that are not significantly different from each other.

of 2017 (Gentemann et al., 2017). Although above-average upwelling winds were evident off Newport, Oregon in the spring of both 2015 and 2016, the resulting cool water was found mainly nearshore and off southern Oregon, and these waters had warmed to above average SSTs by mid-summer (Gentemann et al., 2017). Although we show substantial changes in water temperature and other variables before and after the MHW

event, it is beyond the scope of this paper to present detailed relationships to environmental variables, and this topic is the focus of another paper (Friedman et al., 2018) that examines relationships to modeled, high resolution physical data for many of our dominant taxa collected over a much broader geographic area.

In most respects, the dominant teleost and cephalopod taxa, their relative abundances, and cross-shelf assemblages documented in the present study conform to those identified by Phillips et al. (2009) in a similar study of epipelagic

micronekton collected in the NCC during 2004–2006. Similar to the more recent work, the cross-shelf location (distance offshore or bottom depth) of the sampling was the major determinant of the community composition, with the shelf break serving as the transition region between nearshore and offshore fauna (Phillips et al., 2009). Although all three of these earlier years examined were relatively warm years of reduced ocean upwelling, euphausiids were by far the dominant taxa collected all years, although gelatinous organisms were not examined by Phillips et al. (2009).

The recent increase in gelatinous taxa we observed did not hold uniformly for all gelatinous taxa. Some gelatinous taxa such as the colonial salp, *Salpa* spp., was commonly found in 2011 as well (Supplementary Figure 2), a somewhat cool year inshore but marked with warm water offshore, which led to the incursion of these salps to nearshore waters throughout the northeast Pacific Ocean (Li et al., 2016). Similarly, although the cephalopods and teleosts as a whole did not show a distinct shift related to the arrival of the “warm blob,” some individual species did appear to respond positively (e.g., *M. productus*), whereas others such as *A. felis* and *S. leucopsarus* were relatively more abundant during the two cooler years of 2013 and 2014 (Supplementary Figure 2). The high densities of *M. productus* mainly at the northernmost stations sampled in 2016 were all age-0 fish that have been noted to occur in the NCC only during previous warm years (Brodeur et al., 2006; Phillips et al., 2007). As noted by Auth et al. (2018), this species was observed to be spawning off the coast of Oregon in the winter of 2016, well north of their more typical spawning area in the southern California Bight. We suspect that the distribution of the age-0 *M. productus* extended well north of our sampling area during 2016. With the exception of the along-shelf variation in *M. productus*, there were few latitudinal differences in the distribution of the taxa (Supplementary Figure 2), suggesting that the entire sampling region represented a somewhat cohesive zoogeographical community, as was shown by Friedman et al. (2018) for all stations north of Cape Mendocino (40.5°N).

Although we did not speciate our euphausiids for most of the hauls, Peterson et al. (2017) showed a similar pattern to ours from sampling along a single transect off Newport, Oregon (latitude 44.6°N), where the northern inshore species of euphausiid (*Thysanoessa spinifera*) was extremely rare in both 2015 and 2016 compared to previous years. The smaller offshore species (*Euphausia pacifica*) also showed a decline in 2015 but a rebound in 2016 (Peterson et al., 2017). Even within this species, there appears to be a decline in mean size starting in October of 2014 which would further decrease the biomass per individual (McClatchie et al., 2016). Off Vancouver Island, Canada, Galbraith and Young (2017) found high abundances of euphausiids overall for the last few years, but a demonstrative shift to mostly *E. pacifica* in 2016. We also observed a substantial increase in 2015 and 2016 for a more southern species of euphausiid, *Nematoscelis difficilis* (Galbraith and Young, 2017), which is rarely collected in cooler years. In a similar survey of epipelagic forage taxa off the coast of central California in 1990–2012, Ralston et al. (2015) observed the lowest abundances of euphausiids during their 12-year time series in 1992 and 1998,

which were both strong El Niño years. In contrast, Morgan et al. (2019) found anomalously high larval euphausiid abundances in 2014–2016 from plankton sampling conducted closer to shore in our study area.

The most dramatic increase in gelatinous abundance associated with the warming were predominantly offshore or southern taxa such as *Aequorea victoria* in 2015 and the tropical pelagic tunicate *P. atlanticum*, which dominated the catches in 2016. The latter species was found in even higher densities in the summer of 2017, occurring well into the Gulf of Alaska (Brodeur et al., 2018; Sutherland et al., 2018). Despite the increase in offshore gelatinous taxa such as Hydromedusae, salps, and pelagic tunicates, it should be noted that the normal inshore large medusae, such as *Chrysaora fuscescens* and *Aurelia labiata*, which are dependent on strong upwelling and high productivity (Suchman et al., 2012), showed concomitant decreases in 2015 and 2016 (McClatchie et al., 2016; Sakuma et al., 2016; Morgan et al., 2019).

Our abundance results likely underestimate the impacts of this shift from crustacean to gelatinous taxa on the ecosystem. Unfortunately, we are able to only report changes in abundance, which is what we could measure at sea, since we did not have available a highly-precise, motion-compensated balance needed to get biomass of such relatively small organisms. However, if our abundance estimates were to be converted to a more useful currency in food web models (e.g., biomass or carbon content per individual), then the shifts observed in 2015 and 2016 are likely to be even more dramatic. Many of the crustaceans normally caught in this survey (e.g., euphausiids, sergestid shrimp) are at the smaller (15–25 mm) end of the micronekton size spectrum (Kwong et al., 2018). For example, the average weight of an adult *E. pacifica* is 0.10 g and the average weight of an adult *T. spinifera* is 0.12 g (based on collections in both warm and cold years, Elizabeth Daly, Oregon State University, unpublished data). Most of the gelatinous taxa are much larger in size and even accounting for the high moisture content of many of the taxa we caught, they would still represent per individual a relative high biomass on a dry weight or carbon content basis. A typical *A. victoria* sampled in 2015 was on average 69 mm in bell diameter with an average wet weight of 4.4 g (Sam Zeman, OSU, unpublished data) where a typical *P. atlanticum* averaging 36 mm weighed 1.28 g wet weight and 0.14 g dry weight [based on 28–46 mm individuals measured by Lebrato and Jones (2009); well below our average pyrosome lengths of 64.0 and 86.3 mm measured in 2015 and 2016, respectively].

The abundance we estimated for both these groups may be considered only as an index rather than an absolute abundance, since some taxa such as euphausiids and small salps may be extruded through the larger meshes at the mouth of the trawl. However, we expect that the relative levels we observed between years are likely to be somewhat robust. Observations on the deck of the vessel as the contents of the trawl were emptied showed a stark contrast between multiple large baskets of krill present at almost every station in the earlier cooler years to just a few liters per haul in the latter 2 years, with the gelatinous taxa showing the opposite pattern. In the region north of our study area off southern Vancouver Island, Canada, Galbraith

and Young (2017) found a shift from a crustacean-dominated to a gelatinous-dominated plankton assemblage, and both 2015 and 2016 were the most extreme outliers in their 27-year time series. The dramatic shift we observed in the community composition following the MHW event would have statistically more significance had we included euphausiids in the ordination, thus our results could be considered somewhat conservative. It is interesting to note that the species richness and diversity both peaked in 2015, and then declined in 2016. A possible explanation is that the ecosystem was in transition at this time between the cool nearshore assemblage and the warm offshore assemblage, and both communities were represented in the sampling. Santora et al. (2017) found that diversity was the highest in 2015 of their 26-year time series off California using the same midwater trawl gear we used, although 2016 was not included in their study.

The warming event of 2015 and 2016 contrasted with previous strong El Niño events in that the temperature anomalies were exhibited mainly in the surface layer (upper 50–80 m), while below this layer temperature conditions were close to the climatological mean (Peterson et al., 2017; Auth et al., 2018). As our nighttime trawling occurred for the most part within this warm layer above the sharp thermocline (Figure 3), we cannot ascertain the community composition of the micronekton in the deeper layers which possibly may not have been as affected as much as the surface layer. Our stratified tow series from two stations in 2016 only (Supplementary Figure 3) indicated that, although there were both euphausiids and gelatinous taxa below the target depth of the survey (~30–42 m), they were not substantially different from the depth strata that we examined throughout all years of this study. Moreover, although the net was towed at each target depth for 15 min and quickly retrieved to the surface, there would be some limited catch on the retrieval of the net to the surface and this bias would be the greatest for the deepest stratum sampled. Catches were generally the lowest in the shallowest strata which were mostly within the warm surface layer (Supplementary Figure 3). Concurrent 120 kHz acoustical data along these transects revealed the presence of intense scattering layers below 100 m in 2015 that may have been aggregations of euphausiids and other micronekton that remained below the surface warm layer throughout the diel period (Brodeur, personal observation). Thus, it is possible that many components of the deep-scattering layer, such as crustaceans and fishes, did not undergo their normal diel vertical migration into the surface layers at night in the latter 2 years of our study. Thus, they would not be available to our trawl net, which could therefore skew our midwater abundance estimates. Although the deeper layer may have been exploited by deeper-dwelling fishes (e.g., older age classes of *M. productus*), it is likely to be beyond the diving capacity of many seabirds, possibly contributing to the starvation mortality and reduced reproductive success observed in many populations (Cavole et al., 2016; McClatchie et al., 2016).

The shift from a crustacean dominated system to one dominated by gelatinous taxa is likely to be caused by changes in the physics and mediated through regulation of the size structure and taxonomic composition of the lower trophic-level primary and secondary producers (Parsons and Lalli,

2002; Richardson, 2008). Under strong upwelling conditions, surface waters are cool and nutrients are often in excess, leading to a phytoplankton community dominated by diatoms and a zooplankton community dominated by large crustaceans (Ryckaczewski and Checkley, 2008). The upper trophic level food web is then dominated by planktivorous fishes, which in turn are fed upon by predatory fishes, seabirds, and marine mammals. In contrast, during warm and stratified ocean conditions, the surface waters are limited in nutrients leading to picoplankton and flagellates as the dominant primary producers (Lindegren et al., 2017). The intermediate trophic levels are dominated by gelatinous zooplankton capable of feeding on these fine particles (e.g., salps, tunicates, and appendicularians), which are much less utilized by higher trophic levels. During warm years such as El Niños, food webs tend to be more elongated with additional intermediate trophic levels compared to cool years, leading to less trophic efficiency in the system (Brodeur and Percy, 1992; Ruiz-Cooley et al., 2017). The increased densities of these gelatinous microcarnivorous predators such as *Aequorea victoria* may have depressed populations of grazing copepods, thus creating a trophic cascade typical of many jellyfish blooms (Schnedler-Meyer et al., 2018), leading to the high chlorophyll levels we observed in 2015. In contrast, pelagic tunicates such as pyrosomes feed on smaller particles including phytoplankton (Perissinotto et al., 2007, but see Pakhomov et al., 2019), which may have depressed chlorophyll *a* levels as seen in 2016.

Although most planktivorous forage species consume mainly small pelagic crustaceans such as copepods and euphausiids, the apparent lack of large-bodied crustaceans in 2015 and 2016 (Peterson et al., 2017, this study) appears to have led to a pronounced diet shift in many dominant pelagic fish species. For example, northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*), two of the dominant forage taxa in this region, were observed to be feeding on gelatinous zooplankton such as salps and smaller gelatinous taxa these 2 years, in contrast to a mostly crustacean diet during normal or cool years (Brodeur et al., 2019).

Our cruises during late-spring/early-summer provide a simple “snapshot” of the communities at only one time of the year. In addition to climate-driven changes in productivity, we also see temperature mediated effects on phenology in this region. For example, Auth et al. (2018) provide evidence of earlier and more prolonged spawning of both northern anchovy and Pacific sardine in the NCC since 2015, thus shifting the availability of juveniles of these species in our surveys. Although we did see many younger age-classes of these taxa in our samples, the differences were not striking. However, Auth et al. (2018) also documented a northern shift in the spawning of Pacific hake in 2016, which corresponded to a substantial increase in age-0 hake mostly in the northern part of our sampling region, such that this species became the dominant fish taxa sampled that year (Table 1). Although the normal spawning area of Pacific hake is off southern California, they have been shown to spawn within the NCC during the anomalously warm years that occurred during the mid-2000s, leading to high catches of age-0 fish off Oregon and Washington in the summer (Phillips et al., 2007). Major temperature changes in this region can also

lead to interannual variations in growth rate and survival of larval and juvenile fishes, as observed for northern anchovy in the NCC (Takahashi et al., 2012), thus affecting their availability to predators.

This study and others (Phillips et al., 2009; Friedman et al., 2018) that looked at macrozooplankton and micronekton abundance patterns found temperature to be the dominant environmental variable correlated with interannual variability in catches. The NCC has cycled through warm and cool phases in the past, which led to alternations between a crustacean-dominated and gelatinous-dominated zooplankton system (Francis et al., 2012). Similar patterns have been observed for plankton in other upwelling areas such as off the NW Iberian coast (Bode et al., 2013). The major question is whether these outbursts of gelatinous plankton will continue to occur in the future under projected temperature increases in the North Pacific. However, eastern boundary current regions are not expected to necessarily warm with the projected buildup of greenhouse gases and might actually exhibit enhanced upwelling and cooler temperatures in the future (Wang et al., 2010; Sydeman et al., 2013). Model projections indicate that multiyear marine heat waves are likely to occur more frequently and be of greater intensity in the Northeast Pacific in the coming decades (Joh and Di Lorenzo, 2017), and may be exacerbated by secular trends in anthropogenic warming (Jacox et al., 2018). Frölicher et al. (2018) showed that under projected climate change scenarios, the probability of MHWs will increase by a factor of 41 and be 21 times stronger than pre-industrial conditions, suggesting that these anomalous conditions may be more normal in the future.

It is uncertain whether the intensity and duration of this recent warming event could have exceeded some threshold or tipping point (Duarte, 2014), and result in a long-term increase in gelatinous zooplankton, as seen in some other ecosystems (Atkinson et al., 2004; Attrill et al., 2007; Brotz et al., 2012; Roux et al., 2013), making the return to the previous state quite unlikely without another counteracting major perturbation. Indeed, the extensive bloom of pyrosomes documented here in 2016 continued and actually intensified in 2017 and 2018 (Brodeur et al., 2018; Sutherland et al., 2018), long after the effects of the MHW phenomenon was considered to have abated (Hobday et al., 2018). Conversely, this system may be resilient enough to shift back to cooler conditions, resulting in a lower phase of gelatinous abundance (Lavaniegas and Ohman, 2003; Brodeur et al., 2008; Condon et al., 2013). Only through continual, long-term monitoring of this productive ecosystem will we be able to determine whether this critical trophic level and the apical level taxa that depend on them will continue to be affected by such major ecological perturbations.

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AUTHOR CONTRIBUTIONS

All three authors collected and processed the field data. RB analyzed the physical data and community structure. TA analyzed the diversity indices. AP generated the maps. RB wrote the first draft with later additions by TA and AP. All authors listed have made substantial direct and intellectual contribution to the work, and approved it 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.2019.00212/full#supplementary-material>

Supplementary Figure 1 | Sea surface temperature (SST) time series for the area averaged from 46.625–42.125° N and 124.375–124.875° W. I used the OISST dataset (<https://www.esrl.noaa.gov/psd/>) and the climatology referenced to 1983–2012. The threshold is defined as the 90th percentile defined over the climatology using the marineHeatWave module (Hobday et al., 2016). The shaded categories follow Hobday et al. (2016). The map on the right shows the SST anomalies on Dec. 20, 2014 relative to climatology and denoted by the red triangle marker on the plot. (Figure courtesy of Hillary Scannell, University of Washington).

Supplementary Figure 2 | Distribution maps for the dominant taxa by year. The number in the upper left of each panel indicates the geometric mean catch per haul by year. Note the scale on the plots is logarithmic.

Supplementary Figure 3 | Nighttime vertical distribution of some dominant taxa based on series of three tows made at stations on the Columbia River transect (46.0° N; top) and the Tillamook transect (45.5° N; bottom). Depth indicated on y-axis is the range of depths occupied for most of the tow for each depth stratum. Plots on the right are the vertical distribution of temperature at each location with the approximate depth of the tows at each location indicated by the blue lines.

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Meridional Oceanic Heat Transport Influences Marine Heatwaves in the Tasman Sea on Interannual to Decadal Timescales

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Marine heatwaves (MHWs) pose an increasing threat to the ocean's wellbeing as global warming progresses. Forecasting MHWs is challenging due to the various factors that affect their occurrence, including large variability in the atmospheric state. In this study we demonstrate a causal link between ocean heat content and the area and intensity of MHWs in the Tasman Sea on interannual to decadal time scales. Ocean heat content variations are more persistent than 'weather-related' atmospheric drivers (e.g., blocking high pressure systems) for MHWs and thus provide better predictive skill on timescales longer than weeks. Using data from a forced global ocean sea-ice model, we show that ocean heat content fluctuations in the Tasman Sea are predominantly controlled by oceanic meridional heat transport from the subtropics, which in turn is mainly characterized by the interplay of the East Australian Current and the Tasman Front. Variability in these currents is impacted by wind stress curl anomalies north of this region, following Sverdrup's and Godfrey's 'Island Rule' theories. Data from models and observations show that periods with positive upper (2000 m) ocean heat content anomalies or rapid increases in ocean heat content are characterized by more frequent, larger, longer and more intense MHWs on interannual to decadal timescales. Thus, the oceanic heat content in the Tasman Sea acts as a preconditioner and has a prolonged predictive skill compared to the atmospheric state (e.g., surface heat fluxes), making ocean heat content a useful indicator and measure of the likelihood of MHWs.

Keywords: Tasman Sea, marine heatwaves, climate variability, East Australian Current, Tasman Front, climate extremes, New Zealand, ocean heat content

INTRODUCTION

The Tasman Sea is a region of change, where ocean temperatures (Oliver et al., 2014; Roemmich et al., 2015; Shears and Bowen, 2017) and sea level (Church and White, 2006; Hannah and Bell, 2012; Fang and Zhang, 2015) are rising, exceeding global averages (0.2–0.5°C/decade and 3–5 mm/decade respectively). The difference between air and sea surface temperatures (SST) predominantly controls the air–sea exchange of heat and moisture, which is central to weather and climate. As this region warms (Sutton and Bowen, 2019), it will be vulnerable to experiencing more frequent and more intense extreme events, such as marine heatwaves (MHWs) and tropical storms

(Kuleshov et al., 2008; Oliver et al., 2017, 2018a). Recent studies have shown how MHWs influence the regional climate, terrestrial temperatures, rainfall patterns and ecosystems of Australia, New Zealand and the Pacific Islands (Johnson et al., 2011; Swart and Fyfe, 2012; Purich et al., 2013). Warmer ocean temperatures lead to increased air temperatures, which can hold more water vapor and hence result in more intense rainfall and flooding events. Furthermore, the warm SSTs fuel tropical cyclones, set their intensity (Demaria et al., 1994) and determine how quickly they weaken before making landfall. Around 30 ex-tropical cyclones (e.g., Cyclone Gita, February 2018) made landfall in New Zealand in the past decade, causing severe damage and loss of life due to high wind speeds and flooding. These events are projected to become more intense and more frequent in a warming climate (e.g., Kuleshov et al., 2008). Changes in rainfall distribution and intensity are also of concern, especially for countries with agriculture-based economies, such as New Zealand (Herring et al., 2015).

The ocean circulation in the Tasman Sea is strongly influenced by the energetic East Australian Current (EAC) and the Tasman Front (TF), see **Figure 1**. The eastern Tasman region is less variable and is largely quiescent. The Subtropical Front (STF) is separating northern warm, salty subtropical waters from southern cold, fresh subantarctic waters and crosses the south Tasman Sea at approximately 45°S (e.g., Sokolov and Rintoul, 2009). The EAC transports warm subtropical waters into the Tasman Sea as part of the large-scale South Pacific gyre circulation (e.g., Stammer, 1997; Hu et al., 2015). Volume and heat transports of the EAC are in the order of 22.1 ± 7.5 Sv and 1.35 ± 0.42 PW (Feng et al., 2016; Sloyan et al., 2016). Previous studies have shown that trends and decadal changes in coastal temperatures and salinities in the Western Tasman Sea region are consistent with an intensification in the EAC transport and its poleward extension in response to changes in the South Pacific winds (Hill et al., 2008; Sloyan and O’Kane, 2015). The EAC bifurcates between 30° and 32°S to form the TF which flows to the east (Godfrey et al., 1980; Cetina-Heredia et al., 2014), and the EAC Extension which either continues to the south forming mesoscale eddies that propagate into the Tasman Sea or forms the Tasman Outflow/Tasman Leakage (thereafter TO) (Speich et al., 2002; Ridgway and Dunn, 2007). The mean volume transport of the TF has been found to be 7.6–8.5 Sv (Stanton, 2010) and highly variable (Sutton and Bowen, 2014). The fluctuations of the TF are in phase with the EAC (Hill et al., 2011; Sloyan and O’Kane, 2015), based on hydrographic measurements. We note that the definition of the TF differs in the individual studies depending on the particular data used, with Stanton (2010) and Sutton and Bowen (2014) using eastward flows in the northern Tasman Sea, while Sloyan and O’Kane (2015) and Hill et al. (2011) used shipping routes between New Zealand, Fiji and Australia. In this study we use a north–south cross section along 173°E from New Zealand to 28°S to characterize the flow of the TF. The TF exits the Tasman Sea to the east, between Norfolk Island and the North Cape of New Zealand, to partially source the East Auckland Current (the subtropical western boundary current northeast of New Zealand) (Stanton et al., 1997; Stanton and Sutton, 2003).

Marine heatwaves are characterized by prolonged periods of SST exceeding the 90th percentile of a historical baseline period (Hobday et al., 2016). MHWs in the western Tasman Sea region have been correlated with the variability of the EAC and its extension (Oliver et al., 2017, 2018a), identifying the EAC as the predominant driver of MHWs in the region. This link encourages the exploitation of ocean models to predict heatwaves based on oceanic states, such as heat content and currents. The predictive skill of ocean heat content and currents is higher than that of atmospheric variability, such as blocking high-pressure systems (which contribute to MHWs and caused the recent summer 2017/18 MHW (Salinger et al., 2019)). This is because ocean heat content variability is more persistent in time than weather patterns. Modulations in currents and heat transport due to a changing climate will impact on the heat content and thus the occurrence of MHWs in this region. Progress has been made in predicting SSTs on seasonal timescales, for winter and spring with lead times of up to 3 months (de Burgh-Day et al., 2018), but further work is required to understand precisely how the occurrence of MHWs will be affected by global warming progressing.

In this paper we investigate the connections between MHWs and meridional oceanic heat transport and content in the Tasman Sea on interannual to decadal timescales, using data from a forced ocean model and hydrographic measurements. The paper is structured as follows: section 3 describes the model, the simulation and the methodology used to compute heat content, heat transports and MHWs and provides a model evaluation.

MODEL, METHODS, AND MODEL EVALUATION

Model Description

We use a global sea-ice coupled model to simulate the oceanic fields and investigate the links between oceanic heat content and MHWs in the Tasman Sea. The model output is based on a global forced ocean sea-ice configuration using NEMO (Madec, 2008) and CICE (Hunke and Lipscomb, 2010) as part of UKESM/NZESM (Williams et al., 2016). The global domain is defined by a coarse (nominal 1° × 1° at the equator) tripolar model grid known as eORCA1. Grid sizes in the Tasman Sea, our target region, are around 80 km. Since the model does not resolve oceanic mesoscale eddies, an eddy parameterization has been used following Gent and McWilliams (1990), with an eddy diffusivity coefficient of 2000 m²/s. This configuration uses 75 vertical z-levels, with layer thickness varying between 1 m at the surface and 200 m, and with a maximum depth of 6200 m. Most (55) of the vertical layers are in the upper 2000 m. In addition, a partial cell approach has been used to improve near-bottom flows (Barnier et al., 2006). More specific model details and description of model performance of this configuration can be found in Storkey et al. (2018); Kuhlbrodt et al. (2018), and Salinger et al. (2019).

The model simulation has been started from rest, with climatological temperature and salinity values from EN4 (Good et al., 2013). Atmospheric forcing fields from JRA-55-DO

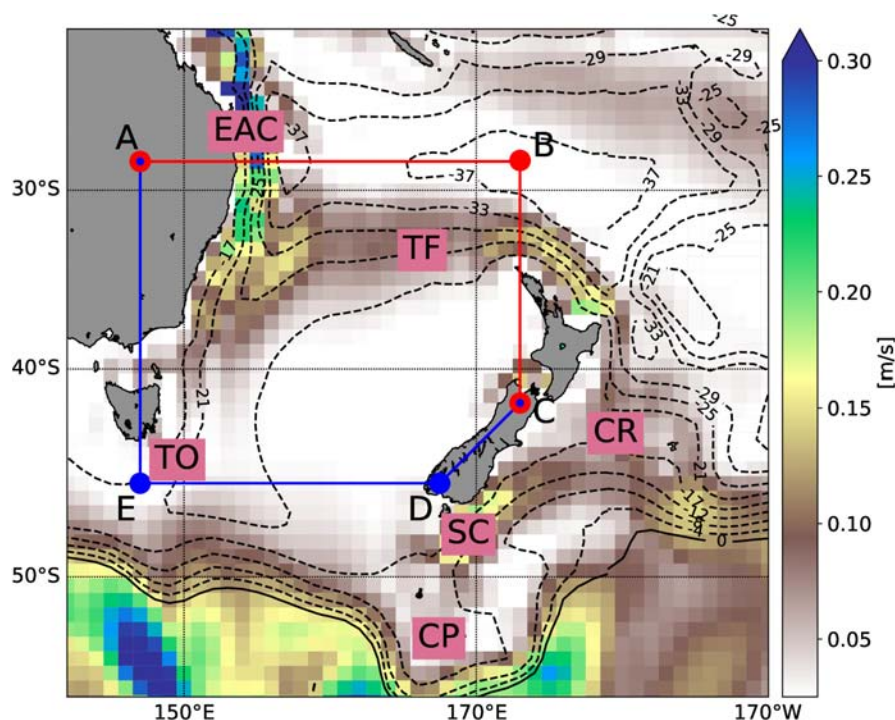


FIGURE 1 | Modeled mean surface speed (shading) in m/s with contour lines representing the barotropic stream-function in Sv. The area enclosed by the polygon ABCDEA is the area of interest for this study, thereafter the Tasman Box. The horizontal boundaries are split into a Tasman North (red lines and dots, section ABC) and Tasman South section (blue lines and dots, section CDEA). See **Table 1** for coordinates. Labels EAC, TO, TF, SC, CP and CR mark the East Australian Current, Tasman Outflow, Tasman Front, Southland Current, Campbell Plateau and Chatham Rise, respectively. The Cook Strait is the passage between New Zealand's North and South Island near corner point C.

version 1.3 (T sujino et al., 2018) have been used to complete a 60-year model hindcast from 1958 to 2018. This hindcast has already been used to characterize the summer 2017/18 MHW in the Tasman Sea (Salinger et al., 2019). The modeled SSTs have been saved as daily averages, while all other oceanic fields are available as monthly means. Since the model has been started from a state of rest and with climatological values for temperature and salinity, the first 12 years of the simulation have been discarded to avoid possible spin-up effects. Therefore, time series and time averages in the manuscript are presented from 1970 onward. Coastal runoff has been prescribed with climatological values (Dai and Trenberth, 2002).

Diagnostics

Marine heatwave diagnostics (i.e., MHW area and MHW intensity) have been calculated from modeled daily SST following

Hobday et al. (2016). Model data have been extracted along the four boundaries (sides) of the Tasman Sea (**Figure 1**) to characterize the inflows and outflows. The enclosed box, thereafter Tasman Box, covers 147° to 173°E and 46° to 28°S (**Table 1**), chosen to include the TF but to exclude most of the Antarctic Circumpolar Current (ACC) and the Southland Current (to avoid large variability in the south). We further split the domain into a northern boundary section (**Figure 1**, A-B-C), thereafter Tasman North (TN), and a southern boundary section (**Figure 1**, C-D-E-A), thereafter Tasman South (TS). Changes in the TN can be attributed to changes in subtropical water masses, while for TS they reflect a mixture of subtropical and subantarctic water masses (Oliver and Holbrook, 2014). Heat content and volume/heat transports have been computed from monthly mean model data. For heat transports and content, 0°C has been selected as reference temperature, and a specific heat capacity of 4000 J/kg/°K has been used. Potential density for the heat content calculation is based on modeled temperature and salinity fields. Time series have been filtered using a 23-month Hanning filter, unless otherwise stated, to eliminate the seasonal cycle. All correlation coefficients presented in this manuscript are significant at a 95% confidence interval (student *t*-test) and have been computed with zero time lag.

Volume and heat transports of the EAC, TF and TO have been defined as extrema of the horizontal cumulated transports of the upper 2500 m (2000 m for TF and 3000 m for TO) over

TABLE 1 | Coordinates for corner points enclosing the Tasman Box (**Figure 1**).

Corner point	Longitude	Latitude
A	147°E	28°S
B	173°E	28°S
C	173°E	42°S
D	168°E	46°S
E	147°E	46°S

the regions, shown by cyan boxes in **Figure 4**. The integration starts from the coast or corner point. The TF transport is the zonal transport between corner point B and the North Cape of New Zealand and excludes transports through Cook Strait (~ 0.9 Sv). The Cook Strait is the passage between New Zealand's North and South Islands, near corner point C in **Figure 1**.

The modeled ocean heat content has been compared with results from the shorter time series (2004–2018) Roemmich–Gilson Argo climatology (Roemmich and Gilson, 2009). The Roemmich–Gilson product consists of optimally interpolated Argo profiles on a $1^\circ \times 1^\circ$ grid of longitude and latitude and can be downloaded from http://sio-argo.ucsd.edu/RG_Climatology.html. The monthly Argo-derived temperature values extend over 58 pressure levels from the surface to 2000 m depth. In this paper, the Argo heat content is depth-integrated from 2000 m to the surface over the same region as the model results. Remotely sensed absolute dynamic topography (ADT), a multi-mission altimeter product (Ssalto/Duacs) from Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO) has been compared to modeled sea surface height (SSH) to evaluate the model and to assess the skill of remote measurements to infer heat content changes in the Tasman Sea. The Ssalto/Duacs altimeter products were produced and distributed by the Copernicus Marine and Environment Monitoring Service (CMEMS)¹. Temperature data from harmonically analyzed high-resolution expendable bathythermograph data (HRXBT) along a shipping line between Sydney and Wellington (PX34) have also been used to evaluate model data (Sutton et al., 2005). We also used large scale climate indices, the Southern Oscillation Index (SOI) and Pacific Decadal Oscillation (PDO) to investigate the influence of the principal modes of climate variability of the Pacific Ocean on MHWs in the Tasman Sea. The SOI is derived from the sea-level pressure difference between Tahiti and Darwin. The PDO is defined as the leading principal component of North Pacific monthly SST variability (poleward of 20°N for the 1900–93 period) and data have been downloaded from <http://research.jisao.washington.edu/pdo/>.

Model Evaluation

The mean barotropic streamfunction and surface speed shown in **Figure 1** provides an impression of the large-scale ocean circulation in this model hindcast. The EAC flows southward along the east coast of Australia. South of 30°S , the EAC bifurcates into the EAC Extension, which continues south, and the TF, which flows eastward toward New Zealand. As the EAC Extension moves southward it transforms into the TO. The largest part of this outflow forms the Tasman Leakage (Ridgway and Dunn, 2007), which leaves the Tasman Sea (see corner point E in **Figure 1**) toward the Indian Ocean, while a second portion recirculates back into the Tasman Sea to the east.

The time mean ADT and the modeled SSH is presented in **Figures 2a,b** respectively. A meridional gradient is present in both datasets, elevated in the subtropics and lower in the subantarctic region. The large decrease, which is associated with the EAC Extension and TF in the northern Tasman

Sea, is well represented (0.7 m contour line) in the hindcast. The central Tasman Sea shows very little change in sea surface height until near 50°S , both in the observations and simulations. Southeast of New Zealand, the Campbell Plateau shows clearly with slightly positive ADT. Flows of the Subantarctic Front along the eastern flank of the plateau are characterized by negative ADT. All these features are well represented in the modeled SSH, despite its coarse resolution. We infer from this good agreement that the near-surface ocean circulation is well captured by the model. We calculate a mean EAC volume transport of 23.3 ± 4 Sv, which is quantitatively consistent with previous reported values (Oliver and Holbrook, 2014; Sloyan and O'Kane, 2015; Ypma et al., 2016).

The mean modeled MHW probability and intensity are shown in **Figures 2c,d**. Both diagnostics highlight that MHWs are predominantly confined to the central Tasman Sea and subtropical waters. The region south of the Tasman Sea is predominantly affected by the energetic ACC, which has a wider spectrum in the temperature climatology, therefore reducing the likelihood of MHW criteria being met. The likelihood of a MHW (**Figure 2c**) varies between 5 and 12% over the Tasman Sea, with hotspots in the EAC Extension, the central Tasman Sea and the eastern TF. Since defining MHWs as ocean temperatures exceeding a 90th percentile above a daily climatology, 10% would reflect the expected likelihood, without considering these conditions to last for at least 5 consecutive days. The mean MHW intensity varies between 0.05 and 0.12°C over the Tasman Sea. The regions that experience more intense MHWs are the EAC Extension, the central Tasman Sea, the northern side of the TF and the ocean south east of Tasmania. These patterns are consistent with results of previous studies (Oliver et al., 2015, 2018a,b). The HRXBT section between Wellington and Sydney (PX34) runs through the Tasman Sea (**Figure 2**) measuring the 0–850 m temperature approximately 4 times a year and can be used to validate the modeled mean structure and temporal variability. The mean temperature structure (for the 1991–2018 period) from the observations and the simulations is shown in **Figures 3a,b** respectively. In the western side of the section, the EAC, which carries warm water into the Tasman Sea, is represented by the down-sloping isotherms (**Figure 3a**). The modeled temperatures (**Figure 3b**), show similar characteristics, although the core of the EAC is not as warm as the observations suggest. This could be due to the coarse horizontal resolution of the model or due to the irregular HRXBT sampling frequency. Despite these differences, the model captures the mean temperature well, which is further demonstrated in the top 850m temperature anomaly over the section (**Figure 3c**). Both upper ocean heat anomalies show similar long-term variations, with the 1990s being cold and the 2000s being warmer. Both time series suggest an ongoing warming of the Tasman Sea since 2010, more evident in the observations. The larger temporal variability in the observations compared to the model can be to some extent explained by the sampling frequency of this HRXBT line.

Overall, the model shows a good degree of consistency with observed key diagnostics in our target region, considering its coarse spatial resolution. For more regional studies, models

¹<http://marine.copernicus.eu/>

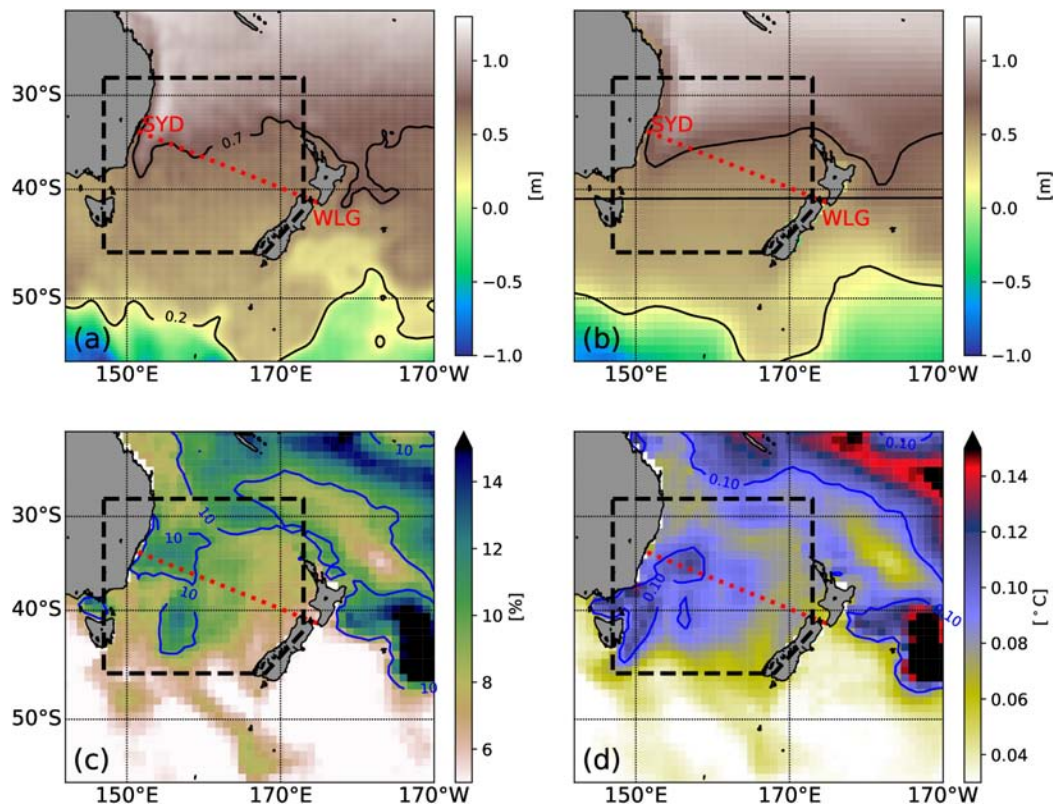


FIGURE 2 | Mean fields (1993–2017) for (a) ADT from a multi-mission altimeter product and (b) SSH from the model hindcast. Mean probability (c) of MHW and its intensity (d) for the period 1970 to 2017. The black box illustrates the Tasman Box and the dashed red line the HRXBT transect between Wellington and Sydney (PX34). The black contour lines in (a,b) represent 0.2 and 0.7 m contour lines to aid the comparison. The blue contour lines in (c,d) represent 10% and 0.1°C contours lines.

with higher spatial resolution, which resolve mesoscale eddies, should be considered.

RESULTS

Time Mean Properties Along the Tasman North and Tasman South Sections

In this section we assess the mean state along the northern and southern sections (TN, TS) that confine the Tasman Box. The EAC and TF dominate the TN section (**Figure 1**). The EAC transports warm, salty, subtropical water into the Tasman Sea and causes a zonal temperature gradient along the TN section, with the maximum temperature found near the Australian Shelf (**Figure 4a**). The modeled EAC occupies roughly the upper 2500m (cyan box labeled EAC). A northward recirculation to the east is part of the EAC boundary current system (**Figure 4b**). East of the EAC recirculation, between 1500 and 2750 km along the TN section, the upper 200m are characterized by a weak northward flow, with velocities around 1–2 cm/s. Flows associated with the TF exit the Tasman Box between corner point B and North Cape (**Figure 1**), represented by positive velocities (eastward flow) in the upper 2000m (cyan box labeled TF) (**Figure 4b**). The TF is surface-intensified and the mean

modeled velocity exceeds 0.2 m/s. The heat transport of the TN section (**Figure 4c**) is dominated by the volume transport and consequently shows the same pattern. The EAC is the largest source of heat advection into the Tasman Sea along the TN section, while the remaining currents, in particular the TF, remove heat from the Tasman Sea. Time averaged volume (and heat transports) for the EAC of -23.3 ± 4 Sv (-1273 ± 232 PW) are in the range of results provided in earlier studies (Oliver and Holbrook, 2014; Sloyan and O’Kane, 2015; Ypma et al., 2016; Bull et al., 2017). Mean transports for the TF of 19.8 ± 3.6 Sv (888 ± 134 PW) are about twice as large. However, the net outflow from the Tasman Sea across the TN is comparable with earlier studies. Those studies suggest a different split for the volume transports, between TF and northward transport across AB than this model hindcast. Their AB outflow is larger, ranges between 8 and 18 Sv, and results to a smaller TF transport.

The TS section is dominated by the TO (Ridgway and Godfrey, 1994), which feeds the Tasman Leakage (Ridgway and Dunn, 2007), and a flow which recirculates back into the Tasman Sea south of Tasmania. This bifurcation was seen in the barotropic streamfunction contour lines in **Figure 1**. The outflow originates from the EAC and is the reason for the warm temperatures close to Tasmania (**Figure 4d**). The modelled TO extend down to about 3000 m and is sub-surface intensified, with its maximum

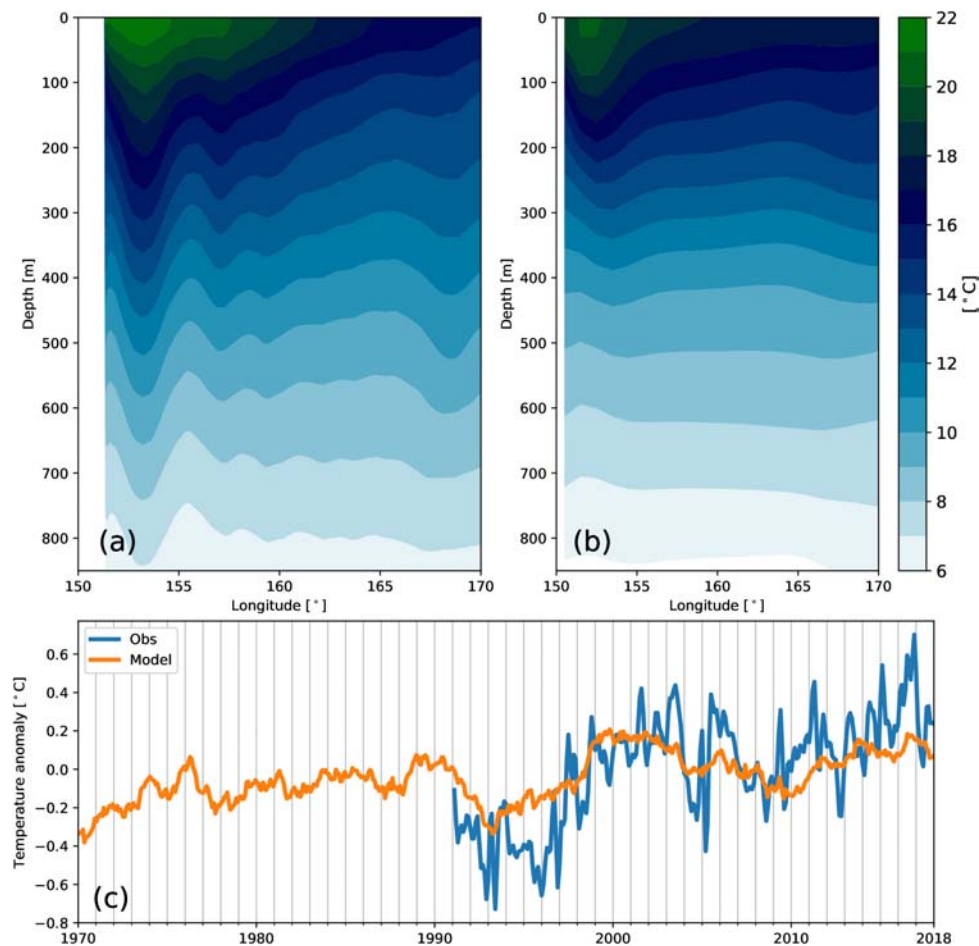


FIGURE 3 | Mean temperature (1991–2018) for the PX34 HRXBT transect **(a)** between Wellington and Sydney (see **Figure 2**) and **(b)** model hindcast. **(c)** top 850 m temperature anomaly over the PX34 HRXBT line from observations (blue) and model (orange). The seasonal cycle has been removed.

around 800–1000 m (**Figure 4e**). The subsurface intensification was also found in earlier studies (Ridgway and Dunn, 2007; van Sebille et al., 2012). Model current speeds of roughly 3–4 cm/s and the total transport of 9.9 ± 4.6 Sv are consistent with other studies (Ridgway, 2007; Hill et al., 2011). At the surface near the New Zealand West Coast, a weak flow associated with the STF is directed southward and then skirts southern New Zealand as a precursor to the Southland Current (Chiswell et al., 2015). Heat transport follows the volume transport (**Figure 4f**) and identifies the TO as the southern export pathway of heat for the Tasman Sea. While some of this heat recirculates back into the Tasman Sea, a substantial portion is carried into the Indian Ocean.

The vertical profiles of mean horizontal transports for the sections are shown in **Figure 5a**. While the net volume transport across both sections totals to a mean southward flow of roughly -3.3 Sv, approximately the upper 150 m of both sections show a northward-directed flow. That is due to the fact that the modeled TF and Cook Strait transport overcompensates the southward transport of the EAC in the near-surface layer (dashed line). Below this transition depth,

the net transport is southward throughout the rest of the water column, with a distinct extremum in the TS section at around 850 m, representing the TO (Ridgway and Dunn, 2007). The net southward transport of about -3.3 Sv through the Tasman Sea is on the lower end of the range suggested by other studies for the TO (usually around 6–7 Sv, Oliver and Holbrook, 2014; Ypma et al., 2016).

With knowledge of the volume transports, the modeled heat transport profile is easier to understand (**Figure 5b**). Due to the large heat transport of the TF (dashed line), the net heat transport of the TN section is not entirely southward as could be expected. Between 30 and 150 m the TF and Cook Strait extract heat from the Tasman Sea, while heat is carried into the Tasman Sea both shallower and deeper. The reversal in heat transport, from northward to southward, is located in the TS section at approximately 150 m. The difference between 180.8 TW along TN and 64.9 TW along TS (**Figure 5b**) reflects a large atmospheric heat flux of approximately 115 TW over the Tasman Box to balance the heat transport convergence. Considering the area of the Tasman Box, this is equivalent to a mean net heat flux of around 22 W/m^2 to the

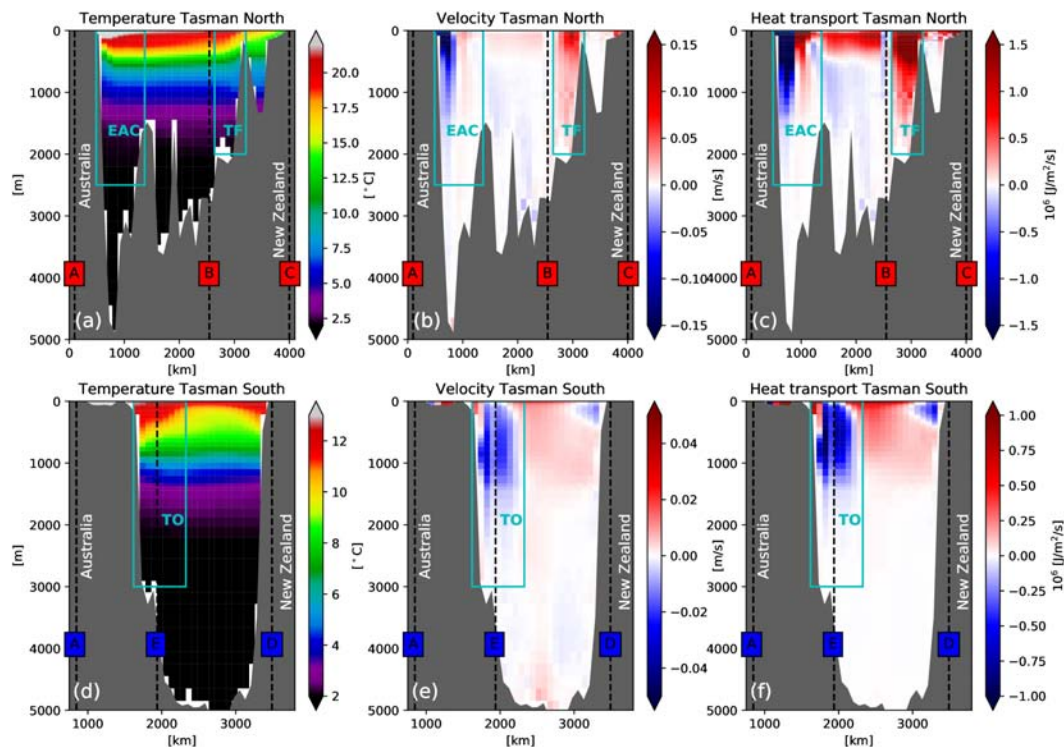


FIGURE 4 | Time averaged (1970–2017) quantities along Tasman North (ABC) and Tasman South section (CDEA). **(a,d)** Temperature in $^{\circ}\text{C}$, **(b,e)** cross section velocity in m/s and **(c,f)** heat transport in $10^6 \text{ J/m}^2/\text{s}$. Specific currents have been labeled, with TF (Tasman Front), EAC (East Australian Current) and TO (Tasman Outflow). In addition the boundary points of the Tasman box have been labeled with (A)–(E). Gray shaded area is the model bathymetry. Transports follow the common sign convention where positive transports show northward or eastward transports. Segments A–B and D–E show meridional transports, while B–C and E toward Australia are zonal transports.

atmosphere, which is in agreement with values from heat flux reanalysis (not shown).

Variability of Volume and Heat Transport and Its Impact on Heat Content

Earlier studies found a relationship between volume transports of EAC, TF and TO/EAC-Extension (Hill et al., 2011; Sloyan and O’Kane, 2015), with increased EAC transports corresponding to increased TF and lower EAC-Extension transports. Here, EAC and TF transports on interannual time scales are correlated at $r = 0.6$. For TO/EAC-Extension and TF transports, the anti-correlation varied from $r = -0.6$ to $r = -0.8$ for different data products on decadal time scales. Our modeled transports (**Figure 6**) also show an anti-correlation between TF and TO using annual means, with slightly a lower correlation coefficient ($r = -0.48$).

We now investigate the interannual variability of transports across TN and TS and compare the transports to heat content changes in the Tasman Box. Transports of TN and TS reflect transports across the entire section. For transports of EAC and TF the cyan boxes in **Figure 4** have been used as regional limits. The time average over the period from 1970 to 2017 has been used as a reference to derive anomalies, except for the ADT and Argo anomalies, where 1993 to 2017 and 2004 to 2017 have been

used, respectively. The volume transport anomalies of TN and TS (**Figure 7a**) present significant interannual to decadal variability. The period from 2003 to 2013 is characterized with an ongoing decline in transport and relatively little interannual variability in both sections. Sloyan and O’Kane (2015) also described lower EAC transports from 2000 to 2004 and lower TF transports from 2000 to the end of their record (2008). Most of the volume transport variability of TN and TS results from the complex interplay between the EAC and TF transports (EAC-TF, black curve). This is reflected in the good alignment between variability across both sections and the difference between the EAC and TF (thick black line) with a correlation of $r = 0.88$. Note this difference is obtained by subtracting the individual time averages of EAC and TF from 1970 to 2017 prior to the subtraction. The EAC and TF transports show general co-variability, in agreement with previous studies (Sloyan and O’Kane, 2015), but the TF exhibits larger interannual variability than the EAC (standard deviation of 2.4 Sv versus 1.6 Sv). Here the very large modeled transport of TF is potentially contributing to this large variability. This co-variability ($r = -0.42$) only emerges when the time series are interannually filtered and is not present in the annual averages.

For the heat transport across TN and TS (**Figure 7b**), the characteristics are similar to the volume transport, with the order of 90% of the interannual variability of the TN section (red) being

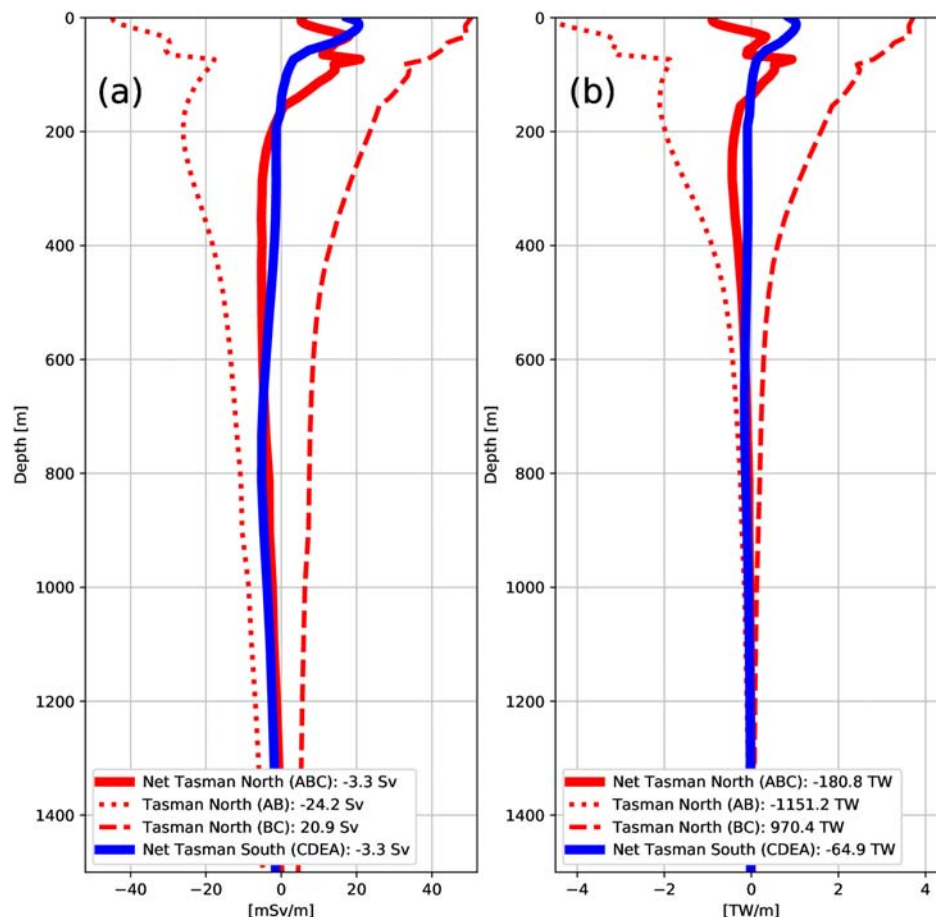


FIGURE 5 | Vertical profiles for time mean (1970–2018) **(a)** volume and **(b)** heat transport for sections TN and TS. Red (blue) curves show cross section transports for the Tasman North (South) section. Net transports are shown as solid thick lines. Positive (negative) values for Tasman North (South) reflect transports leaving the Tasman Sea across this boundary. Mean values are provided in the legend.

attributed to the heat transport differences between the EAC and TF (black). The period from 2003 to approximately 2013 again stands out, with relatively low interannual variability compared with earlier periods. The heat transport variations across the TS section are smaller compared to TN (standard deviation of $0.7 \cdot 10^{14}$ J/s vs. $0.9 \cdot 10^{14}$ J/s), as a result of the colder sub-antarctic water masses being advected, while volume transport variations are the same. The heat transports of the EAC and TF show the same co-variability ($r = -0.6$) as the volume transports. Quantitatively, the EAC imports more heat into the Tasman Sea than is exported by the TF and other outflows along TN, with the imbalance being compensated by atmospheric fluxes, heat content changes and heat transport across TS.

As shown above, the heat transport across the TN section is dominating the heat transport into the Tasman Sea and thus the heat content and its variability (**Figure 7c**). The heat transport across TS only accounts for around 30% of that across TN. Full depth and upper 2000m heat content are linked and show similar variability to the heat content changes, because of the heat transport across the TN section (light blue line in **Figure 7c**). The heat content drop in the early 1990s stands out from the time

series in terms of intensity and persistence. This drop is present in the TN transports, as is the rebound in the late 1990s and is consistent with temperature observations along PX34 (Sutton et al., 2005 and **Figure 3c**). The modeled upper 2000m heat content is correlated to the Argo-derived heat content ($r = 0.7$) in the Tasman Sea (blue line) and shows a positive trend since early 2010, which is within the range of natural variability. From 2015 onward, the modeled heat content is consistently lower than the Argo-derived heat content, while both timeseries share similar variability. Reasons for this mismatch remain unknown, but suggest that the model underestimates the heat extremes during this period. The ADT anomaly (shown by the orange curve) correlates ($r = 0.7$) with heat content, since heat content changes affects the steric component, suggesting that heat content changes can be inferred from remotely sensed observations on interannual to decadal time scales. This provides an opportunity to establish a near real-time measure for inferring heat content trends in the Tasman Sea and therefore a measure for the likelihood of MHWs.

To explain the origin of the variability of the TN heat transport, we computed the correlation of the TN heat transport

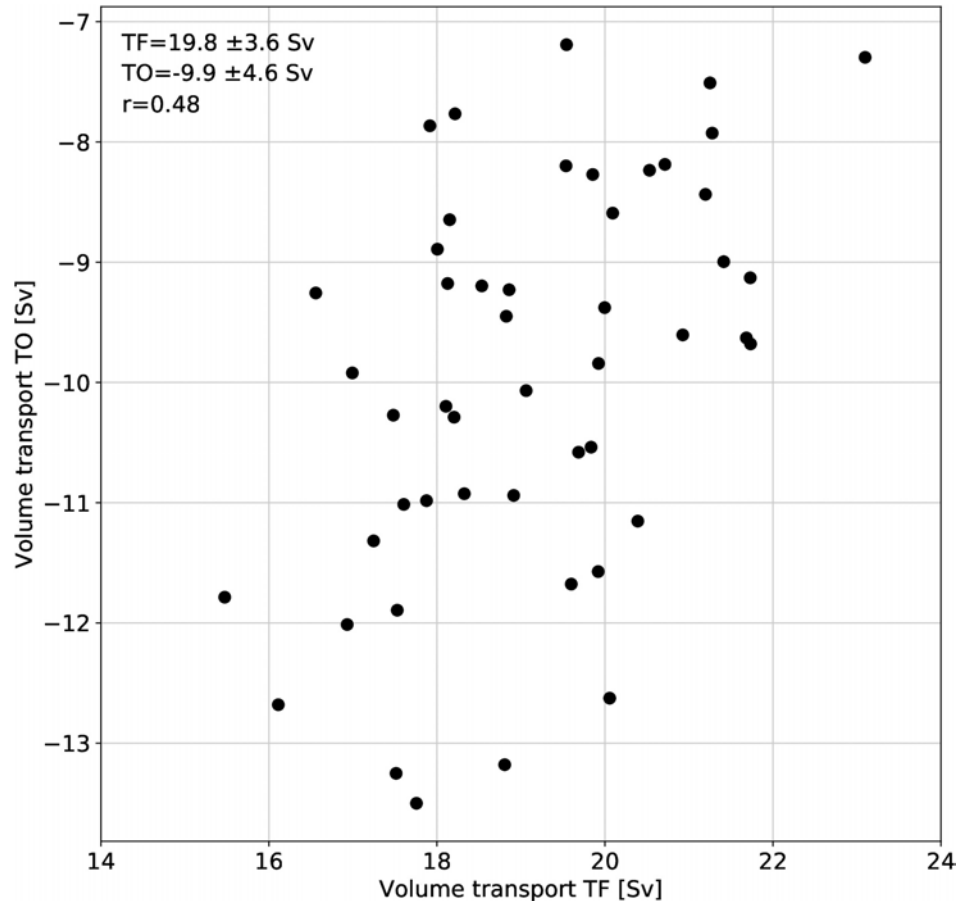


FIGURE 6 | Annual mean modeled volume transports for TF and TO, showing the gating between both transport pathways supplied by the EAC.

with the wind stress curl from JRA-55-DO (**Figure 8**). The correlation coefficient shows a zonal band of positive correlations north of the TN boundary and negative correlations south of it. The coefficients are in the order of $r = \pm 0.25$ over most of the region. In this regard, the positive heat transport anomalies coinciding with positive wind stress curl anomalies between 30°S and 20°S suggest an acceleration of the western boundary current (i.e., the EAC), according to the Sverdrup balance (Sverdrup, 1947), the Island Rule (Godfrey, 1989) and recent studies built on them (Cai, 2006; Hill et al., 2008; Bull et al., 2017, 2018). Without additional wind stress curl changes over the Tasman Sea, both the TF and EAC-Extension heat and volume transports will increase to balance the EAC. In a steady state, the heat content over the Tasman Sea would remain unchanged. However, the negative correlation over most of the Tasman Sea (**Figure 8**) reflects a decrease in wind stress curl and a weaker transport of the EAC-Extension and TO. In this case the TF partially compensates the transport anomaly of the EAC-Extension, but the imbalance may explain the Tasman heat content rise which is in line with previous studies focusing on wind-driven changes on the EAC, EAC Extension and TF (Hill et al., 2010; Oliver and Holbrook, 2014; Sloyan and O’Kane, 2015; Bull et al., 2017). We note that this response is only caused by non-uniform

wind stress curl anomalies between 20°S and 30°S and over the Tasman Sea, in particular the negative anomalies over the Tasman Sea. Recent studies show a positive wind stress curl trend over the entire region, due to intensified westerlies, which leads to an enhanced EAC-Extension transport (Matear et al., 2013; Oliver and Holbrook, 2014; Qu et al., 2018). The drivers for TF variability or outflow across TN and how it balances the heat transport of the EAC, are less well established, with more detailed work required to investigate this sensitive and important balance.

Furthermore, we investigate the vertical coherence of the heat content anomaly, its temporal change and heat transport anomaly across the TN section (**Figure 9**). A time-averaged profile from 1970 to 2017 has been used to compute the anomalies. The temporal evolution of the depth-dependent heat content suggests a separation into three layers: above 250m, between 250 and 750 m and below 750 m. The top 250 m shows a positive–negative alternating signal with downward propagating anomalies through this depth range. In this layer, the 1990s are characterized by a distinct cool phase, followed by a warm phase between 1997 and 2002 and from 2012 until present. The depth of 250 m roughly corresponds to the depth where the net heat transport of TN is southward in the mean vertical profile (see **Figure 5b**). The layer between 250 and 750 m is characterized

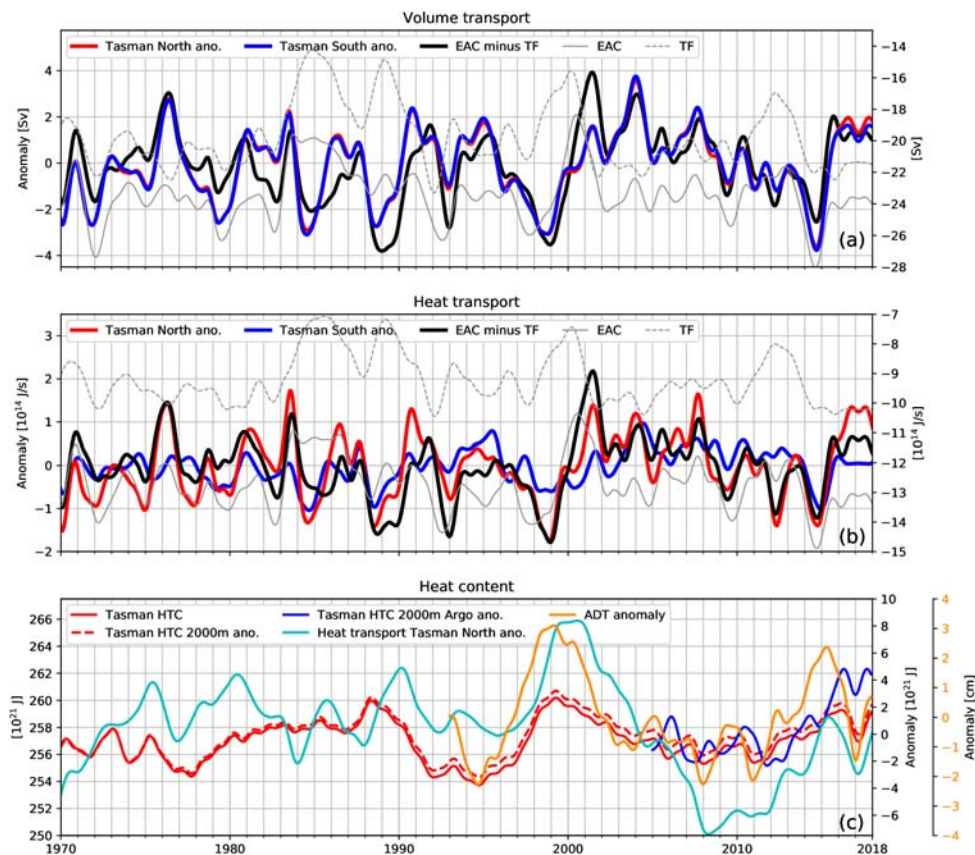


FIGURE 7 | Interannual filtered time series: **(a)** volume transport, **(b)** heat transport and **(c)** heat content (HTC). **(a)** Volume transport anomaly for the Tasman North (red) and Tasman South (blue) section and difference between EAC and Tasman Front (black). Transports of Tasman North and South reflect transports across the entire section. For transports of EAC and TF the cyan boxes in **Figure 4** have been used as regional limits. For anomalies the time mean values from 1970 to 2017 have been used as reference. Net transports for EAC and TF are represented in thin gray lines and use the right hand y-scale. Note that, the sign for TF transport in **(a,b)** has been inverted. **(b)** Heat transport anomalies and net heat transports, as in **(a)**. **(c)** Tasman Sea heat content: full-depth (solid red line, left hand y-scale) and upper 2000 m anomalies (red dashed line, inner right hand y-scale). Heat content anomaly derived from the integrated Northern Tasman section heat transport (light blue line, linear de-trended, inner right hand y-scale). Argo-derived heat content anomaly (dark blue line, inner right hand y-scale) and absolute dynamic topography (ADT, orange line, linear de-trended, in cm and outer right hand y-scale).

by warming until 2000 which then leveled off. The layer below 750m shows the opposite behavior, with a warm phase until 1990, cooling until 2010 and little change afterward.

Computing the temporal change of the heat content anomaly, we obtain strongly barotropic anomalies below 200m, despite the three layers (**Figure 9b**). Most of these anomalies can be connected to heat transport anomalies along TN (**Figure 9c**). Note that the colorscale in **Figure 9c** has been inverted, therefore positive anomalies (blue) indicate that heat is transported out of the Tasman Box across the TN section. The consequence is that the heat content change in **Figure 9b** is negative (blue) and vice versa for negative anomalies. This underpins again the dominant role of the heat transport across TN in the Tasman heat content variability.

Heat Content and MHW

In this section we investigate the relationships between the Tasman Box heat content and MHWs. There is a direct connection via SSTs, since SSTs are used to characterize MHWs

and are also typically correlated with upper ocean heat content. However, predicting SSTs and thus MHWs months ahead is challenging due to large atmospheric variability resulting in low predictive skill (Palmer and Anderson, 1994; Doblas-Reyes et al., 2013; de Burgh-Day et al., 2018). Integrated quantities such as heat content show lower variability and an enhanced predictive skill. This is demonstrated in the close agreement between Tasman Sea heat content and the area identified as MHW (**Figure 10a**). Periods with either a positive heat content anomaly or a sudden increase in heat content correspond with periods where larger parts of the Tasman Sea are under MHW conditions.

The period between 1970 and 1974 shows two sudden increases in heat content, with an increased MHW area during that period, with a short drop around 1972. From 1975 to 1989 the ocean heat content keeps slowly increasing. Despite the steady increase of the heat content, with values exceeding the early 1970s, the MHW area is smaller. However, periods where the ocean heat content increases more strongly than the long-term trend (i.e., 1981, 1985, 1988–1989) have associated

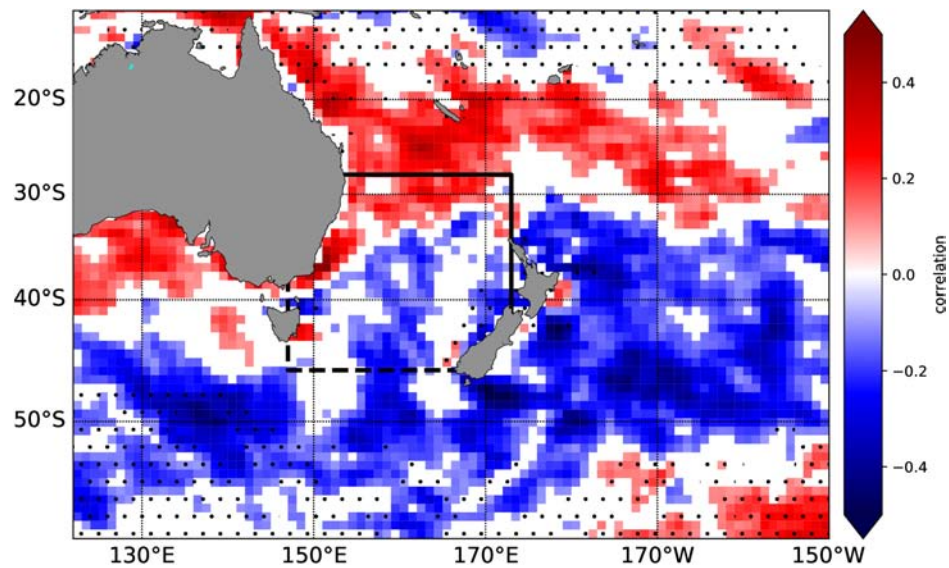


FIGURE 8 | Correlation between Tasman North heat transport and wind stress curl over the period 1970 to 2017 (interannually filtered). Only significant correlations above the 95% confidence level are shown. The dots indicate regions with a negative mean wind stress curl. The Tasman Box is shown by the black lines. The Tasman North section is marked by the solid black line and Tasman South by the dashed black line.

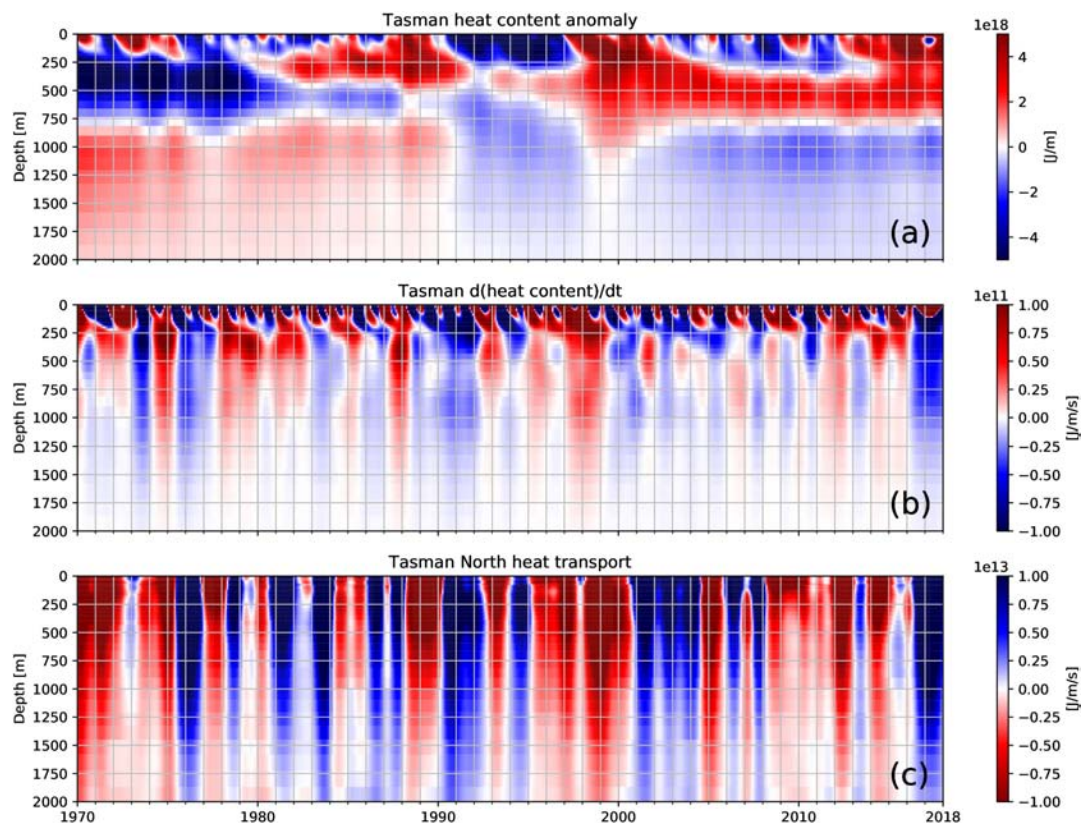


FIGURE 9 | Vertical profiles of (a) Tasman Box heat content anomaly, (b) Tasman Box heat content change and (c) TN heat transport anomalies, interannually filtered. The time averaged profile from 1970 to 2017 has been used as the reference for computing anomalies. Please note the inverted color scale in (c). All anomalies have been normalized using the vertical model layer thickness.

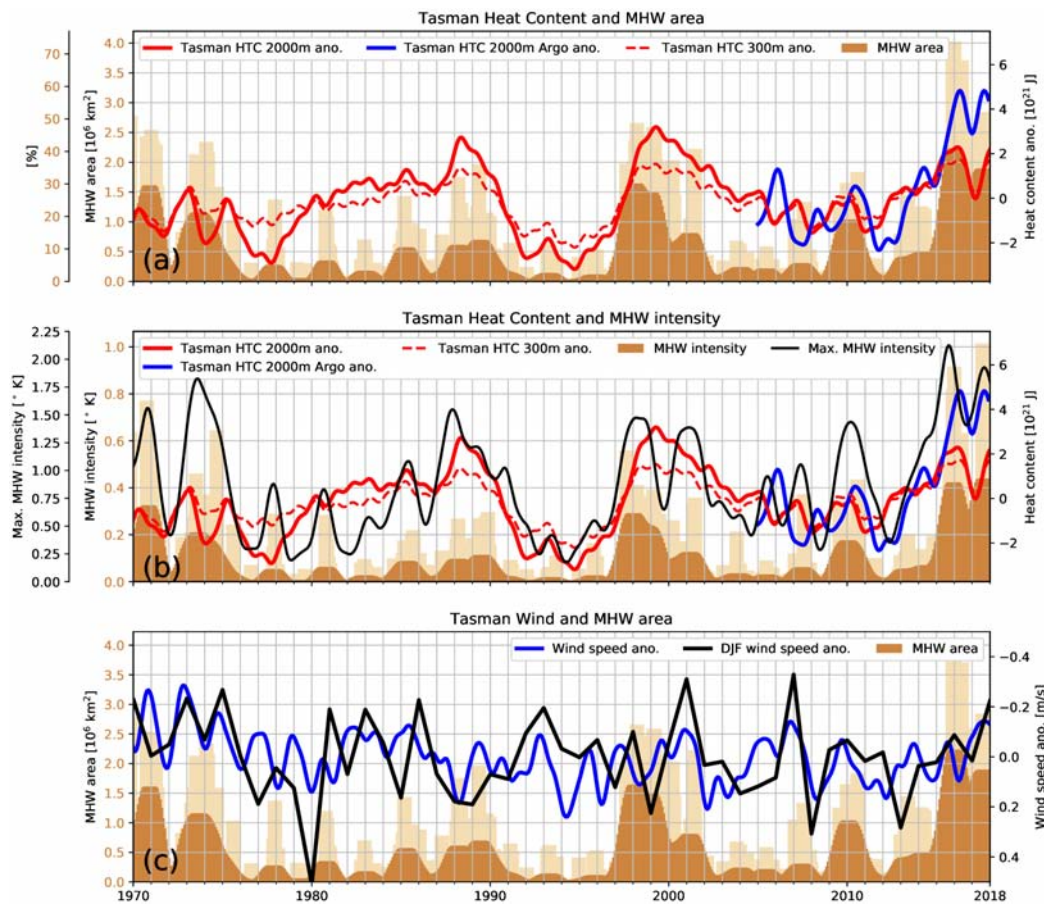


FIGURE 10 | Link between depth-integrated Tasman Box heat content and occurrence of MHWs in the Tasman Sea. **(a)** Upper 2000 m (300 m) heat content in red (red dashed) and area (in 10^6 km^2) identified as marine heatwave as light brown bars (monthly means) and fraction (%) of the Tasman Box (inner and outer left hand y scales). Dark brown area is MHW area interannually filtered. The Argo-derived heat content anomaly is shown in dark blue. **(b)** As for **(a)**, but area-averaged MHW intensity represented by light brown bars (monthly means) and interannually filtered dark brown. Black line shows the maximum MHW intensity over the Tasman Box. **(c)** Area averaged wind speed and December-January-February (DJF) mean anomalies (in blue and black, respectively) and total area identified as in marine heatwave conditions in (light) brown as in **(a)**. All time series have been interannually filtered, except the light brown monthly MHW data and DJF wind anomaly in **(c)**.

MHW activity. From 1989, the heat content decreases rapidly until 1995, with very few signs of MHWs seen during that period. After 1995, the heat content increases sharply, reaching a maximum around the year 1999, with correspondingly larger areas under MHW conditions. The heat content decreases afterward until 2009 and the Tasman Sea experiences less MHW activity, except for 2010 when the heat content increases rapidly. The upward trend of the heat content since 2011 is then reflected in large parts of the Tasman Sea being under MHW conditions. Although the ocean heat content increase after 2015 has leveled off, the MHW activity is still high. The correlation between modeled 2000m depth-integrated heat content and MHW area reaches $r = 0.35$, when the heat content is leading by 4 months. For the top 300m modeled heat content and MHWs, the correlation increases as expected to $r = 0.46$ (ocean heat content leading by 4 months) since the SST contribution becomes more important for a shallower (300m) heat content. The correlation for the Argo-derived heat content and the occurrence of MHWs is $r = 0.43$ with heat content leading by

5 months. The difference in correlation coefficient of model and Argo-derived heat content with MHWs is influenced by the different record length. Although heat content alone does not explain every individual marine heatwave event (e.g., the MHW of the Summer 2017/18 appears (Salinger et al., 2019) to have different characteristics compared to the previous one in 2015/2016), these results suggest that heat content has predictive skill down to even annual timescales, and certainly captures long-term (multi-year) modulations.

Not only can the area of MHWs be inferred from heat content, but also the MHW intensity, as shown in Figure 10b. The link with area-averaged intensity appears to be stronger than that with the MHW area, and periods of larger heat content (e.g., early 2000, 2008–2012, and since 2014) can be connected to MHW intensity. The maximum of the MHW intensity over the Tasman Sea correlates with the oceanic heat content ($r = 0.7$) and for Argo-derived heat content over the top 2000m ($r = 0.66$). Using area-averaged wind speeds or austral summer anomalies (DJF) over the Tasman Sea (Figure 10c) to infer the vertical mixing

or surface heating, which has been found to drive some MHWs (e.g., Summer 2017/18, Salinger et al., 2019), does not provide a robust measure to infer MHWs. No significant relationship has been found between wind speeds and MHWs on longer time scales. Surface winds contribute to the development of MHWs directly, since they affect air–sea fluxes and vertical mixing. Only a few MHW events (i.e., 2001, 2007 and 2018) appear to be dominated by low winds.

The coupling between ocean heat content and MHW area becomes more apparent when just considering annual maximum values for the Tasman Sea (**Figure 11**). Note that annual values refer to the period from June through May, to center diagnostics on the Southern Hemisphere summer, i.e., 2000 refers to the period from June 1999 to May 2000). The correlation coefficient between the annual maximum value for heat content and MHW area is $r = 0.43$ (**Figure 11a**). According to this diagnostic, the 2015/16 MHW (labeled 2016) covered the largest area and was the most intense MHW, while the 2017/18 (labeled 2018) was less intense. There was also a period between June 2016 and May 2017 (labeled 2017) where large parts of the Tasman Sea were under MHW condition but with lower intensity and impact.

A possible explanation for why this 2017 MHW was not as severe is indicated by the wind diagnostics, which show that 2017 had stronger winds than 2016 and 2018 (**Figure 11b**). Strong winds would have caused more vertical mixing of heat into the water column. Comparing **Figures 11a,b** shows the complexity of individual drivers for MHWs. Many years with negative ocean heat content anomaly can still show intense and large MHWs (e.g., 1975, 1998, 2018), which can be attributed to lower winds and reduced vertical mixing of heat into the water column. In these cases, the surface ocean heats up more than usual and the background state, i.e., ocean heat content, is less important for the development of MHW conditions. Conversely, in years with positive heat content anomalies, the background state becomes more important. There are a few exceptions from this generalization on both sides of the regression line (e.g., 2000), highlighting that more factors also need to be taken into account (e.g., cloudiness). According to the described mechanism, the year 2000 should also have been a MHW year, due to low winds and large positive heat content anomaly. Here, it is likely the timing of these maxima also needs to be taken into account, adding another layer of complexity. MHWs occur all year round, but surface heating, which is essential for the development of MHWs, is only strong during austral spring and summer months. If favorable conditions occur during other periods of the year, the weaker surface heating will result in milder MHW conditions compared to what would have occurred during austral spring and summer.

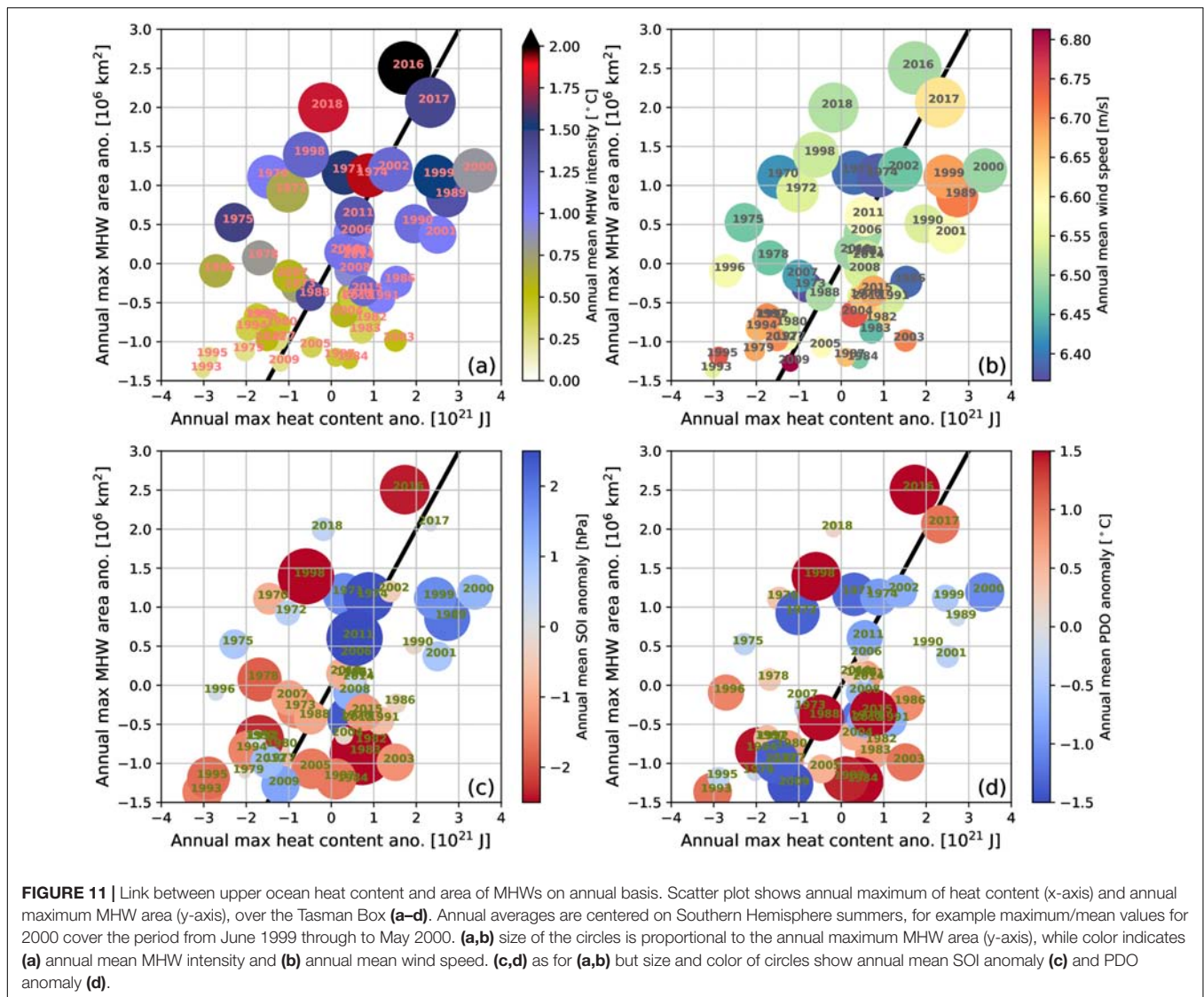
It is worth noting that modeled ocean heat content over the last few years is lower than it has been in the past (i.e., 1989, 1999–2001), which would imply that MHWs have not been as intense as they could have been. However, with SSTs and heat content showing an upward trend over the last decades in the Tasman Sea (Roemmich et al., 2015; Sutton and Bowen, 2019), we could soon reach those higher heat content values again, resulting in more intense MHWs.

Time series presented in **Figures 7, 10** show large interannual to decadal variability. It is therefore tempting to try to link them with large-scale weather patterns such as El Niño Southern Oscillation (ENSO) and PDO (Pacific Decadal Oscillation), as done in **Figures 11c,d**. Previous studies suggested only a very weak ENSO signal is present in the EAC volume transport (Ridgway, 2007) and consequently in the heat transport. Note that we use the SOI as a measure for the ENSO state. A positive SOI index reflects a larger pressure difference between Tahiti and Darwin; stronger trade winds; and La Niña like conditions, where positive SSTs anomalies are located in the west Pacific. A negative SOI describes El Niño conditions, lower trade winds, and positive SSTs anomalies in the east Pacific. Results for the heat content and MHW in combination with ENSO do not show a conclusive pattern (**Figure 11c**). If the positive SST anomalies during La Niña conditions reached into the Tasman Sea or caused an enhanced heat transport of the EAC, the heat content should be elevated, and the converse would be seen for El Niño conditions (**Figure 11c**). The years 1989 and 1999–2001 are years with strong La Niña conditions, positive ocean heat content anomalies and MHWs. However, there are several years which show positive heat content anomalies and El Niño conditions (e.g., 1982, 1988). Likewise, little consistency can be seen for negative heat content anomalies, which could occur during El Niño conditions. Therefore, links between ENSO, Tasman Sea heat content and MHWs are not conclusive. The same applies if we perform the same diagnostic for the PDO, another leading index describing long-term variability in the Pacific (**Figure 11d**). The PDO SST pattern and impact are ENSO-like but on longer time scales. Positive PDOs describe El Niño-like and negative La Niña-like conditions. Similarly to the SOI results, little consistency can be found between the PDO state and MHWs and no preferred heat content state can be identified for either positive or negative PDOs.

DISCUSSION AND CONCLUSION

In this manuscript we investigated the connection between ocean heat content, heat transport and the area and intensity of MHWs in the Tasman Sea, on interannual to decadal timescales, by using a coarse-resolution forced ocean hindcast corroborated by optimally interpolated data from Argo, satellite measurements and *in situ* HRXBT temperature observations. The model results show that meridional heat transports from the subtropics dominate heat content fluctuations in the Tasman Sea. The Tasman Sea is a region of oceanic heat convergence, meaning that average surface heat fluxes are directed toward the atmosphere to balance the oceanic heat convergence. On average around 67% of the ocean heat transported from the subtropics into the Tasman Sea fuels surface heat fluxes.

The heat transport variability from the subtropics is impacted by regional wind stress curl anomalies in this area, which influence the volume and thus the heat transport of the EAC, following Sverdrups' and Godfrey's Island Rule theories. We show that heat transport of TF needs to be considered for the heat content budget of the Tasman Sea. The TF's contribution to



balance the heat transport of the EAC, which is in the order of 85%, is overestimated in our model, due to the overly strong mean volume transport of the TF. Nevertheless, even with half of its modeled contribution it provides a significant portion to the heat budget across TN. A smaller portion does not necessarily affect its temporal variability and interplay with EAC heat transport anomalies, which has been found to control the heat content changes in the Tasman Sea. Volume and heat transport of the TF are usually in phase with the EAC on interannual time scales, in agreement with observations (Hill et al., 2008; Sloyan and O’Kane, 2015). Despite the coarse horizontal resolution of the model, which is not eddy-resolving, volume and heat transports for EAC and TO are within the range of previous studies. We do note that our modeled TF transport is about twice that of previous studies (e.g., Oliver and Holbrook (2014)), while the overall transport which leaves the Tasman Box across the TN sections is in agreement. That reflects that our model shows a different split between TF transports and transports east of the EAC along the

AB section of TN. Here the choice of the location of corner point B could play a role. Our choice was motivated by the modeled barotropic streamfunction (Figure 1), which suggested little flow around corner point B. While the position is in broad agreement with the other studies, a southward shift of corner point B would have resulted in a transport shift from TF toward the transports east of the EAC. Despite the discrepancy in the mean transports of TF, the long-term variability is in agreement (i.e., co-variability between EAC and TO). Furthermore, the model is able to robustly simulate observed variability in the Tasman Sea compared to HRXBT and satellite altimetry observations. For more detailed studies and finer regional focus, models which are capable of resolving mesoscales should be considered, but this is beyond the scope of this study.

We could not find a robust link between Tasman Sea heat content variability and the large-scale climate patterns of ENSO and the PDO on interannual to decadal time scales. Potentially their influence is not instantaneous through direct local wind

changes but affects the heat content through Rossby and Kelvin wave propagation (Bowen et al., 2017). More detailed work is required here.

Our model results and data from Argo show a robust link between Tasman Sea heat content (upper 2000 m) and MHWs, in terms of the area under MHW conditions and MHW intensities on interannual to decadal time scales. The heat content acts as a preconditioner for the development of MHWs. Periods with enhanced heat content or when ocean heat content increases rapidly increase the likelihood of MHWs developing. Periods where the heat content anomalies are negative show less MHW activity. Ocean heat content alone cannot explain every MHW in the Tasman Sea, since strong surface heating can also trigger MHWs, as seen in the MHW in Austral Summer 2017/18. Here, exceptionally low winds over the Tasman Sea led to a reduction in vertical mixing and caused the SSTs to exceed MHW thresholds, while the heat content was almost unchanged relative to previous years (Salinger et al., 2019). Nevertheless, ocean heat content is a measure for the background state of the ocean and if the ocean is already warm then less surface heating is required to develop MHW conditions.

This demonstrates that there are at least two different mechanisms affecting the occurrence of MHWs in the Tasman Sea: the oceanic background state (e.g., heat content), which is persistent and enables better predictability, and the atmospheric forcing (e.g., winds, surface heating), which usually acts on shorter timescales and is thus harder to predict. In the former case, the predictability of heat content changes is further enhanced since the driving mechanisms of EAC dynamics are well understood. Predictability could be further enhanced if a robust understanding of the TF dynamics/outflow from the Tasman Box across TN and its variability were developed. This would reduce the uncertainties in the EAC–TF heat transport difference, or in other words the net heat transport across TN, which sets the heat content of the Tasman Sea in our model.

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AUTHOR CONTRIBUTIONS

EB performed this study. DF and PS helped with the interpretation of the results, supported the writing process, and delivered time series for this study.

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Air-Sea Heat Flux Variability in the Southeast Indian Ocean and Its Relation With Ningaloo Niño

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Previous studies suggest that both air-sea heat flux anomalies and heat advection caused by an anomalous Leeuwin Current play an important role in modulating the sea surface temperature (SST) variability associated with the Ningaloo Niño. However, the estimates of surface heat fluxes vary substantially with the datasets, and the uncertainties largely depend on the time scale and locations. This study investigates air-sea flux variability associated with the Ningaloo Niño using multiple datasets of surface fluxes. The climatological net surface heat flux off the west coast of Australia from six major air-sea flux products shows large uncertainties, which exceeds 80 W m^{-2} , especially in the austral summer when the Ningaloo Niño develops. These uncertainties stem mainly from those in shortwave radiation and latent heat flux. The use of different bulk flux algorithms and uncertainties of bulk atmospheric variables (wind speed and air specific humidity) are mostly responsible for the difference in latent heat flux climatology between the datasets. The composite evolution of air-sea heat fluxes over the life cycle of Ningaloo Niño indicates that the anomalous latent heat flux is dominant for the net surface heat flux variations, and that the uncertainties in latent heat flux anomaly largely depend on the phase of the Ningaloo Niño. During the recovery period of Ningaloo Niño, large negative latent heat flux anomalies (cooling the ocean) are evident in all datasets and thus significantly contribute to the SST cooling. Because the recovery of winds occurs earlier than SST, high SST and strong winds favor large evaporative cooling during the recovery phase. In contrast, the role of latent heat flux during the developing phase is not clear, because the sign of the anomalies depends on the datasets in this period. The use of high-resolution SST data, which can adequately represent SST variations produced by the anomalous Leeuwin Current, could largely reduce the errors in latent heat flux anomalies during the onset and peak phases.

Keywords: air-sea flux, southeast Indian Ocean, Ningaloo Niño, Leeuwin Current, marine heat wave, air-sea interaction

INTRODUCTION

The southeast Indian Ocean (IO) is a region where extreme climate variability and a unique ocean circulation are observed. During 2010–2011, an extreme marine heat wave associated with ocean warming occurred off the west coast of Australia. This extreme warming event is termed as “Ningaloo Niño” (Feng et al., 2013). The 2010–2011 Ningaloo Niño event was associated with

anomalous ocean circulations in the southeast IO. For example, there was an unseasonable surge of the Leeuwin Current, which flows southward against prevailing southerly winds along the west coast of Australia, bringing warm waters from the tropics. These extreme oceanic conditions have a substantial impact on marine ecosystem and regional climate variability (Pearce and Feng, 2013; Wernberg et al., 2013; Caputi et al., 2014; Kataoka et al., 2014; Tozuka et al., 2014).

In the southeast IO near the west coast of Australia, relatively large annual mean surface heat fluxes (cooling the ocean) with the strong seasonal cycle are observed (Feng et al., 2003, 2008). For the annual mean, a large amount of heat loss of the ocean occurs at the air-sea interface in a broad area off the west coast of Australia. The majority of the heat loss is caused by a large evaporative cooling due to warm SSTs in the region of the Leeuwin Current. The annual cycle of net surface heat flux is dominated by shortwave radiation and latent heat flux. During the austral winter, shortwave radiation is weak, but the latent heat flux (cooling) is large due to a stronger Leeuwin Current (and thus warm SSTs) and low near-surface specific humidity associated with the cold air temperature. During the austral summer, shortwave radiation is strong, and the latent heat flux is small due to a weaker Leeuwin Current (Feng et al., 2003, 2008) and higher near-surface specific humidity associated with the warmer air temperature.

In addition to the strong seasonal cycle of air-sea heat fluxes, significant interannual variations of surface heat fluxes are found in this region including those associated with the Ningaloo Niño. Some of the previous studies suggest that the SST warming during the Ningaloo Niño is caused by the heat advection by the strengthening of the Leeuwin Current especially for the 2010–2011 event, whereas air-sea heat fluxes also contribute to the warming (Feng et al., 2013; Zhang et al., 2018). However, the relative importance of heat advection by the Leeuwin Current and surface heat fluxes on the development of the Ningaloo Niño varies substantially between different studies. For example, Benthuisen et al. (2014) indicated that reduced latent and sensible heat fluxes around the peak phase account for 1/3 of the warming during the 2010/2011 event in addition to the heat advection produced by the strengthening of Leeuwin Current. On the other hand, a composite analysis of multiple Ningaloo Niño events indicated that the initial offshore warming is primarily caused by the anomalous latent heat flux (Marshall et al., 2015). Kataoka et al. (2014) classified the Ningaloo Niño to locally and non-locally amplified modes based on the local wind anomalies and suggested that the reduction of latent heat flux enhances offshore warming during the development and coastal warming during the peak in both modes. Recently, Kataoka et al. (2017) calculated the mixed layer temperature balance associated with Ningaloo Niño events and found that shortwave radiation contributes to the coastal warming in both locally and non-locally amplified modes due to the warming produced by the climatological surface heat flux enhanced by the shallow mixed-layer depth (MLD) anomaly during the onset. Moreover, Xu et al. (2018) compared the difference in SST warming patterns between the 2012/2013 event with the 2010/2011 event and found that the difference in the relative importance of surface heat fluxes

and heat advection between the two events is mostly responsible for the different spatial distribution of the warming.

As described above, a variety of different conclusions on the role of surface heat fluxes in the warming during the Ningaloo Niño have been obtained in previous studies. These differences could partly be due to the different source of surface flux datasets, which include various satellite observations, reanalysis products, and model simulations. The systematic analysis of air-sea heat flux variability associated with the Ningaloo Niño using multiple datasets is thus necessary to reconcile previous studies and determine the uncertainties on the role of air-sea fluxes.

While most of the previous studies focus on processes during the onset and development (warming period) of the Ningaloo Niño, processes that control the cooling during the recovery phase have received little attention. A recent study by Kataoka et al. (2017) discussed processes during both the development and demise of the Ningaloo Niño and suggested that the mixed layer temperature is influenced by not only heat flux anomalies but also MLD anomalies which change the heat capacity. They concluded that the net effect of latent heat flux is not as important as earlier studies suggested during the recovery phase because of the anomalously deep mixed layers and thus a large heat capacity. In addition, the significant role of sensible heat flux for the locally-amplified mode is suggested. However, these conclusions are based on the analysis of a single numerical model simulation and it is possible that different results could be obtained using different datasets. Accordingly, it is necessary to examine the processes during the recovery phase using multiple datasets, and such analyses will provide better insights into the role of air-sea fluxes during the recovery phase.

In addition to the large influence of surface heat fluxes on SST and upper ocean during the Ningaloo Niño, air-sea heat fluxes influence the atmospheric conditions and the large-scale atmospheric circulations, and in turn they can feedback on SSTs. Various feedback mechanisms between the atmosphere and ocean associated with the Ningaloo Niño have been suggested in recent years. For example, Tozuka and Oettli (2018) showed that during the Ningaloo Niño, positive SST anomalies increase the formation of cloud and thus decrease the shortwave radiation, which will weaken the initial warming. Zhang and Han (2018) found that SST anomalies in the southeast IO associated with the Ningaloo Niño lead to the enhancement of western Pacific trade winds and the cooling in the central Pacific. The enhanced trade winds could strengthen the ITF and the cooling anomalies in the central Pacific could induce cyclonic wind anomalies in the southeast IO, both of which will amplify the initial warming of Ningaloo Niño. As changes in air-sea fluxes in the southeast IO are essential components of these feedback mechanisms, assessing the uncertainties of surface fluxes using multiple datasets is necessary for further exploring these air-sea interaction processes.

The uncertainties of air-sea heat fluxes arise from the errors in bulk atmospheric variables and SST, which are derived from reanalysis products and satellite observations, and use of different bulk flux algorithms (Brunke et al., 2002; Wu et al., 2006; Kubota et al., 2008; Valdivieso et al., 2017). In the area off the west coast of Australia, the uncertainties and thus the difference between the

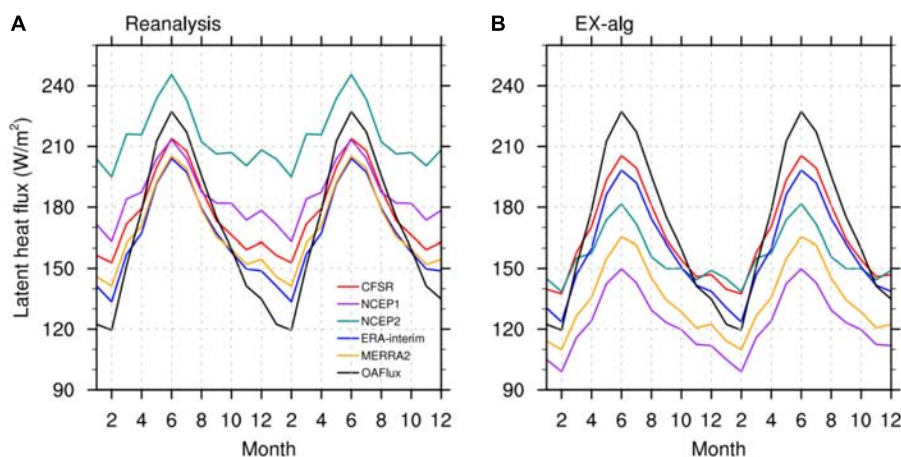


FIGURE 1 | Climatological seasonal cycle of latent heat flux calculated for the area around the west coast of Australia (110°E–116°E, 22°S–32°S) from **(A)** reanalysis products, **(B)** sensitivity calculations using COARE3.5 algorithm (EX-alg). Positive values indicate the flux from the ocean to the atmosphere.

TABLE 1 | Mean absolute deviation of annual and seasonal mean latent heat flux calculated from reanalysis, EX-alg, EX-wspd, EX-sst, and EX-qa.

	Annual mean	DJF	MAM	JJA	SON
reanalysis	13.3	19.4	13.0	10.2	14.0
EX-alg	15.0	11.7	16.5	21.5	13.4
EX-wspd	7.7	6.0	8.6	10.1	6.7
EX-sst	1.5	1.3	1.6	2.2	1.1
EX-qa	9.3	9.0	9.9	11.8	9.4

Units are in $W\ m^{-2}$.

datasets could be very large because of the large variability of SST and associated atmospheric variables caused by Leeuwin Current variations. Hence thorough description of air-sea fluxes in this region using multiple datasets and their comparisons are crucial for the investigation of climate variability in this region including the Ningaloo Niño.

The purpose of this study is to investigate the air-sea heat fluxes associated with the development and decay of Ningaloo Niño and to identify the major sources of uncertainties in the interannual variability using multiple datasets. In particular, the air-sea heat flux variations during the decay phase of the Ningaloo Niño is emphasized. The rest of this paper is organized as follows. Section “Materials and Methods” describes the data and method used in this study. In Section “Results”, climatological air-sea fluxes from different datasets are compared, and the effect of latent heat flux variability on the Ningaloo Niño is studied based on the composite analysis. A discussion and summary are presented in Sections “Discussion and Summary.”

DATA AND METHODS

Reanalysis

Daily short and longwave radiation, and latent and sensible heat fluxes from five major reanalysis products are used in this

study. These are the National Center for Environmental Prediction-National Centers for Atmospheric Research (NCEP/NCAR) reanalysis-1 (NCEP1; Kalnay et al., 1996), the NCEP-Department of Energy (NCEP/DOE) reanalysis (NCEP2; Kanamitsu et al., 2002), the European Centre for Medium-Range Weather Forecasts (ECMWF) Interim reanalysis (ERA-Interim; Dee et al., 2011), NASA’s Modern-Era Retrospective analysis for Research and Applications, Version 2 reanalysis (MERRA-2; Gelaro et al., 2017), and NCEP Climate Forecast System Reanalysis (CFSR; Saha et al., 2010, 2014). NCEP1 and NCEP2 are available on the T62 Gaussian grid with a spatial resolution of about $1.875^\circ \times 1.875^\circ$. CFSR reanalysis is based on a coupled ocean-atmosphere-land data assimilation system that consists of an atmospheric component at a resolution of T382 (38 km) and an ocean component at a resolution of 0.5° beyond the tropics. ERA-Interim data is on $0.75^\circ \times 0.75^\circ$ grid, and MERRA2 uses an approximate resolution of $0.5^\circ \times 0.625^\circ$. The data for the period 1985–2016 is analyzed during which all these datasets are available. To investigate the effect of MLD variation on SSTs (Kataoka et al., 2017), MLD obtained from $1/12^\circ$ Hybrid Coordinate Ocean Model (HYCOM) reanalysis (Metzger et al., 2014) for 1994–2015 is used.

OAFflux

We also used daily gridded ($1^\circ \times 1^\circ$) bulk flux state variables (i.e., wind speed, air and sea surface temperature, and humidity) from WHOI Objectively Analyzed Ocean-Atmosphere Flux (OAFflux) product (Yu et al., 2008) to calculate the latent heat flux using the state-of-the-art COARE3.5 bulk algorithm (Fairall et al., 2003). The state variables provided by OAFflux blended observational and reanalysis data from various sources based on an objective analysis to obtain an optimal estimate of the atmospheric and oceanic conditions. The daily state variables for the period 1985–2016 are used in the analysis. The latent heat flux estimates calculated here are well correlated with those from the gridded flux provided by OAFflux ($r = 0.997$) but

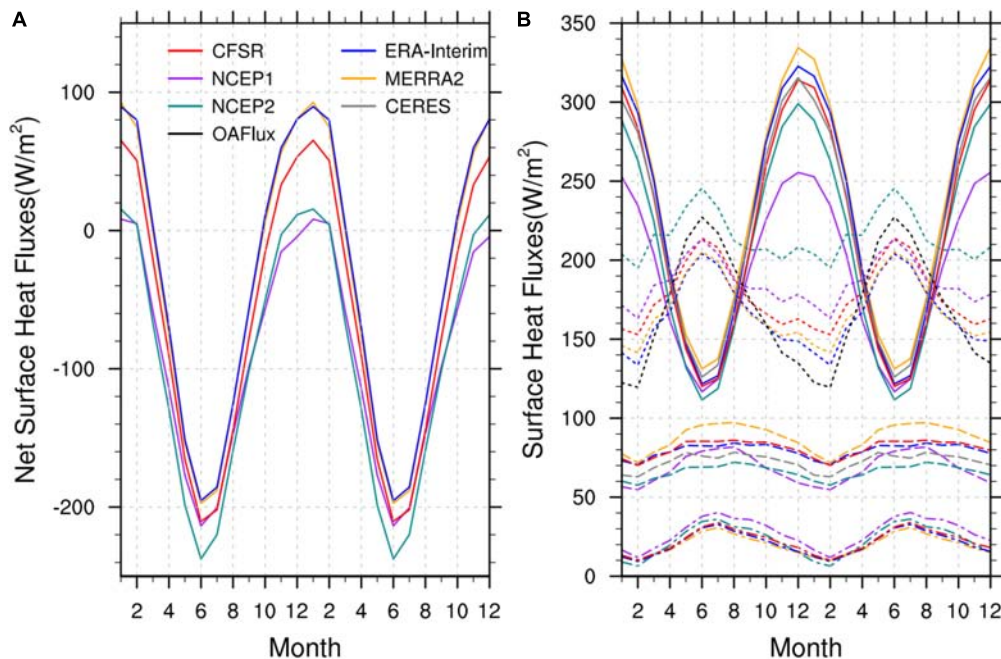


FIGURE 2 | (A) Climatological seasonal cycle of the net surface heat flux calculated for the area around the west coast of Australia (110°E – 116°E , 22°S – 32°S). **(B)** Same as in **(A)**, but for net shortwave radiation (solid line), net longwave radiation (dashed line), latent heat flux (dotted line) and sensible heat flux (dot-dashed line). Colors indicate different datasets. Positive values indicate the flux into the ocean (atmosphere) for net surface heat flux and shortwave radiation (longwave radiation, latent and sensible heat flux).

have a Root Mean Square error (RMSE) of 7.8 W m^{-2} . This difference is primarily caused by the lack of SST correction associated with the cool skin and warm layer in our calculation, and the difference due to the use of different versions of bulk formula (COARE3.5 and COARE3.0) is very small (RMSE: 0.6 W m^{-2}). Note that the RMSE between latent heat flux estimates using COARE3.5 and those provided by OAFlux is much smaller (2.1 W m^{-2}) during DJF when Ningaloo Niño develops, and thus the effect of the cool skin and warm layer is very small during this season.

Satellite and Buoy Observations

Monthly satellite-derived radiation fluxes from Clouds and Earth's Radiant Energy Systems (CERES; Kato et al., 2018) for the period 2000–2016 are used. Surface fluxes and bulk flux state variables from the Research Moored Array for African-Asian-Australian Monsoon Analysis and Prediction (RAMA) at 25°S , 100°E (McPhaden et al., 2009) from September 2012 to 2014 are also used for the comparison with gridded flux data products. The surface air-sea fluxes were estimated using COARE3.0b.

Besides flux datasets, we also use daily high resolution SST products obtained from National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature based on Advanced Very High Resolution Radiometer (AVHRR) observations (OISST; Reynolds et al., 2007; Banzon et al., 2016; $0.25^{\circ} \times 0.25^{\circ}$; 1985–2016) and Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature

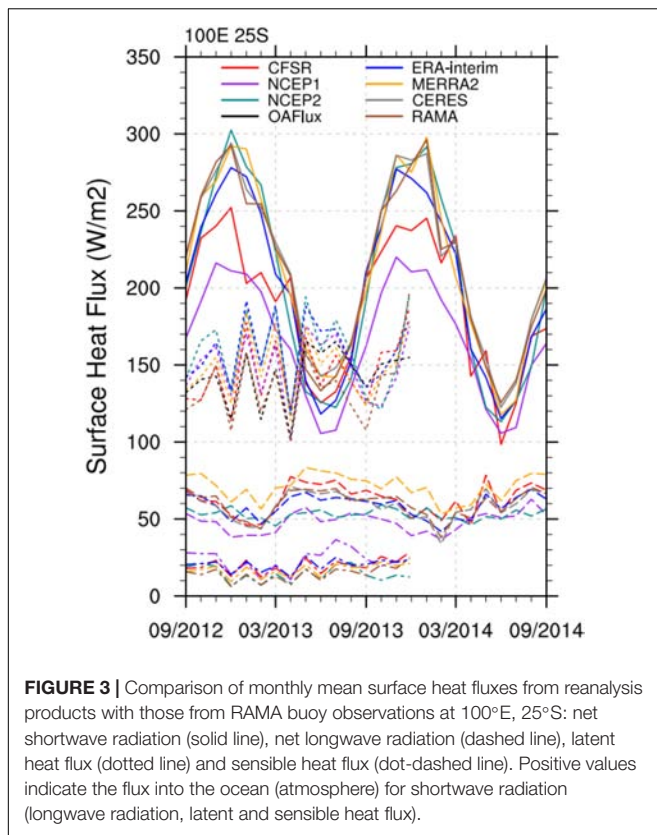
(SST) analysis produced at Jet Propulsion Laboratory (Chin et al., 2017; $0.01^{\circ} \times 0.01^{\circ}$; 2002–2016).

RESULTS

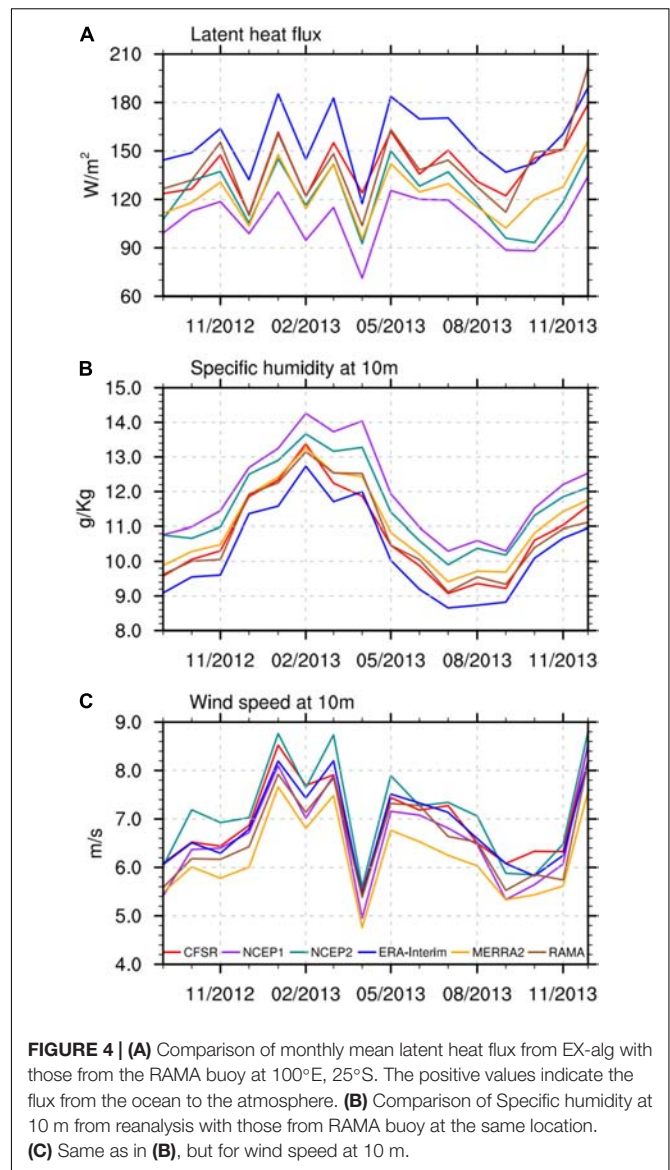
Climatology

Before examining the air-sea flux variations associated with the Ningaloo Niño, climatological air-sea fluxes in this region and their uncertainties are investigated by comparing those from different datasets (Figure 1A and Table 1). The seasonal cycle of latent heat flux from all products are similar, in which large (small) latent heat release in the austral winter (summer) is found. However, remarkable quantitative differences are found especially in summer (Figure 1A), during which the maximum difference can be as large as $\sim 80 \text{ W m}^{-2}$.

To further quantify the uncertainties, mean absolute deviation (MAD) defined as $MAD = \frac{\sum_{i=1}^n |X_i - \bar{X}|}{n}$, where X_i is surface heat flux from reanalysis, $\bar{X}$ is the mean value of all datasets, and n is the number of datasets, is calculated (Table 1, first row). Since MAD measures the magnitude of inter-data spread, the difference in uncertainties between the datasets could be determined quantitatively by calculating MAD. While large uncertainties are found in all seasons, the uncertainty is particularly large during summer with the MAD of 19.4 W m^{-2} when the difference between the highest and lowest latent heat flux exceeds 80 W m^{-2} .



Uncertainties of latent heat fluxes could partly be due to the use of different bulk flux algorithms. To evaluate the uncertainties caused by the use of different bulk flux algorithms, we recalculated the daily latent heat flux by using COARE3.5 flux algorithm and the state variables from each reanalysis product (referred to as EX-*alg*, where “EX” and “*alg*” stand for “experiment” and “algorithm”). **Figure 1B** show the climatological seasonal cycle of latent heat flux from EX-*alg*. The difference between the values in **Figures 1A,B** is a measure of uncertainty caused by the use of different algorithms. Based on the comparison, the algorithms used in reanalysis products tend to produce higher values than COARE3.5. For example, the difference is $\sim 60 \text{ W m}^{-2}$ for NCEP1 and NCEP2, $\sim 30 \text{ W m}^{-2}$ for MERRA2, and $\sim 10 \text{ W m}^{-2}$ for ERA-Interim and CFSR. Higher values of latent heat flux in reanalysis data have been documented in previous studies at various locations (e.g., Kubota et al., 2008; Zhang et al., 2016). For example, Kubota et al. (2008) evaluated the latent heat flux from NCEP1 and NCEP2 by comparing with the measurement at the Kuroshio Extension Observatory site. Both datasets overestimated the latent heat flux with a bias of 41 and 62 W m^{-2} . They suggest that this bias is primarily caused by the use of different algorithms. The major difference between bulk flux algorithms is how the transfer coefficients vary with wind speeds, atmospheric stability and other physical processes that influence the transfer of heat and moisture at the sea surface. Yet further details why the algorithms used in reanalysis tends to produce higher values



are still unknown. The MAD of algorithm-caused uncertainty is 21.3, 25.0, 26.0, and 22.5 W m^{-2} during DJF, MAM, JJA and SON, respectively, showing a weak seasonal variation. This is because the uncertainty depends on both the magnitude of latent heat flux (larger in winter) and wind speed (smaller in winter). Further details of the seasonal dependence are discussed in the **Appendix**.

The shortwave radiation also reveals a strong seasonal variation (**Figure 2B**). Similar to latent heat flux, large uncertainties are found in summer. Assuming the satellite derived estimate (CERES) is more accurate than reanalysis products, the estimate of NCEP1 has the largest bias ($\sim 80 \text{ W m}^{-2}$) in summer, and estimates in other datasets have smaller biases of $\sim 20 \text{ W m}^{-2}$. Shortwave radiation and latent heat flux are dominant components of the seasonal variations of net surface heat flux. Considerable net surface heat flux differences between the datasets are found during summer when

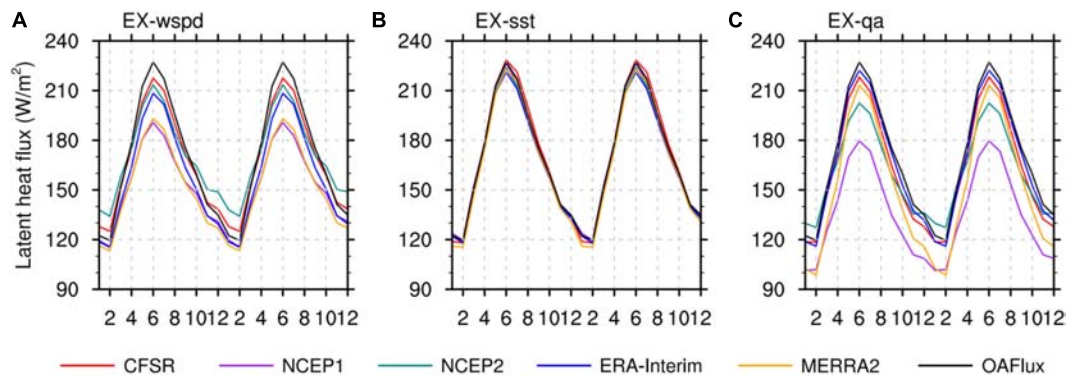


FIGURE 5 | Climatological seasonal cycle of latent heat flux (into the atmosphere) over the region (110°E-116°E, 22°S-32°S) from (A) EX-wspd, (B) EX-sst, (C) EX-qa.

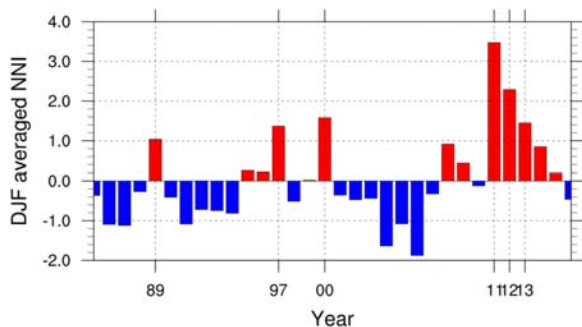


FIGURE 6 | DJF averaged Normalized Ningaloo Niño Index calculated from the NOAA 1/4° daily Optimum Interpolation Sea Surface Temperature. The year shown in the horizontal axis corresponds to the year of January and February.

the Ningaloo Niño develops (Figure 2A). Most of the differences arise from latent heat flux and shortwave radiation as discussed above. The contribution of the difference in longwave radiation and sensible heat flux between the different datasets is minimal.

Figure 3 compares the monthly surface heat flux from reanalysis products with the RAMA buoy at 100°E, 25°S for the 2-year period during which buoy measurements are available. The variations of latent heat flux from OAFlux and shortwave radiation from CERES agree well with those from the RAMA buoy. Large differences in shortwave radiation between the datasets are found during the austral summer. Both NCEP1 and CFSR greatly underestimate the net shortwave radiation. The seasonal variations of latent and sensible heat flux at the buoy site are weaker, and the mean value is smaller than those near the west coast of Australia due to the weaker influence of the Leeuwin Current at this location. An overestimate of 10–50 W m^{-2} in latent heat flux from reanalysis products is found throughout the analysis period, suggesting that these differences are partly due to the use of different bulk flux algorithms. The use of COARE3.5 improves the latent heat flux for most of the datasets (Figure 4A). MAD decreases from 11.5 to 7.5 W m^{-2} for CFSR, 25.3 to 13.7 W m^{-2} for NCEP2,

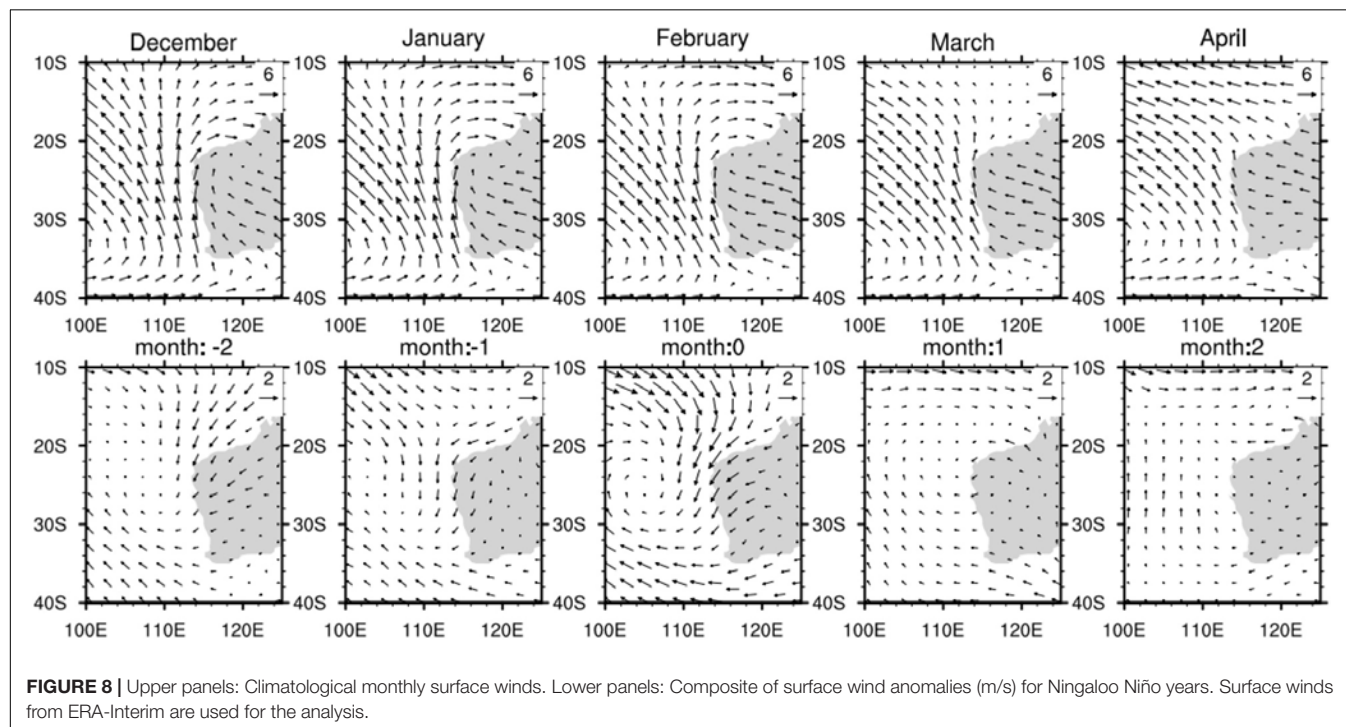
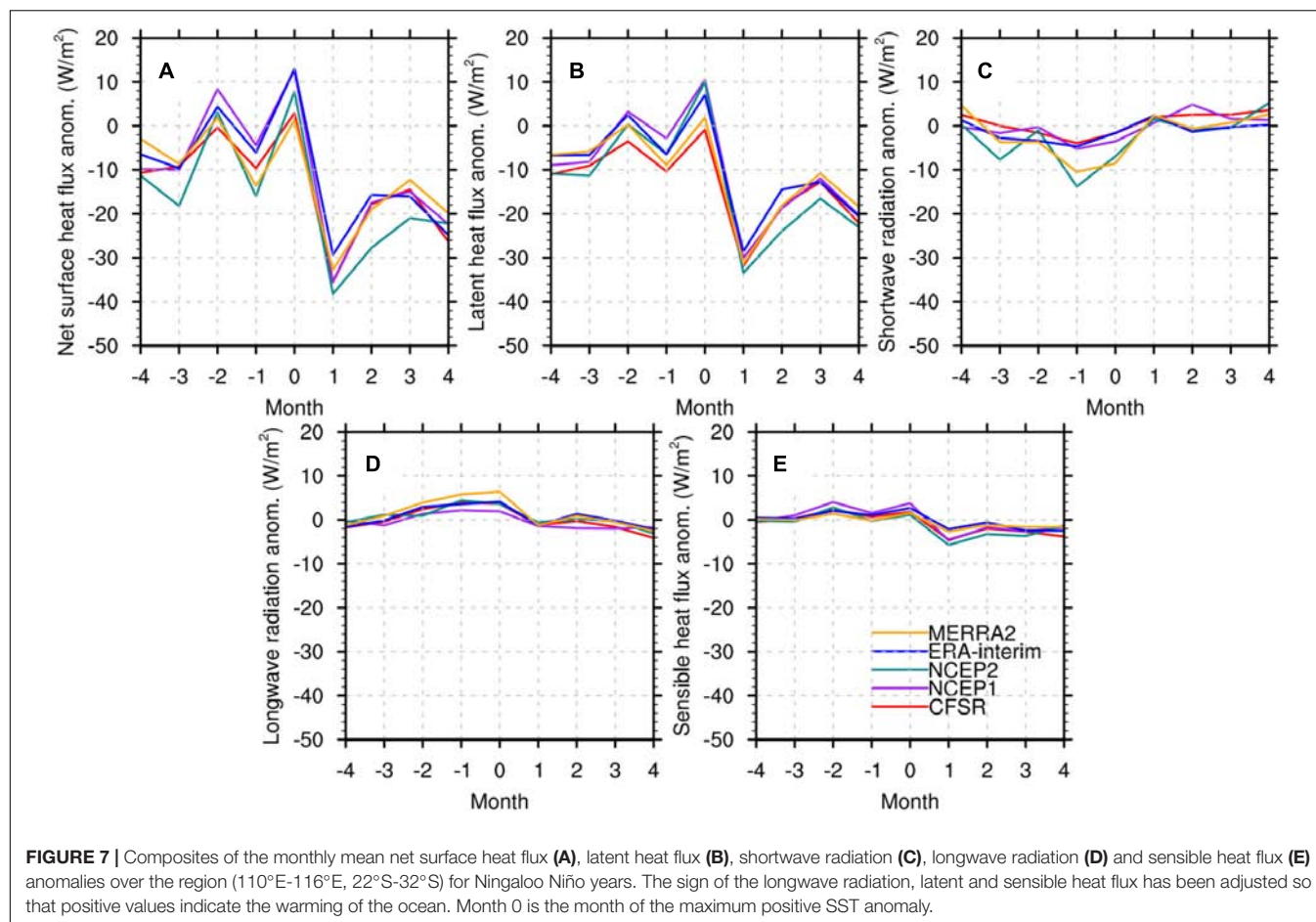
24.7 to 23.4 W m^{-2} for ERA-Interim and 15.9 to 13.2 W m^{-2} for MERRA2, but it increases from 17.7 to 28.2 W m^{-2} for NCEP1 due to large errors in the specific humidity and wind speed (Figures 4B,C).

While the use of different bulk flux algorithms causes significant difference in estimated fluxes, large differences still exist when using the same algorithm (Figures 1B, 4A), indicating that the difference in bulk variables largely influences the estimates of latent heat flux. To evaluate the uncertainties caused by each bulk variable, we calculated the daily latent heat flux using COARE3.5 for three different cases, in which bulk variables are (1) surface wind speed only from each reanalysis and other variables from OAFlux (EX-wspd), (2) SST only from each reanalysis and other variables from OAFlux (EX-sst), (3) air humidity only from each reanalysis and other variables from OAFlux (EX-qa). The uncertainties caused only by windspeed, SST and air humidity can be estimated from EX-wspd, EX-sst, and EX-qa, respectively. Both surface wind speed and humidity largely contribute to the difference between the datasets, whereas the contribution of SST is much smaller (Figure 5). The MAD of annual mean latent flux is 7.7 and 9.3 W m^{-2} for EX-wspd and EX-qa, and that of EX-sst is 1.5 W m^{-2} (Table 1). All latent heat fluxes calculated with reanalysis state variables are underestimated in EX-wspd and EX-qa during winter, but not during summer. The MAD during winter is also larger than in summer in EX-wspd and EX-qa.

Air-Sea Fluxes Associated With Ningaloo Niño

In the previous subsection, large uncertainties of air-sea fluxes are identified in the climatological seasonal cycle. In this subsection, surface heat fluxes associated with the Ningaloo Niño, which is the major interannual variability in this region, are investigated and their uncertainties are determined using the same datasets.

Ningaloo Niño events are identified based on the Ningaloo Niño Index (NNI) defined as the average of SST anomalies over the region 110°E-116°E, 22°S-32°S (Marshall et al., 2015). Years when the DJF averaged NNI is above one standard deviation are

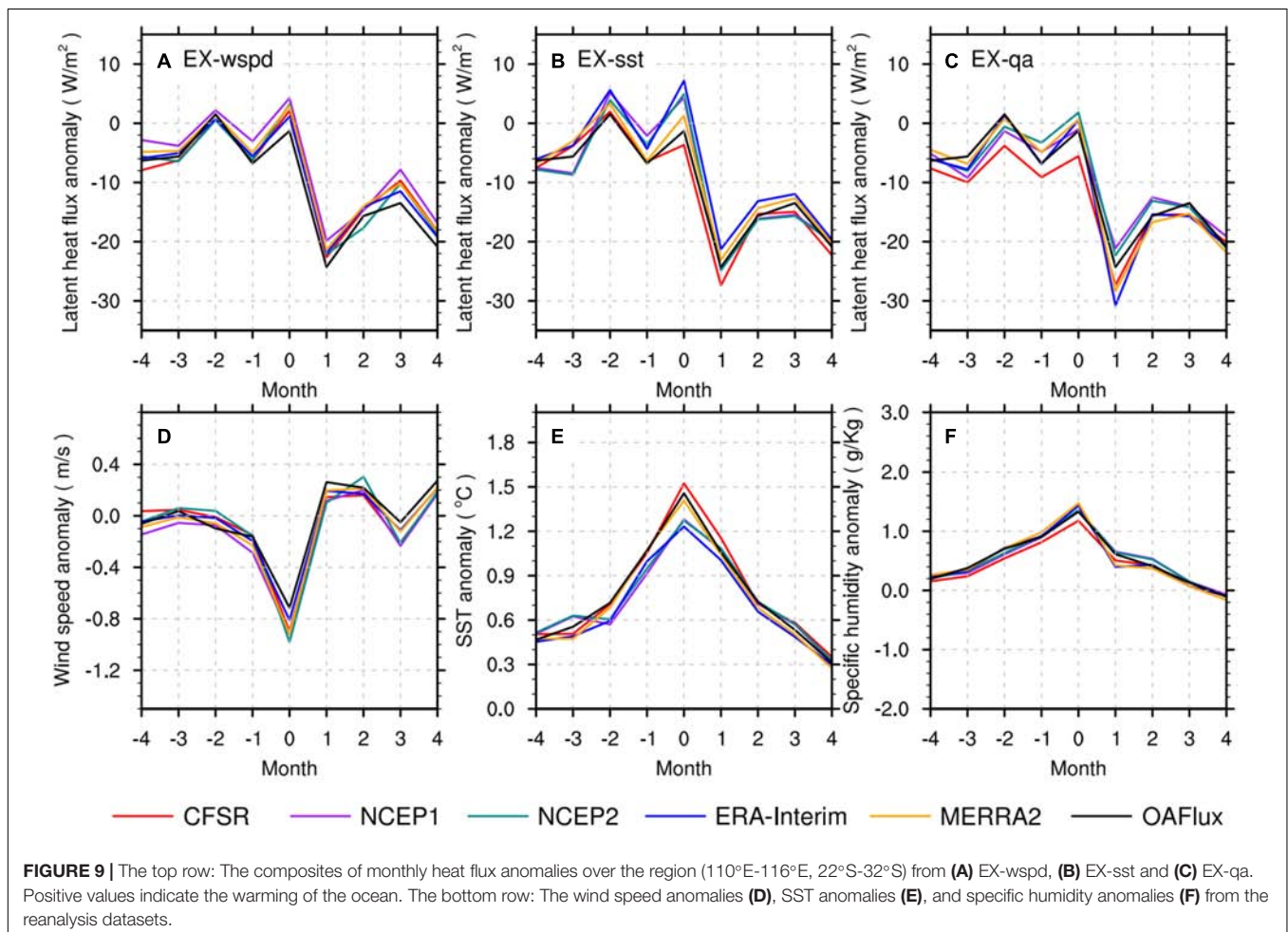


defined as the Ningaloo Niño years. For the entire period of the analysis, six events are identified: 1988/89, 1996/97, 1999/2000, 2010/11, 2011/12, and 2012/13 (**Figure 6**). The composite time series of surface heat flux anomalies, which cover the period of onset, development, and recovery of the events, are constructed by averaging all six events. Month 0 in the composite is defined as the month of the maximum positive SST anomaly in the region used for the NNI calculation.

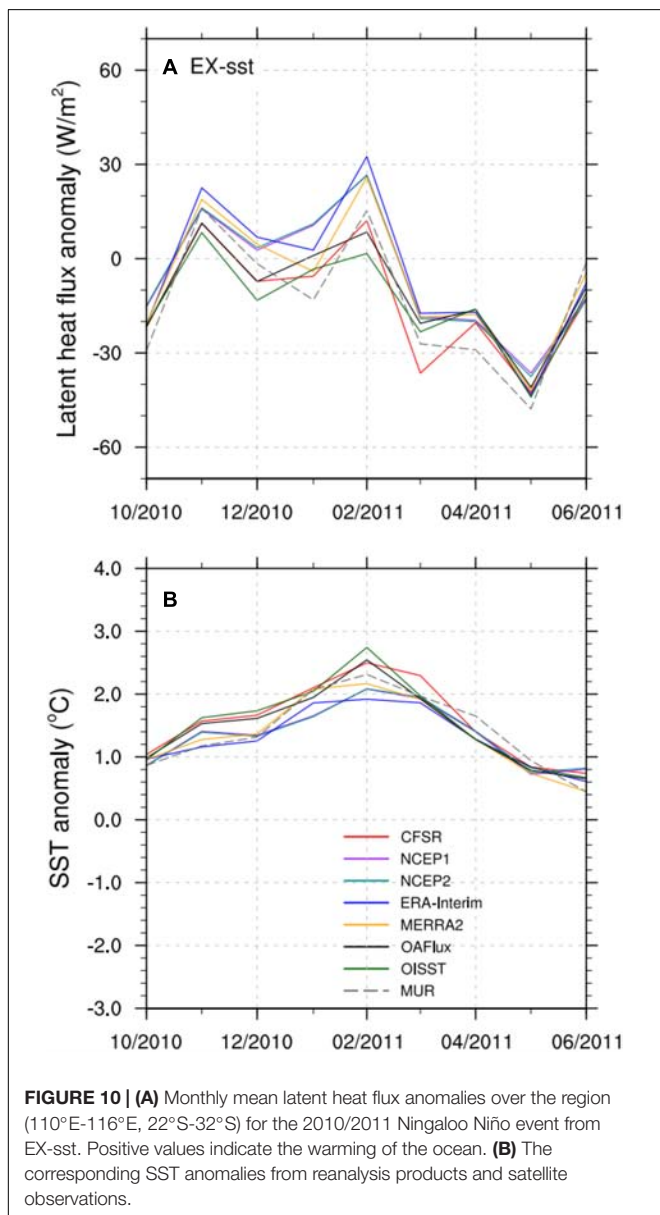
Despite the large uncertainties in climatology, anomaly fields show much smaller differences between the datasets. However, these uncertainties are still significant because they are in the same order of the amplitude of the anomaly particularly during the warming period. In addition, the sign of the latent heat flux anomalies varies between the datasets during the developing phase of Ningaloo Niño, suggesting the opposite role of latent heat flux. Large variations associated with the Ningaloo Niño are detected in all datasets (**Figure 7**). For instance, during the developing phase, a significant increase of net surface heat flux is found from month -3 to -2 and month -1 to 0. Then the anomalous surface heat flux decreases sharply from month 0 to month +1, resulting in substantial cooling during the recovery phase (**Figure 7A**). The sharp decrease (cooling) in the recovery phase is seen clearly in all datasets and it is dominated

by the latent heat flux anomaly fluctuation (**Figures 7B–E**). Similar variations are found for the composite using turbulent heat fluxes from OAFlux and shortwave and longwave radiation from CERES (not shown), but only the last three events are used for this composite because of the shorter period the CERES data cover.

To further examine how the fluctuation of the latent heat flux associated with the Ningaloo Niño event occurs, spatial patterns of surface wind anomalies are compared with those of climatological surface winds (**Figure 8**). During December–April, climatological southeasterly winds prevail around the west coast of Australia. When the Ningaloo Niño is fully developed at month 0, the northerly wind anomalies reach the peak, which largely decrease the climatological southeasterly and thus reduce the wind speed. Such reduction of wind speed is also found in month -2 although it is much weaker. The latent heat flux anomalies from some of the datasets are positive during the development and peak phases due to the weakening of surface winds described above, which are consistent with the windspeed–evaporation–SST (WES) feedback mechanism suggested in previous studies (e.g., Nicholls, 1979; Marshall et al., 2015). However, the positive latent heat flux anomalies are not found in some of the datasets during this period.



During month +1 soon after the peak, the wind anomaly rapidly changes to weak southerly, resulting in an increase of wind speed by 1 m/s. Since SSTs recover much more slowly and thus they are still anomalously high in month +1 (**Figure 9E**), the evaporative cooling (negative latent heat flux anomaly) is rapidly enhanced, which contributes to the SST cooling. By month +2, evaporative cooling is reduced because of the decrease of SST although wind speed similar to month +1 is maintained. The variation of latent heat flux anomaly including the rapid increase of negative anomalies in month +1 are found in all datasets. The cooling anomalies in longwave radiation and sensible heat flux, which are associated with high SSTs, are found (**Figures 7D,E**), but their contributions to SST recovery are much smaller than those of latent heat flux.



In contrast to the recovery phase, the variation of latent heat flux and its contribution to SST growth during the developing phase show disagreement between the datasets. NCEP1 shows warming anomalies during month -2 to 0, while others reveal cooling anomalies (CFSR, MERRA2) or alternate between cooling and warming (NCEP2, ERA-Interim). It is not clear whether the latent heat flux anomaly significantly contributes to the SST warming during the Ningaloo Niño onset. These results are consistent with those of previous studies, which used different surface heat flux products and concluded different roles of surface heat fluxes during the onset and development phases (e.g., Feng et al., 2013; Marshall et al., 2015; Kataoka et al., 2017).

The major sources of the uncertainty during the onset period are further investigated based on the additional analysis using EX-wspd, EX-sst and EX-qa described in Section "Climatology." Composites of latent heat flux anomalies from EX-wspd, EX-sst and EX-qa are displayed in **Figure 9**. The mean of the difference between the maximum and minimum latent heat flux anomaly during the entire period of composite is 4.1, 4.7 and 5.0 W m^{-2} for EX-wspd, EX-sst and EX-qa, respectively. This suggests that air specific humidity errors could cause larger uncertainties of latent heat flux anomalies, which is similar to the results from the analysis of climatological latent heat flux. However, the largest differences between the datasets during the peak phase are found in EX-sst (**Figure 9B**), which is 10.9 W m^{-2} , and the sign of latent heat flux anomaly also shows a disagreement between the datasets. While a significant difference (7.4 W m^{-2}) is also found in EX-qa in month 0, the sign of the latent heat flux anomaly is the same in most datasets. This result indicates that the uncertainties in SST significantly contribute to the errors in latent heat flux during this period. Since the SST is highest at the peak month, the latent heat flux is most sensitive to changes in SSTs during this period. In other words, even small errors in SST could impact the latent heat flux significantly during the onset and peak periods.

The SST difference between the datasets is largest in the peak period (month 0) (**Figure 9E**). While SSTs used in the flux products are based on similar satellite observations, their spatial resolutions could influence the accuracy since SST in this region is largely affected by Leeuwin Current variability (Huang and Feng, 2015). Such SST differences caused by the resolution are demonstrated for the 2010–2011 Ningaloo Niño case. The monthly latent heat flux and SST anomaly during the event are shown in **Figure 10**. To exclude the latent heat flux uncertainties caused by algorithm, wind speed, and humidity, we use fluxes from EX-sst instead of the original reanalysis. In addition to SST products used in the original EX-sst, high resolution OISST and MUR are also included in this case study.

The peak of this Ningaloo Niño occurred in February 2011. From November 2010 to February 2011, warm SST anomalies were built up near the west coast of Australia (**Figure 10B**). During this time, significant positive latent heat flux anomalies (10–30 W m^{-2} , positive value denote heat going into the ocean) are evident in NCEP1, NCEP2, ERA-Interim and MERRA2, suggesting that air-sea fluxes may contribute to the SST warming. In contrast, CFSR, OAFux, MUR and OISST show very small positive anomalies into the ocean, or even negative anomalies in December 2010 and January 2011

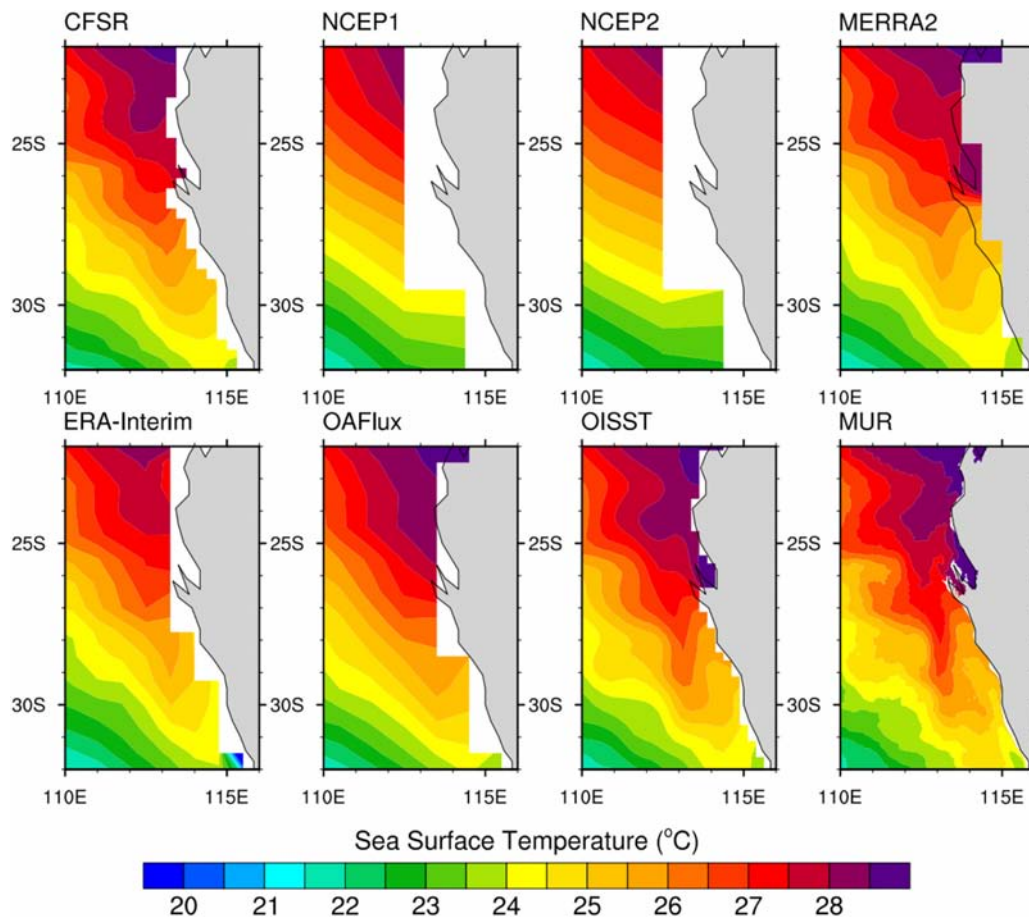


FIGURE 11 | Mean SST of January and February 2011 over the west coast of Australia from different SST datasets.

(Figures 10A, 12). These differences are caused by warmer area average SSTs for the relatively high-resolution SST products (MUR, OISST) (Figure 10B).

Figure 11 shows SST maps from different datasets during the peak period of the 2010–2011 Ningaloo Niño event. The southward extension of warm waters carried by the Leeuwin Current is evident clearly in the high-resolution data (MUR and OISST), while it is not well represented in the low-resolution data. Accordingly, higher area average SSTs and thus higher evaporative cooling are found in the case of high-resolution SSTs (Figure 12). The results demonstrate that it is crucial to resolve SST changes caused by Leeuwin Current variability adequately for the latent heat flux estimates especially during the peak period of Ningaloo Niño.

DISCUSSION

The results in the previous section demonstrate that large negative surface heat flux anomalies are found during the decay periods of the Ningaloo Niño in all datasets, and that the latent heat flux anomaly is the dominant component. Such large latent heat fluxes (evaporation)

could significantly impact the atmospheric conditions and circulation.

In addition to the air-sea flux anomalies, MLD changes associated with the Ningaloo Niño could influence the SST evolution (Kataoka et al., 2017). Kataoka et al. (2017) suggested that the cooling due to latent heat flux anomalies during the decay period could be largely reduced by MLD variability, and the sensible heat flux significantly contributes to the SST cooling for some events.

To further investigate the relative importance of latent and sensible heat fluxes for the SST variations during the decay phase, these flux terms in the following mixed layer heat budget equation are calculated (Equation 7 in Kataoka et al., 2017):

$$\left(\frac{Q}{\rho c_p h} \right)' = \frac{Q'}{\rho c_p h} - \frac{\bar{Q}}{\rho c_p h} \frac{h'}{\bar{h}} + Res \quad (1)$$

where Q is the surface heat flux, ρ is seawater density, c_p is the specific heat of seawater, h is the MLD. An overbar represents monthly climatology and a prime represents anomaly. The first term on the RHS represents the contribution of the surface heat flux anomaly, and the second term represents the contribution of MLD variability through the change of the mixed layer heat

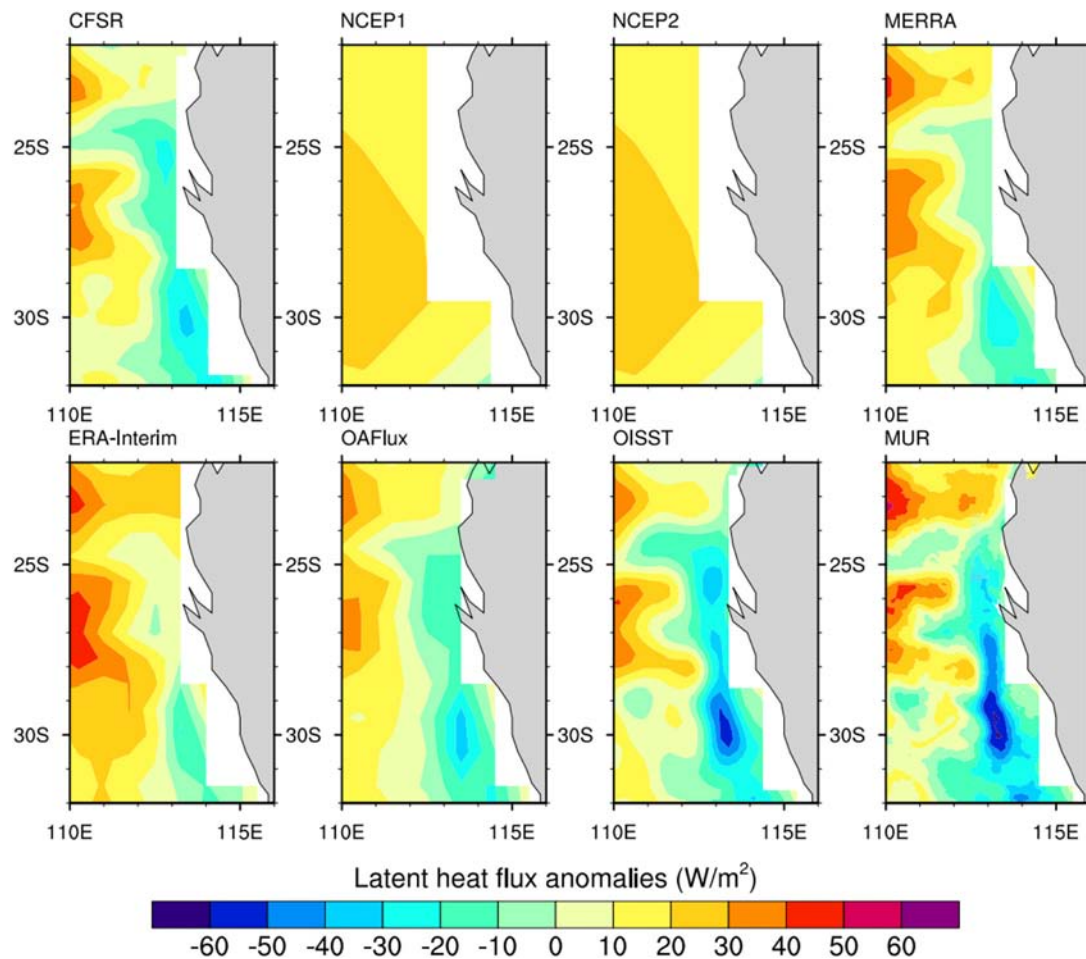


FIGURE 12 | Mean latent heat flux anomalies of January-February 2011 over the west coast of Australia from EX-sst. Positive values indicate the warming of the ocean.

capacity. The MLD is derived from the HYCOM reanalysis which is defined as the smaller depth at which the temperature is decreased by 0.2°C or the salinity is increased by 0.03 psu from the surface values. The seasonal variation of MLD from the HYCOM reanalysis agrees well with observations (e.g., CARS, **Supplementary Figure 1**). The composite latent and sensible heat flux anomalies, which include the effect of MLD changes, are shown in **Figure 13**, and the composites of the first and second term on the RHS of Eq. (1) are shown in **Figure 14**. Significant contributions of MLD changes are evident (**Figures 13, 14**). For example, the weak cooling (negative anomaly) is found during the onset and peak phase in the latent heat flux term (**Figure 13**) in all datasets whereas the weak warming is found in some datasets when the effect of MLD change is not included (**Figure 7**). The contribution of the MLD change (second term) is relatively large during the onset and peak phase as the first term is small. Yet the latent heat flux term is still dominant and contributes to the cooling during the decay period much more than the sensible heat flux term. The variation of latent heat flux in **Figure 13** is similar to that of non-locally amplified Ningaloo Niño in Kataoka

et al. (2017). It should be noted that there are no significant differences between locally and non-locally amplified modes in the analysis of this study.

Although the reason for the differences between the results of this study and Kataoka et al. (2017) is unknown, it is likely that different sources of the data including air-sea fluxes and MLD are primarily responsible for the differences. In particular, the interannual variation of MLD could be largely model dependent. Thus, further studies which focus on the interannual variability of upper ocean structures including the MLD are necessary.

While earlier studies suggest that a reduction of latent heat flux partially contributes to SST anomalies at the peak of Ningaloo Niño, an opposite conclusion could be obtained when taking account of MLD variation. **Figure 13** shows that the latent heat flux damps SST anomalies in all stages of Ningaloo Niño and the cooling reach the maximum during the peak. At the peak phase, large differences in latent heat flux anomaly between the datasets and thus large uncertainties are found. Again, these uncertainties are likely to be related to the resolution of SST.

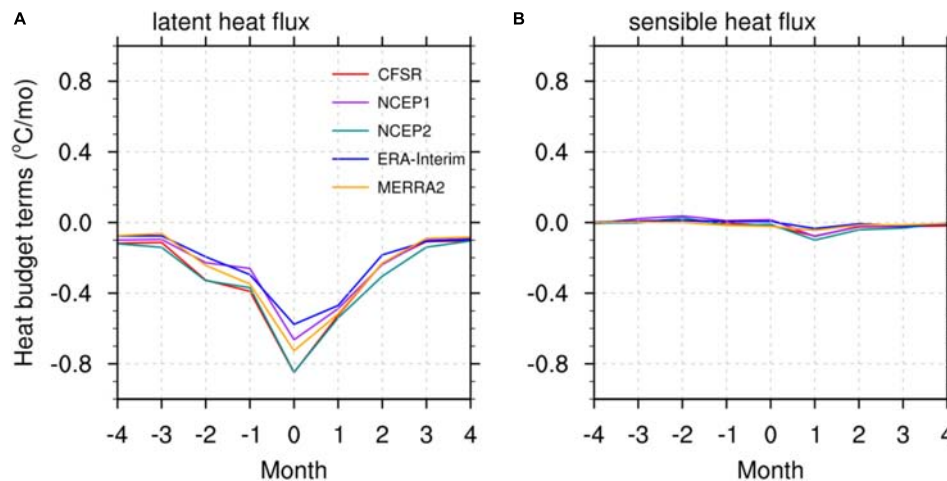


FIGURE 13 | Composites of monthly mean heat flux anomaly term in the mixed layer heat budget equation over the region (110°E–116°E, 22°S–32°S): **(A)** latent heat flux term, **(B)** sensible heat flux term.

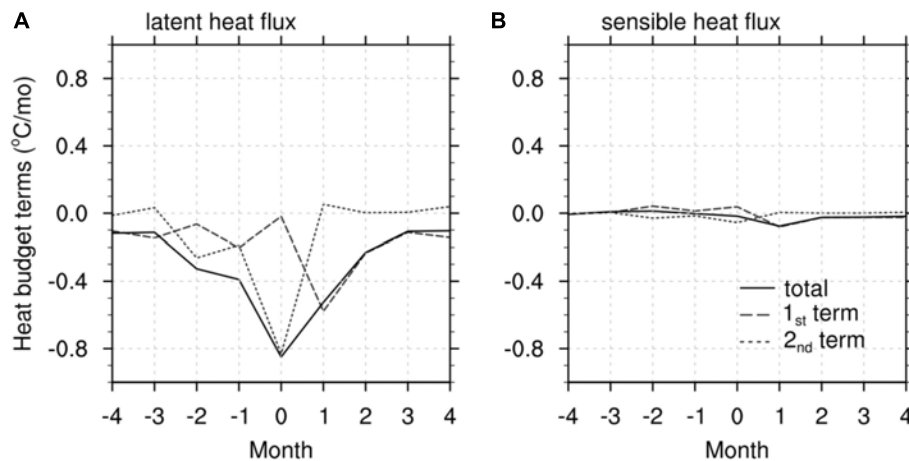


FIGURE 14 | Composite monthly mean heat flux anomaly terms calculated from the mixed layer heat budget equation for the region (110°E–116°E, 22°S–32°S): **(A)** latent heat flux, **(B)** sensible heat flux. First and second terms on the RHS of Eq. (1) are compared. Only the results from CFSR are shown. The first term represents a temperature tendency produced by the flux anomaly with the climatological MLD, and the second term represents a temperature tendency produced by climatological fluxes and the MLD anomaly.

In addition to the influence of air-sea fluxes on the upper ocean temperature, these heat and moisture fluxes directly affect the atmosphere. In particular, the latent heat fluxes (evaporation) could largely contribute to moisture budget changes in the atmosphere during the period of Ningaloo Niño and thus air-sea interaction. A recent modeling study demonstrates that the Ningaloo Niño could develop without ENSO, and the intrinsic air-sea interaction alone may induce atmospheric cyclonic circulation anomalies and a stronger Leeuwin Current (Kataoka et al., 2018). As the present study suggests the importance of the resolution of SST for the latent heat flux estimates off the west coast of Australia, coupled model simulations using the high-resolution ocean component would be useful to investigate the feedbacks between the atmosphere and ocean that control the development of Ningaloo Niño.

SUMMARY

This study investigates the air-sea flux variability off the west coast of Australia using multiple datasets and satellite observations. We found large uncertainties in climatological net surface heat fluxes. The uncertainties result primarily from latent heat flux and shortwave radiation. The possible causes of the uncertainty for latent heat flux are investigated with additional calculations which isolate the effects of wind speed, SST, humidity, and bulk flux algorithm. The results of these calculations suggest that the use of different bulk flux algorithms largely contributes to the uncertainties. The bulk atmospheric variables also significantly contribute to the uncertainties.

The role of air-sea fluxes in the development and decay of Ningaloo Niño is investigated based on the composite analyses

over the life cycle of Ningaloo Niño. Large differences in air-sea flux anomaly fields associated with the Ningaloo Niño between the datasets are evident although they are smaller than the climatology. Large negative air-sea heat flux anomalies (cooling the ocean) in the recovery phase are found in all datasets, and the anomalous latent heat flux is the dominant component. This suggests that the latent heat flux plays an important role in damping the positive SST anomalies during the recovery stage. The composite evolution of surface winds suggests that WES feedback is responsible for the variations of latent heat flux. Since SSTs recover much more slowly than surface winds after the peak of SST warming, large evaporative cooling is favored under the condition of strong winds and warm SST especially during the early stage of the recovery phase. Then the evaporative cooling is reduced as the SST gradually recovers.

During the developing phase, however, the contributions of air-sea heat flux have large uncertainties. Sensitivity calculations show that the differences in SST anomaly between the datasets largely contribute to the uncertainties. Large uncertainties around the period of SST peak are partly due to the warmer SST than other periods, since the small errors in SST could generate large latent heat flux changes. Also, SST anomalies are directly related to the strengthening of the Leeuwin Current, and thus the resolution of SST datasets significantly affects the SST anomalies. A case study of the 2010–2011 Ningaloo Niño event demonstrates a close relationship between the SST anomaly and the resolution of the datasets. Southward extension of warm waters transported by the Leeuwin Current can be adequately resolved only by high-resolution SST datasets. As a result, a relatively cold SST and thus smaller evaporative cooling are estimated using the low-resolution SST datasets.

AUTHOR CONTRIBUTIONS

Both authors conceived and designed most of the analyses. XF analyzed the data and wrote the manuscript. TS contributed to the discussion of the results and assisted in writing.

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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.2019.00266/full#supplementary-material>

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Conflict of Interest Statement: 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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APPENDIX

Uncertainty of Latent Heat Flux Caused by Bulk Flux Algorithm and Its Seasonality

The bulk flux algorithm calculates latent heat flux by using the mean value of bulk state variables (Yu et al., 2008):

$$Q_{LH} = \rho L C_e U (q_s - q_a) \quad (2)$$

where ρ is the density of air, L is the latent heat of vaporization, C_e is the transfer coefficient for moisture, U is surface wind speed relative to surface current, q_s is sea surface saturated specific humidity estimated from SST and q_a is air specific humidity. The direction of the latent heat flux calculated with this equation is from the ocean to the atmosphere for the positive values. While latent heat flux is directly proportional to wind speed and humidity gradient, the transfer coefficient for moisture, which represents the physical processes involved in the heat transfer at the air-sea interface, can change with wind speed and atmosphere stability. The transfer coefficient is calculated differently in different algorithms.

Figure A1 shows the uncertainties of latent heat flux caused by the algorithms used in reanalysis products. While latent heat flux based on the algorithm in NCEP1 and NCEP2 have a larger difference compared to that from COARE3.5, CFSR and ERA-Interim indicate a better agreement with COARE3.5. The uncertainties also depend on the magnitude of latent heat flux and larger latent heat flux usually have larger uncertainties. However, results from NCEP1 and CFSR show the uncertainty is larger in summer than in winter, although latent heat flux is higher in winter. This difference between summer and winter is likely due to the difference in wind speed. Zeng et al. (1998) showed that the neutral exchange coefficient for latent heat flux from different algorithms diverge at higher wind speed. During summer, winds are stronger although the latent heat flux is relatively smaller. The wind effect on the transfer coefficient is likely to account for the larger uncertainty during summer.

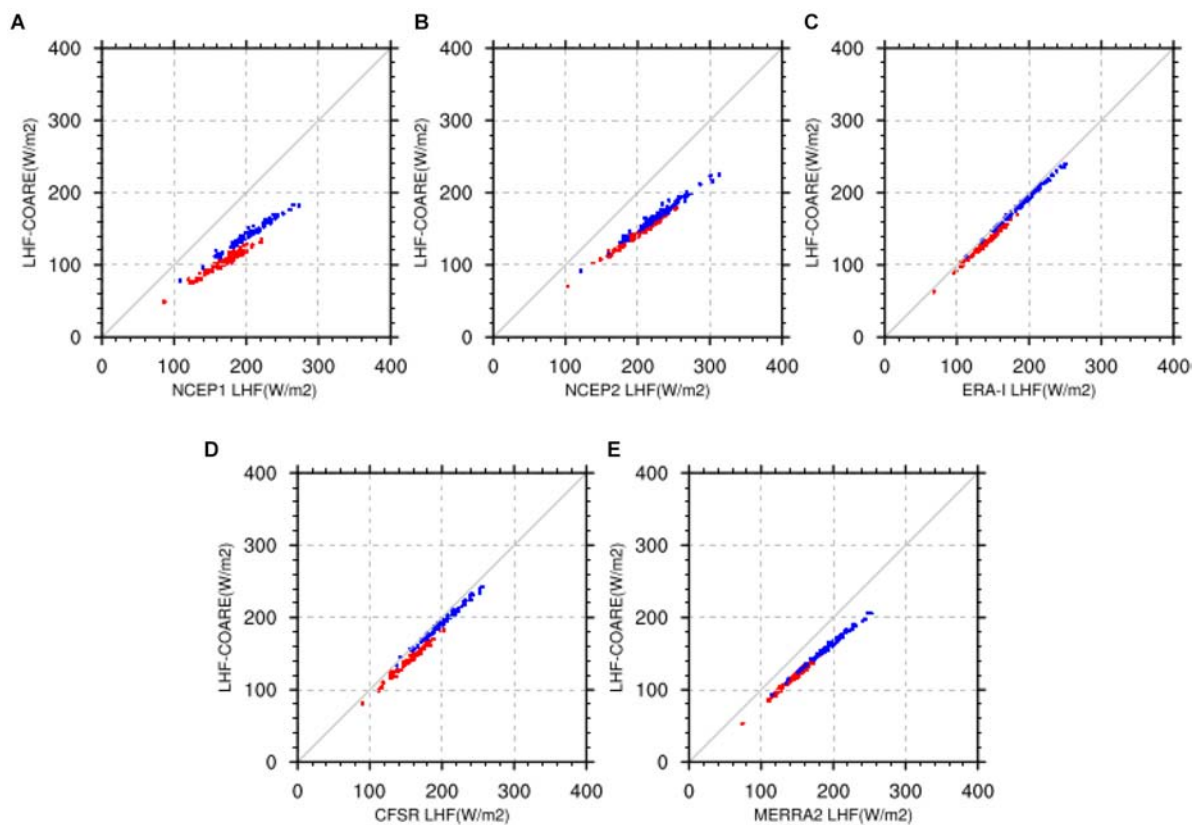


FIGURE A1 | Comparisons of monthly latent heat fluxes (LHF) from EX-alg (vertical axis) with those (horizontal axis) obtained from (A) NCEP1, (B) NCEP2, (C) ERA-Interim, (D) CFSR and (E) MERRA2. JJA (DJF) data points are shown in blue (red).



Simmered Then Boiled: Multi-Decadal Poleward Shift in Distribution by a Temperate Fish Accelerates During Marine Heatwave

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Sillago schomburgkii inhabits coastal waters of south-western Australia, where it occurs over a wide latitudinal range (22–35°S). The species has occupied this range for at least the past century. It is a valuable fishery species, particularly in northern (warmer) areas where it has historically been most abundant. Fishery trends indicate a gradual poleward shift in the center of abundance since the 1950s, coinciding with gradual ocean warming over the same period. This shift dramatically accelerated after the 2010/2011 marine heatwave, when abundance abruptly declined at the northern edge of the range but increased in southern areas. The heatwave drew attention to the significant, but previously unrecognized, distributional shift of *S. schomburgkii*. It also helped to elucidate the recruitment-related mechanism by which the shift is occurring. There was evidence of exceptionally strong recruitment by the 2010/2011 year class in southern areas, but weaker recruitment at the northern edge. Spawning by *S. schomburgkii* is associated with ocean temperatures of approximately 20–26°C. Temperatures are in this range for most of the year in the north, but only briefly during the height of summer in the south. During the heatwave, coastal temperatures were up to 5 degrees above average. It is likely that the spawning period was reduced in the north but extended in the south, due to higher temperatures, which would explain the recruitment trends in each area. All evidence suggests the distributional shift is primarily due to altered spawning success by resident fish in each area (i.e., self-recruitment), rather than by the movement of adults, or larval dispersal. The accelerated shift during the heatwave was probably due to major changes in self-recruitment, but possibly supplemented by atypical southward larval dispersal. For commercial and recreational fisheries that capture this species, the ongoing poleward range shift could have significant negative, and positive impacts in the northern and southern areas, respectively. Fisheries in southern areas are expected to benefit from an increasing availability of this species, although a predicted climate-induced loss of critical habitats could negate any gains at the southern edge of the range.

Keywords: yellowfin whiting, ocean warming, fisheries impact, spawning duration, Western Australia, Peel-Harvey

INTRODUCTION

A global redistribution of marine species is predicted to occur in response to climate change (Pinsky et al., 2013; Poloczanska et al., 2016). Poleward range shifts have already been documented for many fish species in response to warming temperatures (Perry et al., 2005; Dulvy et al., 2008; Nye et al., 2009; Last et al., 2011; Cheung et al., 2013; Fossheim et al., 2015). These range shifts pose major challenges for fisheries, which will need to adapt to minimize the socio-economic costs of the changes, take advantage of emerging opportunities, and ensure appropriate regulations are in place to allow adaptation whilst preventing overexploitation of declining or new fishery resources (Rice and Garcia, 2011; Madin et al., 2012; Pinsky and Fogarty, 2012; Bell et al., 2016; Caputi et al., 2017).

As oceans warm, marine heatwaves (MHWs) are becoming more frequent (Lima and Wetthey, 2012; Frölicher and Laufkötter, 2018; Oliver et al., 2018). These events can have damaging and long-term impacts on ecosystems, but can also provide a useful “preview” into future ecosystem changes, and the human responses to them, that will occur as temperatures continue to rise and become more variable (Mills et al., 2013). MHWs can therefore assist fisheries to prepare for production losses, or gains, associated with future climate change.

In the austral summer of 2010/2011, an unprecedented MHW affected about 2000 km of the western Australian coastline. During this La Niña-driven event, sea surface temperatures (SST) along the coast between 22 and 34°S exceeded the typical summer level by 3°C on average, including peaks of 5°C above average at numerous sites over this range (Feng et al., 2013; Pearce and Feng, 2013; Wernberg et al., 2013). The MHW was superimposed on a long term, increasing SST trend of about 0.1°C per decade off south-western Australia (Pearce and Feng, 2007; Pearce et al., 2016).

Dramatic effects of the 2010/2011 MHW included mortality of fish, invertebrates, seagrasses and habitat-forming algae, coral bleaching, and the sudden appearance of tropical species in temperate waters (Pearce et al., 2011; Moore et al., 2012; Wernberg et al., 2013, 2016; Arias-Ortiz et al., 2018). Less obvious effects, such as impacts to growth or recruitment of longer-lived species, have also become apparent in the years following the event (Foster et al., 2014; Cure et al., 2015, 2018; Lenanton et al., 2017).

Sillago schomburgkii (Peters, 1864) (Sillaginidae) is a temperate marine fish that is endemic to south-western Australia, where it is distributed over a wide latitudinal range (22–35°S) (Hutchins and Swainston, 1986). It occurs on sheltered, sand flats in shallow coastal waters and the saline parts of estuaries (Hyndes et al., 1996; Hyndes and Potter, 1997). The species, commonly known as “yellowfin whiting,” is a popular target for shore-based commercial and recreational fishers. In 2014, the commercial catch of *S. schomburgkii* unexpectedly rose to a record high level in the Peel-Harvey Estuary (Figure 1), generating concerns among fishery managers, and stakeholders about the sustainability of this fishery. It then became apparent that changes in *S. schomburgkii* catches were also occurring in other fisheries across the species range. This study was

undertaken to (i) determine the full extent of spatio-temporal changes in abundance of *S. schomburgkii* and (ii) identify reasons for the observed changes.

MATERIALS AND METHODS

Biology of *Sillago schomburgkii*

In Western Australia (WA), *S. schomburgkii* occurs from Exmouth (22°S, 114.5°E) to Albany (35°S, 118°E) (Figure 1). A second, separate population of this species occurs in South Australia from Spencer Gulf to Fleurieu Peninsula (33–35°S, 136–138.4°E). The population structure in WA has not been directly investigated. However, there is evidence of low rates of alongshore movement by adults, and thus low connectivity of adults at different latitudes in WA (Smith, unpubl. data). The entire life cycle, including spawning, is completed in sheltered, shallow waters (mostly <2 m) (Hyndes and Potter, 1997; R. Lenanton pers. comm). Adults and juveniles inhabit estuaries and ocean waters, although spawning occurs in ocean waters only. Similar to other sillaginids, *S. schomburgkii* has a protracted spawning period in which multiple batches of pelagic eggs are released by each female (Lenanton, 1970; Hyndes and Potter, 1997; Ferguson, 2000; Coulson, 2003). Fecundity is regarded as indeterminate and thus total annual fecundity is likely to be a function of the duration of the spawning period. *S. schomburgkii* has a maximum recorded total length (TL) of 427 mm and age of 12 years (Hyndes and Potter, 1997; Brown et al., 2013). Both sexes attain maturity at approximately 200 mm TL and age 2 years (Hyndes and Potter, 1997; Coulson et al., 2005).

Ocean Temperature Data

Ocean temperatures from 1981 onward at Exmouth Gulf (22.375°S, 114.375°E), Shark Bay (25.625°S, 113.635°E), Perth Zone (near Rottnest Island, 32.125°S, 115.625°E), and South Coast (near Albany, 34.875°S, 118.625°E) (Figure 1) were obtained from satellite-derived continuous daily sea surface temperature (SST) data from the NOAA OIv2 dataset at 1/4 degree (~28 km) resolution¹.

In Geographe Bay mean daily ocean temperatures from February 2001 onward were obtained from the Busselton Jetty Underwater Observatory (33.630°S, 115.338°E). Water temperatures at the Observatory (1.7 km from the shore) are recorded hourly at about 4 m depth using automatic temperature loggers accurate to $\pm 0.2^\circ\text{C}^2$.

To examine temperature variations during the main *S. schomburgkii* spawning period (see section “Results”), the “spring” (October–December) and “summer” (January–March) temperature anomalies at each location were calculated against mean levels in pre-MHW years (i.e., 2001/2002–2009/2010 for Busselton; 1981/1982–2009/2010 for other locations). For a more detailed view of the progression of the MHW at each location, mean monthly ocean temperatures in 2010/2011, 2011/2012, and 2012/2013, which all had exceptionally warm summers,

¹ <https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html>

² <https://www.busseltonjetty.com.au>

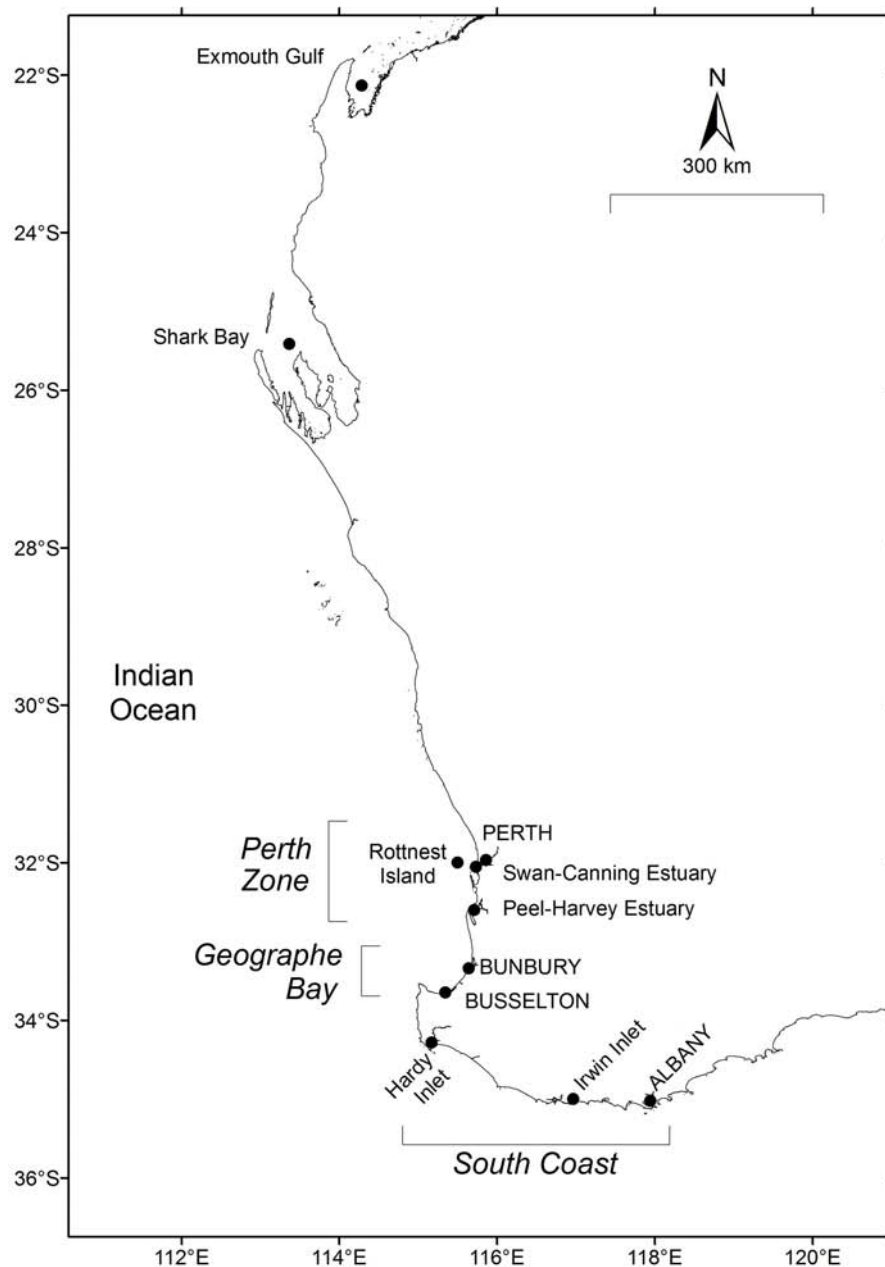


FIGURE 1 | Location of fisheries and sampling locations for *Sillago schomburgkii* in Western Australia.

were plotted against mean ($\pm$ SD) monthly temperatures in pre-MHW years.

Compared to satellite-derived coastal SST, shallow nearshore waters in WA typically experience slightly higher (0 to $^{\circ}\text{C}$) summer maxima, and substantially lower ($\sim 2^{\circ}\text{C}$) winter minima (e.g., Baldock et al., 2014; Pearce et al., 2016). Thus, SST is generally indicative of spring and summer temperatures experienced by *S. schomburgkii* in nearshore waters at the same latitude. SST may have underestimated the temperatures experienced by *S. schomburgkii* during the MHW. In late February/early March 2011, SST anomalies averaged $+2.7^{\circ}\text{C}$

along the west coast of WA but anomalies of $+3$ to $+5^{\circ}\text{C}$ were recorded at very shallow sites due to atypically high air-sea flux (Depczynski et al., 2013; Feng et al., 2013; Pearce and Feng, 2013).

Fishery Descriptions and Catch Rates

Sillago schomburgkii is taken commercially and recreationally throughout its range in WA. Commercial catches are taken by numerous small-scale net fisheries that are beach or estuary-based. Since 1976, it has been compulsory for commercial fishers in WA to provide monthly summaries of their catch (kilograms of each species, for each gear type) and effort (number of crew,

total days fished by each gear type). Prior to 1976, more limited catch and effort data are available and only for certain fisheries. To assess trends in *S. schomburgkii* abundance, annual catches and catch rates were examined in a suite ($n = 7$) of commercial fisheries that collectively span the full latitudinal range of this species (Table 1). In these fisheries, *S. schomburgkii* is taken as part of a multi-species catch. Due to the monthly aggregation of reported data, effort spent directly targeting *S. schomburgkii* is not known for any fishery. Therefore, a mean annual “targeted catch rate” was developed by restricting the catch and effort data to the primary gear type, the primary fishing months, and the primary boats that captured *S. schomburgkii* in each fishery (Table 1). Targeted catch rates of *S. schomburgkii* for each commercial fishery were calculated for recent years, 1990–2017.

The targeted catch rate was regarded as the most reliable index of abundance of *S. schomburgkii* for each fishery. In earlier years, where insufficient data were available to calculate targeted catch rates, nominal (raw) annual catch rates (kg/day or kg/boat), and total catches were plotted to provide longer term indicators of abundance. *S. schomburgkii* has always fetched relatively high wholesale prices (approximately twice the average price per kilogram for finfish captured in these fisheries). It is targeted when available and always retained. Hence the catch in these fisheries is a reasonable indicator of *S. schomburgkii* availability. The nominal annual catch rate for each fishery was calculated from the total annual catch of *S. schomburgkii* and total annual effort. The best available measure of long-term annual effort (sum of fishing days by all boats, or mean monthly number of active boats) was used for each fishery. The methods used by each fishery have not substantially changed over time and so fishing efficiency was assumed to be constant. Note: effort in these fisheries has declined substantially since 1970 as a result of a WA government policy to reduce the number of commercial fishers in nearshore and estuarine areas (Anonymous, 1999).

Limited data are available about recreational catches of *S. schomburgkii* in WA. The annual recreational catch level is not monitored. Most recreational catches of *S. schomburgkii* are taken in summer, and occur on ocean beaches with smaller amounts also taken in estuaries. To provide an indication of recreational catch rate trends in ocean waters, catch and effort data recorded by an avid recreational angler who fished regularly on ocean beaches in Geographe Bay (Figure 1), were examined.

A mean annual catch rate of *S. schomburgkii* was calculated from the total catch (number of fish, kept, and released) and total effort (number of fishing days) recorded in a voluntary daily logbook by the angler from 2005/2006 to 2016/2017. All fishing was shore-based and restricted to the warmer months (November–February).

Sampling and Analysis of Fish

During 2014–2017, the age composition of *S. schomburgkii* was sampled from commercial catches at Shark Bay, Perth Zone (in Peel-Harvey Estuary), Geographe Bay (on ocean beaches near Busselton and Bunbury), and South Coast (in Hardy Inlet) (Figure 1). Recreational fishery catches were sampled from the Perth Zone (in Peel-Harvey Estuary and on ocean beaches), and from the South Coast (in Hardy Inlet).

For each fish, the TL (in mm), total weight (g), sex and gonad weight (g) was recorded, and sagittal otoliths were extracted. Fish were later aged by enumerating the number of annually deposited opaque zones in their sagittal otoliths (Hyndes and Potter, 1997; Coulson et al., 2005). Age in months was estimated, assuming a nominal birthday of 1 October at Shark Bay, and a nominal birthday of January 01 at other locations (Hyndes and Potter, 1997; Coulson et al., 2005). Otoliths were aged by two independent readers. Agreement between readers was achieved for all otoliths.

Fish were sampled from commercial nets with a mesh size of 50 mm, which retain fish of approximately 260 mm TL and greater (i.e., 50% selection at this length). This length corresponds to an age of 2 or 3 years depending on sex and region (Hyndes and Potter, 1997; Coulson et al., 2005; Smith, unpubl. data). The selectivity of the recreational fishery was unclear, but the age composition of the recreational catch was similar to that of the local commercial catch, suggesting similar ages at selection. In this study, fish were assumed to be fully selected by each fishing gear at > 2 years.

At each site, age composition was similar for females and males, and also similar for commercial and recreational fisheries, so age data for all fish were pooled at each site. To assess recruitment variability, age frequencies of fully selected year classes were $\log_e$ transformed, and then residuals were examined against a simple linear regression, i.e., a “regression catch curve” approach (Maceina, 1997). This method assumes all fully selected age classes are subject to a similar rate

TABLE 1 | Location of commercial fisheries for which catch rates were examined, years for which annual catch and effort data are available, and the primary fishing gear and primary fishing months for capturing *S. schomburgkii*.

Fishery location (latitude and longitude)	Data years	Net type (mesh size, in mm)	Fishing months	Age at recruitment to fishery (years)
Exmouth Gulf (22.3°S, 114.3°E)	1976–2017	Haul (35–38)	July–November	1–2
Shark Bay (25.6°S, 113.6°E)	1956–2017	Haul (50)	May–October	2
Swan-Canning Estuary (32.0°S, 115.8°E)	1952–2007	Haul (60)	All	~4
Perth ocean beaches (32.4°S, 115.7°E)	1995–2017	Haul (20–55)	November–January	1–3
Peel-Harvey Estuary (32.6°S, 115.7°E)	1952–2017	Haul (50)	March–November	3
Hardy Inlet (34.3°S, 115.2°E)	1977–2017	Haul (50)	All	3
Irwin Inlet (35.0°S, 117.0°E)	1964–2017	Gill (57)	May–October	~4

The average age at which *S. schomburgkii* recruits to each fishery varies according to mesh size, and local growth rates.

of total mortality (Z), represented by the regression slope, and positive (or negative) residuals indicate above (or below) average recruitment.

The timing of spawning was determined from monthly trends in gonad development at four latitudinal zones: 26°S (Shark Bay), 32°S (Perth Zone), 33.5°S (Geographe Bay), and 34.5°S (South Coast) (**Figure 1**). Samples were obtained in each month in each zone, except Shark Bay where only 6 months were represented. To provide adequate monthly sample sizes at each latitude, all available gonad data from that latitude were pooled, including additional fish from other sites not used in the analysis of age composition. The majority of South Coast fish were obtained from Hardy Inlet, with the remainder from various estuaries located between Hardy Inlet and Albany. There were no obvious differences in the timing of gonad development between estuaries and so all South Coast sites were pooled. A gonadosomatic index (GSI) for each fish was calculated as $GSI = 100 \times [W1/(W2 - W1)]$, where $W1$ is weight of the gonad and $W2$ is total weight of the fish. Gonads from fish below the length at 50% maturity ($L50$) were excluded. $L50$ values previously estimated by Coulson et al. (2005) were assumed, i.e., 220/195 mm TL for females/males in Shark Bay, and 200/190 mm TL for females/males elsewhere. A monthly mean (+ SD) GSI for each sex was calculated at each location. Mean monthly GSI is a good indicator of relative spawning activity in *S. schomburgkii* (Hyndes and Potter, 1997; Coulson et al., 2005).

RESULTS

Ocean Temperatures

Along the WA coast, mean monthly ocean temperatures generally follow a latitudinal gradient, with highest temperatures in northern areas, and lowest in southern areas (**Figure 2**). The exception in this study was Geographe Bay, where temperatures in autumn/winter are substantially lower than those of the Perth and South Coast Zones.

In pre-MHW years, the mean monthly SST ranged from 22°C (in August/September) to 28°C (March) at Exmouth, 20°C (August/September) to 26°C (February/March) at Shark Bay, 19°C (September/October) to 22°C (February–April) at Perth, and 17°C (September/October) to 20°C (February–April) on the South Coast (**Figure 2**). In Geographe Bay, mean monthly temperature ranged from 15°C (July/August) to 22°C (February/March) (**Figure 2D**).

During 2010/2011, summer temperatures were well above their pre-MHW mean levels at all sites. In 2010/2011, the summer temperature anomaly was ~3°C at Shark Bay, ~0°C at Exmouth, Perth, and Geographe Bay, and ~1°C on the South Coast (**Figure 3**). At Exmouth the spring temperature anomaly was also high (~2°C) in 2010/2011. In 2011/2012 and 2012/2013, spring and summer temperatures were generally lower than in 2010/2011 but still relatively high compared to pre-MHW levels, with the exception of relatively cool summer temperatures at Geographe Bay in 2011/2012. Notably, on the South Coast the summer temperatures in 2011/2012 and 2012/2013 were both higher than in 2010/2011. In Geographe

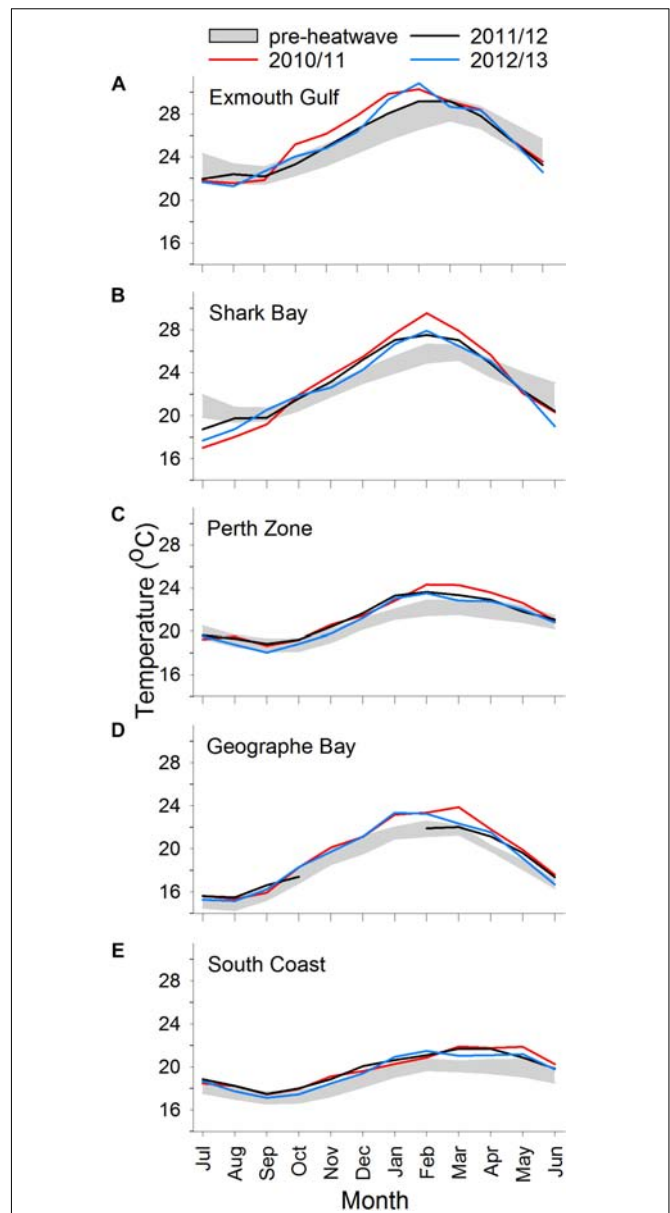


FIGURE 2 | Mean monthly ocean temperatures in individual years 2010/2011, 2011/2012, and 2012/2013 vs. pre-heatwave years (years pooled; shaded area is mean $\pm$ SD) at (A) Exmouth, (B) Shark Bay, (C) Perth Zone, (D) Geographe Bay, and (E) South Coast. Pre-heatwave years are 1981/1982–2009/2010, except for Geographe Bay which are 2001/2002–2009/2010.

Bay, warm conditions continued in 2014/2015 and 2015/2016, when spring temperatures were higher than in 2010/2011.

Catch and Catch Rate Trends

In Exmouth Gulf, the nominal commercial catch rate of *S. schomburgkii* was variable but displayed no obvious directional trend between 1976 and 2017 (**Figure 4A**). There was a shift toward a higher number of crew per boat, which contributed to higher nominal catch rates in the mid-2000s. The targeted

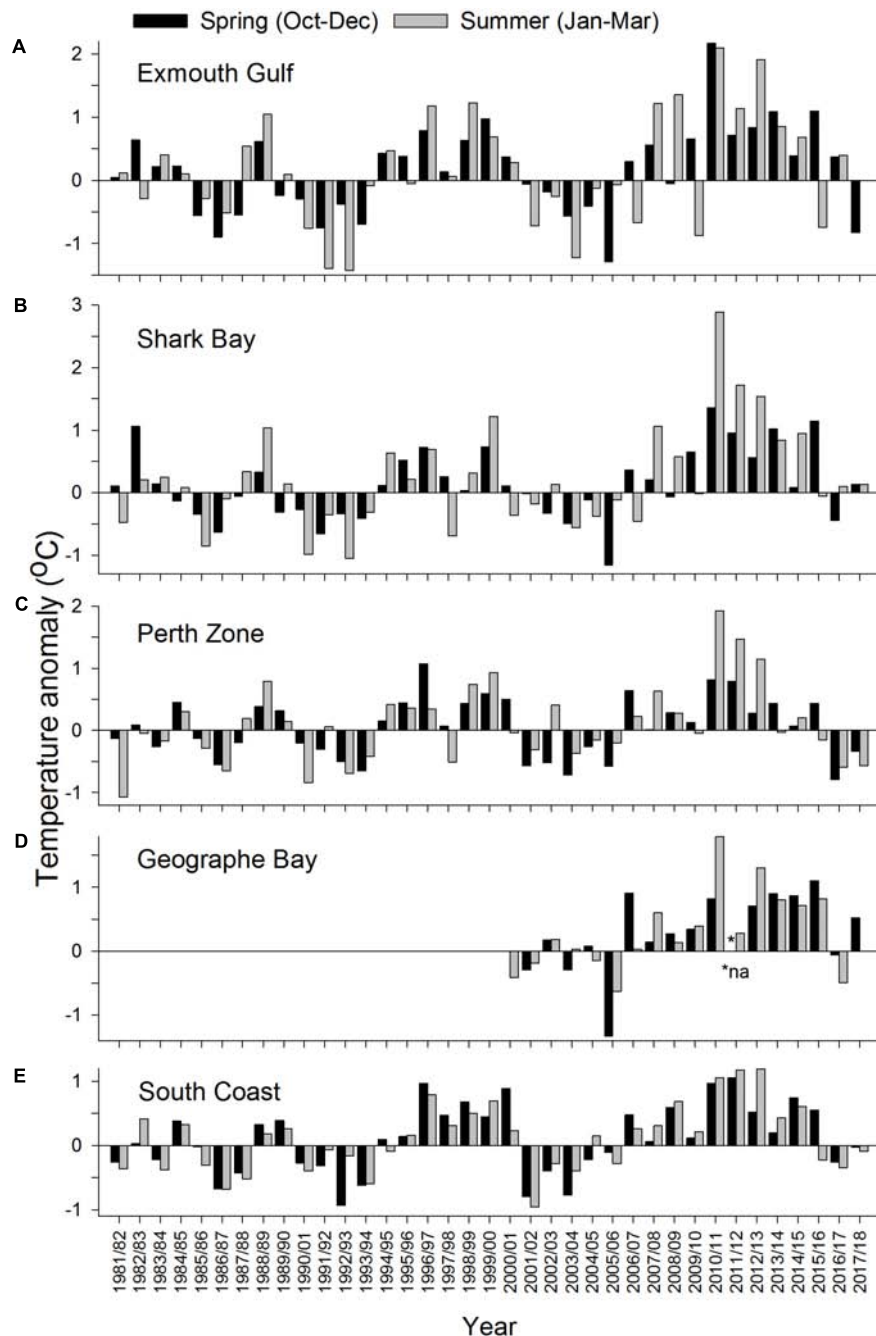


FIGURE 3 | Anomalies in mean ocean temperature during spring (October–December) and summer (January–March) at **(A)** Exmouth, **(B)** Shark Bay, **(C)** Perth Zone, **(D)** Geographe Bay, and **(E)** South Coast.

catch rate (which was standardized for crew number) followed a declining trend during 1990–2017 (**Figure 5A**). From a peak in 1994, it gradually declined to low levels during 2012–2014, then increased slowly until 2017. The targeted catch rate was also relatively low in 2001.

In Shark Bay, the nominal commercial catch rate was stable from the mid-1960s until 1991, then followed an increasing trend until 2017, including a pronounced peak in 2013 (**Figure 4B**).

After 1991, there was a shift toward the use of larger nets, which contributed to the rise in nominal catch rates. During 1990–2017, the targeted catch rate (which was standardized for net length) varied, but displayed no clear directional trend. There was a relatively small peak in the targeted catch rate in 2013 (**Figure 5B**).

In the Perth Zone, the commercial catch of *S. schomburgkii* in the Swan-Canning Estuary was negligible prior to 2000. The

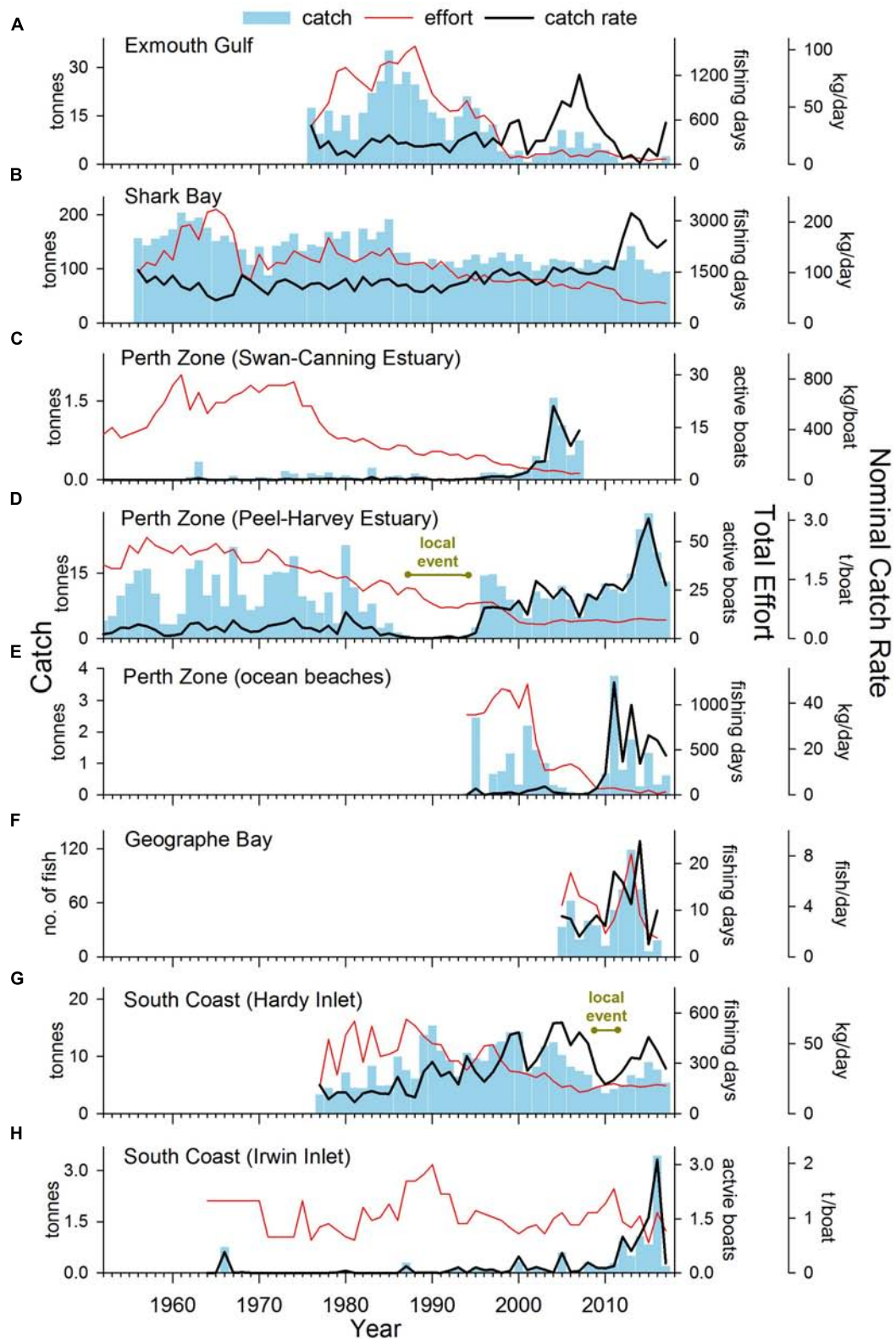


FIGURE 4 | Total annual catch, effort, and nominal catch rates of *S. schomburgkii* for commercial fisheries in (A) Exmouth Gulf, (B) Shark Bay, (C) Perth Zone (Swan-Canning Estuary), (D) Perth Zone (Peel-Harvey Estuary), (E) Perth Zone (ocean beaches), (G) South Coast (Hardy Inlet) and (H) South Coast (Irwin Inlet), and (F) recorded by a recreational fisher on ocean beaches in Geographe Bay. “Year” refers to calendar years except for (E–G) which are fiscal years.

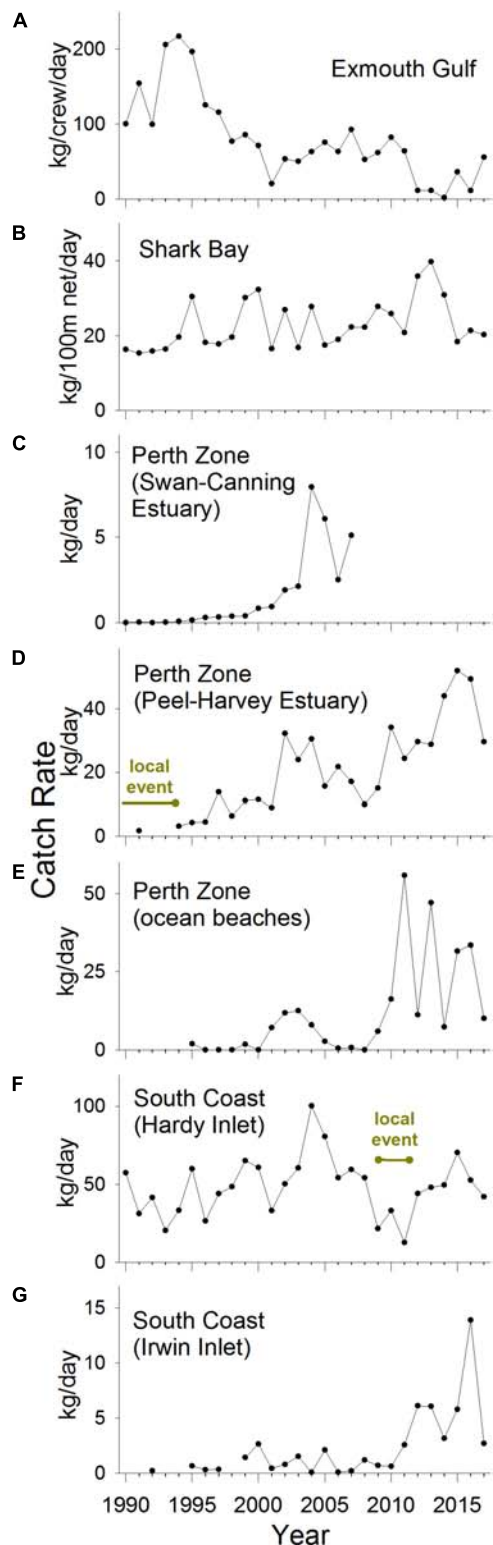


FIGURE 5 | Targeted annual commercial catch rates of *S. schomburgkii*, 1990–2017, in (A) Exmouth Gulf, (B) Shark Bay, (C) Perth Zone (Swan-Canning Estuary), (D) Perth Zone (Peel-Harvey Estuary), (E) Perth Zone (ocean beaches), (F) South Coast (Hardy Inlet), and (G) South Coast (Irwin Inlet). “Year” refers to calendar years except for (E,F) which are fiscal years.

nominal and targeted catch rates both abruptly increased after 2000 to peak in 2004 and remained relatively high until 2007 when this fishery ceased (Figures 4C, 5C). In the Peel-Harvey Estuary, the nominal commercial catch rate followed a gradual increasing trend from 1952 until 2013, except during 1987–1994 when it was almost zero (Figure 4D). The nominal catch rate peaked sharply during 2014–2016, then declined in 2017. The targeted catch rate followed an overall increasing trend during 1990–2017, including two localized peaks during 2002–2004, and 2015–2016 (Figure 5D). On ocean beaches in the Perth Zone, the nominal commercial catch rate was relatively low until 2009/10, then increased abruptly in 2011/2012 and remained relatively high until 2017/2018 (Figure 4E). The targeted catch rate was negligible until 2000/2001, increased to a small peak in 2003/2004 then returned to zero (Figure 5E). The targeted catch rate increased sharply to peak in 2011/2012, then remained relatively high until 2017/2018.

In Geographe Bay, the recreational logbook fisher reported his highest catch of *S. schomburgkii* in 2013/2014 (Figure 4F). His catch rate was relatively high during 2011/2012–2014/2015, compared to other years (Figure 4F).

On the South Coast, the nominal commercial catch rate in Hardy Inlet steadily increased during 1977/1978–2008/2009, then fell during 2009/2010–2012/2013, before returning to relatively high levels (Figure 4G). The targeted catch rate increased slightly during 1990/1991–2008/2009, fell during 2009/2010–2011/2012, then returned to pre-2009/2010 levels in subsequent years (Figure 5F). In Irwin Inlet, the commercial catch of *S. schomburgkii* was typically zero until 1986, then relatively low until 2011 (Figure 4H). The nominal and targeted catch rates in Irwin Inlet were both relatively low until 2011, then increased sharply to a peak in 2016, then fell in 2017 (Figures 4H, 5G).

Age Composition and Recruitment Variability

The age composition of the commercial catch of *S. schomburgkii* in Shark Bay was sampled in 2014. The ages of both females and males ranged from 1 to 9 years at this site. There was no evidence of recruitment variation, i.e., no obviously strong or weak year classes (Figure 6A).

In the Perth Zone, the age composition of the commercial catch was sampled in the Peel-Harvey Estuary in 2015 and 2016. Recreational catches were sampled in 2016 in this estuary and in ocean waters. At this location the ages of females ranged from 1 to 9 years, while males ranged from 1 to 8 years. In all samples a strong year class, which was aged 4 years in 2015 and 5 years in 2016, was evident (Figures 6B,C). This age class was estimated to have been spawned during summer 2010/2011.

In Geographe Bay, the age composition of the commercial catch was sampled in 2016 and 2017. Ages of females ranged from 1 to 10 years, while males ranged from 2 to 12 years. The 2010/2011 year class was relatively strong in 2016 (then aged 5 years) and again in 2017 (aged 6 years) (Figures 6D,E). The 2011/2012 year class (aged 4 years in 2016, 5 years in 2017) was relatively weak. Despite not being fully selected by the fishing

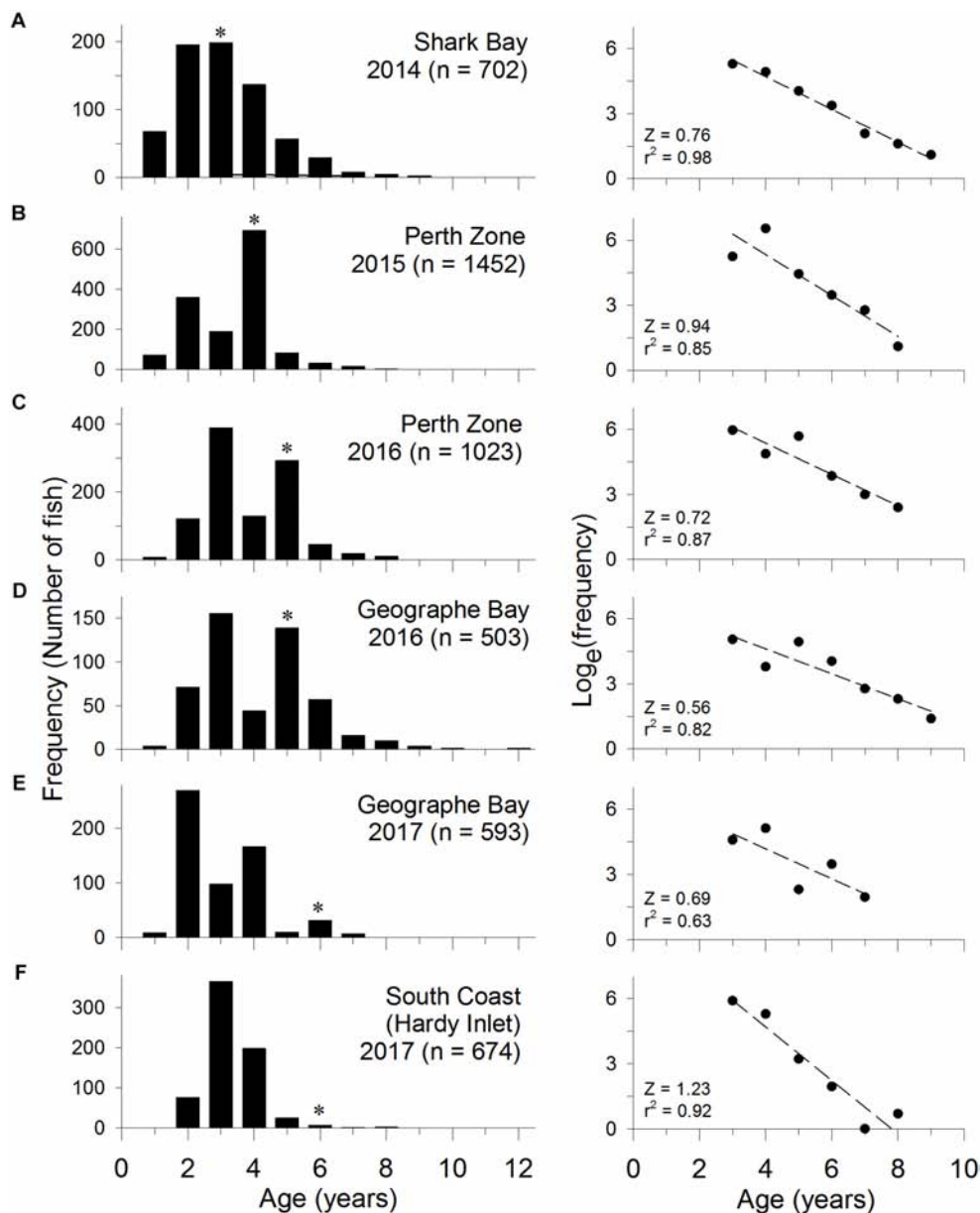


FIGURE 6 | Age frequency distribution of *S. schomburgkii* in fishery catches sampled at (A) Shark Bay in 2014, (B) Perth Zone in 2015, (C) Perth Zone in 2016, (D) Geographe Bay in 2016, (E) Geographe Bay in 2017, and (F) South Coast (Hardy Inlet only) in 2017. (*year class spawned during 2010/2011). Raw frequencies shown in left column and natural log transformed values in right column, with linear regression fitted to fully selected ages.

gear, the 2014/2015 year class (age 2 years) was the most abundant age group in 2017, which suggests that it was relatively strong (Figure 6E). Overall, there was evidence of more variability in annual recruitment strength at this location than Shark Bay or the Perth Zone.

On the South Coast, the age composition of commercial and recreational catches were sampled in Hardy Inlet in 2017. Females ranged from 1 to 6 years, and males from 2 to 8 years. Catches in Hardy Inlet were dominated by fish aged 4 years or less, which were spawned in 2012/2013 or later (Figure 6F). The proportion of older fish (>4 years) was lower than at other sites. Due to the

truncated nature of the age composition, it was not possible to discern the relative strength of any age classes in Hardy Inlet.

Monthly Spawning Trends at Each Latitude

At latitude 26°S (Shark Bay), almost all gonads of *S. schomburgkii* were collected during May, June, August, or September. Only 9 fish (all male) were collected outside these months. Male and female mean GSI values at 26°S were relatively high in August–September and low in the other sampled months (Figure 7A).

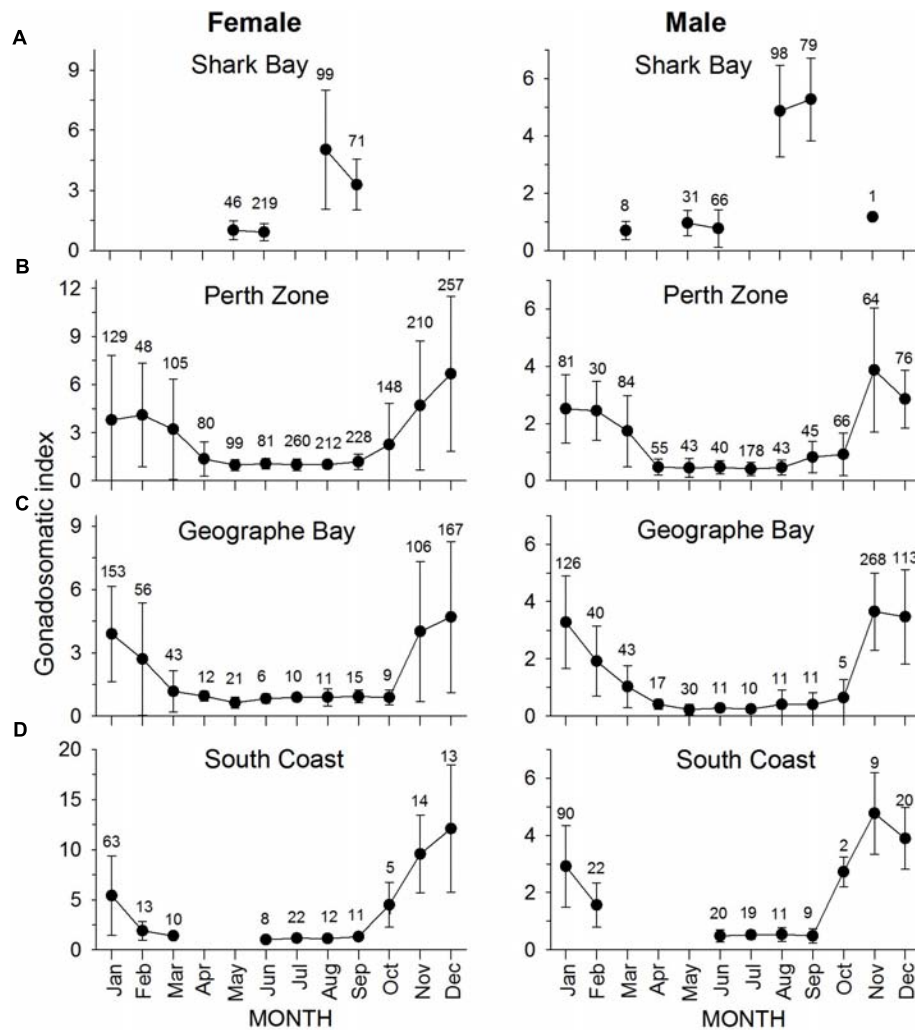


FIGURE 7 | Monthly mean ($\pm$ SD) gonadosomatic index for female (left column) and male (right column) *S. schomburgkii* in (A) Shark Bay, (B) Perth Zone, (C) Geographe Bay, and (D) South Coast. Each data point is labeled with number of fish sampled.

At latitude 32°S (Perth Zone) and 33.5°S (Geographe Bay), gonads were collected in every month. Mean GSI values were elevated from November to March at 32°S, and from November to February at 33.5°S (Figures 7B,C). At latitude 34.5°S (South Coast), gonads were collected in all months except April and May. GSI values at 34.5°S were relatively high for both sexes from November to January, with some relatively high values for males also observed in February and October (Figure 7D).

DISCUSSION

Evidence for Poleward Shift by *S. schomburgkii*

There is evidence of a multi-decadal, poleward shift in the center of abundance of *S. schomburgkii* in WA, including a gradual increase in abundance in the southern part of its range since the 1950s, stable abundance in the center (also since the 1950s), and

a more recent decline in abundance at the northern edge of its range since 1990.

In WA, intermittent commercial fishing records for *S. schomburgkii* commence around the start of the 20th century and, in combination with anecdotal reports, provide good information about the historical distribution of this species. Records of commercial “whiting” catches that are almost certainly *S. schomburgkii* are available from 1899 in the Peel-Harvey Estuary and from 1904 in estuaries around Albany (Lenanton, 1984). “Whiting” was reported to be relatively abundant in the 1920s in Shark Bay (Lenanton, 1970) and the 1950s in Geographe Bay (Gaynor et al., 2008). Specific catches of *S. schomburgkii* are recorded from south coast estuaries since the 1940s (Lenanton, 1984). Thus *S. schomburgkii* has occupied its current latitudinal range in WA (i.e., 22–35°S) since at least the 1940s and probably much earlier.

Of the sites examined in this study, Shark Bay is the closest to the center of the species range. Shark Bay hosts the largest

commercial fishery for *S. schomburgkii* and has consistently yielded relatively large annual catches since it commenced in the 1940s (Lenanton, 1970). Apart from a period of overfishing in the early 1960s (Lenanton, 1970), there is no evidence of major changes in abundance of *S. schomburgkii* in Shark Bay since records commenced.

About 700 km to the south, fishery trends in the Peel-Harvey and Swan-Canning Estuaries provide long-term records of abundance in the Perth Zone. These data indicate a gradual rise in abundance of *S. schomburgkii* since the 1950s. In adjacent ocean waters, fishery records are limited (commencing in 1995) but these also follow an increasing trend.

At the southern edge of the species range, early recorded catches of *S. schomburgkii* in various estuaries on the South Coast of WA were typically small and infrequent, indicating relatively low historical abundance in this region (Lenanton, 1984). In Hardy Inlet, which currently yields the largest commercial and recreational fishery catches of *S. schomburgkii* on the south coast, this species was reported to be rare or absent in the 1940s and 1950s (“there were no yellowfin whiting to be caught” C. Price, retired commercial fisher, in Gaynor et al., 2008). By 1974/1975, when commercial catch records commence, *S. schomburgkii* had become relatively abundant in Hardy Inlet (Lenanton, 1977). The commercial catch rate indicates a steady increase in the abundance of *S. schomburgkii* in this estuary between the 1970s and the late 2000s. Limited observations of the recreational fishery in Hardy Inlet also suggest an increase. In 1974, *S. schomburgkii* was estimated to be the most common species retained by recreational fishers, comprising 42% of the total recreational catch in this estuary (Caputi, 1976). By 2005, the species was estimated to comprise 58% of the recreational catch in this estuary (Prior and Beckley, 2007), suggesting a further increase in abundance. In Irwin Inlet, located about 180 km southeast of Hardy Inlet, the earliest recorded catches of *S. schomburgkii* were in 1946, but the catch rate suggests abundance was very low until 1990, and then began to gradually rise.

The increase in abundance of *S. schomburgkii* at high latitudes is not restricted to WA. There is also evidence of increasing abundance in South Australian waters, where commercial catch rates have steadily increased since 1990, following a similar trend to WA catch rates at the same latitudes (33–35°S) (Steer et al., 2018).

After the 2010/2011 MHW, the southward shift of *S. schomburgkii* temporarily accelerated. At the northern edge of the range, abundance in Exmouth Gulf abruptly declined to a very low level as indicated by historically low catch rates during 2012–2014. In the southern half of the range, all sites examined in this study (except Hardy Inlet, but see section “Importance of Habitat” discussion below for reasons why) experienced a major spike in abundance of *S. schomburgkii* after the MHW. For example, catch rate trends implied an approximately twofold increase in abundance in the Peel-Harvey Estuary, and a 10-fold increase in Irwin Inlet. Toward the center of the range, in Shark Bay, *S. schomburgkii* abundance also briefly increased after the MHW, as suggested by a peak in the catch rate in 2013. However,

the magnitude of the increase was less than at southern sites. After the MHW, fishery trends suggested that abundances at each site returned to levels consistent with the long-term trends in that area.

Reproductive Output Is Controlled by Ocean Temperature

The poleward distributional shift of *S. schomburgkii* (both long-term and during the MHW) can be largely explained in terms of changes in reproductive output at each latitude in response to rising ocean temperatures. Field observations in WA indicate that spawning by *S. schomburgkii* is associated with a temperature range of approximately 20–26°C (Hyndes and Potter, 1997; Coulson et al., 2005; this study). The same temperature range has also been indicated for spawning by *S. ciliata* and *S. japonica*, which are morphologically and ecologically similar (Hotta et al., 2001, 2003; Payne et al., 2016). *Sillago* species in temperate and subtropical regions predominantly spawn in spring and/or summer, suggesting that rising water temperature and/or photoperiod may be environmental cues for gonad maturation (Tongnunui et al., 2006; Kendall and Gray, 2009; Wang et al., 2010; Lowerre-Barbieri et al., 2011). The onset of spawning (i.e., actual release of gametes) in these species is likely to be primarily controlled by temperature (Lee, 1981; Lee and Hirano, 1985; Hotta et al., 2001; Tongnunui et al., 2006). Thus, we propose for *S. schomburgkii* that (i) rising temperature and/or photoperiod is required for gonad development and (ii) spawning is restricted to a temperature range of approximately 20–26°C.

The duration of the spawning period of *S. schomburgkii* declines from latitude 26°S to 35°S, consistent with the declining gradient in ocean temperatures over the same range. At 26°S (Shark Bay), spawning primarily occurs over a 5-month period from August to December, with small amounts of spawning in other months (Coulson et al., 2005; this study). At 32°S (Perth Zone), spawning also occurs over a 5-month period, from November to March, but with little evidence of spawning in other months (this study). Further south, the spawning period commences at approximately the same time but is progressively shorter with increasing latitude, i.e., November–February at 33.5°S (Geographe Bay) and November–January at 34–35°S (South Coast) (this study). Additionally, *S. schomburgkii* populations in South Australia (latitude 33–35°S) have a spring/summer spawning period of 3 or 4 months (Ferguson, 1999, 2000), similar to WA populations at the same latitudes.

In Shark Bay, SST typically remains within the preferred range (20–26°C) all year, potentially facilitating spawning throughout the year. In contrast, SST at the southern edge of the species range rarely exceeds 20°C, and at the northern edge is often above 26°C during spring/summer, limiting spawning potential in both cases. During the 2010/11 MHW, significantly higher spring/summer SST in each region could have dramatically increased spawning activity at the southern edge, and reduced it at the northern edge. Relatively warm summer SST in 2011/2012 and 2012/2013, particularly on the South Coast, could have altered spawning

activity in these years too. The dramatic 10-fold increase in abundance in Irwin Inlet may be the product of three consecutive years of elevated summer temperatures and enhanced local spawning success.

It is noteworthy that the 5-month spawning period in the Perth Zone observed in our study is longer than the 3-month spawning period reported from the same area in the early 1990s (Hyndes and Potter, 1997). This difference is consistent with the substantially higher summer SST in this Zone during our study.

Localized Variations in Recruitment Linked to Local Ocean Temperatures

The evidence presented here indicates that the changes in *S. schomburgkii* abundance that occurred in each region after the 2010/2011 MHW were primarily due to variations in juvenile recruitment strength in each region and not due to movement between regions by older fish. In each fishery, a lag of one or more years between the MHW and the catch rate response indicates that older fish did not migrate in/out of the fishery area during, or immediately after, the MHW. In each fishery, the magnitude of the lag was consistent with the age at which *S. schomburgkii* becomes vulnerable to capture by their respective fishing gears. This suggests that the increase (or decrease) in each catch rate was due to strong (or weak) recruitment into each fishery by the year class that was spawned during 2010/2011. Thus, the catch rate trends imply that the MHW led to weaker recruitment at the northern edge of the range, but led to stronger recruitment in southern areas.

The age composition of *S. schomburgkii* sampled during 2015–2017 provides further evidence of stronger recruitment by the 2010/2011 year class in the southern part of the range. In the Perth Zone and Geographe Bay, fish spawned during the MHW were two or three times more abundant than expected, based on the relative strengths of each age class. The recruitment of the 2010/2011 year class into local fisheries would account for the abrupt increase in their catch rates 1–3 years later, and for the maintenance of elevated catch rates for several years while this year class survived in the population.

In Shark Bay, toward the center of the range, the age composition sampled in 2014 provided no indication of strong recruitment by the 2010/2011 year class and was similar to the age composition prior to the MHW [sampled in 2001–2003 (P. Coulson, unpubl. data)]. The age data are inconsistent with the catch rate trends at this site, which suggested an increase in abundance after the MHW. However, the abundance increase was relatively small compared to the increases at southern sites, so there may have been a minor change in recruitment that was not detected in the age composition at Shark Bay.

The unique temperature regime in Geographe Bay provides an explanation for the stronger variability in annual recruitment by *S. schomburgkii* observed here compared to other sites. Geographe Bay lies outside the influence of the warm Leeuwin current (LC), which flows poleward along the west coast and extends eastward along the south coast (Feng et al., 2003). The LC has a distinct seasonal cycle, with southward transport

reaching a maximum during autumn/winter (April–August), thus maintaining relatively warm ocean temperatures along the south coast in winter (Smith et al., 1991; Feng et al., 2003). The LC bypasses Geographe Bay and, as a consequence, the Bay typically experiences colder winter temperatures than the Perth Zone and South Coast (Fahrner and Pattiaratchi, 1995). Additionally, the cold capes current (CC) exerts a stronger influence in Geographe Bay, which can cause summer temperatures here to be significantly cooler than nearshore waters in the Perth Zone (Fahrner and Pattiaratchi, 1995; Pearce and Pattiaratchi, 1999). The CC originates near Cape Leeuwin (34°S) as cold, upwelled water, which flows into Geographe Bay and then northward against the coast in summer. Hence the fish populations in Geographe Bay and Perth are exposed to quite different temperature regimes, despite being separated by an alongshore distance of only ~100 km, which is likely to result in differences in the duration of spawning and strength of local recruitment. Relatively weak recruitment in 2011/2012 in Geographe Bay compared to Perth was consistent with the summer temperature anomalies at each site, i.e., low in Geographe Bay and high in Perth.

Larval Dispersal or Self-Recruitment?

Broadly speaking, there are two mechanisms by which an increase in juvenile recruitment at higher latitudes could potentially occur: (i) an influx of remotely spawned recruits dispersed by ocean currents (“larval dispersal”), or (ii) an increase in the production of locally spawned recruits (“self-recruitment”). All lines of evidence suggest that enhanced self-recruitment by populations at higher latitudes, and not southward larval dispersal, is facilitating the gradual poleward shift by *S. schomburgkii*.

Overall, the location and the timing of spawning by *S. schomburgkii* greatly limits the potential for alongshore dispersal of their larvae. On the west coast of WA, alongshore flow in nearshore waters is not driven by the LC, but rather, is largely driven by the prevailing winds which result in primarily northward flows between September and February and no dominant direction in other months (Fahrner and Pattiaratchi, 1995; Woo et al., 2006; Zaker et al., 2007; Gallop et al., 2012; Ruiz-Montoya and Lowe, 2014). Thus, under typical oceanographic conditions, there is limited potential for the poleward dispersal of eggs or larvae of *S. schomburgkii* that are primarily spawned in spring/summer. At this time, larvae spawned in nearshore waters are likely to be retained within their natal region, with a low probability of being advected large (>200 km) distances alongshore, either northward or southward (assuming a larval duration of 3–4 weeks; Feng et al., 2010; Berry et al., 2012). The very shallow (mostly <2 m), sheltered habitats occupied by *S. schomburgkii* further reduces the likelihood of larval dispersal. Along the west coast, this habitat type is concentrated within marine embayments, such as Exmouth Gulf, Shark Bay and Geographe Bay, that are sheltered from the direct influence of alongshore currents, and where larval retention rates are high (Fahrner and Pattiaratchi, 1995; Nahas et al., 2003; Feng et al., 2010; Breheny et al., 2012).

The region from Cape Naturaliste to Cape Leeuwin is a prominent geographical feature that acts as a partial barrier to dispersal from the west coast to the south coast, particularly for summer-spawned larvae (Berry et al., 2012). The CC originates in this area during spring and flows into Geographe Bay, potentially capturing larvae that have been advected from northern areas (Pearce and Pattiaratchi, 1999). On the south coast, Hardy Inlet lies in the shadow of Cape Leeuwin, beyond the direct influence of the southward flowing LC. The probability of larvae from “upstream” spawning areas on the west coast being entrained in the LC and then recruiting into Hardy Inlet is particularly low (Feng et al., 2010; Berry et al., 2012). Despite this isolation, there has been a gradual increase in the abundance of *S. schomburgkii* in Hardy Inlet over many decades, which suggests that self-recruitment is maintaining this population.

The accelerated shift during the 2010/2011 MHW was probably due to greatly enhanced self-recruitment at higher latitudes, but may also have been supplemented by atypical larval dispersal. In 2010/2011, three unusual factors combined to greatly increase the likelihood of southward advection of *S. schomburgkii* larvae. First, the early onset of the LC provided atypical southward transport in spring and summer along the outer shelf (Feng et al., 2013; Pearce and Feng, 2013). Secondly, at higher latitudes, suppression of the CC resulted in unseasonal southward flows over the inner shelf in February/March (Pearce and Feng, 2013; Benthuyssen et al., 2014). Thirdly, at higher latitudes, an extension of the spawning period due to warmer nearshore temperatures may have increased the production of larvae in late summer/early autumn when the LC velocity was peaking. Together, these conditions provided an unprecedented opportunity for southward advection of *S. schomburgkii* larvae along the west coast in 2010/2011. The larvae of numerous tropical species, including summer-spawning fish, were dispersed to higher latitudes in 2010/2011 (Pearce et al., 2011; Wernberg et al., 2013; Caputi et al., 2014; Cure et al., 2017; Lenanton et al., 2017), which suggests that the southward advection of *S. schomburgkii* at this time is possible.

The Importance of Habitat Availability

In WA, further increases in abundance of *S. schomburgkii* at higher latitudes may be limited by the availability of suitable habitats, particularly along the south coast. This coastline is subject to high wave energy and so the shallow, sheltered habitats favored by *S. schomburgkii* are largely restricted to estuaries. However, the quality and accessibility of estuarine habitats in south-western Australia is predicted to decline in future due to the impacts of climate change and catchment processes (Hallett et al., 2018). In particular, declining streamflow and ongoing eutrophication of estuaries are likely to strongly affect *S. schomburgkii*, as already demonstrated in several estuaries.

In the Peel-Harvey Estuary, commercial catches of *S. schomburgkii* almost ceased during 1986–1994, coinciding with a period of intense algal blooms in this estuary due to eutrophication (Brearley, 2005). The abrupt decline in catch was partly due to fishing nets becoming clogged with algae and difficult to deploy in many parts of the estuary (Lenanton et al., 1985). However, the abundance of *S. schomburgkii* probably

also declined as benthic habitats within the estuary deteriorated. Firstly, there was reduced availability of bare sand habitat due to an increase in macro-algae. Secondly, hypoxia in bottom waters led to fish kills and presumably reduced the availability of benthic invertebrate prey (Potter et al., 1983). In 1994, the construction of an artificial entrance (the “Dawesville Channel”) led to increased tidal exchange, higher salinity, reduced nutrient loads, and a reduction in algal blooms in the estuary basin (Kelsey et al., 2011). By 1996, commercial catches of *S. schomburgkii* had resumed.

In Hardy Inlet, the commercial catch of *S. schomburgkii* started to decline in late 2009 and remained at a relatively low level until 2013. As a consequence of declining streamflow and eutrophication, nuisance blooms of macroalgae and cyanobacteria occurred in this estuary prior to and during 2010, which reduced the quantity and quality of bare sand habitat (White, 2012). Very few *S. schomburgkii* were observed in mid-2010, and their abundance in Hardy Inlet had reportedly been declining for several years prior to 2010 (T. Price, commercial fisher, pers. comm.). Additionally, the sand bar at the entrance (normally permanently open) temporarily closed in 2010 after low winter rainfall (White, 2012; Brearley, 2013), preventing juvenile recruitment into the estuary. Juvenile *S. schomburgkii* use this estuary, as well as adjacent coastal habitats, as a nursery area (Lenanton, 1977; Valesini et al., 1997). Hence, unfavorable conditions prior to and during 2010–2012 may have encouraged adult fish to emigrate from Hardy Inlet, and restricted recruitment into this estuary. The age composition sampled in 2017 had a low representation of fish spawned prior to 2012/13, which is consistent with poor recruitment during 2010–2012.

CONCLUSION

In the coastal waters of WA, *S. schomburgkii* occurs over a very wide latitudinal range (22 to 35°S) which it has occupied for at least the past century. Since the 1950s, there is evidence of a gradual, poleward shift in the center of *S. schomburgkii* abundance, coinciding with long-term ocean warming off South-Western Australia. The distributional shift briefly accelerated after the 2010/2011 MHW, further implicating temperature as the key driver.

Multiple lines of evidence suggest the range shift has primarily occurred via changes in spawning success by resident fish in each area (i.e., self-recruitment). There is no evidence of alongshore migration by adults of this species, including during the MHW, and the alongshore dispersal of larvae is probably very limited in most years. Unprecedented conditions during the MHW could have resulted in some atypical larval dispersal, and this may have also contributed to the accelerated range shift.

Sillago schomburgkii appears to spawn within a temperature range of approximately 20–26°C. Temperatures are typically in this range for several months in northern areas, but only briefly during the height of summer in southern areas. Being a multiple batch spawner, the length of the spawning period is a key factor determining the annual reproductive output of *S. schomburgkii*. During the 2010/2011 MHW, ocean temperatures were up to 5°C

above average in some nearshore areas (Feng et al., 2013). As a consequence, it is likely that the spawning period was reduced in the north but extended in the south, which would explain the recruitment trends observed in each area. The age composition and fishery catch rates examined in this study provided evidence of exceptionally strong recruitment by the 2010/2011 year class in southern areas, but not in northern areas.

The dramatic response of *S. schomburgkii* to the 2010/2011 MHW focused attention on the significant, yet previously unrecognized, distributional shift by this species. It also helped to elucidate the mechanism by which this shift is occurring. The insights gained about the effects of ongoing ocean warming on *S. schomburgkii* have important implications for the commercial and recreational fisheries that harvest this valuable species. In future, fisheries at lower latitudes are expected to suffer a decline in availability of this species while those at higher latitudes

(32–35°S) are expected to benefit from increasing availability, although gains on the south coast could be negated by the loss of critical estuarine habitats.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

KS conceived the study, prepared the manuscript, and analyzed the data and aged fish. CD and JB collected the fish and conducted the laboratory processing and ageing of fish.

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Spatial Variability in the Resistance and Resilience of Giant Kelp in Southern and Baja California to a Multiyear Heatwave

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In 2014–2016 the west coast of North America experienced a marine heatwave that was unprecedented in the historical record in terms of its duration and intensity. This event was expected to have a devastating impact on populations of giant kelp, an important coastal foundation species found in cool, nutrient rich waters. To evaluate this expectation, we used a time series of satellite imagery to examine giant kelp canopy biomass before, during, and after this heatwave across more than 7 degrees of latitude in southern and Baja California. We examined spatial patterns in resistance, i.e., the initial response of kelp, and resilience, i.e., the abundance of kelp 2 years after the heatwave ended. The heatwave had a large and immediate negative impact on giant kelp near its southern range limit in Baja. In contrast, the impacts of the heatwave were delayed throughout much of the central portion of our study area, while the northern portions of our study area exhibited high levels of resistance and resilience to the warming, despite large positive temperature anomalies. Giant kelp resistance throughout the entire region was most strongly correlated with the mean temperature of the warmest month of the heatwave, indicating that the loss of canopy was more sensitive to exceeding an absolute temperature threshold than to the magnitude of relative changes in temperature. Resilience was spatially variable and not significantly related to SST metrics or to resistance, indicating that local scale environmental and biotic processes played a larger role in determining the recovery of kelp from this extreme warming event. Our results highlight the resilient nature of giant kelp, but also point to absolute temperature thresholds that are associated with rapid loss of kelp forests.

Keywords: giant kelp, resilience, Baja California (Mexico), heatwave, Southern California (United States)

INTRODUCTION

Extreme warming events in the ocean have been linked to habitat loss and major changes in the community structure and function of marine ecosystems (Johnson et al., 2011; Wernberg et al., 2013; Smale et al., 2019). These events are often large scale phenomenon that span 100 s to 1000 s of km (Oliver et al., 2018), which can result in spatially variable ecosystem responses

(Berkelmans et al., 2004; Edwards, 2004). Such spatial variability can arise from differences in physical and chemical ocean characteristics (e.g., temperature, nutrients, swell height) or biological processes (e.g., local adaptation, biotic interactions, dispersal, migration) within the affected region (e.g., Hughes et al., 2003; Wernberg et al., 2010). Characterizing spatial patterns in the response of ecosystems to large-scale disturbances such as heatwaves can provide insight into the processes and environmental thresholds that control these responses. A spatial approach can also help address the challenge of inferring ecological thresholds from large events that occur infrequently at a single locality (Turner et al., 2003).

Considerable insight into the ecological consequences of extreme warming events such as marine heatwaves can be gained by differentiating between ecosystem resistance (the initial response of the system to disturbance) and resilience (the ability of the system to recover after being disturbed; Hodgson et al., 2015). This is because different processes may control resistance and resilience, which can lead to variability in spatial patterns between the two metrics. For example, even if an ecosystem is initially sensitive to a disturbance, it may still exhibit high resilience, returning relatively quickly to its pre-disturbance state (Pimm, 1984).

Interactions between marine heatwaves and other physical stressors can also control spatial patterns of resistance and resilience. In the northeastern Pacific, severe El Niño conditions are often associated with positive sea surface temperature anomalies and large wave disturbance events (Storlazzi and Griggs, 1996; Chavez et al., 2002). Both of these factors can have negative effects on the growth and survival of the giant kelp *Macrocystis pyrifera*, an important coastal foundation species (Graham et al., 2007; Castorani et al., 2018; Miller et al., 2018). Warm sea temperatures are typically associated with reduced upwelling and nutrient limited conditions in Southern California, United States, and Baja California, Mexico (Zimmerman and Kremer, 1984), and heat stress can itself cause mortality in giant kelp (Clendenning, 1971; Rothäusler et al., 2011). In addition, large waves can physically remove giant kelp from the seafloor. During particularly strong El Niño events in 1982/1983 and 1997/1998, large waves and warm, nutrient poor waters resulted in widespread loss of giant kelp throughout its range in the United States and Mexico (Dayton and Tegner, 1989; Edwards and Estes, 2006). These events led to northward contractions of the distribution of giant kelp in Baja California (Edwards and Hernández-Carmona, 2005), and altered the community structure of kelp forests in Southern California (Dayton et al., 1992). However, there was substantial spatial variability in the resilience of giant kelp following these events. For example, after the 1997–1998 El Niño, recovery time for sites across southern and Baja California ranged from 6 months to several years (Edwards and Estes, 2006).

Some of this spatial variability in the response of giant kelp to heatwaves may be due to local adaptation to environmental conditions, a process which has been observed in a number of marine species (Howells et al., 2011; Sanford and Kelly, 2011; Bennett et al., 2015). The broad geographic distribution of giant kelp spans large environmental gradients (Graham et al., 2007),

and the scale of these gradients is much larger than the scales of giant kelp dispersal (Reed et al., 2006). Limited connectivity among distant populations constrains the homogenizing effects of gene flow, and creates conditions suitable for population level selection (Alberto et al., 2010, 2011; Johansson et al., 2015). Empirical evidence suggests that kelp populations are adapted to local nutrient conditions, as Kopczak et al. (1991) demonstrated that plants from nutrient limited locations (Catalina Island, CA, United States) exhibited more efficient nitrate uptake and assimilation than those from nutrient-rich areas (Monterey, CA, United States). There is also evidence of adaptation to thermal stress in the microscopic reproductive stages of giant kelp (Ladah and Zertuche-González, 2007). Local adaptation may create temperature or nutrient thresholds in populations that are relative to their local conditions, as opposed to all populations sharing a similar absolute threshold (Sanford and Kelly, 2011). If this is the case, then we would expect that spatial variability in the response of giant kelp to a heatwave would reflect relative SST variability, such as temperature anomalies. On the other hand, if there is a universal tolerance threshold for giant kelp, then absolute temperatures may better explain resistance and resilience.

Between 2014 and 2016, the west coast of North America experienced exceptional warming due to a sequence of climatic events (Di Lorenzo and Mantua, 2016). This phenomenon began in the winter of 2013/2014 as a persistent atmospheric ridge that led to abnormally high sea surface temperatures in offshore areas of the Northeastern Pacific (Bond et al., 2015). By the summer and fall of 2014 this warm water mass had spread to the coastal regions of North America and SST anomalies reached record highs in southern and Baja California (Di Lorenzo and Mantua, 2016). This warm anomaly was followed by one of the strongest El Niño events on record, which led to sustained positive SST anomalies through early 2016. This multiyear marine heatwave was associated with decreased primary productivity in the northeast Pacific and changes in the biological structure and composition of communities of fish, birds, and marine mammals (Di Lorenzo and Mantua, 2016). While SST anomalies were comparable to the 1982/1983 and 1997/1998 El Niño events, the 2014–2016 heatwave differed from these earlier events in that it was not associated with large wave disturbances, and the initial impacts of the warm anomaly on giant kelp forests and their associated communities in parts of Southern California were smaller than expected (Reed et al., 2016). However, it is unclear whether the effects of this heatwave were more pronounced or longer lasting in other parts of Southern California or Baja California.

Here we combine satellite data of kelp biomass and SST to examine the canopy dynamics of giant kelp across more than 7° of latitude in Southern California and Baja California before, during, and after the 2014–2016 marine heatwave. The unique conditions associated with this event provided us with an opportunity to examine the impacts of a severe marine heatwave on giant kelp biomass in the absence of confounding effects from large wave disturbances. Our primary goals were: (1) to characterize patterns of giant kelp resistance and resilience to the 2014–2016 marine heatwave across all of southern and Baja

California, and (2) to determine whether relative sea surface temperature anomalies or absolute sea surface temperature thresholds better predicted spatial variability in the resistance and resilience of giant kelp to the warming.

MATERIALS AND METHODS

Study Region

In the northeast Pacific giant kelp is distributed from Alaska to Baja Mexico (Graham et al., 2007). Our study area encompassed the distribution of giant kelp along the mainland coasts of Southern California, United States and Baja California, Mexico, spanning more than 7 degrees of latitude (approximately 1600 km) from Point Conception (34.5°N) to the southern range limit of giant kelp near Bahía Asunción (27.1°N). This southern portion of giant kelp's range is most likely to be impacted by high temperatures (Bell et al., 2015). We binned this region into sixteen 100 km coastline segments and examined variability in sea surface temperature and kelp canopy biomass in each of these segments. All offshore islands were excluded from our analysis to simplify binning and latitudinal comparisons. We chose 100 km as the length for coastline segments in our analyses because we were interested in regional scale responses of giant kelp to SST variability.

Sea Surface Temperature Variables

We obtained daily SST data between 1984 and 2018 for our study area from the National Climatic Data Center Optimal Interpolation Sea Surface Temperature product (Banzon et al., 2016). This 35-y dataset combined observations from satellite, ships, and buoys to create a daily global SST dataset at a 0.25° resolution. We created a daily SST time series for each 100 km coastline segment by averaging the pixels adjacent to the coastline along each segment.

These daily data were used to calculate time series of relative and absolute metrics of SST variability in each coastline segment. Daily SST values were averaged over each calendar month to produce a time series of mean monthly SST for each coastline segment. We calculated monthly SST anomalies as the difference between the mean value for a given month and the 35-year average (1984–2018) for that month. The number and duration of marine heatwaves were calculated as periods of five or more consecutive days when daily SST was greater than the 90th percentile based on our 35-year baseline (Hobday et al., 2016).

We used the above time series of relative and absolute metrics of SST variability to develop time series of annual metrics of SST variability for each coastline segment. The annual metrics that we calculated were the mean monthly SST anomaly, the total number of heatwave days, and the mean temperature of the warmest month of the year. Mean monthly anomaly and total number of heatwave days are relative measures of temperature variability, as these variables are based on temporal averages and percentiles. In contrast, mean temperature of the warmest month of the year characterizes absolute temperature variability. Instead of following the calendar year, we calculated these annual metrics for a “temperature year” (July 1–June 30)

so that the warmest months were positioned at the beginning of each year (e.g., temperature year 2014/2015 = July 1, 2014–June 30, 2015).

Spatiotemporal Variability in Giant Kelp Canopy Biomass

We used Landsat satellite imagery to estimate giant kelp canopy biomass across our study area at 30 m resolution on seasonal timescales from 2009 through 2018 following methods described in Cavanaugh et al. (2011) and Bell et al. (2018). The 30 m × 30 m pixels of kelp canopy biomass were binned into 100 km coastline segments to match the SST data. There were three coastline segments in the study region that historically contained very little kelp canopy (<0.1 km² of kelp canopy area), and these were removed from our analysis (hence, $n = 13$ coastline segments).

In order to control for differences in canopy biomass between coastline segments, we normalized the canopy biomass of each coastline segment by the maximum biomass observed in that segment from 2009 to 2018 to produce a time series of seasonal values that were bounded between 0 and 1. The normalized seasonal values of canopy biomass in each temperature year were averaged to produce a time series of annual normalized canopy biomass. This facilitated comparisons of canopy dynamics among the coastal segments.

Giant Kelp Resistance and Resilience

We defined the resistance and resilience of giant kelp to the 2014–2016 marine heatwave as a proportional change in canopy biomass, prior to the normalization described above, relative to a 5-year baseline period (2009–2013) that immediately preceded the heatwave. Heatwave resistance for each coastal segment was calculated as the proportion of the lowest annual average biomass during the heatwave (2014/2015–2016/2017) relative to the mean canopy biomass during the 5-year baseline period. Heatwave resilience of each coastal segment was calculated as the proportion of the average canopy biomass in 2017/2018 relative to the mean canopy biomass during the 5-year baseline period. Resistance and resilience were not correlated ($p = 0.33$; **Supplementary Figure S1**).

Statistical Analysis

We specified univariate regression models to examine the amount of variation in giant kelp resistance and resilience explained by the relative and absolute temperature metrics. Specifically, we modeled kelp resistance as separate functions of the average SST anomaly, maximum monthly SST, and total number of heatwave days calculated over the 2-year (2014/2015–2015/2016) duration of the heatwave (three models). Likewise, we modeled kelp resilience as separate functions of the SST anomaly, maximum monthly SST, and total number of heatwave days calculated both during (2014/2015–2015/2016) and after (2016/2017–2017/2018) the heatwave (six models). For each response variable (resistance or resilience), we used an AIC-based model comparison approach to assess which temperature variable(s) fit the data best (Burnham and Anderson, 2002).

Comparing temperature variables against one another using a single multiple regression model was not possible due to moderate to strong collinearity among some predictors.

Because kelp resistance data were continuous proportions (i.e., $0 < y < 1$), we used beta regression models with a Cauchy latent variable link function (Ferrari and Cribari-Neto, 2004). We used ordinary least squares (OLS) regression to estimate temperature effects on kelp resilience. We analyzed models in R 3.5.3 (R Core Team, 2019), using the package “betareg” (Cribari-Neto and Zeileis, 2010) for beta regression models. We assessed the significance of model predictors for OLS and beta regressions using *F*-tests and likelihood ratio tests, respectively (Ferrari and Cribari-Neto, 2004). We estimated the explanatory power of OLS models using R^2 and of beta regression models using a pseudo- R^2 metric (the squared correlation between the linear predictor and the link-transformed response; Ferrari and Cribari-Neto, 2004).

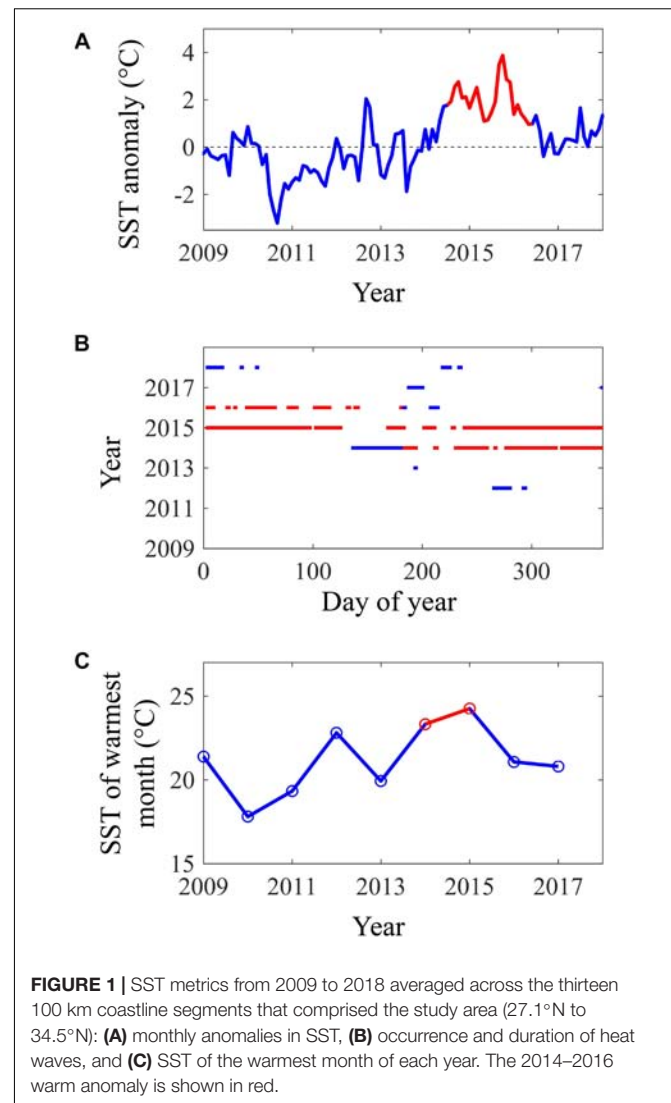
We checked for homogeneity of variance by plotting Pearson residuals against model predictions and individual predictors (Zuur et al., 2009, 2010; Zuur and Ieno, 2016). We ensured normality of residuals using histograms and quantile-quantile plots. We utilized the R packages “ape,” “geosphere,” and “ncf” (Paradis et al., 2004; Hijmans, 2016; Bjornstad, 2018) to check for spatial autocorrelation among model residuals using tests of Moran’s *I* (Moran, 1950) and visual inspection of spline correlograms. For all models, spatial autocorrelation was not detected ($p > 0.23$). Hence, all models satisfied assumptions of independent, homogeneous, and normally distributed Pearson residuals.

Our analyses consisted of several statistical tests, increasing the likelihood of false positives. Thus, we controlled the false discovery rate (i.e., the proportion of false positives among all significant hypotheses) using the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995; García, 2004). All reported *p* values are Benjamini–Hochberg adjusted.

RESULTS

Patterns in SST During and After the Warm Anomalies

The coasts of southern and Baja California experienced a period of exceptionally warm SST from summer 2014 to spring 2016 (Figure 1). July 2014 to June 2016 was the warmest 2-year period from 1984 to 2018 according to all three of our temperature metrics. During this period, monthly SST anomalies across our study region averaged 2.0°C and reached a high of 3.9°C in October 2015 (Figure 1A). Our study region as a whole experienced 542 heatwave days between July 2014 and June 2016, and so was in a heatwave state for 74% of this 2-year period (Figure 1B). Because of the extended nature of these heatwaves, we refer to this period as the 2014–2016 heatwave, even though it actually consisted of multiple heatwaves. However, there were brief periods during 2014–2016 when the heatwaves abated in the spring of 2015 and 2016 (Figure 1B). SST anomalies and heatwave days were slightly higher in the southern part of the study area, but this latitudinal pattern was relatively weak



(Figures 2A,B, 3A,B). There was more latitudinal variability in absolute temperatures. SST of the warmest month between July 2014 and June 2016 ranged from 21.1°C for the coastline segment that included Santa Barbara to 26.7°C for the Bahía Asunción segment. However, SST of the warmest month did not strictly follow latitude, and was slightly lower in northern Baja, $30.5 - 32^{\circ}\text{N}$ (23.3°C), than in Southern California, $32^{\circ}\text{N} - 33.5^{\circ}\text{N}$ (23.7°C ; Figure 4).

By the summer of 2016, SST returned to more normal conditions across our study area (Figures 2C, 4C). In 2016/2017 SST anomalies and heatwave days averaged 0.3°C and 21 days, respectively. The temperature of the warmest month similarly, declined across the study region from 2015/2016 to 2016/2017 (Figure 4C). However, temperature in the San Diego region (33°N) remained high (warmest month = 22.5°C) in 2016/2017 relative to all of the other coastline segments except the southernmost segment at Bahía Asunción (22.6°C). By comparison the temperature of the

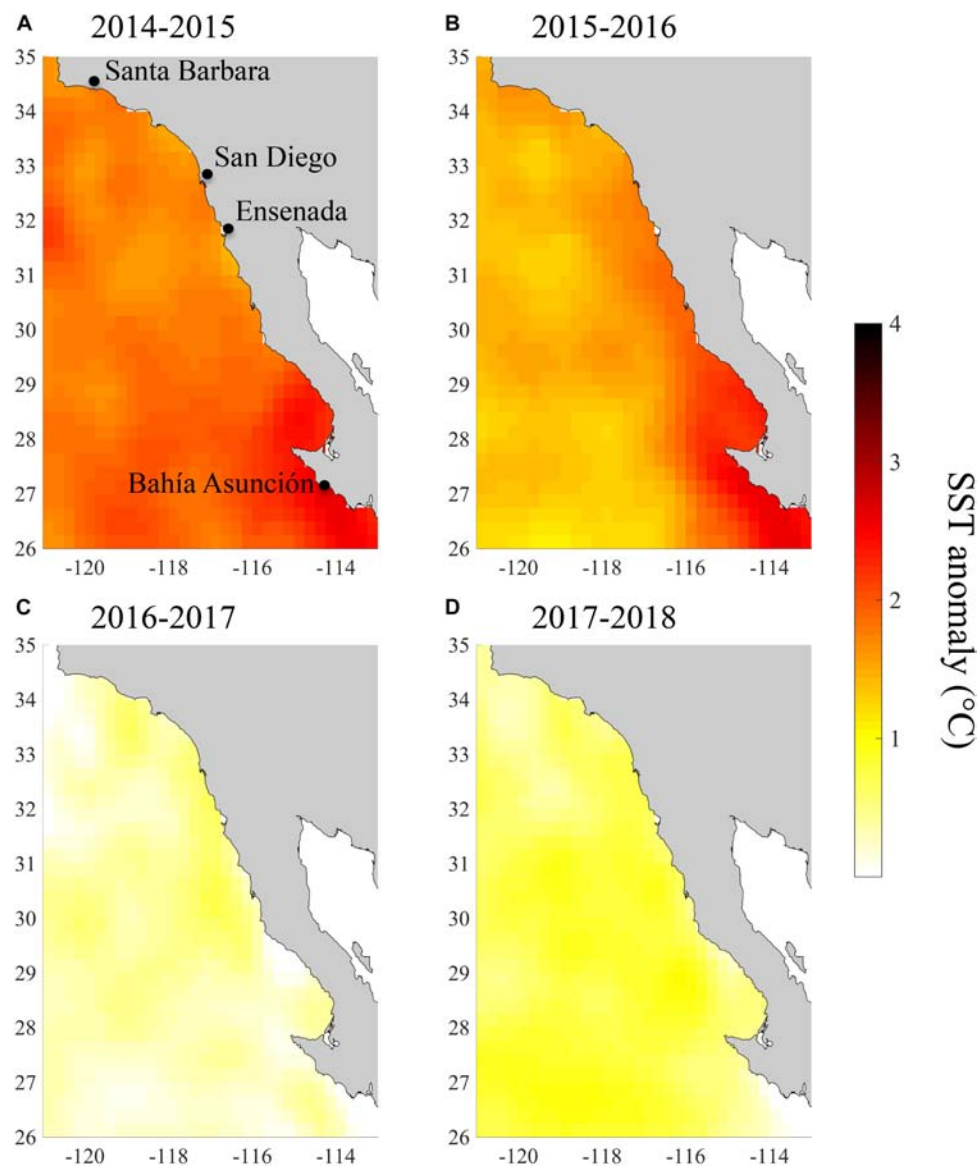


FIGURE 2 | Mean SST anomalies across the study region for (A) July 2014–June 2015, (B) July 2015–June 2016, (C) July 2016–June 2017, and (D) July 2017–June 2018.

warmest month in Northern Baja (30.5°N – 32°N) was 20.6°C in 2016/2017 (Figure 4D).

Spatiotemporal Variability in Giant Kelp Canopy Biomass

Giant kelp canopy biomass exhibited high intra- and inter-annual variability throughout the study region during the 5-year period prior to the onset of the heatwave in 2014. Seasonal patterns varied from year to year, but in most of the coastline segments, canopy biomass was typically highest in the spring or summer and lowest in winter (blue lines in Figure 5). These seasonal patterns were likely due to wave disturbance, which is typically strongest during the winter across most of our study area (Reed

et al., 2011; Bell et al., 2015). However, during the heatwave this seasonal pattern changed, as canopy biomass in all the coastline segments reached minimums in the summer and fall of 2014 (Figure 5). Interestingly, in most regions this decline in kelp was followed by rapid recovery during the winter and spring of 2015, even though SST anomalies remained high with persistent heatwaves during this period (Figures 2, 3). This winter/spring recovery did not occur in the southern portions of the range (south of 30°N ; Figures 5K–M) or in the coastline segment centered at 33.5°N , just north of San Diego (Figure 5D).

Kelp canopy declined rapidly across all coastline segments during the summer and fall of 2015 (Figure 5). Recovery from this decline during the following winter and spring was less prevalent, and mean canopy biomass in 2015/2016 was lower

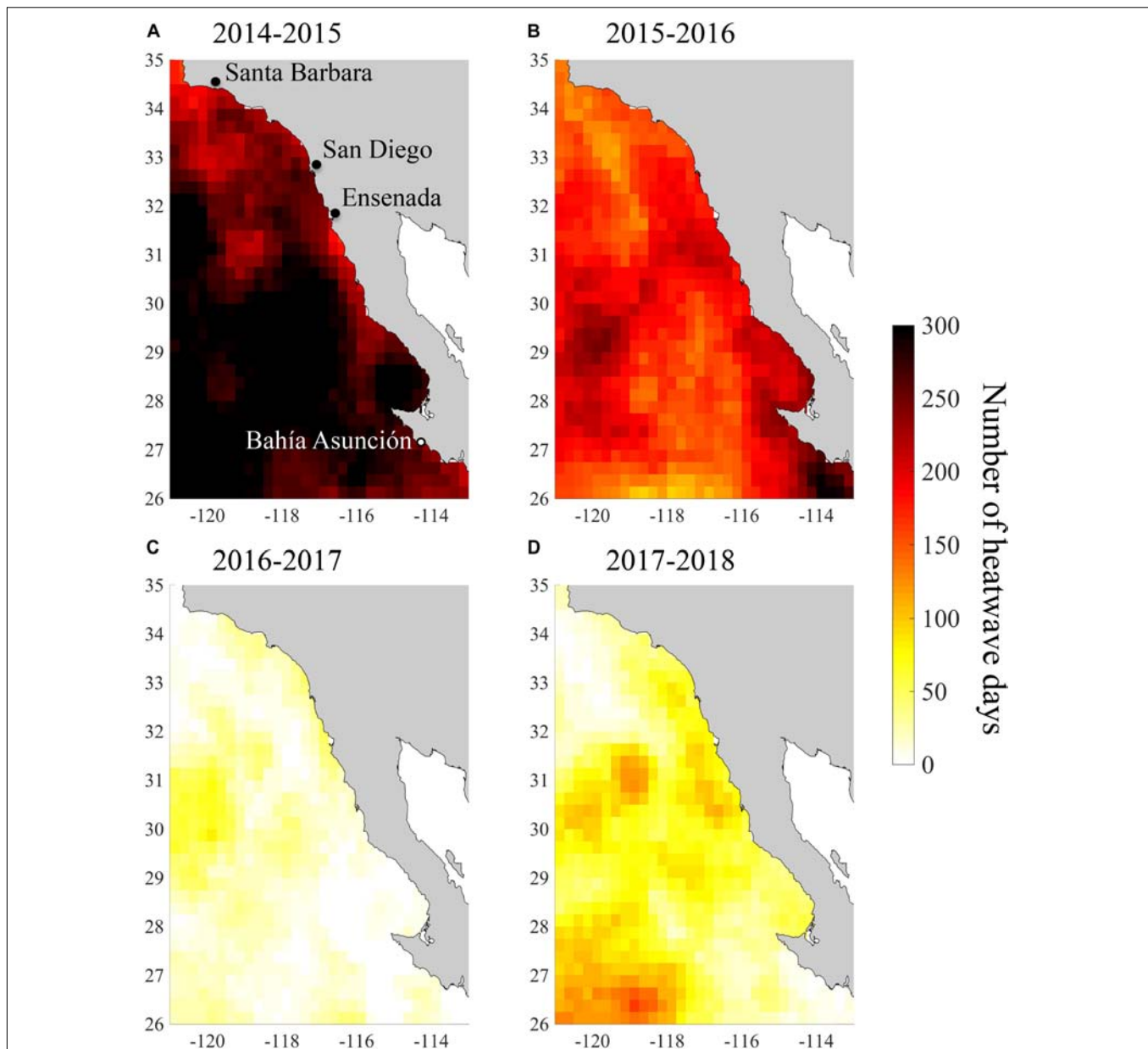


FIGURE 3 | Total number of heatwave days across the study region for (A) July 2014–June 2015, (B) July 2015–June 2016, (C) July 2016–June 2017, and (D) July 2017–June 2018.

than it had been in 2014/2015 for all but one coastline segment (**Figure 6**). During this period, the coastline segment near San Diego and Baja segments south of 29.5°N experienced a near complete loss of kelp canopy. The only two segments where kelp canopy biomass remained near the 2009–2013 average were Santa Barbara (34.5°N) and Ensenada (31.5°N).

In the summer of 2016 the positive SST anomalies abated (**Figure 2C**), and kelp canopy biomass started to recover in the northern coastline segments ($>33.5^{\circ}\text{N}$). However, kelp canopy biomass continued to decline in 2016/2017 across much of the rest of study area, particularly in northern Baja between 33° and 29°N (**Figures 5, 6**). Canopy biomass remained close

to 0 near San Diego and in the southernmost portion of the range ($<29.5^{\circ}\text{N}$).

Recovery of giant kelp canopy biomass in 2017/2018 showed a high degree of spatial variability. In the northernmost portions of our study area ($>34.0^{\circ}\text{N}$), kelp canopy biomass continued its recovery from the previous year, and reached levels even higher than the 2009–2013 average (**Figure 6**). Canopy biomass near San Diego increased slightly from 2016/2017, but remained at historically low levels. In northern Baja, canopy biomass increased, but was still below baseline levels in all but one segment. Surprisingly, we documented a dramatic increase in kelp canopy in the southern portion of our study area near Bahía

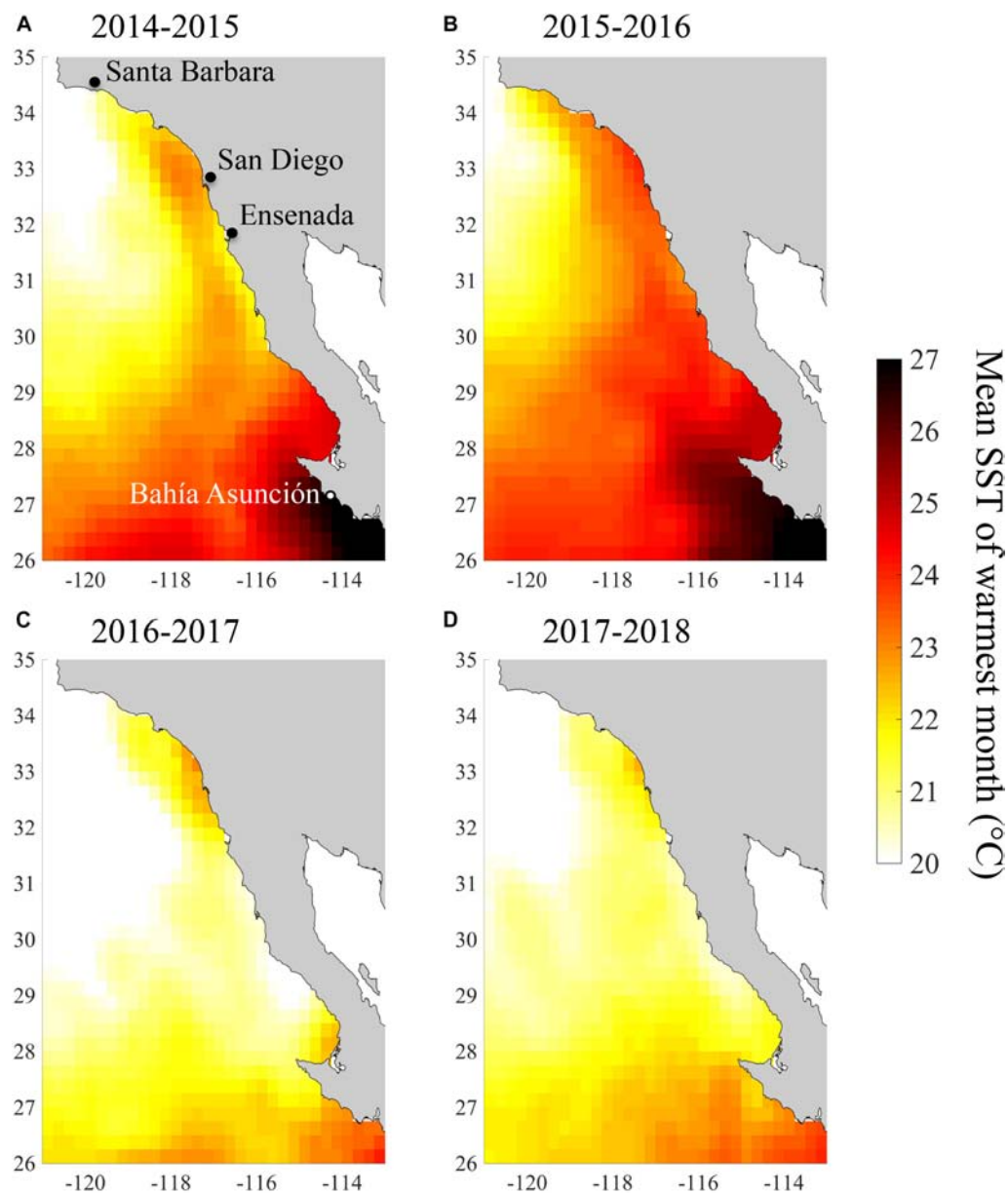


FIGURE 4 | Mean SST of the warmest month across the study region for (A) July 2014–June 2015, (B) July 2015–June 2016, (C) July 2016–June 2017, and (D) July 2017–June 2018.

Tortugas (27.5°N). Canopy biomass in this coastline segment increased nearly 10-fold between 2016/2017 and 2017/2018, and by 2017/2018 canopy biomass was $1.7 \times$ greater than the 2009–2013 baseline. By contrast, canopy biomass in the adjacent southernmost coastline segment near Bahía Asunción remained close to 0.

Giant Kelp Resistance and Resilience

The timing of canopy loss varied across our study area, and in most segments there appeared to be a delayed response to the onset of the heatwave in summer 2014. Only one of the 13 coastline segments experienced its lowest kelp canopy biomass

during the first year of the heatwave (2014/2015). Six segments reached their minimums in 2015/2016, five in 2016/2017, and one in 2017/2018 (**Supplementary Table S1**). On average, annual canopy biomass was 40% of the baseline in 2015/2016 and 32% of baseline in 2016/2017. Resistance to the heatwave (i.e., the lowest annual canopy biomass relative to the average of the 5-years prior to the heatwave) ranged from 0 to 0.75 (mean = 0.23). There was a significant negative relationship ($p < 0.05$) between giant kelp resistance and both the number of heatwave days and the mean SST of the warmest month between July 2014 and June 2016 (**Figure 7**). The absolute metric, mean SST of the warmest month, was the best predictor of resistance based on

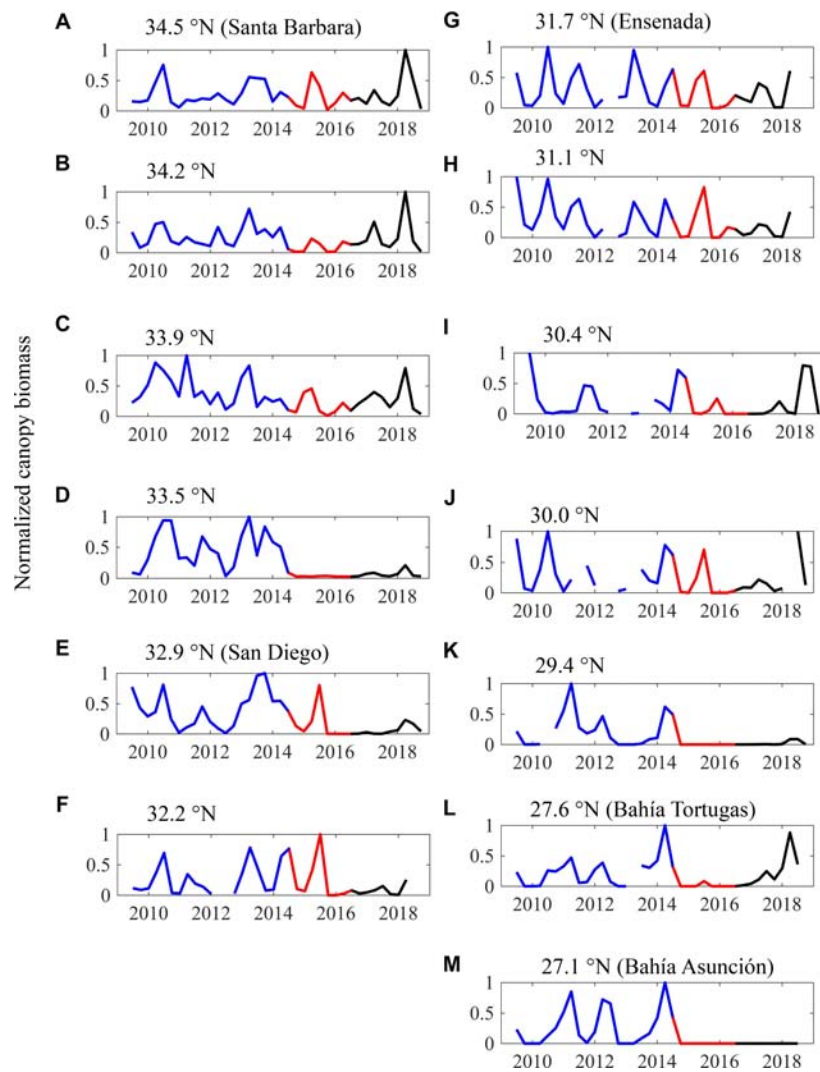


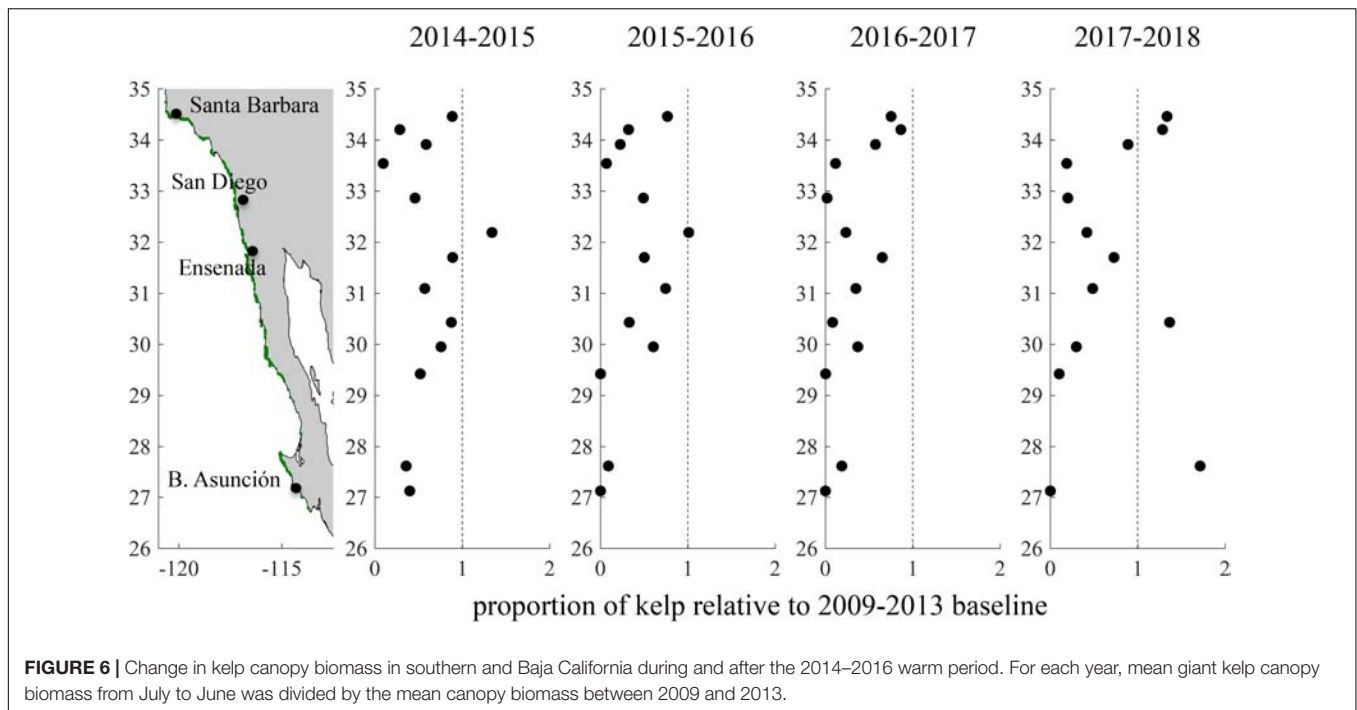
FIGURE 5 | (A–M) Time series of seasonal giant kelp canopy biomass from 2009 to 2018 for the thirteen 100 km coastline segments. Biomass is normalized to the maximum biomass observed in a segment over the time series. The baseline period (July 2009–June 2014) is shown in blue, the heat wave period (July 2014–June 2016) is shown in red, and the recovery period (July 2016–December 2018) is shown in black.

model AIC, explaining approximately 41.3% of the variability in spatial patterns of kelp resistance (**Table 1**).

Kelp resilience (i.e., the proportion of canopy biomass in 2017/2018 relative to the 2009–2013 baseline) ranged from 0 to 1.7 (mean = 0.69) across all coastline segments. Resilience was not significantly correlated with any of the SST metrics calculated during (2014/2015–2015/2016) or after (2016/2017–2017/2018) the heatwaves ($p > 0.35$), suggesting that the severity of warming did not affect recovery (**Figure 8** and **Supplementary Figure S2**, and **Table 2**). The resilience of the two southernmost coastline segments at Bahía Tortugas and Bahía Asunción are notable in that their resilience differed dramatically despite being adjacent to each other. Both of these segments experienced high SST during the 2014–2016 heatwave, but Bahía Asunción exhibited the lowest resilience of any coastline segment while Bahía Tortugas showed the highest.

DISCUSSION

The exceptional warming of 2014–2016 had unexpected impacts on giant kelp abundance in southern and Baja California. Kelp canopy biomass declined at the onset of the heatwave in 2014 throughout the entire study region, however, the magnitude of this decline and the subsequent recovery varied dramatically and inconsistently with latitude. Several coastline segments showed an immediate decline in kelp abundance with little signs of recovery 2 years after the heatwave ended, including the segment at the southern range limit. In contrast, many of the coastline segments experienced a relatively strong recovery in spring 2015. This recovery was short-lived, however, and was followed by a sharp decline in the summer and fall of 2015. The specific reasons for the recovery of the canopy at these locations during the middle of the heatwave



and its subsequent decline following the cessation of the heatwave remain unknown.

The variability in patterns of kelp resistance that we documented for the 2014–2016 heatwave differs substantially from the immediate and near complete loss of giant kelp observed throughout southern and Baja California during the heatwaves associated with the 1982/1983 and 1997/1998 El Niño events (Dayton and Tegner, 1989; Edwards and Estes, 2006). Both of these previous heatwaves were associated with catastrophic wave disturbance (Griggs and Brown, 1998), which caused the initial large-scale mortality in giant kelp populations throughout southern and Baja California, with warm, nutrient limited conditions negatively impacting subsequent recovery in some locations (Dayton and Tegner, 1984; Edwards, 2004; Edwards and Estes, 2006). The 2014–2016 heatwave was not associated with major wave disturbance (Reed et al., 2016), which likely explains the greater variability in the initial response and recovery of giant kelp that we observed. Near the southern range limit of giant kelp, high temperatures and/or low nutrients may have been severe enough in 2014/2015 to cause rapid mortality of adult giant kelp and suppress subsequent recruitment. However, in northern Baja and most of southern California, some kelp survived the first year of the heatwave, and conditions were suitable for recruitment and/or regrowth of the canopy by the summer of 2015.

The delayed reaction of giant kelp to the warm anomaly across much of our study area may indicate that a major part of the heatwave's impact was on giant kelp recruitment. Previous studies have identified "recruitment windows," where spore release coincides with suitable temperature, nitrate, and irradiance conditions (Deysher and Dean, 1986). Environmental conditions may have been suitable for recruitment across parts of our study area in the winter and spring of 2015, which

would explain the recovery observed during this period in many segments (Figure 5). Alternatively, it is possible that observed declines in canopy biomass during the summer and fall of 2014 resulted from a prolonged dieback of the canopy without mortality of plants below the surface. This canopy dieback was then followed by canopy recovery from surviving plants when conditions briefly improved in early 2015. The low rates of canopy recovery observed during the spring of 2016 when cooler temperatures prevailed suggests low adult densities and widespread recruitment failure during this time. That lack of recruitment in spring 2016 would have led to low adult abundance and sparse kelp canopies during the following year (2016/2017). While we cannot directly observe subsurface dynamics with our satellite data, the prolonged (> 12 months in some segments) and widespread lack of canopy recovery after the heatwave ended in early 2016 is consistent with the hypothesis that canopy loss was the result of kelp mortality and not simply canopy dieback because giant kelp typically regrows its surface canopy within 6 months (Schiel and Foster, 2015).

The spatial patterns of resistance in giant kelp were better explained by an absolute thermal threshold (i.e., mean SST of the warmest month) than by relative increases in temperature as measured by SST anomalies and heatwave days. This finding contradicts that of Smale et al. (2019), who found that variation in the canopy biomass of giant kelp in our study region was best explained by the number of heatwave days. This contradiction in findings is likely related to confounding effects of wave disturbance. The negative relationship between canopy biomass and heatwave days observed by Smale et al. (2019) resulted primarily from low biomass during the exceedingly warm 1982–83 and 1997–98 El Niño events, which as noted above resulted from extremely

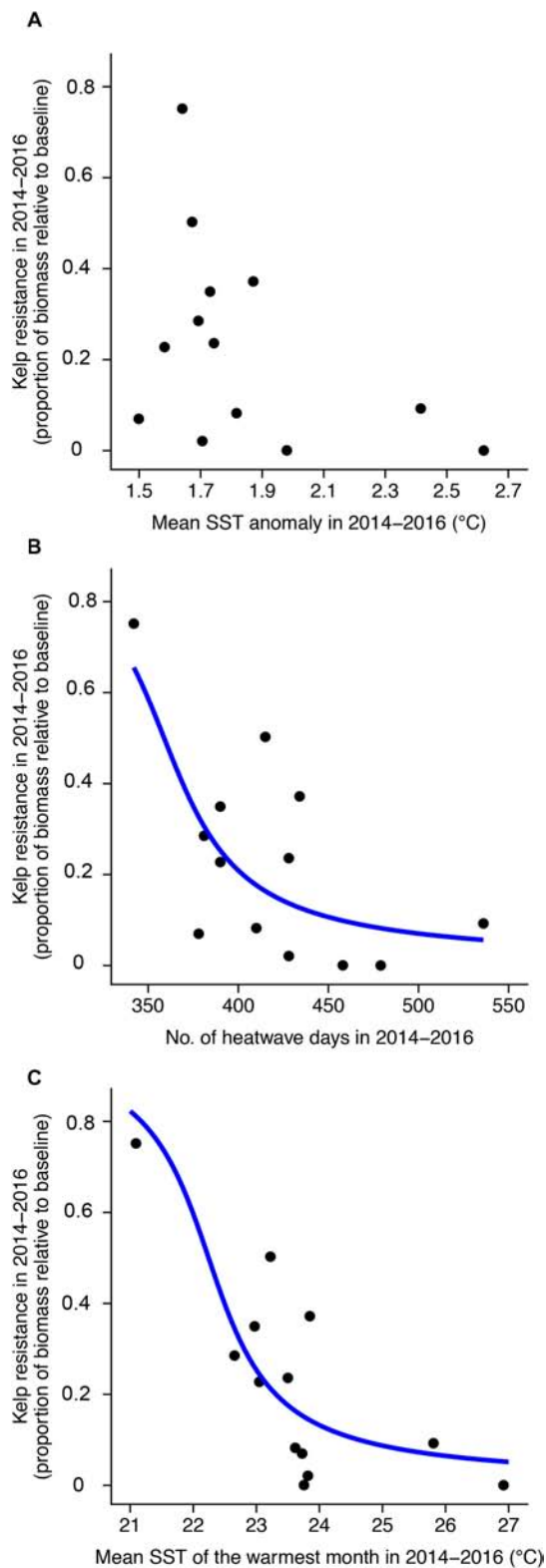


FIGURE 7 | Relationship between kelp resistance and 2014–2016 sea surface temperature metrics: **(A)** SST anomaly, **(B)** number of heatwave days, and **(C)** mean SST of the warmest month. Blue lines show beta regression model fits for significant relationships ($p < 0.05$).

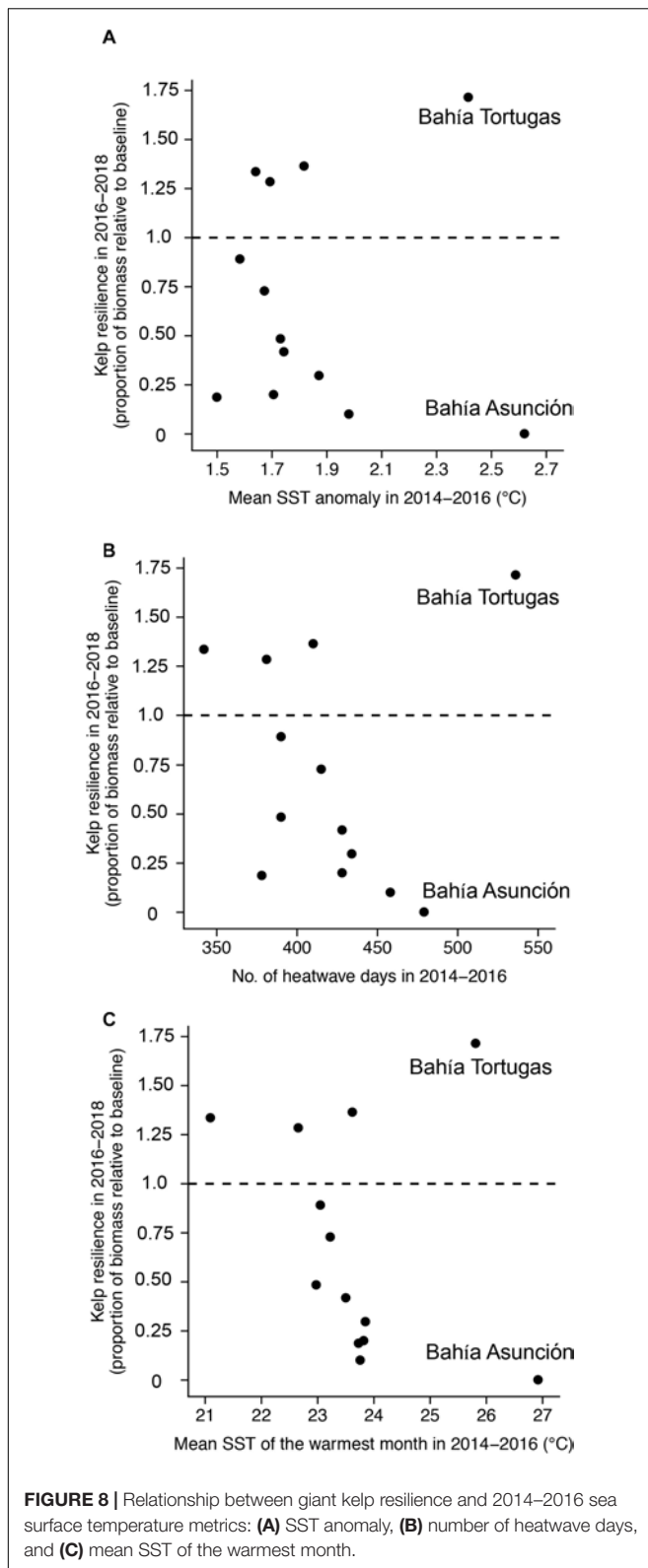
TABLE 1 | Summary of model comparisons examining the relationship between giant kelp resistance and the three SST metrics from July 2014 to June 2016.

Predictor	ΔAIC	Pseudo- R^2	P	Model rank
Mean SST of the warmest month	0	41.3	0.006	1
Number of heatwave days	2	18.6	0.013	2
Mean SST anomaly	5.8	51.9	0.082	3
Intercept only (null model)	8.4	0	1.000	4

large waves rather than warm water. Our finding that kelp was more responsive to an absolute temperature maximum than to the magnitude of relative temperature change suggests that local adaptation to heat stress did not have a major impact on the response of kelp to this warming event throughout much of its range.

Relative temperature metrics have been shown to explain variability in resistance to heat stress in other marine systems. For example, coral reef bleaching has been correlated with degree heating weeks, a relative metric calculated using the baseline climatology of a given location (Hughes et al., 2017). Coral reefs consist of an assemblage of different coral species, which may give them a higher capacity for local adaptation than ecosystems where the foundation species is a single species. However, relative temperature anomalies also explained variability in growth, survivorship, and reproduction across the distribution of *Scytothalia dorycarpa*, a temperate fucoid alga common to western Australia (Bennett et al., 2015). It is important to note that our results do not rule out the possibility that local adaptation may play an important role in controlling giant kelp dynamics. Instead, we suggest that there may be some absolute threshold beyond which local adaptation to temperature stress or nutrient limitation is no longer effective, and the 2014–2016 warming event exceeded that threshold throughout much of southern and Baja California.

Disentangling the effects of heat stress and nutrient limitation on giant kelp during heatwaves is challenging because temperature and nitrate concentration are strongly negatively correlated in the California Current system (Zimmerman and Kremer, 1984). Other sources of nitrogen are unrelated to temperature (e.g., ammonium and urea) and help to sustain kelp during warm periods when nitrate concentrations are low (Brzezinski et al., 2013; Smith et al., 2018). These other forms of nitrogen help account for the relatively high growth rates maintained by giant kelp ($>2\%$ dry mass per day) that we observed at our long-term study sites near Santa Barbara during the 2014–2016 heatwave (Rassweiler et al., 2018) despite positive temperature anomalies $>4^\circ\text{C}$. Thus, it seems reasonable that heat stress rather than nutrient stress caused giant kelp to display its lowest resistance at locations with the highest temperatures. This contention is supported by our finding that most coastline segments where the mean SST of the warmest month during the 2014–2016 heatwave approached or exceeded 24°C suffered near-complete loss of giant kelp canopy, whereas those that did not exceed this threshold exhibited less kelp loss. Experimental studies have found that water temperatures $>24^\circ\text{C}$ exceed



giant kelp's physiological tolerance, leading to rapid mortality (Clendenning, 1971; Rothäusler et al., 2011). Similar patterns of kelp loss were observed near the southern range limit of

TABLE 2 | Summary of model comparisons evaluating the relationship between giant kelp resilience and the three SST metrics during (July 2014 to June 2016) and after (July 2016 to June 2018) the heatwave.

Predictor	Δ AIC	R^2	P	Model rank
Mean SST of the warmest month (2016–2018)	0	16.3	0.368	1
Intercept only (null model)	0.3	0	1	2
Mean SST of the warmest month (2014–2016)	1.4	6.8	0.912	3
Number of heatwave days (2016–2018)	2.1	1.7	0.354	4
Mean SST anomaly (2016–2018)	2.2	0.3	1	5
Number of heatwave days. (2014–2016)	2.2	0.2	1	6
Mean SST anomaly (2014–2016)	2.3	0	1	7

giant kelp during the summer of 1997 when SST reached 25°C for 2 months, leading to a complete loss of both canopy and subsurface kelp at Bahía Tortugas (Ladah et al., 1999).

Recovery of kelp after the heatwaves was spatially variable and not related to any of the SST metrics that we analyzed. We observed high levels of resilience in the coastline segments in the north of our study area ($>34^\circ\text{N}$) and in certain parts of Baja. Surprisingly, the most resilient coastline segment was in Bahía Tortugas (27.5°N), which is close to the southern range limit of giant kelp. This is in sharp contrast to the adjacent coastline segment at the southern range edge, which did not have any detectable kelp canopy by mid-2018, 2 years after the heatwave subsided. Kelp canopy biomass also remained well below baseline levels near San Diego (32.9°N). The Bahía Tortugas segment showed high levels of resilience, even though absolute and relative SST were high during the heatwave period. The area near Bahía Tortugas is characterized by strong localized coastal upwelling (Dawson, 1951; Woodson et al., 2018), which may have reduced heat and nutrient stress and promoted canopy regrowth and recruitment during and after the heatwave. Some of this small-scale temperature variability may not have been captured by our relatively coarse SST data. Other studies have reported rapid recovery of kelp in Bahía Tortugas following previous heatwaves (Ladah et al., 1999; Edwards and Estes, 2006), and this area could serve as an important refuge for giant kelp near its southern range edge following extreme warming events.

Biological processes such as dispersal, recruitment, competition, and grazing influence giant kelp population dynamics, and likely interact with environmental controls to explain local variability in resilience. For example, highly isolated giant kelp populations have lower persistence and resilience due to diminished demographic connectivity (Reed et al., 2006; Castorani et al., 2015, 2017) and, in some locations, inbreeding depression (Raimondi et al., 2004). Likewise, competition with understory algae can inhibit giant kelp recruitment (Reed and Foster, 1984; Reed, 1990), thereby negatively impacting population recovery following disturbance from warm temperatures or large waves (Edwards and Hernández-Carmona, 2005). Grazing by herbivores can have a strong impact on giant kelp abundance, and so spatial variability in grazing pressure due to processes such as top-down trophic controls may also influence resilience (Shears and Babcock, 2002; Lafferty, 2004; Ling et al., 2009). Interactions among environmental

and biological processes may also be important, as increased temperatures can make kelp forests more vulnerable to other physical or biotic disturbance (Wernberg et al., 2010).

Our results highlight both the resilient nature of giant kelp in southern and Baja California, as well as the limits of that resilience. Populations near the equatorial range limit of giant kelp, which exist near temperature tolerance thresholds, are likely the most vulnerable to future increases in the frequency of marine heatwaves. However, marine microclimates, such as regions of localized upwelling, may provide spatial refuges from heatwaves that help repopulate neighboring areas following these disturbances. Other stressors, such as wave disturbance and grazing, may interact with positive temperature anomalies, and push giant kelp systems beyond their capacity for recovery. Interacting stressors may be especially important in the center of species distributions, where the system would otherwise be resilient to warming on its own.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

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AUTHOR CONTRIBUTIONS

DR, KC, and TB conceived the study. KC and TB processed the satellite-based datasets. KC, DR, TB, and MC performed data analysis. KC wrote the first draft of the manuscript. All authors contributed substantially to revisions of 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.2019.00413/full#supplementary-material>

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Severe Continental-Scale Impacts of Climate Change Are Happening Now: Extreme Climate Events Impact Marine Habitat Forming Communities Along 45% of Australia's Coast

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Recent increases in the frequency of extreme climate events (ECEs) such as heatwaves and floods have been attributed to climate change, and could have pronounced ecosystem and evolutionary impacts because they provide little opportunity for organisms to acclimate or adapt. Here we synthesize information on a series of ECEs in Australia from 2011 to 2017 that led to well-documented, abrupt, and extensive mortality of key marine habitat-forming organisms – corals, kelps, seagrasses, and mangroves – along >45% of the continental coastline of Australia. Coral bleaching occurred across much of northern Australia due to marine heatwaves (MHWs) affecting different regions in 2011, 2013, 2016, and 2017, while seagrass was impacted by anomalously high rainfall events in 2011 on both east and west tropical coasts. A MHW off western Australia (WA) during the 2011 La Niña extended into temperate and subtropical regions, causing widespread mortality of kelp forests and seagrass communities at their northern distribution limits. Mangrove forests experienced high mortality during the 2016 El Niño across coastal areas of northern and north-WA due to severe water stress driven by drought and anomalously low mean sea levels. This series of ECEs reflects a variety of different events – MHWs, intense rainfall from tropical storms, and drought. Their repeated occurrence and wide extent are consistent with projections of increased frequency and intensity of ECEs and have broad implications elsewhere because similar trends are predicted globally. The unprecedented and widespread nature of these ECE impacts has likely produced substantial ecosystem-wide repercussions. Predictions from ecosystem models suggest that the widespread mortality of habitat-forming taxa will have long-term and in some cases irreversible consequences, especially if they continue to become more frequent or severe. The

abrupt ecological changes that are caused by ECEs could have greater long-term impacts than slower warming that leads to gradual reorganization and possible evolution and adaptation. ECEs are an emerging threat to marine ecosystems, and will require better seasonal prediction and mitigation strategies.

Keywords: extreme climate events, kelp, coral, seagrass, mangrove, marine heat wave, modeling, ecosystem

INTRODUCTION

Extreme climate events (ECEs), statistically rare or unusual climatic periods that alter ecosystem structure and/or function well outside normal variability (Smith, 2011), are receiving increasing attention as drivers of change in ecological and evolutionary communities (IPCC, 2012; van de Pol et al., 2017). ECEs are also associated with climate change, becoming more frequent and more intense (e.g., Herring et al., 2018). In coastal marine systems, heatwaves and floods could have greater ecosystem and evolutionary impacts than the more gradual effects of climate change (Campbell-Staton et al., 2017; Grant et al., 2017), and essentially represent a “pulse vs. press” dichotomy in terms of climate impact regime (Harris et al., 2018). For example, heatwaves compound the effects of underlying warming trends and provide little opportunity for organisms to acclimate or adapt, whereas slower warming is more likely to allow time for these processes to occur (Walther, 2010). Although there is a common perception that high-latitude areas will be most affected by climate change because the magnitude of warming is greater there (Burrows et al., 2011), low-latitude areas with dampened seasonal cycles, have the greatest emergence of extreme heat (Diffenbaugh and Scherer, 2011) and host many species that inhabit environments already close to the limits of their thermal tolerance (Sunday et al., 2011, 2012; Frieler et al., 2013; Pinsky et al., 2019). Global warming is increasingly affecting marine ecosystems including habitat forming sessile organisms (Poloczanska et al., 2013), which are often key ecosystem engineers and particularly vulnerable to heatwaves as individuals cannot physically move to cooler locations (Mislán and Wetthey, 2015).

Here we synthesize the unprecedented large-scale impacts of a series of ECEs on coastal marine habitats around the Australian continent (**Figure 1**) between 2011 and 2017, spanning both strong El Niño and La Niña phases of the El Niño Southern Oscillation (ENSO). We also model how impacts on habitat forming organisms propagate through food webs and ecosystems under a range of impact scenarios. The impact of ECEs throughout most of northern Australia has broad implications as the climate change phenomena driving the ECEs are being experienced globally (Oliver et al., 2018a). These conditions are also a precursor of a future in which ECEs are increasingly common, since ECEs are episodic, thus providing little or no time for acclimation and evolution, thus potentially exacerbating damage through the shocks they create within ecosystems (IPCC, 2012).

ECE Impacts in Australia

Vulnerability to marine extremes, such as heatwaves, has been demonstrated for many marine species (Poloczanska et al., 2013),

but impacts to habitat-forming species may be most damaging. Around Australia and globally, coral reefs, kelp forests, mangroves, and seagrasses are all foundation species supporting diverse ecological communities (Steneck et al., 2002; Orth et al., 2006; Blaber, 2007; Nagelkerken et al., 2008; Waycott et al., 2009; Pratchett et al., 2011; Graham, 2014). Direct losses of significant portions of these habitats have been reported (e.g., McKenzie et al., 2014; Thomson et al., 2015; Wernberg et al., 2016a; Duke et al., 2017; Hughes et al., 2017), with predictions of wide-ranging effects that will significantly alter the communities associated with these ecosystems.

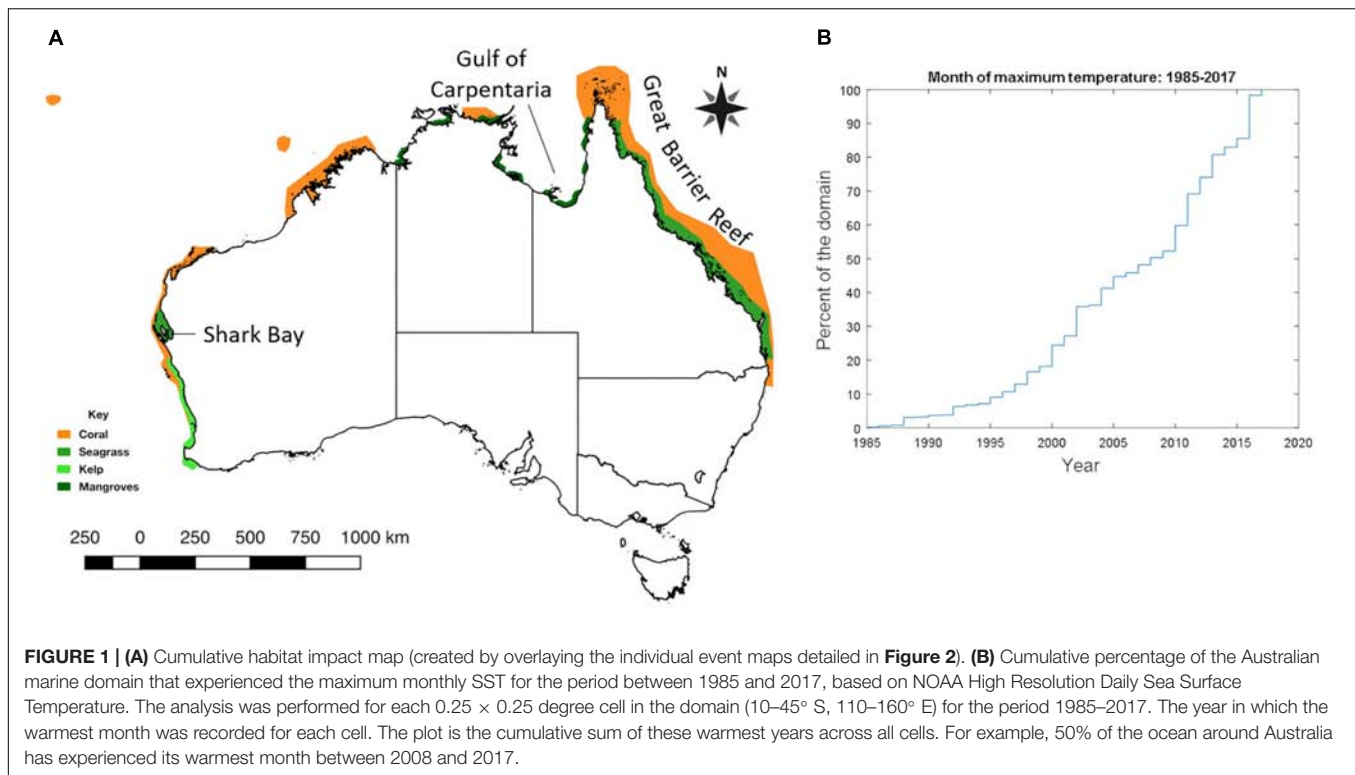
Half of Australian coastal waters have experienced their warmest ever monthly temperatures since 2008 (**Figure 1**), which reflects the increased extent, frequency and magnitude of marine heatwaves (MHWs; Hobday et al., 2016). The duration and magnitude of these events is also extending, with warmer sea temperatures persisting for longer than was recorded during previous extreme events (Hughes et al., 2017; Oliver et al., 2017). MHWs have increased around Australia and globally (Oliver et al., 2018a) and global climate models indicate that such MHWs are orders of magnitude more likely as a result of anthropogenic climate change (Oliver et al., 2017, 2018b). There is now a high level of consensus that, in addition to extreme warming events, climate change is also leading to extremes in other aspects of climate and weather, such as more severe storms (Herring et al., 2014, 2018; Stocker, 2014; Cheal et al., 2017). For example, extreme 1-day rainfall events estimated to occur once every 20 years in the 1950s are now expected to occur once every 15 years (Zhang et al., 2013; McInnes et al., 2015).

Extreme warming events have contributed to the abrupt, severe, and extensive impacts on key marine habitat-forming species including corals, kelp, seagrass, and mangroves along the Australian coastline in recent years. Below, for each key habitat forming biota, we briefly discuss their importance and their threats and then detail the recent ECEs in Australia and their impacts. We then use ecosystem models to estimate the overall impacts of ECEs of varying frequency on different ecosystems, and compare whether temperate or tropical environments are more likely to be impacted. We also discuss how understanding climate variability and change in marine ecosystems might be used to develop adaptation strategies to reduce potential impacts of ECEs.

MATERIALS AND METHODS

Extreme Climate Impacts

We reviewed the literature relating to impacts on Australia's coastal marine ecosystems of ECEs during the recent ENSO cycle, which spanned the La Niña of 2011 and the El Niño of 2016.



We examined the nature of the events as well as the extent and severity of impacts. This provided the basis for modeling of current and future ecosystem-wide impacts under a range of possible scenarios.

Modeling Ecosystem-Wide Impacts

The magnitude of habitat change caused by ECEs will have significant impacts on species dependent upon them and their associated food webs (Thomson et al., 2015; Wernberg et al., 2016a; Richardson et al., 2018). However, long-term implications are not yet clear because of short time series and the recent increase in such events. To address the potential long-term consequences, ecosystem models were used to explore ecosystem-wide impacts of ECEs and the sensitivity of these systems to differing disturbance patterns. There are ecosystem models for much of Australia's coastline and the models available for the areas affected by the ECEs (**Table 1**; with more detailed descriptions available in the **Supplementary Materials**) were used to explore the magnitude of potential trophic and habitat-mediated indirect effects. To account for uncertainty about the structure and linkages in the systems, a multi-model approach was taken. All systems had Ecopath with Ecosim (EwE) models (Christensen and Walters, 2004), and these were supplemented with Atlantis (Fulton et al., 2011) and InVitro (Fulton et al., 2011) models where available. The use of published EwE models across almost all systems provided a uniform basis for comparison across the various ecosystems, with the addition of the Atlantis and InVitro models providing insight into uncertainties regarding the level of potential change (or robustness) that

result from uncertainty around the structure and dynamics of the ecosystems.

The Jurien Bay EwE model had the smallest spatial extent (823 km^2) but the highest number of trophic groups (81), while at the other extreme the Great Barrier Reef (GBR) EwE model had the fewest trophic groups (31). The Atlantis-SE model for south-eastern Australia had the greatest spatial extent (at 3.7 million km^2).

The use and dependency on habitats by reef and other species are explicit in Atlantis and InVitro. Mediation functions (where the state of the habitat influences the success of trophic interactions targeting the habitat dependent prey group) were used to capture the same dependency on biogenic habitats in the EwE models. Parameterizations of these dependencies were drawn from the same literature as the original model implementations or from the Atlantis and InVitro models of the same systems where available (**Table 1**).

An additional "ECE mortality" source was added to each model, and affected the main habitat forming primary producers, initially at low levels (causing biomass losses of only $3.4 \times 10^{-4} \text{ tonnes km}^{-2} \text{ d}^{-1}$), so that under standard conditions mortality is negligible. Major ECEs were then represented by forcing this mortality source to produce short-term mortalities with the same magnitudes of habitat decline as those reported in the literature discussed above. For instance, if corals suffered 50% mortality due to severe bleaching in a particular region, then the mortality source was increased for simulated ECEs of 2 months duration, to a level that resulted in 50% realized mortality in the relevant model. In the currencies of the models the magnitudes of all trophic groups are represented in units of biomass and realized

TABLE 1 | Details of the models used to investigate primary and indirect effects of extreme climate events.

Region	Model type	Number of functional groups	Area (km ²)	Notes	References
Jurien Bay	EwE	81	823		Lozano-Montes et al., 2011
Ningaloo	EwE, InVitro	52 43	28,700	Both models include fisheries, tourism, agriculture, and oil and gas extraction. InVitro also includes trucking, shipping, and local urban areas; as well as forcing time series for temperature, salinity, ocean currents, and precipitation.	Fulton et al., 2011; Gray et al., 2013
North west Shelf	EwE	37	70,000		Bulman, 2006
Kimberley	EwE	58	93,000	In addition to commercial and recreational fishing, the model contains: collection of specimen shells, Trochus, marine aquarium fish, pearl oyster and Beche-de-mer mariculture, tourism, oil- and gas-related stressors, shipping and coastal habitat deterioration.	Boschetti et al., 2017
Gulf of Carpentaria	EwE	53	396,483	Fisheries include indigenous collection, charter vessels, and IUU activities.	Bustamante et al., 2011; Dichmont et al., 2013
Great Barrier Reef	EwE	32	325,848		Gribble, 2003
New South Wales Coast	EwE, Atlantis	57 54	48,000 50,000	Atlantis includes drivers for temperature, salinity, ocean currents, and terrestrial run-off.	Forrest et al., 2015
South East Australia	EwE, Atlantis	59 58	30,263* 3,700,000	Atlantis includes drivers for temperature, salinity, ocean currents, and terrestrial run-off. In addition to fisheries the model contains aggregate mining, shipping, marine energy sectors, and coastal development.	Bulman et al., 2006; Fulton et al., 2014
Tasmania	EwE	47	137,000	Contains the potential for a pinniped cull.	Watson et al., 2013

*Models for south east Australia and Tasmania have been included, as this region has experienced a number of MHWs, but has not yet seen the same extent of habitat impact due to the decline of kelp in the area pre-dating the events (this does not, however, preclude further ECE-related change in the future). EwE, Ecopath with Ecosim. Unless noted otherwise, EwE models were non-spatial, were forced only with the ECE driver, and the only anthropogenic components included were fisheries. Further details of models including definitions of trophic groups are presented in **Supplementary Table S1**. *The EwE model extent represents a small subset of the Atlantis domain (around the eastern end of Bass Strait and the coast of Victoria).*

mortalities are represented as reductions in total biomass of habitat formers. For the spatially explicit models, the footprint of the simulated ECE was set to match that of the real-world ECE in the same region.

To explore the full implications of extreme events for habitat formers and the stability of ecosystems dependent on them (Bender et al., 1984), three forms of extreme events scenario were considered with each model in which the frequency of ECEs was varied to assess the sensitivity of systems to disturbance frequency. We simulated a single major “pulse” event (with mortality rate returning to normal negligible levels after the ECE and remaining at those low levels for the rest of the 50 year run); “episodic” ECE-driven mortality events every 5 years; and a “step-change” such that the mortality-induced change in biomass becomes a permanent feature of the system. All of these are variations of “pulse” disturbances rather than a more gradual “press” impact of climate change. To provide first-order estimates of effects, these simulated ECEs were simplistic in that they did not account for synergies among different types of ECE, or the capacity of species to adapt to changing ECE frequency, duration, and intensity. The single exception to this is the Atlantis model for SE Australia. That model has the capacity to represent acclimation and evolution and simulations were run for that

model, with and without that capacity enabled, to see what difference it made to the results. The effects of ECEs on the systems included assessment of the ability of the systems to recover to their original biomass and structure (Bender et al., 1984), and the speed at which this occurred.

RESULTS AND DISCUSSION

Australia has been impacted by an unprecedented number of ECEs since 2011, impacting >45% of the coastline (**Figure 2**). We now describe in detail these impacts on the four major habitats around the coast.

ECE Impacts

Corals

Coral reefs are home to >83,000 species (Fisher et al., 2015), more than any other marine ecosystem. The global economic value of coral reefs from both direct and indirect services is estimated to be in the billions to trillions of \$US per annum (Costanza et al., 2014; Spalding et al., 2017). Corals face a wide range of threats, including diminishing water quality, overfishing, and construction (Wilkinson, 2004). However, processes related

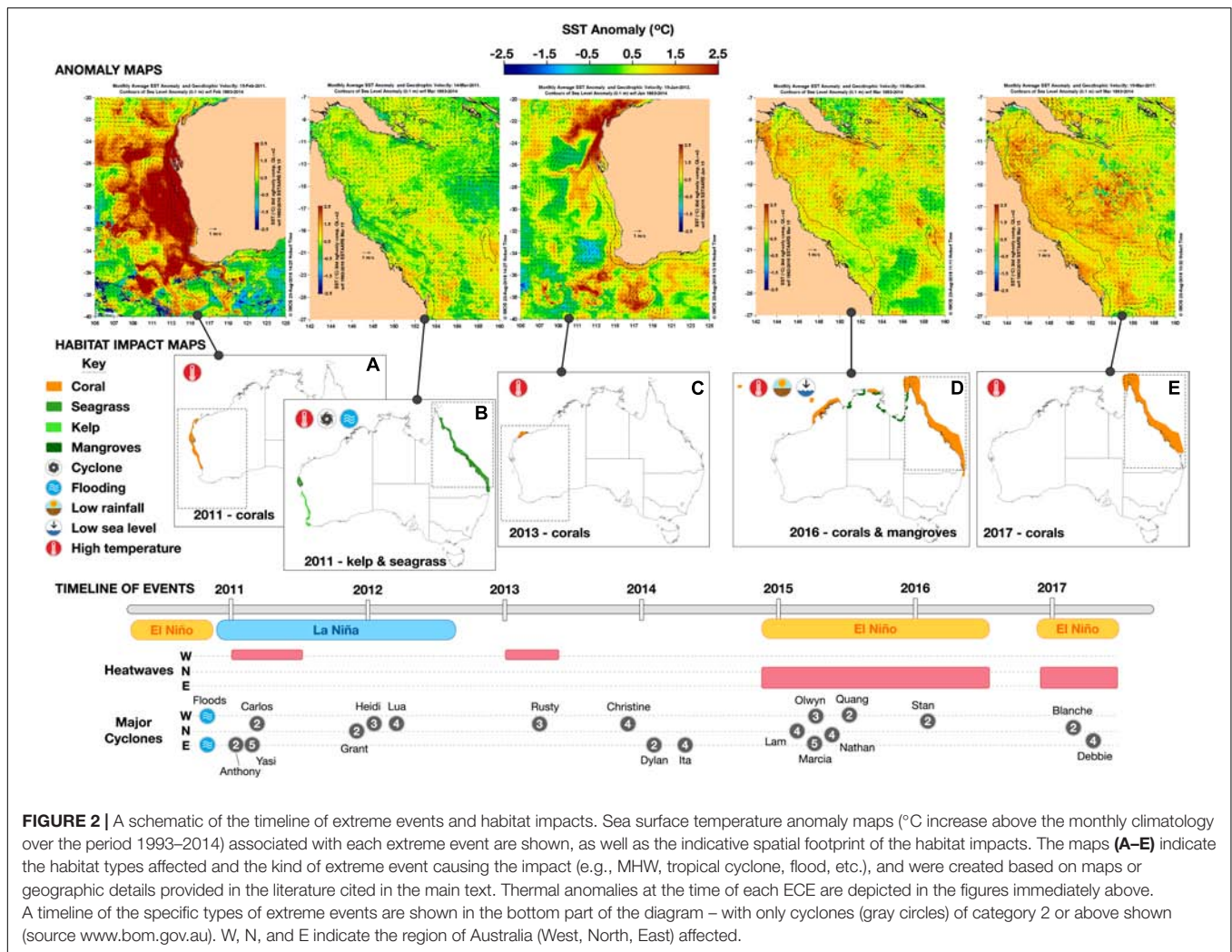


FIGURE 2 | A schematic of the timeline of extreme events and habitat impacts. Sea surface temperature anomaly maps (°C increase above the monthly climatology over the period 1993–2014) associated with each extreme event are shown, as well as the indicative spatial footprint of the habitat impacts. The maps (A–E) indicate the habitat types affected and the kind of extreme event causing the impact (e.g., MHW, tropical cyclone, flood, etc.), and were created based on maps or geographic details provided in the literature cited in the main text. Thermal anomalies at the time of each ECE are depicted in the figures immediately above. A timeline of the specific types of extreme events are shown in the bottom part of the diagram – with only cyclones (gray circles) of category 2 or above shown (source www.bom.gov.au). W, N, and E indicate the region of Australia (West, North, East) affected.

to climate change, in particular warming and ocean acidification, are increasingly threatening coral reefs (Heron et al., 2017). Bleaching of corals due to heat-induced breakdown in the relationship between corals and their symbiotic algae (Glynn et al., 2001; Smith et al., 2005) can lead to coral mortality, declines in total coral cover, changes in the composition of coral communities (Perry and Morgan, 2017b), subsequent reductions in reef calcification rates and physical structure (Perry and Morgan, 2017a), and drops in recruitment and recovery rates (Hughes et al., 2019). These changes in reef ecosystems will fundamentally change the nature of coral reefs (Stuart-Smith et al., 2018), with concomitant changes in the biodiversity and biomass of associated fish (Pratchett et al., 2011; Graham, 2014; Hughes et al., 2018; Richardson et al., 2018) and invertebrate (Przeslawski et al., 2008) communities. Coral reefs of Australia, including the world's largest reef, the GBR, are not immune to these threats, despite receiving a high level of legal protection (De'ath et al., 2012).

In the eastern Indian Ocean off Western Australia (WA) in 2011 there was an intense MHW, unprecedented in the 140-year local record (Wernberg et al., 2013). The 2010–2011 extreme La

Niña conditions in WA resulted in sea surface temperatures up to 5°C above normal (Figure 2). The MHW persisted for months along most of the west coast of Australia, resulting in widespread effects on corals. Bleaching and mortality were reported along a stretch of coast from Perth (32° S) to the Exmouth Gulf (21.75° S) (Abdo et al., 2012; Moore et al., 2012; Depczynski et al., 2013; Speed et al., 2013; Bridge et al., 2014). Effects of bleaching were most severe in parts of the northern extent (e.g., >90% in Exmouth Gulf), with 19–50% reduction at the Abrolhos Islands (28.7° S) (Abdo et al., 2012; Bridge et al., 2014). Further south at Rottnest Island (32°S), levels of bleaching and mortality were lower, around 17% (Moore et al., 2012).

Heatwave conditions on the west coast abated in 2012, but anomalously warm waters returned in 2013 – this time to northwestern Australia (21.75° to 20.3° S), to the north of the region worst affected by the 2011 MHW. Bleaching and mortality of corals (Figure 2) were recorded on inshore (51–68%; Lafratta et al., 2017) and offshore reefs (69.3%; Ridgway et al., 2016). The MHW was the result of La Niña conditions and the development of the “Ningaloo Niño” in the eastern Indian Ocean (Feng et al., 2013), which brings anomalously

warm surface waters along the west coast of Australia (Zhang et al., 2017). Ningaloo Niño conditions were persistent during 2012 and 2013 (Feng et al., 2015), and have become increasingly frequent since the late 1990s. This is consistent with climate change projections (Cai et al., 2015).

By 2016, the ENSO index indicated an El Niño state with warm surface waters across much of the central western Pacific, and temperatures between Papua New Guinea and Australia were the warmest ever recorded (Oliver et al., 2018a; **Figure 1B**). Heating lasted much longer in 2016 than during previous bleaching episodes (e.g., 2002; Berkelmans et al., 2004), and more than twice as many reefs on the GBR experienced > 8 Degree Heating Weeks (Hughes et al., 2017, 2018). Bleaching of corals in 2016 was the most severe and extensive so far recorded, with the most severe impacts seen in the northern GBR (**Figure 2**); there was severe bleaching (>60% of coral cover) and mortality recorded on most reefs between Torres Strait (9.5° S) and Lizard Island (15° S) and significant bleaching (30–60%) on reefs as far south as 19° S (Hughes et al., 2017). Bleaching and recovery were observed in corals further to the south, off the subtropical coast of eastern Australia (27.2–30° S; Hughes et al., 2017; Kennedy et al., 2018). Severe bleaching was also recorded at the same time along the northwestern coastline of the Northern Territory (12° S, 134° E to 16.45° S, 123.1° E), and on oceanic reefs between Australia and Indonesia (Scott Reef, 14° S, 121.8° E; Christmas Island 10.5° S, 105.6° E; Hughes et al., 2017).

In 2017, for the first time on record, there was a second consecutive year of bleaching on the GBR (**Figure 2**), extending south to 19° S (Great Barrier Reef Marine Park Authority, 2017; Hughes and Kerry, 2017). Approximately 50% of the remaining corals were severely bleached, overlapping in spatial extent with bleached areas from 2016 but extending further south. The severity of these consecutive events, combined with the vulnerability of particular corals such as members of the genus *Acropora* to bleaching (Hughes et al., 2017), means that the composition of coral assemblages on reefs in the worst affected northern half of the GBR are unlikely to return to their former state in the foreseeable future (Hughes et al., 2018).

El Niño conditions that push a pool of warm-water toward the western Pacific and drive sea surface temperature anomalies on the GBR are projected to increase in frequency under climate change (Cai et al., 2014); long-term environmental proxy records already show a recent increase in ENSO variability in the central Pacific (Liu et al., 2017). Observations of coral bleaching in response to anomalously warm sea temperatures on the GBR extend back to 1998, with bleaching also recorded in 2002. Analysis of these records shows that reefs more frequently exposed to bleaching conditions in the past were more likely to bleach again (Hughes et al., 2017). Consequently, the likelihood of more frequent, more extensive, and increasingly severe bleaching of corals across the tropics of Australia appears to be increasing, as predicted, both for east and west coasts (Heron et al., 2017). Local weather features such as cyclones (Moore et al., 2012; Hughes et al., 2017) and upwelling (Xu et al., 2013) may lead to cooling that mediates bleaching effects in specific subregions; however, the location of such events will vary over time, reducing the likelihood of corals in any given

area avoiding impact in the longer term. Further, the warm, oligotrophic waters of Australian coasts have localized and weak upwelling by global standards, which provides little abatement to the surface warming.

Kelp Forests

Kelp forests provide habitat for highly diverse assemblages of flora and fauna (Steneck et al., 2002) and make vital contributions to the productivity and economy of coastal habitats. For example, the estimated value of kelp forest habitats to the Australian economy is at least AU\$10 billion per year (Bennett et al., 2016). Kelp forests globally are facing threats from overfishing (Steneck et al., 2004), eutrophication (Coleman et al., 2008), and climate change (Wahl et al., 2015; Smale and Vance, 2016). Consequently, their loss has serious implications for the stability, productivity, and economic value of temperate coastal ecosystems. Declines in kelp forests lead to reductions in biodiversity (Airoldi et al., 2008; Ling, 2008), the biomass of fish and invertebrates such as abalone (Edgar et al., 2004), and recruitment of commercially important lobsters (Hinojosa et al., 2014; Hesse et al., 2016).

As a result of the WA MHW in 2011, abundance of the kelp *Ecklonia radiata* decreased by >90% in the northern extent of its range, between 29 and 27.7° S (**Figure 2**), with local extinction of *E. radiata* on 370 km² of reef during 2011 (Wernberg et al., 2016a). These warmer temperatures resulted in slower growth and impaired physiological performance of *E. radiata* adults and juveniles (Wernberg et al., 2010, 2016b; Bearham et al., 2013). More than 50% of *Ecklonia* stands were lost as far south as 30.5° S and effects extended to south of 32.0° S. Another large brown alga, *Scytothalia doryocarpa*, disappeared from 5% of its range, with a range contraction of >100 km from 30.1 to 30.9° S and reductions in abundance as far as 31.9° S (Smale and Wernberg, 2013). The MHW in 2011 almost certainly caused the localized extinction of these two species of canopy-forming brown algae along 100 km of coast (Smale and Wernberg, 2013; Wernberg et al., 2016a). Since 2011, there has been no recovery of the kelp canopy in areas affected by the MHW, due to impaired recruitment and grazing by tropical herbivorous fish. It is thus likely that the shift in ecosystem structure throughout this region will persist for the foreseeable future even without further MHWs (Bennett et al., 2015; Wernberg et al., 2016a).

In contrast, kelp communities on the Australian east coast have undergone gradual declines in response to long-term warming (**Supplementary Figure S1**), providing insight into the contrasting mechanisms and impacts between gradual warming and ECEs. The east coast is experiencing long-term ocean warming due to more frequent and prolonged poleward penetration of the East Australian Current extension (Ridgway, 2007). At the Solitary Islands (29.7–30.1° S), 10 years of video evidence showed that the decline of *E. radiata* near its northern range limits, during a period in which SST warmed by 0.6°C, was caused by increased abundance of herbivorous fish, which ate the kelp (Vergés et al., 2016). Similarly in Tasmania, the sea urchin *Centrostephanus rodgersii* has become established since the 1960s because water temperatures are now routinely warmer than the lower limits for larval survival (Ling, 2008). Sea urchins have now expanded along the Tasmanian coast (39.6–43.4° S), facilitated by

the rarity of large rock lobsters *Jasus edwardsii*, due to fishing, which are important urchin predators (Johnson et al., 2011). Sea urchins in turn have consumed much of the macroalgae in substantial areas of northern Tasmania, especially for canopy-forming species *E. radiata* and *Phyllospora comosa* (Ling, 2008). While rapid on geological time scales, the gradual effects of warming temperatures in eastern Australian kelp forests over the past decades are more characteristic of changes in distribution commonly found in marine and terrestrial systems (Rosenzweig et al., 2008; Poloczanska et al., 2013) than are changes attributable to the WA MHW in 2011. Perhaps because kelp abundance was already reduced, the Tasman Sea MHW in 2016 apparently had little effect on remaining kelp forests of Tasmania (Oliver et al., 2017). In temperate Australia, as elsewhere, both gradual and extreme changes in temperature are shaping kelp ecosystems.

Seagrasses

Seagrasses form a critical component of many nearshore environments, helping to stabilize sediments and store carbon, providing food for megafauna such as turtles and dugong, and affording critical habitat for birds and recreationally and commercially important fish and invertebrates (Orth et al., 2006). Globally, the decline of seagrass meadows is accelerating (Waycott et al., 2009), attributed primarily to coastal development and deteriorating water quality (Waycott et al., 2009; Grech and Coles, 2010), although growing evidence suggests ECEs have also played a major role (Wetz and Yoskowitz, 2013). Cyclonic conditions can destroy seagrasses in shallow water through physical damage and smothering, while the associated heavy rainfall often results in turbid flood plumes that reduce available light for seagrasses (Longstaff and Dennison, 1999; Campbell and McKenzie, 2004; McKenzie et al., 2012). Elevated nutrient levels transported to the nearshore environment by floods can promote phytoplankton and epiphyte growth, further limiting the light and oxygen available to seagrasses (McKenzie et al., 2012).

During the 2010–2011 wet season along the north Queensland coast, combined impacts of a prolonged period of low salinity, light deprivation, and increased contaminant load (via terrestrial runoff) (Devlin et al., 2012) resulted in a major loss of seagrasses (Figure 2; Babcock et al., 2012; McKenzie et al., 2012, 2014; McKenna and Rasheed, 2013; Hanington et al., 2015). During this time, the formation of one of the strongest La Niñas (McKenna and Rasheed, 2013) brought a series of extreme events to the coast of north-eastern Australia (Hodgkinson et al., 2014). During this period, three tropical cyclones, including one category 5, crossed the coast of tropical eastern Australia. This resulted in record river flows, with the total flow for all rivers adjacent to the GBR being 2.6 times the median flow. At their peak, flood plumes during this period covered 39% of the GBR (Devlin et al., 2012). There were similar levels of flooding as far south as Moreton Bay, where an estimated sediment load > 1 million tonnes (three times average annual load) was deposited into Moreton Bay over a 10-day period (DERM, 2011).

Severe declines in seagrasses were recorded in 2011 for regions within the GBR, with >70% of all seagrass beds declining by >20% and seagrass condition in all regions rated as “very poor”

and at historically low levels (McKenzie et al., 2014). Similar, though less-extreme trends were reported in coastal areas south of the GBR, also associated with unusually high rainfall and flooding (Babcock et al., 2012). In February 2011, Tropical Cyclone Yasi (Category 5, Figure 2) not only brought high rainfall but also resulted in extensive physical damage to seagrasses within a 300-km wide band across the continental shelf (Kennedy et al., 2018). Approximately 98% of intertidal seagrass was lost in its path, and only a few isolated shoots remained in coastal and reef habitats (McKenzie et al., 2012). Following floods in 2011 in Queensland, there were record numbers of strandings of green turtles and high levels of strandings of dugongs that rely on seagrass for food (Meager and Limpus, 2014).

After the floods in early 2011, colonizing species of coastal seagrasses showed some recovery (e.g., <10% of original cover) between Townsville and Moreton Bay during the ensuing 12 months (Babcock et al., 2012; McKenna and Rasheed, 2013; McKenzie et al., 2014), as did some deep-water seagrasses to the north of Townsville (McKenna and Rasheed, 2013). In contrast, there was no evidence of recovery in coastal inshore seagrasses by September 2012 (McKenna and Rasheed, 2013).

Seagrass meadows in Shark Bay on the west coast (~26° S) also experienced mortality during the 2011 MHW (Thomson et al., 2015; Arias-Ortiz et al., 2018), possibly exacerbated by an extreme rainfall event in late December 2010 that led to prolonged (December 2010 to February 2011) flooding and high turbidity. Within the eastern embayment of Shark Bay, impacts of the heatwave and the flooding potentially acted synergistically on the seagrass damaging 36% of the seagrass community, causing 22% loss of extent and exposing organic carbon in sediments to oxic conditions (Arias-Ortiz et al., 2018). *Amphibolis antarctica* is close to its northern limit of distribution at Shark Bay, suggesting it could be sensitive to increases in temperature (Walker and Cambridge, 1995) or deterioration in conditions. Similar to the east coast, turtle health was affected in Shark Bay following declines in seagrass cover (Thomson et al., 2015). The slow growth rate of *A. antarctica* and observations that below-ground biomass continued to decline for several years following the MHW (Fraser et al., 2014; Thomson et al., 2015) suggest future recovery will be slow. These events are an example of how different types of ECEs that are linked to larger-scale variability in climate such as ENSO (e.g., Figure 2) can be clustered in time, and thus compromise the natural coping mechanisms of many species.

Mangroves

Remote tropical Australian coasts support undisturbed mangrove forests and adjacent estuarine and shallow coastal waters of global significance (Halpern et al., 2008). Mangrove forests are responsible for major components of the primary productivity of coastal habitats that support fish and fisheries, both globally and in northern Australia (Blaber, 2007). The physical structure of mangrove forests provides both shelter and a stable substrate for flora and fauna, as well as increasing soil stability on which subterranean communities of fish, crustaceans, and detritus recyclers rely (Nagelkerken et al., 2008).

During the summer of 2015–2016, a significant area (7400 ha) of mangroves in the Gulf of Carpentaria (GOC) died (**Figure 2**), mostly in tracts along the coastline from the western GOC to the south-east GOC (Duke et al., 2017; Harris et al., 2018). The

scale of this dieback, over 1000 km in linear extent of saltflat- and beach-backed coasts, was far more extensive than any reports of previous diebacks (e.g., Paling et al., 2008). The dieback affected 6% of the overall GOC mangrove community, and in some

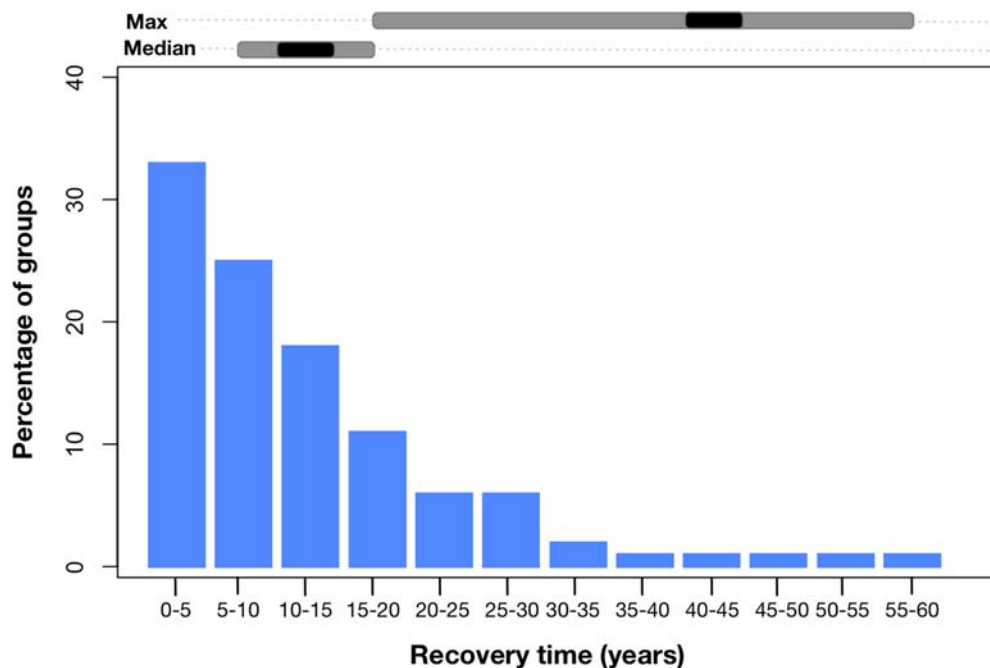


FIGURE 3 | Distribution of recovery times (across all groups in all models). The spread of the median and maximum ranges of recovery times at a system level are shown in gray bars above the plot, with the median across systems shown in black.

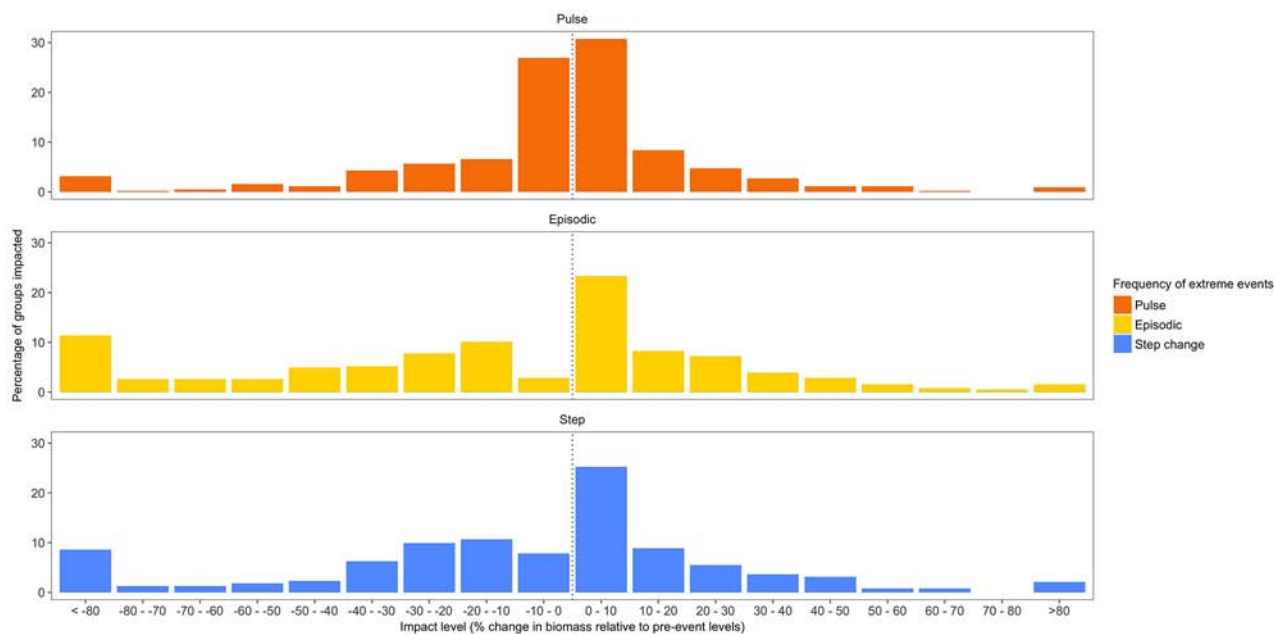


FIGURE 4 | Ecosystem impact plots showing the distribution of percentage change in relative biomass (in comparison to pre-event levels) under the three scenarios: pulsed, episodic, or step-change in the frequency of extreme events (plots aggregate results across all groups in all models).

regions dieback affected up to 26% of the mangrove stands. At locations in the eastern GOC ($\sim 17.5^\circ$ S, 140.9° E), the coastal *Avicennia marina* community suffered complete mortality. In other locations, such as in the western GOC (15° S, 138.7° E), two species of mangrove died (*A. marina* and *Rhizophora stylosa*), each along the landward edge of the upper tidal limit of their distribution, despite the two species inhabiting different tidal levels. Mortality of mangroves was also reported in early 2016 as far away as the Northern Territory (12.2° S, 132.7° E; Lucas et al., 2017) and the Australian west coast (22.0° S) and was due to ENSO-linked sea level changes (Lovelock et al., 2017) that affect the whole northern Australian region, suggesting that there may have been further diebacks in remote areas that were unreported.

By late 2015, affected areas of the GOC had experienced lower-than-average rainfall for the previous 3 years, record hot temperatures in the preceding 6 months, and abnormally low sea-level (>20 cm below mean sea level) (Duke et al., 2017). This was coincident with a strong El Niño, resulting in ECE conditions across northern Australia. Mangrove forests require freshwater for survival and, though they use saltwater as well, many mangroves live close to their salinity tolerance levels (Parida and Jha, 2010). It is likely that mangrove tracts suffered from a combination of soil moisture stress, loss of monthly inundation of the upper intertidal on neap tides, and abnormally hot temperatures over an extended period. The recent mangrove diebacks in northern Australia took place within otherwise pristine mangrove ecosystems, few of which remain worldwide, and illustrate impacts on tropical stands suffering dieback from soil moisture stress (see Duke et al., 2017; Lovelock et al., 2017).

Modeling ECE Impacts

Results from the ecosystem models of simulations of extreme event scenarios indicate that there are clear and potentially substantial effects of ECEs (Figure 3). After a single extreme event, recovery times for individual functional groups ranged from 4 to 60 years. While median recovery time was more typically 10–15 years, a long tail of continuing small-scale effects was evident (Figure 3), with biomass of primarily slower-growing or longer-lived groups departing from pre-event levels for decades.

Since median recovery time is estimated to be 10–15 years (Figure 3), and the frequency of ENSO-related ECEs is projected to be 1 in 15 years (Cai et al., 2014), coastal ecosystems are unlikely to recover fully between ECEs, resulting in compounding effects on ecosystem structure and function. For example, if events were once-off or relatively infrequent, longer-term shifts were small for the majority of groups ($<5\%$), however, as frequency increased so did the mean size of the impact on biomass each functional group – increasing to be 8–10% for most groups (Figure 4). This mean hides considerable variation, with biomass of habitat-forming groups and species dependent upon them – particularly large-bodied reef or meadow-dependent species – declining substantially (e.g., by $>80\%$), while other generalist or more opportunistic species increase in abundance (e.g., small herbivorous fish in Jurien Bay, WA, increase by 48%; fish species characteristic of degraded and

disturbed habitats increasing in tropical models and demersal omnivores and invertebrate feeders increasing in temperate models). For fisheries, these shifts in biomass had substantial negative effects on landed catches, which were predicted to fall by 15–25% overall.

Across the different types of models, those capturing the time delays inherent in habitat recovery (Atlantis, InVitro, and EwE models with stanza representations of corals) predicted the longest recovery times. Maximum recovery times ranged from 15–20 to 55–60 years, with median values between 40 and 45 years (Figure 3). Moreover, tropical systems took longer to recover than temperate systems and showed a greater propensity for the consequences of individual ECE to last decades. Allowing for acclimation and evolution in the Atlantis model of south east Australia lessened the effect of ECEs, halving the magnitude of biomass declines and shortening recovery times by $\sim 40\%$, but did not negate all impacts.

CONCLUSION

Widespread and severe impacts of climate change are not simply a problem we might face in the future, they are happening now. We have detailed recent severe, abrupt, and widespread impacts of climate change related to environmental extremes affecting globally significant habitat-forming corals, seagrasses, kelps, and mangroves around Australia. Since 2011, $>45\%$ of the coastline of the Australian continent has been affected by ECEs, which are unprecedented in intensity, and are becoming more frequent, such as the multiple bleaching episodes of coral reefs in WA and on the GBR. This manifestation of climate change – an increase in episodic ECEs – differs from a more gradual model of climate change driven solely by changes in mean temperature assumed in most modeling of future biodiversity distribution (e.g., Burrows et al., 2014; Lenoir and Svenning, 2015). Marine life is more likely to be able to adapt to the gradual climate change in coastal marine ecosystems that is occurring in Australia (e.g., in kelp forests of southeastern Australia; Ling, 2008; Vergés et al., 2016) and globally (Bates et al., 2018), than to the abrupt ECEs that we describe here.

When effects of gradual climate-related change in coastal habitats around southeastern Australia are added to ECE impacts (Supplementary Figure S1), the proportion of coastline affected around Australia reaches almost 50%. Regardless of the mechanisms, the public reaction to these vast impacts has been relatively muted, particularly relative to the concern that results from localized accidents such as oil spills, shipwrecks, or coastal developments. For example, the Deepwater Horizon accident in the Gulf of Mexico caused a global outcry far larger than for any of the events documented here, yet it affected at most 2100 km of coast (Beyer et al., 2016) with apparently short-lived impacts so far (Lin and Mendelssohn, 2012). In contrast the length of coastline affected by the ECEs in the last decade described here is around 8000 km, nearly four times greater in extent and includes impacts that appear likely to be irreversible at least on decadal scales and possibly longer (Wernberg et al., 2016a; Hughes et al., 2018). Recent

modeling strongly suggests that the reduction in extent of key habitats such as kelp forest will continue to change rapidly with a reduction in extent of kelp forests of up to 70% by 2100 (Martínez et al., 2018).

Climate change is exacerbating ECEs on land (Christidis et al., 2015; Mann et al., 2017; Harris et al., 2018), including recent hurricanes in the Caribbean and the United States, and in the ocean (e.g., Wetz and Yoskowitz, 2013; Brown et al., 2016; Oliver et al., 2018a). In the future, atmospheric (Fischer et al., 2013) and marine (Oliver et al., 2017) heatwaves are expected to increase in frequency and duration under climate change. The Coupled Model Intercomparison Project (CMIP5) models project terrestrial heatwaves to become more frequent, hotter, and last longer across Australia by the end of the 21st century (Cowan et al., 2014). Projections for northern Australia show the largest increase in heatwave days, due to the narrow temperature distribution in the tropics (e.g., Diffenbaugh and Scherer, 2011). Given that global climate models project significant increases in extreme El Niño and La Niña events (Cai et al., 2014, 2015) and a continuation of positive Southern Annual Mode trends in the Representative Concentration Pathways (RCP8.5) scenario (Zhang et al., 2013), there is likely to be an increase in MHWs and ECEs in Australia (and globally), with impacts felt more acutely in northern Australia (Oliver et al., 2018b). Tropical storms (Walsh et al., 2016) are likely to become more intense, and rainfall events and sea levels (Zhang et al., 2013; Widlansky et al., 2015) will also become more extreme and more likely. The scale of the ECE impacts observed around the Australian coastline is also an issue of concern, since sessile species rely on recruits (whether larvae, spores, or seeds) from outside the impacted area for recovery, with likely implications for the resilience of affected systems (e.g., Hughes et al., 2017).

Based on our literature synthesis and modeling, ECE impacts to ecosystems are likely to become more severe and extensive in the relatively near future. Indeed, they are happening now, and based on this Australian analysis, may be more common globally than currently appreciated, and have longer lasting impacts in the tropics than in temperate regions. ECE impacts on kelp in south WA are consistent with this hypothesis, since seasonal temperature extremes in this region are moderated by the poleward-flowing Leeuwin current, which is strongest during winter (Rochford, 1984). Widespread ECE impacts are not restricted to the Australian coast but are widespread globally (Smale et al., 2019). These events are changing ecosystems in profound ways that in some cases are unlikely to be reversible. ECE impacts also suggest that while climate change may be viewed as gradual, in many cases it manifests through a series of often extreme and abrupt changes. It is significant that impacts of climate change may manifest through ECEs because heatwaves provide little opportunity for acclimation or adaptation, in contrast to more gradual warming (Walther, 2010) such as on Australia's temperate east coast. Whereas studies of mobile species suggest that ECEs may lead to rapid evolution because of the dramatic selective pressures they impose (van de Pol et al., 2017), the implication for habitat-forming sessile marine species may be quite different and more serious as they can be

particularly vulnerable to heatwaves. Sessile organisms lack the ability to physically move to cooler locations (Mislan and Wethey, 2015) except by establishing new populations via larval transport; therefore, for marine species in particular the velocity of climate change may exceed the ability of most species' populations to extend their range (Burrows et al., 2011). Further, it is uncertain whether immigrant species arriving in new latitudes would actually be able to adapt (Sommer et al., 2018). In addition, disrupted ecosystems that have been stable for millennia have non-biological consequences, such as the release of carbon from stable sediment accumulation (Arias-Ortiz et al., 2018). As such, ECEs will have significant consequences not only for coastal marine ecosystems but also for the human economic, social, and political systems that depend on them.

The results of modeling ECE impacts on coastal habitats around Australia provide insights into a range of potential futures for marine ecosystems around the continent, some of which may have serious ecological and social implications. As such they provide a useful assessment of the risks faced in the future but also hypotheses that must be evaluated by targeted observations if we are to refine our understanding of climate and ECE impacts. Such refinements are essential if we are to make practical steps to minimize or manage these impacts, particularly since combined press (incremental global warming) and pulse (ECE) disturbances may produce unpredictable interactions and outcomes (Underwood, 1989).

Extreme climate events can act as a catalyst for transformational adaptation to climate change (Travis, 2014). We need to combine our efforts to forecast the climate on seasonal to multi-year timescales with our understanding of marine ecosystem responses at both species and ecosystem level to develop and test strategies to minimize impacts of ECEs. In developing adaptation strategies, we need to consider that ECEs can trigger fundamental shifts in ecosystems (van de Pol et al., 2017), and that the loss of resilience often precedes ecosystem shifts (Scheffer et al., 2001). Therefore, adaptive management strategies that maintain ecosystem resilience continue to be important. Adaptation strategies also need to be flexible and adaptive in response to the information revealed by monitoring and assessment (Schindler and Hilborn, 2015). It is also likely that such strategies must include active restoration approaches (Anthony et al., 2017). This requires close integration between management interventions with ecosystem research.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

RCB, RHB, EF, MH, AR, and MV conceived the manuscript. RCB, RHB, EF, DF, MH, AH, RK, RM, EP, AR, and MV wrote the manuscript. EF performed the ecosystem modeling. DF, MH, and AH conceived and executed the figures.

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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.2019.00411/full#supplementary-material>

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Corrigendum: Severe Continental-Scale Impacts of Climate Change Are Happening Now: Extreme Climate Events Impact Marine Habitat Forming Communities Along 45% of Australia's Coast

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A Corrigendum on

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In the original article, there was a mistake in **Figure 2** as published. Monthly SST mean plots obtained from OceanCurrents (<http://oceancurrent.imos.org.au/>) contained an error at the time that we downloaded our data. This error has subsequently been corrected, and we were notified of the error by OceanCurrents after the publication of our article. The correct SST anomalies are lower than those suggested in the original **Figure 2**. The corrected **Figure 2** appears below.

Additionally, there was an error in affiliation Mathew A. Vanderklift. Instead of having both affiliation 3 and 5, Matthew A. Vanderklift should only have affiliation 5.

The authors apologize for these error 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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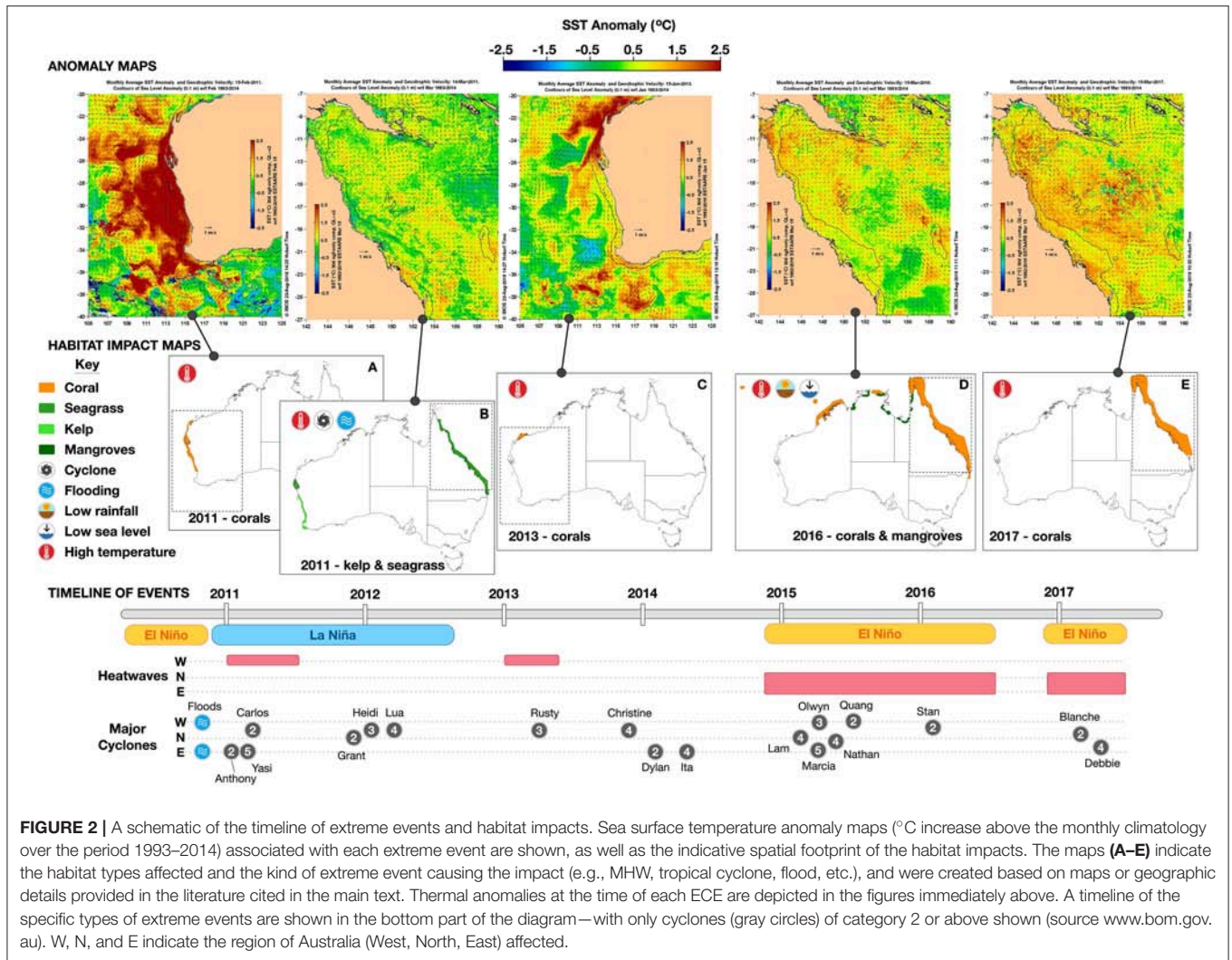


FIGURE 2 | A schematic of the timeline of extreme events and habitat impacts. Sea surface temperature anomaly maps ($^{\circ}\text{C}$ increase above the monthly climatology over the period 1993–2014) associated with each extreme event are shown, as well as the indicative spatial footprint of the habitat impacts. The maps (A–E) indicate the habitat types affected and the kind of extreme event causing the impact (e.g., MHW, tropical cyclone, flood, etc.), and were created based on maps or geographic details provided in the literature cited in the main text. Thermal anomalies at the time of each ECE are depicted in the figures immediately above. A timeline of the specific types of extreme events are shown in the bottom part of the diagram—with only cyclones (gray circles) of category 2 or above shown (source www.bom.gov.au). W, N, and E indicate the region of Australia (West, North, East) affected.



A Systematic Review of How Multiple Stressors From an Extreme Event Drove Ecosystem-Wide Loss of Resilience in an Iconic Seagrass Community

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A central question in contemporary ecology is how climate change will alter ecosystem structure and function across scales of space and time. Climate change has been shown to alter ecological patterns from individuals to ecosystems, often with negative implications for ecosystem functions and services. Furthermore, as climate change fuels more frequent and severe extreme climate events (ECEs) like marine heatwaves (MHWs), such acute events become increasingly important drivers of rapid ecosystem change. However, our understanding of ECE impacts is hampered by limited collection of broad scale *in situ* data where such events occur. In 2011, a MHW known as the Ningaloo Niño bathed the west coast of Australia in waters up to 4°C warmer than normal summer temperatures for almost 2 months over 1000s of kilometers of coastline. We revisit published and unpublished data on the effects of the Ningaloo Niño in the seagrass ecosystem of Shark Bay, Western Australia (24.6–26.6° S), at the transition zone between temperate and tropical seagrasses. Therein we focus on resilience, including resistance to and recovery from disturbance across local, regional and ecosystem-wide spatial scales and over the past 8 years. Thermal effects on temperate seagrass health were severe and exacerbated by simultaneous reduced light conditions associated with sediment inputs from record floods in the south-eastern embayment and from increased detrital loads and sediment destabilization. Initial extensive defoliation of *Amphibolis antarctica*, the dominant seagrass, was followed by rhizome death that occurred in 60–80% of the bay's meadows, equating to decline of over 1,000 km² of meadows. This loss, driven by direct abiotic forcing, has persisted, while indirect biotic effects (e.g., dominant seagrass loss) have allowed colonization of some areas by small fast-growing tropical

species (e.g., *Halodule uninervis*). Those biotic effects also impacted multiple consumer populations including turtles and dugongs, with implications for species dynamics, food web structure, and ecosystem recovery. We show multiple stressors can combine to evoke extreme ecological responses by pushing ecosystems beyond their tolerance. Finally, both direct abiotic and indirect biotic effects need to be explicitly considered when attempting to understand and predict how ECEs will alter marine ecosystem dynamics.

Keywords: extreme climate events, marine heatwaves, seagrass, resilience, multiple stressors, resistance, recovery

INTRODUCTION

A key question at the forefront of ecology and evolutionary research in the anthropocene is “how will climate change alter the structure and function of ecological systems?” Evidence suggests widespread, dramatic, climate driven changes to ecosystems with negative consequences including the local extinction of species, major shifts in geographic range and phenology, disruption of fundamental biotic interactions, and a reduction in ecosystem productivity (Poloczanska et al., 2013; Hyndes et al., 2016; Pecl et al., 2017). Recent examples of range shifts and local extinctions that have been documented in marine environments (Johnson et al., 2011; Wernberg et al., 2016) include seagrasses (Kim et al., 2009; Gorman et al., 2016).

Identifying stressors that negatively affect the resilience of ecosystems is fundamental to managing the impacts of climate change (Peterson et al., 1998). Marine ecosystems are being impacted through increasing ocean temperatures, ocean acidification, deglaciation, reduced ocean ice cover, rising sea levels, increasing storm frequency, and intensity (Doney et al., 2012), and strengthening boundary currents (Vergés et al., 2014). These stressors are decreasing ocean productivity, altering food web dynamics, reducing abundance of habitat-forming species, shifting species distributions, and increasing the incidence of diseases (Hoegh-Guldberg and Bruno, 2010; Wernberg et al., 2016). Impacts have been widely documented, despite average global warming of just 1°C (Scheffers et al., 2016). While some of these changes are clearly visible and have received much public attention, such as coral bleaching events, others are much more insidious.

Climate change is predicted to increase the frequency, duration, and intensity of extreme climate events (ECEs), including marine heatwaves (MHWs) (Cai et al., 2014; Pachauri et al., 2014; Oliver et al., 2015; Frölicher and Laufkötter, 2018). ECEs can act as strong and acute agents of change that can generate widespread mortality and collapse of ecosystem services (Smale et al., 2019). ECEs rarely occur in isolation, but generally cause impacts through the combination of multiple abiotic, (e.g., temperature, salinity, pCO₂ concentration), and biotic drivers (e.g., changes in food resources, herbivory, predation, competition, disease) acting additively or synergistically through time (Brook et al., 2008). ECEs, including MHWs, can push populations beyond their functional threshold, where range contractions and extinctions are likely (Hyndes et al., 2016; Wernberg et al., 2016). Furthermore, the indirect, biotic effects

that ECEs trigger (e.g., biogenic habitat loss) can even affect species that were resilient to the initial abiotic effects of an ECE. Despite the critical need to understand the potential for multiple stressors to affect resilience synergistically, many studies instead treat co-occurring stressors as independent phenomena (Orth et al., 2006; Wernberg et al., 2012). Finally, because studies of ECE impacts are often opportunistic, insights into community scale impacts of these events are relatively rare, at least in marine systems. Understanding how ecosystems respond to stressors is necessary to be able to quantify and ultimately predict the resilience of ecosystems exposed to the increasing stressors of the Anthropocene (Pecl et al., 2017).

Summer temperature extremes associated with MHWs are important drivers for the survival and growth of seagrasses globally and will heavily impact their biogeographical distributions and, therefore, have indirect effects to species that are dependent on seagrass ecosystem services (Orth et al., 2006). For example, during the summers of 2005 and 2010, severe MHWs (Hobday et al., 2018) in Chesapeake Bay resulted in 58% loss of *Zostera marina* (2005) along with declines in blue crabs, silver perch and bay scallops followed by a further 41% loss of seagrasses (2010) (Lefcheck et al., 2016). Two strong MHWs in 2003 and 2006 in the western Mediterranean caused shoot mortality of *Posidonia oceanica* to exceed recruitment (Diaz-Almela et al., 2007; Marba and Duarte, 2010). However, with the exception of these studies, monitoring of extreme MHWs in seagrass ecosystems has been rare and generally focussed on individual organisms.

In this paper, we focus on resilience to extreme events in a seagrass-dominated ecosystem, specifically in one of the largest in the world, Shark Bay, Western Australia. We define resilience as “the capacity to undergo disturbance without permanent loss of key ecological structures and functions” (O’Brien et al., 2018; based on Holling, 1973). We focus on the processes of resistance and recovery to assess resilience (*sensu* Hodgson et al., 2015) in relation to 3 seagrass ecosystem trajectories outlined in O’Brien et al. (2018): *reversible degradation* where the ecosystem recovers post-disturbance; *hysteretic degradation*, where feedbacks maintain the disturbed state which requires a lower environmental threshold or another perturbation to start recovery, and; *recalcitrant (irreversible) degradation* where the damage done by the disturbance is not reversible and the environment is not suitable for recovery of seagrass habitat. We also investigate how the life history strategy of major seagrass species found in Shark Bay, as

described by Kilminster et al. (2015), influence resistance and recovery trajectories.

Shark Bay is a large marine embayment (13,500 km²) (Figure 1) on the tropical temperate transition zone on the west coast of Australia that has obtained World Heritage Site (WHS) listing because of its unique environmental values (whc.unesco.org). One of these values is the extensive seagrass meadows that support high marine biodiversity, including significant consumer populations of dugongs, turtles, and their major predator, tiger sharks (Heithaus et al., 2012; Kendrick et al., 2012). Shark Bay is characterized by high seagrass biodiversity as it sits in the transition between the temperate and tropical biomes, with 13 species of temperate and tropical seagrasses, most at the extremes of their respective distributions (Walker et al., 1988). These species also encompass multiple life history strategies including colonizing, opportunistic and persistent (Kilminster et al., 2015). The large temperate seagrasses *Amphibolis antarctica* and *Posidonia australis* have historically dominated Shark Bay seagrass cover, creating extensive, persistent meadows measuring 3,676 km² and 200 km² of 4,176 km² total seagrass cover, respectively (Walker et al., 1988). Both species lack a seed bank and exhibit relatively slow rates of rhizome expansion, resulting in slow rates of recovery from disturbance. The remaining 500 km² of seagrass meadows are dominated by the small tropical colonizing seagrasses *Halodule uninervis*, *Halophila ovalis*, *Halophila ovata*, *Halophila spinulosa*, and *Halophila decipiens* and opportunistic tropical species *Cymodocea serrulata*, *Cymodocea angustata*, and *Syringodium isoetifolium*. These tropical species have low initial resistance to disturbances but can recover quickly through seed banks, vegetative fragments, and rapid rhizome elongation rates (Sherman et al., 2018). There is also minor coverage by other persistent temperate species *Posidonia angustifolia* and *Posidonia coriacea*.

The severity of several MHWs has been characterized (Hobday et al., 2018) and the marine heatwave of austral summer 2011 along the Western Australian coast (Figure 2) was among the most extreme on record (Category IV). An unusual combination of conditions led to this event (Feng et al., 2013). The Western Australian coastline is influenced by the poleward flowing Leeuwin Current (LC) that transports tropical waters from the eastern Indian Ocean southward along the continental slope, particularly during winter. The LC is heavily influenced by the El Niño Southern Oscillation (ENSO) through oceanographic and atmospheric connectivity to the Pacific Ocean. During La Niña years (e.g., 1999–2000, 2011–2012) the LC flows stronger resulting in transport of elevated ocean temperatures down the west coast (Feng et al., 2003). The region is typically dominated by strong southerly wind patterns through the summer months that oppose the LC, contributing to its seasonality, and also acting to moderate heating of coastal ocean temperatures through upwelling (Woo et al., 2006; Rossi et al., 2013) and air-sea heat flux (e.g., evaporative cooling) processes (Feng and Shinoda, 2019). However, relaxation or reversal of the southerly winds can further enhance heating, as occurred during the La Niña event of 2010–2011, when weak, northerly winds combined with an unusually strong summer Leeuwin Current to elevate

summer maximum sea temperatures by 2–4°C in the region. This extraordinary build-up of warm Indian Ocean water along the Western Australian coast was coined the “Ningaloo Niño” (Feng et al., 2013; Pearce and Feng, 2013) and has recently been proposed to occur even in the absence of ENSO influences (Kataoka et al., 2018). The shallow, semi-enclosed geography of Shark Bay means it is particularly susceptible to anomalous air-sea heat fluxes such as the conditions observed during the Ningaloo Niño and other climatic events, a factor which has generally been overlooked in broad scale regional studies. Whilst extreme temperatures were experienced over the entire region (Figure 2i), within the bay the local SST response to the extreme conditions varied (Figures 2a–h).

Here, we review published literature and unpublished data to characterize the resilience (i.e., resistance and recovery) of a large seagrass-dominated marine ecosystem using a case study focussed on the influence of the 2011 MHW on the seagrasses of Shark Bay. First, we summarize our knowledge of individual species resistance to this environmental “perfect storm” and the trajectory of recovery for seagrasses and seagrass-dependent organisms in Shark Bay across multiple scales from *whole ecosystem* (>10,000 km²), to *regions* that cover areas of >100 km², and *local scales* of single to multiple sites within a *region* (<10 km²). Finally, we discuss the future of the system and the management of the WHS values of Shark Bay.

METHODS

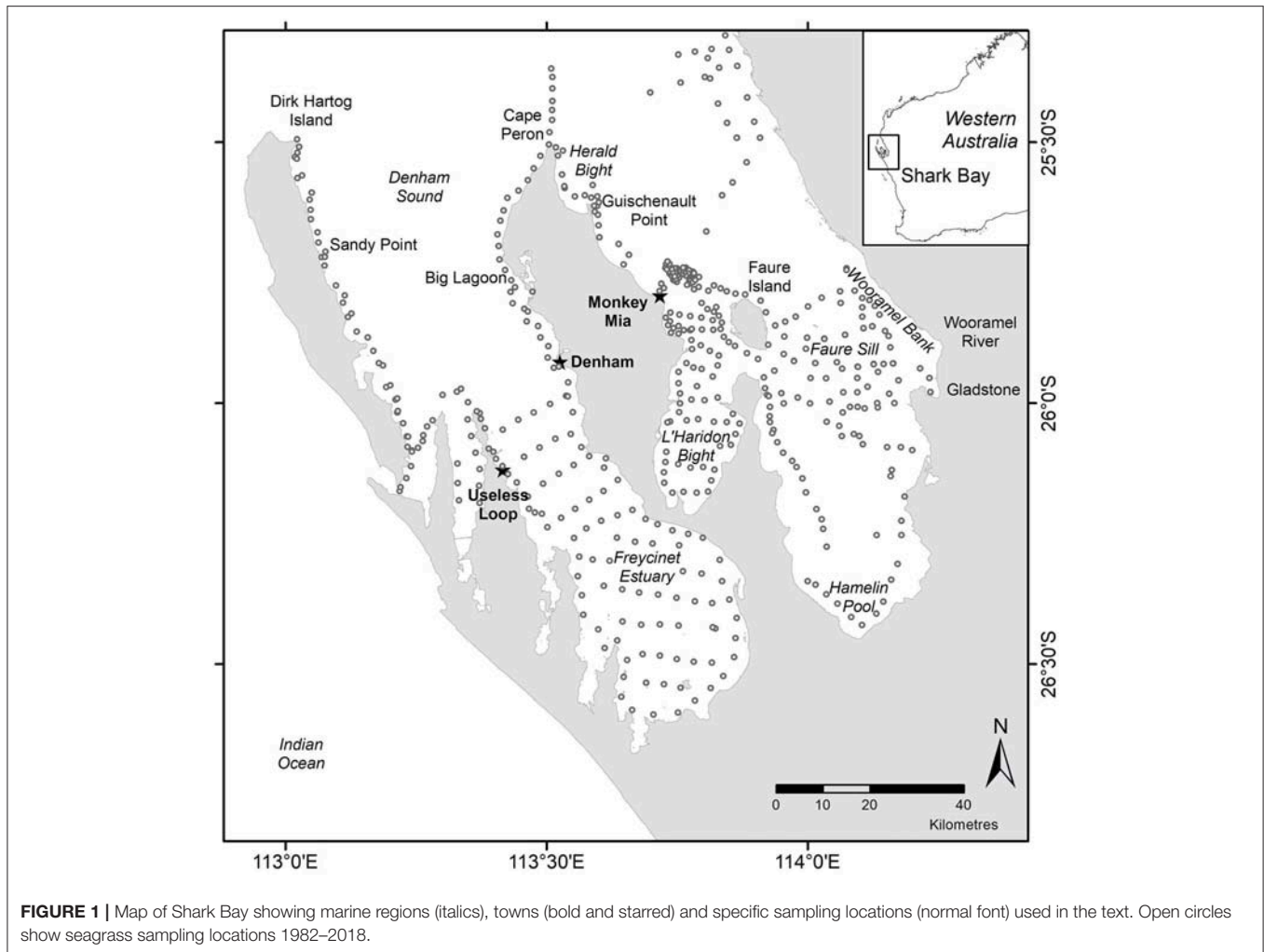
The size of Shark Bay (13,500 km²), its isolation from major research institutes (>900 km), and the varying taxonomic and regional foci of its researchers has resulted in heterogeneous data on the impact and recovery from the MHW. Furthermore, the data available have been collected during studies not specifically aimed at addressing questions around the MHW. Here we combine the best available science from these studies, both published and unpublished, to address the loss of resistance and the trajectory of recovery in the system.

Satellite Sea Surface Temperature (SST) Data

In order to examine details of the MHW within the bay and avoid biases intrinsic in some coarser SST datasets, high-resolution (2 km) daily nighttime AVHRR L3S SST data available through the Integrated Marine Observing System (IMOS) (<http://imos.org.au/facilities/srs/sstproducts/sstdata0/>, Griffin et al., 2017) were combined with the SST Atlas of Australian Regional Seas (SSTAARS) (1993–2016) climatology (Wijffels et al., 2018) to produce monthly mean SST and anomaly maps from 1993 to 2019. Time series of these variables were extracted by calculating the spatial means over the region shown in Figure 2.

Seagrasses

We collated published and unpublished seagrass data from before, during and after the MHW in Shark Bay to address the magnitude of the disturbance and change in state in relation to the return time of the Shark Bay ecosystem and characterized the scale of impact to one of three scales: ecosystem-wide, regional,



and local. Ecosystem-wide data represent the entire 13,500 km² Shark Bay ecosystem with 4,176 km² of seagrass-dominated banks and sills (**Figure 1**). Regional studies represent regions of >100 km² within the ecosystem, like Faure Sill, Eastern Cape Peron, L'Haridon Bight, Western Cape Peron, Denham Sound, Freycinet Estuary and sills and banks offshore from Monkey Mia. Local studies are those at individual locations <10 km², like Useless Loop. We only included data that allowed us to address changes across multiple years and that was appropriately collected using comparable methods.

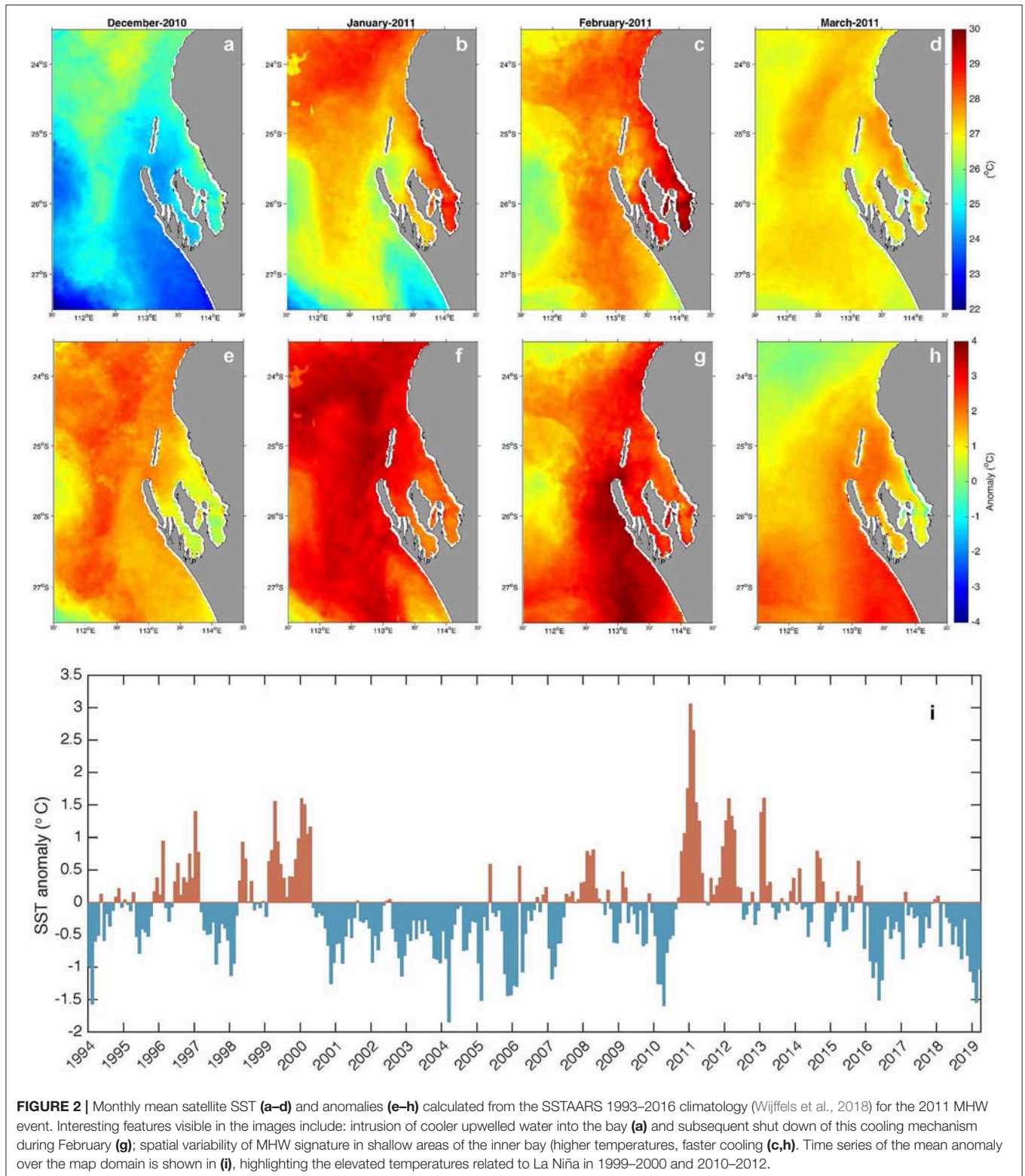
Mapped Changes

Historical mapping of seagrasses between 1983 and 1985 was conducted by Walker et al. (1988). Ecosystem-wide changes in seagrass coverage were determined from a comparison of satellite imagery collected between 2002 and 2014 that mapped 68% of the Shark Bay Marine Park, which were extrapolated to cover the whole Shark Bay region (Arias-Ortiz et al., 2018). We updated these data to include unpublished studies that are currently underway by the Department of Biodiversity Conservation and Attractions (DBCA) in Western Australian to improve both

spatial and temporal resolution and coverage of this dataset. The final data set allowed us to illustrate changes in seagrass coverage across multiple years before and after the MHW throughout Shark Bay.

Regional Changes in Shoot Density and % Cover

Regional loss of seagrasses were recorded as changes in presence/absence, percent cover, and shoot density in quadrats (**Tables S1, S2**). These data were collected before, during and after the 2011 MHW. Shoot densities at 14 locations were collected from six 0.2 × 0.1 m quadrats at each location in the western and eastern Cape Peron and Faure Sill regions in 1982, three decades before the heatwave (Walker, 1985). Similar shoot density data were collected from five 0.04 m⁻² cores taken at multiple locations from Useless Loop, Freycinet Estuary (Statton, unpublished data) and from Faure Sill (2011, 2013), and eastern and western Cape Peron (2013–2014, 2017–2018) (Fraser et al., 2014; Fraser and Kendrick, unpublished data). Seagrass density data predominantly from the western embayment and Freycinet Estuary were also included (Seagrass monitoring program for the Shark Bay Marine Park, DBCA, Strydom, unpublished data).



Briefly, in the DBCA survey, shoot density was determined at six locations by randomly placing eight 0.2×0.2 m quadrats along three 10 m transects at each location and counting shoot densities (Table S2).

Regional changes in seagrass cover were also monitored more frequently at five offshore banks north of Monkey Mia, where occurrence and percent cover of *A. antarctica*, *H. uninervis*, and macroalgae were determined from 3×0.36 m² across 63

locations between 2007 and 2017 (Nowicki et al., 2017; Nowicki, unpublished data). Seagrass % cover was also taken across Faure Sill and Wooramel Bank regions in March 2011 (28 locations, $5 \times 0.25 \text{ m}^2$ quadrats location⁻¹) at the height of the MHW, in September 2011 (14 locations, $5 \times 0.25 \text{ m}^2$ quadrats location⁻¹) and in February 2013 (5 locations, $5 \times 0.25 \text{ m}^2$ quadrats location⁻¹) (Fraser et al., 2014).

Finally, to attempt an analysis of system resistance and recovery, we took the most complete dataset, shoot density for *A. antarctica* and *P. australis*, and plotted it by field program (mean $\pm$ SE) for field programs that collected that data between 1982 and 2011–2018. For *A. antarctica*, there were four field programs between 1982 and 2013, and for *P. australis* there were 11 field programs between 1982 and 2018. Sampling locations within each field program were treated as replicates to reduce confounding data in space and time. This approach also addressed the effect of differences in both number and placement of locations from each program. Note also that some programs sampled existing seagrass meadows so have a bias over time toward seagrass loss. Statistical differences between each program's data were tested using one way ANOVA, and significance differences determined using Tukeys HSD pairwise tests (aov and Tukeys HSD: R Core Team, 2013).

Local Observations

Local observations of seagrass reproduction and recruitment were used to assess the capacity for recovery. A series of recruitment studies using transplants of both *P. australis* and *A. antarctica* were undertaken between 2010 and 2018 at Useless Loop as part of a seagrass restoration program (Poh, Statton, unpublished data). Surveys of flowering and seed production in *P. australis* were carried out mainly at Useless Loop and Guischnault Point but opportunistic collections were also made at Monkey Mia, Denham, Big Lagoon and Eagle Bluff in 2011, 2012, 2016 and 2017 (Statton and Kendrick, unpublished data).

Effect on Seagrass Associated Fauna

Effects of seagrass loss were assessed on all major species of air-breathing megafauna that occur in Shark Bay via visual transect surveys at the surface (Nowicki et al., 2019). These surveys, running continuously since 1998, have been part of a wider community research project on the seagrass banks immediately north of Monkey Mia (see Heithaus et al., 2012 for descriptions). Briefly, long-term transects 3–4 km in length were established over shallow seagrass banks ($\sim 2\text{--}4 \text{ m}$ depth) or deep sandy channels ($\sim 10 \text{ m}$ depth). Each transect was run by driving a 5.5 m vessel along the transect at 6–9 km per hour approximately four times per month, with most sampling occurring between Feb–Oct. All air breathing fauna (Indo-Pacific bottlenose dolphins *Tursiops aduncus*, dugongs *Dugong dugon*, loggerhead turtles *Caretta caretta*, green turtles *Chelonia mydas*, Pied Cormorants *Phalacrocorax varius*, and sea snakes) that were sighted at the surface within a species-specific sighting band were quantified and recorded.

In addition to air-breathing fauna, Nowicki et al. (2019) also quantified changes to the large shark community via standardized

drumline fishing. ~ 4 days per month (mostly between Feb–Oct), 10 drumlines baited with $\sim 1.5 \text{ kg}$ of fish each were set at dawn. All sharks captured were identified, measured, tagged, and released. Catch-per-unit effort (expressed as sharks per 100 hook hours) was compared between 1998–2010 and 2012–2014 to assess whether seagrass loss related to the Ningaloo Niño significantly impacted large shark densities, which are historically dominated by tiger sharks (*Galeocerdo cuvier*, Heithaus, 2001). We also examined data on bioturbation on establishing seeds (Johnson et al., 2018) at Useless Loop.

RESULTS

Scales of Loss and Recovery in Seagrasses: Ecosystem-Wide

The seagrass-dominated ecosystem in Shark Bay displayed high resistance to change in seagrass cover before the MHW, which varied little between that determined by hand drawn polygons in 1983–85 and computerized mapping from satellite imagery in 2002 (area change of -183 km^2 to $+124 \text{ km}^2$ (Table 1). Differences in aerial coverage between 2002 pre-MHW and 2014 post-MHW resulted in $696\text{--}921 \text{ km}^2$ lost and $190\text{--}261 \text{ km}^2$ of dense meadows thinning dramatically becoming sparse meadows of $<10\%$ coverage. A brief visual survey of landsat imagery indicated seagrass losses in the landscape occurred 1–2 years after defoliation of *A. antarctica* (2012–2013), and was most evident in shallow offshore banks and sills and deeper seagrass environments (Figure 3).

Regional Loss and Recovery of Seagrasses

Using long term and multi-institutional data on shoot density (m^{-2}) we demonstrate there were significant loss in above ground shoot and stem densities in temperate seagrasses during (*P. australis*) and within a year after (*A. antarctica*) the 2011 MHW (Figure 4, Table S3). *A. antarctica* stem densities had not recovered by 2015 [Figure 4A, Table S2: ANOVA $F = 9.139$, $p = 4.28 \times 10^{-6}$, $df = 4, 77$; Pairwise Tukey HSD DW1 (1982) = GAK1 (March 2011) $\neq$ GAK2 (September 2011) $\neq$ GAK3 (2013) $\neq$ DPAW1 (2015)]. In contrast, *P. australis* shoot density collapsed to a third of historical values in 2011 and remained low in 2014, and 2016 [Tukey's HSD DIW (1982) $\neq$ DBCA1 (2011) $\neq$ DBCA2 (2014) $\neq$ DBCA3 (2016)], but by 2016 was showing signs of recovery (DBCA3 = CG1 $\neq$ JS1). By 2017–2018 shoot densities of *P. australis* were not significantly different than those recorded in 1982 [Figure 4B, Table S3: ANOVA $F =$

TABLE 1 | Change in total area of seagrasses between 1983–85 (Walker et al., 1988), and dense and sparse seagrasses between 2002 and 2014 (DBCA monitoring program, no brackets) with the larger estimates of Arias-Ortiz et al. (2018) in brackets.

Year	Total (km ²)	Dense (km ²)	Sparse (km ²)
1988	4,176		
2002	3,993 (4,300)	2,729 (3,096)	1,264 (1,204)
2014	3,297 (3,371)	1,772 (2,906)	1,525 (1,394)
2002–2014 change	−696 (−921)	−957 (−190)	+261 (+190)

11.23 $p = 2.35 \times 10^{-9}$, $df = 9, 50$; Tukey's HSD DIW (1982) = JS2 (2017) = GAK 1, 2, 3 (2018 seasonal sampling)]. Note we show these data with the major caveat that the different sources of data were from field programs that sampled different locations and numbers of locations with different sampling densities (Table S2).

The state change from *A. antarctica* meadows to low cover of tropical colonizing and opportunistic seagrasses has persisted to 2017 across five shallow offshore banks near Monkey Mia from 2007–2008, 2011–2014, 2016, 2017 (Figure 5). Statistically significant losses in *A. antarctica* occurrence and % cover were

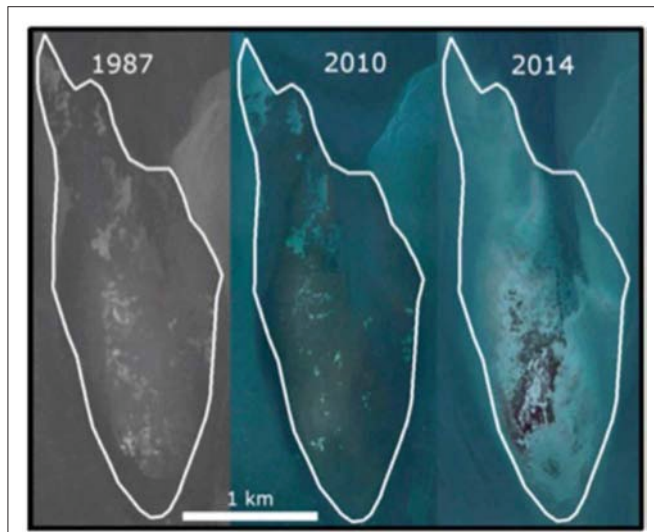


FIGURE 3 | Imagery illustrating changes to seagrass cover (dark areas) within a single seagrass bank (white outline) before and after the 2011 MHW. The decadal stability of small bed features such as sand patches across almost 3 decades illustrates the natural resistance of the system to change, as well as the unusual impact of the MHW on the Shark Bay seagrass landscape (from Nowicki et al., 2017, with permission to reuse from MEPS, Images from Google Earth).

documented between 2007–2009 and 2012 (% cover of 89.5–4.8% (Friedman test, $\chi^2 = 59.7$, $df = 2$, $P < 0.0001$), and no recovery between 2012 and 2014 [% cover 3.8 ± 0.9 ; One-way repeated-measures ANOVAs on ranks, $F_{(1,125)} = 3.16$, $p = 0.08$] was observed. However, the tropical colonizing species, *H. uninervis*, increased in occurrence and cover by almost 3-fold from 2007–2009 to 2014 (occurrence: 12–29%; logistic regression, $t_{(124)} = 6.94$, $p < 0.0001$, and cover: 3.1 ± 0.5 to 8.5 ± 2.6 ; One-way repeated-measures ANOVAs on ranks, $F_{(1,125)} = 23.64$, $p < 0.0001$), a trend which continued into 2016 (Figure 5). Importantly, this increase is small in comparison to the loss of *A. antarctica* on these banks from >80 to $<5\%$ cover (Figure 5) and does not represent functional ecosystem recovery.

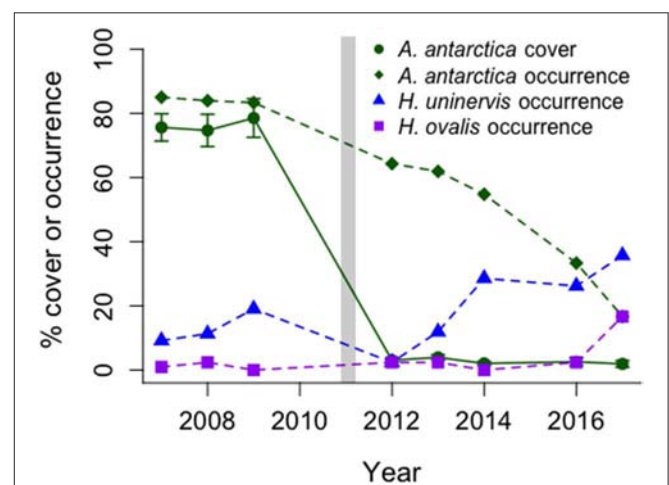


FIGURE 5 | Changes over time in occurrence of two common tropical seagrasses (*H. uninervis*, *H. ovalis*) and percent occurrence (as a total) and percent cover (mean $\pm$ SE, $n = 63$) of the dominant temperate seagrass, *A. antarctica*, before and after the MHW (vertical bar). Data collected from 42 long-term monitoring stations north of Monkey Mia, Shark Bay.

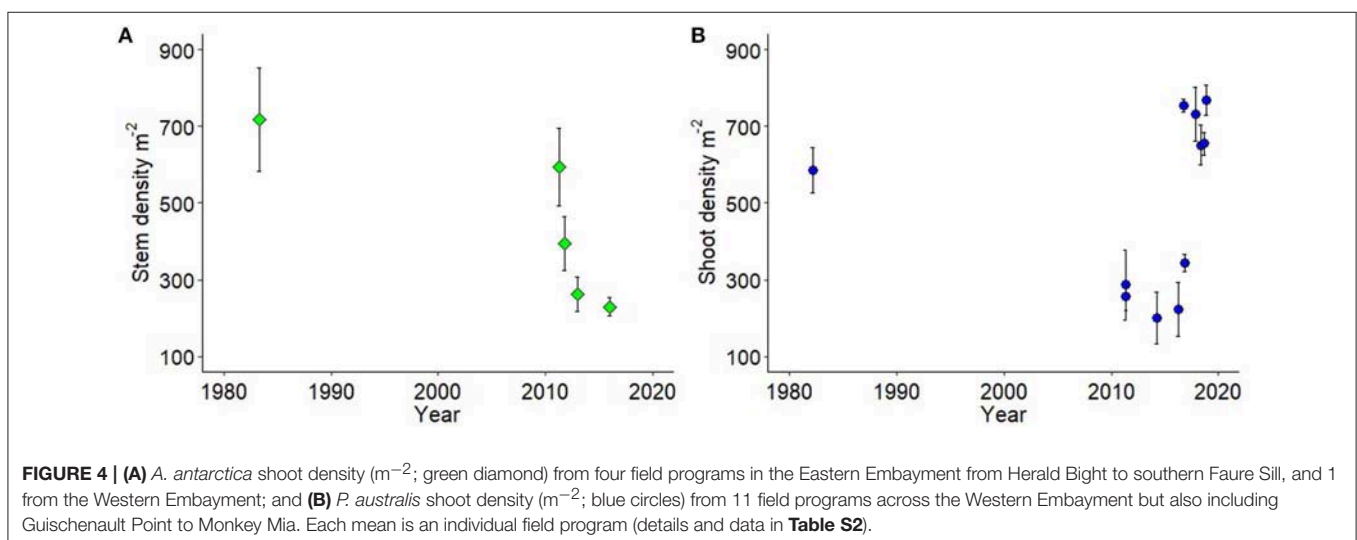


FIGURE 4 | (A) *A. antarctica* shoot density (m^{-2} ; green diamond) from four field programs in the Eastern Embayment from Herald Bight to southern Faure Sill, and 1 from the Western Embayment; and **(B)** *P. australis* shoot density (m^{-2} ; blue circles) from 11 field programs across the Western Embayment but also including Guiskenault Point to Monkey Mia. Each mean is an individual field program (details and data in Table S2).

Local Loss and Recovery of Seagrasses

Local studies of shoot mortality and growth at Useless Loop indicated *P. australis* was not resistant to MHWs although it showed some recovery after 5 years. Higher shoot mortality and slower shoot growth was recorded in *P. australis* transplants after the 2011 MHW at Useless Loop from restoration studies (Poh, unpublished data 2011). Interestingly, seagrass restoration experiments conducted between 2015 and 2018 at Useless Loop show annual doubling of shoot densities for transplants of both *A. antarctica* and *P. australis* suggesting these temperate species do have the ability to recover at the plant scale, but this has not translated into system-wide recovery yet.

Though meadow mortality was low for *P. australis*, recruitment from seed was heavily impacted. Although *P. australis* continued to flower, 100% seed abortion was observed in 2011–2012. Subsequent observations of flowering in 2016 and 2017 recorded much higher successful seed production from flowering (Table S4). In 2016, Guischnault Point and Useless Loop produced 350 and 0.65 viable seeds m^{-2} and in 2017, 350 and 116 viable seeds m^{-2} , respectively. Clearly, reproductive propagules have been missing from Shark Bay until 2016–2017 and have not made a major contribution to recovery for *P. australis*. Similarly, large numbers of viviparous seedlings of *A. antarctica* were observed in August 2018 in the Western Gulf (Kendrick and Sinclair, pers obs), though whether this will result in meadow level recovery remains unclear.

Other Published Observations—Wooramel River

Other 2011 MHW observations that are already published include dramatic loss of *A. antarctica* adjacent to the Wooramel River due to combined high surface sea temperatures and unprecedented flooding. Flooding released over 500 gigaliters of floodwater (Table S5) containing large amounts of fine sediments. The flood was the largest recorded between 1994 and 2015. Reduced light availability over weeks to months associated with resuspended fine sediments, exacerbating the effect of extreme temperatures resulting in a change in state from seagrass meadows to bare sand and patchy meadows in that area. This flood effect was small in area (300 km^2) in relation to the total size of Shark Bay and the scale of loss of seagrasses across the whole system where flooding effects were not observed. Though leaf biomass in the area recovered slightly in the 2 years following the event, it was still at 7–20% of historical averages. Belowground biomass decreased by an order of magnitude over the same time period, indicating change in biomass allocation associated with physiological stress and likely reducing the recovery capacity and increasing the return time for extensive seagrass meadows.

Seagrass Associated Biota

The impacts of seagrass loss within Shark Bay on vertebrate consumers varied with species. For example, long term surface transect data from the Eastern Gulf of Shark Bay offshore of Monkey Mia showed significant population declines in Indo-Pacific bottlenose dolphins (39%), dugongs (68%), cormorants (35%), green turtles (39%), and sea snakes (77%) (Figure 6). The mechanisms of decline (i.e., emigration vs. mortality) likely

differ by species, and consumers more strongly associated with seagrass for food or habitat were more impacted by seagrass loss. Also, seagrass associated fish populations declined significantly, though density of fish in remaining seagrass habitats actually increased following the MHW (Table S1). The ecological impacts of the MHW and seagrass loss on invertebrate fauna have been less well-studied, with existing studies focusing on impacts to fisheries. The 2011 MHW impacted invertebrate fisheries with closure of scallop and blue swimmer crab fisheries and modification in the size to maturity of prawns in the prawn fishery in Shark Bay (Table S1).

DISCUSSION

The “Ningaloo Niño” MHW in 2011 pushed the temperate persistent meadow-forming seagrass species *A. antarctica* and *P. australis* past their capacity to resist high temperatures in Shark Bay, Western Australia. This drove a change in state where extensive leaf defoliation in *A. antarctica* (Fraser et al., 2014) and subsequent death of shoots and whole meadows resulted in bed erosion, sediment resuspension and movement (Thomson et al., 2015; Nowicki et al., 2017), and major losses to seagrass-dependant biota (Caputi et al., 2016; D’Anastasi et al., 2016; Nowicki et al., 2019) (Figures 6, 7). The breakdown in resistance is among the largest observed in Australia (Statton et al., 2018) (Figure 7). Several years after the MHW there has been little documented recovery in seagrass extent (Arias-Ortiz et al., 2018). Shark Bay has the largest C stock reported for a seagrass ecosystem globally with up to 1.3% of total C sequestered by seagrasses worldwide stored within the top meter of sediments (Fourqurean et al., 2012). It also experiences a relatively high sediment accumulation rate of 1.6–4.5 $mm\ y^{-1}$ (Arias-Ortiz et al., 2018). The 2011 MHW resulted in loss of seagrass stored carbon of between 1.8 and 9 Tg as CO_2 over the 3 years between 2011–2013 (Arias-Ortiz et al., 2018). This represents a significant loss to C sequestration.

Similar large-scale seagrass declines have been recorded from other seagrass-dominated ecosystems. A downward trend in coverage of eelgrass (*Zostera marina*) in Chesapeake Bay has been observed since 1984 and was driven by multiple disturbance events including heating, cooling, turbidity and freshwater inputs from flooding ECEs (Lefcheck et al., 2016). More locally in Western Australia, system-wide loss of seagrasses between 1968 and 1972 produced a recalcitrant state change to bare sediments in over 700 ha of previous seagrass habitat in Cockburn Sound, Western Australia that has lasted for 47 years (Kendrick et al., 2002). High inputs of nutrients and other pollutants were determined to be the cause of the initial rapid loss of seagrasses but subsequent reduction in nutrient inputs and a shift in the system toward oligotrophic conditions have not resulted in recovery of the seagrasses in either system.

Time and Space Scales of Loss and Recovery

Fast local scale (individual to population, weeks to months) responses of temperate seagrass to the MHW included

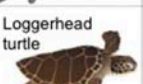
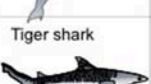
Fauna	During heat-wave	+1 yr	+2 yr	+3 yr	+4 yr	+5 yr	+6 yr
Scallop 	X	X					
Prawn 						Size Decline	
Crab 			X	X			
Sea snake 			76%				
Cormorant 			35%				
Green turtle 			38%				
Loggerhead turtle 							
Dugong 			67%				
Dolphin 			39%				
Tiger shark 							

FIGURE 6 | Generalized timeline of change in seagrass associated biota before to after the 2011 heatwave. Red, population decline; Yellow, other change to population; Green, no decline in population; Gray, no data; "X", fishery closure (see Nowicki et al., 2019 for details).

defoliation of large areas of *A. antarctica* and higher shoot mortalities and seed abortion in *P. australis* (Figure 7). Loss of both species resulted in landscapes changing from seagrass-dominated to sand dominated but this slower, larger scale process took 1–2 years to develop after the 2011 MHW. These sand- and silt-dominated areas have persisted years after the MHW ended (Nowicki et al., 2017). Since 2016, both *A. antarctica* and *P. australis* (2016–2017) have been reproductive and in some locations have produced numbers of seedlings and seeds, respectively. However, limitations remain to recruitment and re-establishment of temperate seagrasses from seeds or seedlings. For example, seed predation has been observed near

Useless Loop as well as seedling disturbance by bioturbators in the sediments (especially the heart urchin *Breynia desori*: Johnson et al., 2018).

The slower 1–2 year system-wide seagrass loss after the 2011 MHW demonstrate how indirect, biotic legacies of MHWs can be significant, even for organisms that are resistant to the direct abiotic effects (Figure 7) (Nowicki et al., 2019). This multi-faceted nature of resistance needs to be considered in the context of ECEs, including MHWs. Indeed, changes to seagrass-associated fauna have continued for 4 years after the influence of the initial stressor (temperature). Nowicki et al. (2017) also reported increased turbidity and sediment

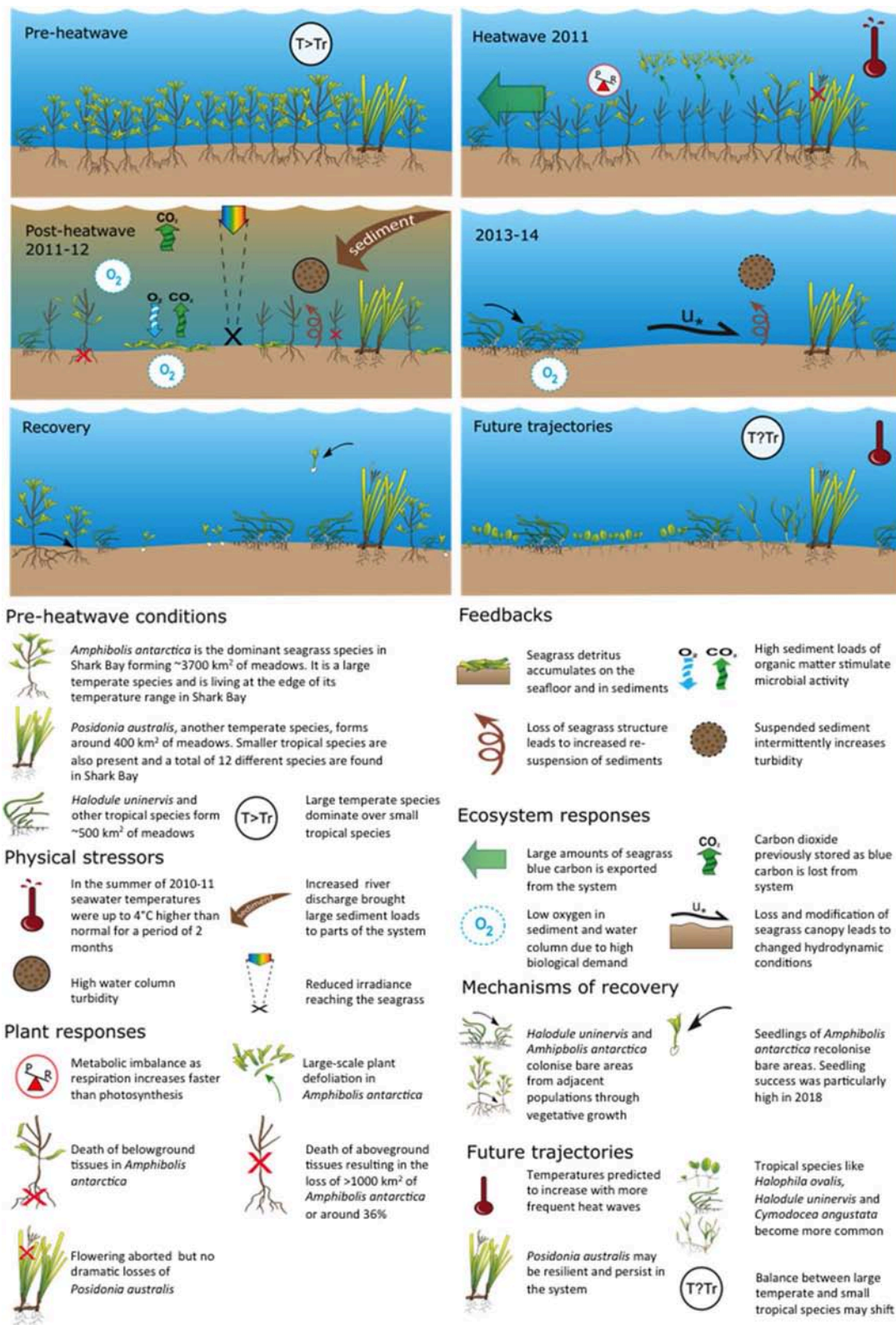


FIGURE 7 | Generalized timeline of change in seagrass structure and composition before during and after the 2011 MHW with potential future shown (Data and publications shown in Table S1).

resuspension and movement after *A. antarctica* was lost from offshore banks near Monkey Mia, affecting both stability of sediments and incident light reaching seagrasses. There were also local observations of phytoplankton blooms across many locations suggesting continuing microbial remineralization of organic matter associated with the high input of organic detritus into the system since defoliation in 2011 (Thomson et al., 2015; Nowicki et al., 2017).

Impacts to Seagrass

Life history traits of temperate and tropical seagrass species (Kilminster et al., 2015) have influenced both the scale of loss and extremely slow rate of recovery of the Shark Bay ecosystem (Figure 7) (Kilminster et al., 2015). Energy budgets of the persistent temperate species *A. antarctica*, indicate a strong dependency on high photosynthesis rates to compensate for respiratory load associated with the complex aerial canopy of multiple leaf clusters, some in full sunlight and others significantly shaded by the canopy above, and little ability to store carbohydrates in rhizomes. Without sufficient light, respiration will exceed production in plants of *A. antarctica* (Carruthers and Walker, 1997). Also, experiments on the temperature tolerance of *A. antarctica* indicate increased mortality above water temperatures of 28°C (Walker and Cambridge, 1995). Therefore, *A. antarctica* is at the limits of its physiological tolerance in Shark Bay and based purely on physiology, would expect to become locally extinct under climate change scenarios (Hyndes et al., 2016) unless thermally resistant genets exist among surviving beds.

The persistent temperate species *P. australis* appeared more resistant to the 2011 MHW, however it still underwent loss in shoot density (Figure 4B) and showed a multi-annual reproductive collapse despite widespread flowering (Figure 7). This is important to note because some *Posidonia* species (like *P. oceanica* in the Mediterranean) increase flowering intensity during warm events (Ruiz et al., 2018), suggesting some persistent seagrasses may demonstrate resilience to warming through reproduction. However, the total seed abortion of *P. australis* documented in Shark Bay in 2011–2012 (Sinclair et al., 2016) suggests flowering alone may be a poor proxy for resilience. More than 7 years after the MHW there is no evidence that recruitment from seed has occurred in Shark Bay.

The tropical colonizing seagrass, *H. uninervis* appear to be less impacted by the 2011 MHW and increased in cover during post-MHW recovery (Nowicki et al., 2017) (Figure 7). *H. uninervis* is a colonizing and sediment stabilizing species common in the Indo-Pacific (Ooi et al., 2011a) and has a low level of clonal integration making it resistant to physiological stress and sediment burial (Ooi et al., 2011b). However, it is one of the preferred seagrasses in fish, turtle and dugong diets and top down control has been shown to limit its abundance and distribution (Anderson, 1986; Burkholder et al., 2012, 2013; Thomson et al., 2015; Bessey et al., 2016). As such, certain biotic legacy effects of MHWs may be more important to these species than they are for persistent species.

Community to Ecosystem Response

Little research has focussed on community to ecosystem responses to ECEs (Langtimm and Beck, 2003; Cahill Abigail et al., 2013), particularly in marine ecosystems. Most consumer species in Shark Bay were negatively impacted by the seagrass loss, although some remained less affected (Figure 6). In general, the level of population decline was roughly correlated to the direct reliance of the species on seagrasses. For example, sea snakes, which use seagrass meadows as both foraging grounds and refuge, suffered the largest declines from seagrass losses, while dugongs, obligate seagrass herbivores, suffered the second highest loss (Nowicki et al., 2019). Resource loss can influence the capacity of consumers to engage in anti-predator behavior because they must balance anti-predator behavior with other needs (such as obtaining food) (Clark, 1994; Werner and Peacor, 2006). Indeed, green turtles in poor body condition in Shark Bay spend more time in the middle of shallow seagrass habitats, which offers higher quality food resources but also reduces the potential for escape from tiger shark encounters (Heithaus et al., 2007). Long-term demographic data on Shark Bay's resident Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population revealed a significant decline in female reproductive rates following the MHW, with capture-recapture analyses indicated 5.9 and 12.2% post-MHW declines in the survival of dolphins that use tools to forage relative to those that do not (Wild et al., 2019). Lower survival has persisted, suggesting that habitat loss following extreme weather events may have prolonged, negative impacts on even behaviourally flexible, higher-trophic level predators, but that the tool-using dolphins may be somewhat buffered against the cascading effects of habitat loss following the MHW (Wild et al., 2019). The Indo-Pacific bottlenose dolphins altered their habitat use patterns similarly following seagrass loss, increasing their use of profitable but dangerous shallow banks during periods of high tiger shark abundance, suggesting a need to increase foraging in these habitats despite predation risk (Nowicki et al., 2019). Finally, surface surveys and shark fishing data indicated that loggerhead turtles and tiger sharks, which are both generalist and opportunistic consumers (Matich et al., 2011; Thomson et al., 2012), showed no short-term population declines following seagrass loss (Nowicki et al., 2019). This aligns with the theory that generalist consumers are likely to be more resilient to habitat loss than specialists (Ryall and Fahrig, 2006). Indeed, seagrass loss may increase foraging success of these species, which often hunt species that can be obscured by dense seagrass meadows. However, even these generalists may be impacted if seagrass recovery does not occur.

The mechanism of decline likely differs by species and can be inferred with knowledge of the species' biology. For example, sea snakes are known to have extremely small home ranges (Burns and Heatwole, 1998; Lukoschek et al., 2008; Lukoschek and Shine, 2012) and to be highly reliant on seagrass for both foraging ground and refuge in Shark Bay (e.g., Kerford et al., 2008; Wirsing and Heithaus, 2009), suggesting that population declines are likely mostly driven by starvation and predation mortality (D'Anastasi et al., 2016; Nowicki et al., 2019). In contrast, dugong population declines are almost certainly driven by emigration; indeed, dugongs often migrate between foraging

regions in response to resource loss, including between Shark Bay and Ningaloo reef (Preen and Marsh, 1995; Holley et al., 2006). This, combined with a lack of strandings that would be expected if mass mortality had occurred (Marsh, 1989; Preen and Marsh, 1995), suggest that dugongs left the interior of Shark Bay in response to seagrass loss.

These different mechanisms of population decline have important ecological implications for the recovery of Shark Bay's seagrasses. A rapid functional return of dugongs is more likely than for sea snakes, and will likely alter the relative functional role of the seagrass consumer community (Preen et al., 1995). For example, dugongs structure seagrass ecosystems via herbivory, that targets tropical species, but their grazing can damage climax species *when they co-occur*. Because dugong foraging decisions and modes are risk sensitive (Wirsing et al., 2007a,b,c), their overall impact on systems and climax species may be greater with the loss of top predators or reductions in predation risk sensitivity that are predicted under conditions of resource scarcity (Heithaus et al., 2008). Dugongs can actively choose habitat based on the location of preferred seagrass forage, and they maintain a spatial memory of these locations (Holley et al., 2006; Sheppard et al., 2010). Similarly, the species-specific changes in risk-sensitive foraging (Nowicki et al., 2019) suggest that the possible magnitude and nature of top-down control by tiger sharks (i.e., predation risk vs. direct predation) has likely changed for some prey species within Shark Bay. Understanding how consumer populations, habitat use patterns, and species interactions change in response to the direct impacts (i.e., physical forcing) and indirect impacts (i.e., resource loss) of MHWs will remain critically important to accurately predicting the recovery trajectories of primary producer communities to these disturbances (Nowicki et al., 2019). This is particularly important because overfishing continues to be a major problem for true apex predators, like tiger sharks, in most areas of the world and overfishing likely is a multiplier of ECE effects.

Flow on Effects to Human Activities

Impacts of the MHW to human activities in the Shark Bay WHS can be measured in terms of changes to commercial and recreational fisheries and tourism. The response to recruitment and catch declines in the Blue Swimmer crab and scallop fishery was 1–3 year closures and catch has returned to pre-MHW levels subsequent to the fisheries being opened (Caputi et al., 2016). The economic and social impact to fishermen was severe and points to a need to build in climate adaptation strategies for fisheries management. These include early identification of temperature hot spots, early detection of abundance changes (preferably using pre-recruit surveys), and flexible harvest strategies that allow a quick response to minimize the effect of heavy fishing on poor recruitment to enable protection of the spawning stock (Caputi et al., 2016). Major declines in the tourism experience also occurred. Sightings recorded in daily operator logs declined for dugongs, turtles, sharks, dolphins, and fish that forced operators to move their activities spatially to compensate although total loss of tourism revenue was not determined.

CONCLUDING REMARKS

To be able to predict future impacts from climate change and increased frequency of MHWs, we need a detailed ecosystem level understanding of how and when such events exceed the ecological resistance of foundation species. Also we need to understand how the ensuing habitat loss can impact fisheries, species of conservation concern, or other species that may be resistant to the direct abiotic forcing of MHWs, but not to the ensuing biotic effects of habitat loss. Furthermore, we need an understanding of the role of species interactions in generating feedbacks. This requires us to be able to identify which interactions are likely to be dominant drivers of patterns (including competition between seagrasses, predation, etc.). Understanding mechanisms that drive dominant interactions will better allow us to predict whether those interactions will remain strong or not after a system changes.

We also need to understand the potential for surviving seagrass to persist through future extreme events. Genomic tools offer new insights into local adaptation (Savolainen et al., 2013) to increase our understanding of species' response to climate change (Stillman and Armstrong, 2015), although there are challenges for translating into conservation practice (Shafer et al., 2015). More importantly, the factors that allow us to “future-proof” seagrasses warrant substantial consideration to ensure contemporary restoration efforts are not compromised by future conditions. In Shark Bay and the west coast of Western Australia, genomic studies designed to understand the interaction between plasticity, adaptation and range shifts will contribute to better translation for adaptive management and conservation responses to ECEs for the dominant habitat-forming temperate seagrasses. This is needed for both temperate and tropical seagrasses that are at both (trailing and leading edge, respectively) extremes of their geographical distributions. Recent research on terrestrial plants has shown such edge populations show similar or less resilience than core populations and are typically characterized by lower levels of genetic diversity, increasing genetic differentiation due to reduced gene flow, lower effective population sizes, and reduction in sexual reproduction although it is unknown whether trailing edge populations have a lower or higher capacity for plasticity (Donelson et al., 2019). A decline in genetic diversity was not observed in tropical colonizing species *H. ovalis* and *H. uninervis* along a Western Australian tropical to subtropical gradient with Shark Bay as the most southerly location. Instead the biggest trend was that areas of high dugong grazing show higher genetic diversity in both *H. ovalis* and *H. uninervis*, so for these species loss of dugongs may lead to lower genetic diversity over time (McMahon et al., 2017).

Finally, we stress that long term and broad spatial monitoring of iconic flora and fauna, and the initiation of continuous recording of *in-situ* environmental data linked to oceanographic models is required to better understand resilience of seagrass-dominated ecosystems to MHWs into the future, as well as a commitment to continue funding existing long term biological research. Individual researchers and government scientists volunteered their research effort to the understanding of the 2011 MHW, but this is not the best model for

future events. A more interdisciplinary approach is required to facilitate greater understanding of the complex interactions among seagrasses and their environment, seagrass-dependent communities and trophic webs, and seagrass ecosystems. Several such models already exist and could be adapted to an Australian context, including the U.S. National Science Foundation Long Term Ecological Research Network (LTER) (<https://lternet.edu/>), the *Zostera* Experimental Network (Zenscience.org), or the U.S. NSF National Ecological Observatory Network (NEON) (Neonscience.org). Such initiatives are critical to increasing our ability to understand and predict ecosystem resilience to change in the Anthropocene.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

GK conceived the study. GK, RN, YO, SS, MF, ES, JS, RH, JT, DB, KM, KK, JF, MH, and RO designed the study. GK, RN, SS, MF, ES, JS, JT, DB, JF, and MH supplied published and unpublished data. GK, RN, YO, SS, RH, YH, JT, KM, and KK analyzed data. GK, RN, YO, SS, MF, ES, JS, RH, JT, DB, KM, YH, KK, JF, MH, and RO wrote and edited 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.2019.00455/full#supplementary-material>

Table S1 | Impacts to marine organisms and data sources by year before, during and after the 2011 MHW in Shark Bay. All cited papers are in the reference list of the main paper.

Table S2 | Stem and shoot density (Mean, SE, and *n*) for *Amphibolis antarctica* and *Posidonia australis*, respectively, for field programs in Shark Bay held between 1982 and 2018.

Table S3 | Description of results of a one way ANOVA and *post-hoc* Tukeys HSD statistics with field trip as the factor and shoot density of *Posidonia australis* and stem density of *Amphibolis antarctica* as dependent variables.

Table S4 | *Posidonia australis* inflorescence densities and seed production between 2011 and 2018.

Table S5 | Wooramel River Discharge by month (megaL) and sea temperatures between 1994 and 2015 (courtesy of WA Dept. of Water and Environmental Regulation).

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Predicting the Evolution of the 2014–2016 California Current System Marine Heatwave From an Ensemble of Coupled Global Climate Forecasts

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Throughout 2014–2016, the California Current System (CCS) was characterized by large and persistent sea surface temperature anomalies (SSTa), which were accompanied by widespread ecological and socioeconomic consequences that have been documented extensively in the scientific literature and in the popular press. This marine heatwave and others have resulted in a heightened awareness of their potential impacts and prompted questions about if and when they may be predictable. Here, we use output from an ensemble of global climate forecast systems to document which aspects of the 2014–2016 CCS heatwave were predictable and how forecast skill, or lack thereof, relates to mechanisms driving the heatwave's evolution. We focus on four prominent SSTa changes within the 2014–2016 period: (i) the initial onset of anomalous warming in early 2014, (ii) a second rapid SSTa increase in late 2014, (iii) a sharp reduction and subsequent return of warm SSTa in mid-2015, and (iv) another anomalous warming event in early 2016. Models exhibited clear forecast skill for the first and last of these fluctuations, but not the two in the middle. Taken together with the state of knowledge on the dominant forcing mechanisms of this heatwave, our results suggest that CCS SSTa forecast skill derives from predictable evolution of pre-existing SSTa to the west (as in early 2014) and the south (as in early 2016), while the inability of models to forecast wind-driven SSTa in late 2014 and mid-2015 is consistent with the lack of a moderate or strong El Niño or La Niña event preceding those periods. The multi-model mean forecast consistently outperformed a damped persistence forecast, especially during the period of largest SSTa, and skillful CCS forecasts were generally associated with accurate representation of large-scale dynamics. Additionally, a large forecast ensemble (85 members) indicated elevated probabilities for observed SSTa extremes even when

ensemble mean forecasts exhibited limited skill. Our results suggest that different types or aspects of marine heatwaves are more or less predictable depending on the forcing mechanisms at play, and events that are consistent with predictable ocean responses could inform ecosystem-based management of the ocean.

Keywords: heatwave, prediction, predictability, forecast, California Current System, Blob, El Niño

INTRODUCTION

In 2013, a region of highly anomalous warm ocean anomalies (i.e., a marine heatwave), colloquially known as “the Blob,” developed in the surface ocean of the northeast Pacific (Bond et al., 2015). The California Current System (CCS) was subsequently impacted by rapid anomalous warming in early 2014, and large positive sea surface temperature anomalies (SSTa) persisted in the region at least through mid-2016 (**Figure 1**; Gentemann et al., 2017). While marine heatwaves have been defined in multiple ways, at least one study categorized this one as a “severe” heatwave with a duration of over 700 days (Hobday et al., 2018). This unprecedented physical anomaly brought with it widespread ecological consequences including dramatic range shifts of species at all trophic levels (Cavole et al., 2016; Peterson et al., 2017; Sanford et al., 2019), a coastwide outbreak of toxic algae (McCabe et al., 2016; Ryan et al., 2017) and mass strandings of marine mammals and seabirds (Cavole et al., 2016). As a result of these ecological changes, a number of commercially important fisheries were closed either in response to adverse conditions (Cavole et al., 2016; McCabe et al., 2016) or in anticipation of them (Richerson et al., 2018). Similar impacts have been documented for other marine heatwaves around the globe (e.g., Mills et al., 2013; Wernberg et al., 2013; Oliver et al., 2017), and increasing emphasis is being placed on the role of these types of events in disrupting marine ecosystem functioning (Smale et al., 2019).

While the CCS was persistently anomalously warm throughout 2014–2016 (**Figure 1**), regional and broad-scale anomalies during that period evolved in response to a suite of forcing mechanisms (Amaya et al., 2016) including (i) the “Ridiculously Resilient Ridge,” a blocking high pressure system (Swain et al., 2014) that gave rise to the Blob by reducing wind-driven mixing and wintertime cooling in the northeast Pacific (Bond et al., 2015), (ii) the subsequent impact of offshore warm anomalies on the CCS, likely through both lateral advection and anomalous atmospheric forcing (Zaba and Rudnick, 2016; Chao et al., 2017; Jacox et al., 2018), (iii) evolution from the Blob warming pattern characteristic of North Pacific Gyre Oscillation (NPGO) variability to an arc-pattern warming resembling Pacific Decadal Oscillation (PDO) variability, a transition that may have been facilitated by tropical-extratropical teleconnections through an El Niño event in 2014–2015 that was initially predicted to be very strong but ultimately was weak (McPhaden, 2015; Amaya et al., 2016; Di Lorenzo and Mantua, 2016), and (iv) the 2015–2016 El Niño event that was one of the strongest on record based on equatorial Pacific SSTa, but whose CCS expression was quite different from that expected based on past strong El Niños (Jacox et al., 2016; Frischknecht et al., 2017).

Advance warning of events like the 2014–2016 CCS heatwave, whether it be for the onset of anomalous warming or its evolution thereafter, would enable ocean managers and other stakeholders to be proactive in their decision making. To that end, the overarching aim of this paper is to determine what about this heatwave was predictable, and why. Hu et al. (2017) examined seasonal forecasts from the National Center for Environmental Prediction’s Climate Forecast System (NCEP-CFSv2) to assess predictions in the region of the Blob, centered on $\sim 140^\circ\text{W}$, 45°N (see November–December 2013 in **Figure 1**). They found little forecast skill for the initiation of this extreme warm anomaly, which was forced by atmospheric internal variability that is inherently unpredictable. However, anomalous warming of the CCS occurred following the establishment of the offshore warm anomaly, and so prediction of CCS anomalies was not necessarily limited in the same way. It is conceivable that while the Blob was not predictable, subsequent impacts on the CCS were; such is the case for El Niño – Southern Oscillation (ENSO) events that once developed in the tropics can impart predictability in the CCS for the following months (Doi et al., 2015; Jacox et al., 2017).

Here, we explore seasonal forecasts from eight global climate forecast systems that have contributed to the North American Multi-Model Ensemble (NMME; Kirtman et al., 2014) and assess their ability to predict different phases of the 2014–2016 CCS warm anomalies. We examine variability averaged over the CCS domain as well as the spatial evolution of forecast and observed SST anomalies in the northeast Pacific, and link the success or failure of model forecasts to the mechanisms responsible for the SSTa variability. Finally, we combine individual ensemble members from each model to create a large (85-member) forecast ensemble, which can indicate the probability of extreme warm anomalies even when they are largely missed by ensemble mean forecasts.

MATERIALS AND METHODS

Seasonal Forecasts

Seasonal SST forecasts are obtained from global coupled climate models contributing to the NMME. We focus on eight models whose SST forecasts are publicly available for a long re-forecast period as well as for the recent years that are the focus of this study (i.e., 1982–2016). The models are CMC1-CanCM3 and CMC2-CanCM4 (Merryfield et al., 2013) from the Canadian Meteorological Center (CMC), NCEP-CFSv2 (Saha et al., 2014) from the National Center for Environmental Prediction (NCEP), COLA-RSMAS-CCSM4 (Infanti and Kirtman, 2016) from the National Center for Atmospheric Research (NCAR), GFDL-CM2p1-aer04 (Delworth et al., 2006), GFDL-CM2p5-FLOR-A06

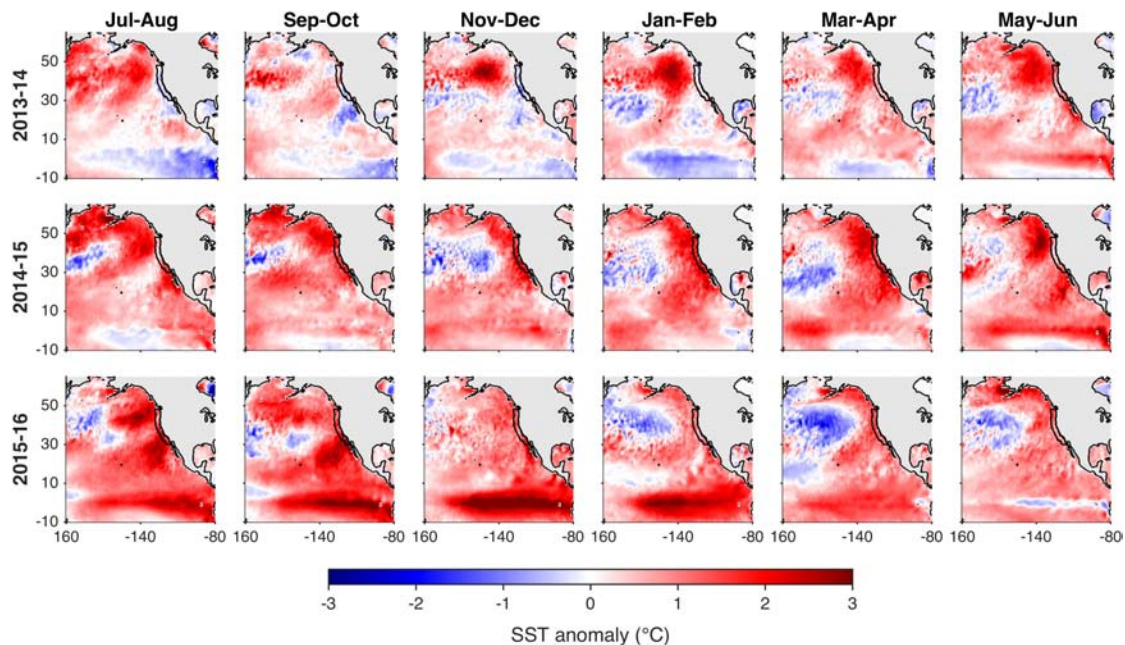


FIGURE 1 | Observed evolution of northeast Pacific SST anomalies from July 2013 to June 2016. Anomalies are calculated relative to the 1982–2010 climatology using the 0.25° OISSTv2 product. The CCS region of interest to this paper, extending along the North American west coast from 30 to 48°N and from the coast to 300 km offshore, is outlined in black.

(Vecchi et al., 2014), and GFDL-CM2p5-FLOR-B01 (Vecchi et al., 2014) from the Geophysical Fluid Dynamics Laboratory (GFDL), and NASA-GMAO-062012 (Vernieres et al., 2012) from the National Aeronautics and Space Administration (NASA). For each model, forecasts are initialized monthly and an ensemble of forecasts is produced. For all models except CFSv2, forecasts are initialized on the first day of the month and an ensemble of 10–12 members is produced at each initialization time. Individual ensemble members are generated by introducing small perturbations to the initial conditions, which grow in time to large differences due to the chaotic nature of the climate system (Lorenz, 1963). For CFSv2, four ensemble members are initialized every fifth day, for a total of 24 per month. For consistency with other models, we use only 10 ensemble members from CFSv2, the four initialized on the first of the month and the last six initialized the previous month. Monthly average output is saved for lead times from 0 (e.g., a January 1st forecast of mean January conditions) to 11 months, except for the CFSv2 and NASA-GMAO models, which have forecasts available for lead times up to 8 months.

Skill Evaluation

As global climate models have in some cases large SST biases, especially in eastern boundary upwelling systems like the CCS, forecasts must be bias corrected for comparison with observations. Additionally, models drift from their initialized state toward their preferred (biased) state over the course of a forecast, so bias correction is initialization month- and lead time-dependent. For each initialization month and lead time, forecast SST anomaly (SSTa) is computed by removing the 1982–2010

forecast climatology, and observed SSTa is calculated similarly by removing the 1982–2010 climatology from NOAA's 0.25° Optimum Interpolation SST, version 2 (OISSTv2; Reynolds et al., 2007; Banzon et al., 2016). This method assumes that forecast biases are stationary in time, which is an oversimplification (Supplementary Figure 1; Kumar et al., 2012). However, there is no established protocol for dealing with non-stationarity in forecast biases. We discuss this issue more in Section “California Current System SST Anomalies,” particularly with reference to the NCEP-CFSv2 forecasts.

We evaluate SSTa forecasts with respect to observed conditions in the CCS, which we defined as extending 30–48°N and from the coast to 300 km offshore, as well as in the broader northeast Pacific (Figure 1). Past analyses of NMME forecast SSTa (Stock et al., 2015; Hervieux et al., 2017; Jacox et al., 2017) have relied on several skill metrics for evaluation: the deterministic metrics anomaly correlation coefficient (ACC) and root mean square error (RMSE), and the probabilistic Brier Score. In each case, skill scores have been calculated based on interannual variability over a long (~30-year) time series. Such analyses have demonstrated that NMME forecasts have significant skill for SSTa in the CCS at lead times of at least 5 months and up to 11 months depending on initialization month. Furthermore, NMME SSTa forecasts outperform persistence forecasts in the CCS, primarily due to the ability of the model forecasts to capture anomalies associated with moderate to strong ENSO events (Jacox et al., 2017). While long-term skill assessments offer a baseline evaluation of model forecasts capabilities, here we aim to evaluate predictions for individual fluctuations over a much shorter time period (3 years),

so the same skill metrics are not appropriate. Instead, we focus on the SSTa forecast error (forecast minus observed SSTa) to evaluate predictions of mean CCS conditions and spatial anomaly correlations to evaluate the ability of models to predict the spatial evolution of SSTa more broadly in the northeast Pacific.

Persistence Forecasts

We use a “damped persistence” forecast as a baseline against which to evaluate the skill of model forecasts. The damped persistence forecast assumes that observed SSTa decays toward zero over some characteristic timescale, and it is a more rigorous baseline for forecast skill than the climatology (which has zero skill for predicting anomalies) or a simple persistence forecast (which unrealistically maintains anomalies in the absence of additional forcing) (e.g., Mason and Mimmack, 2002). The damped persistence forecast SSTa at lead t is calculated from $SSTa(t) = aSSTa(i)$, where $SSTa(i)$ is the observed SSTa at forecast initialization and a is the autocorrelation coefficient of SSTa at lag t .

RESULTS

California Current System SST Anomalies

While warm SSTa generally persisted along the North American coast from early 2014 through at least 2016, on monthly timescales the CCS saw distinct periods of increasing and decreasing SSTa. Models were able to forecast some of these fluctuations with clear skill, while in other cases they performed no better than a damped persistence forecast (**Figure 2**). All models predicted increasing SSTa in late winter and early spring 2014, albeit this anomalous warming was more gradual in forecasts than in observations. A warmer than average 2014 early summer was predicted by all models with a January initialization, and the multi-model mean SSTa forecast for summer 2014 fell halfway between the persistence forecast (0°C) and the observed anomaly (0.8°C). However, a second pulse of anomalous warming in late 2014, which increased observed SSTa from 0.8 to 2°C , was absent from the January initialized forecasts. In fact, even forecasts initialized in July – approximately 2 months before this second period of rapid SSTa increase – predicted SSTa to decrease toward zero rather than increase. CCS temperatures remained elevated throughout much of 2015, interrupted only by a brief but strong cooling in May–June. This pattern was missed by forecasts initialized in January 2015, which generally predicted decreasing SSTa throughout the year following the damped persistence forecast. Finally, 2016 was characterized by yet another brief period of increased SSTa in spring followed by cool and warm SSTa in summer and fall, respectively. The spring 2016 warm period was captured with impressive fidelity by model forecasts, with the January initialized multi-model mean matching observations almost exactly through June (**Figure 2**), although forecast skill dropped off later in 2016.

The findings outlined above – that forecasts exhibited skill for SSTa changes in early 2014 and early 2016, but not for mid-2014 through 2015 – generally hold true across models and lead times

(**Figure 3**). For longer leads (e.g., 8 months), skillful forecasts of early 2014 anomalous warming led to improvements over a damped persistence forecast throughout 2014, and in fact the multi-model mean forecast outperformed a damped persistence forecast for much of the study period. However, the most intense warm anomalies in late 2014 were largely missed by all models even at lead times of 2 months, as was the persistence of those anomalies into 2015. In contrast, the evolution of the early 2016 warm period, with SSTa exceeding 1°C , was forecast with very high skill even 8 months in advance (**Figure 3**). Forecasts from individual models differ quantitatively but exhibit skill during the same time periods, consistent with findings for large marine ecosystems around the U.S. and elsewhere (Stock et al., 2015; Hervieux et al., 2017).

One model, NCEP-CFSv2, emerges as a potential outlier with forecast SSTa that is in some cases much higher than that seen in other models (**Figure 2**). However, interpretation of this result is challenging for several reasons. First, CFSv2 anomalies are warmer than those of other models throughout 2013–2016, not just during the observed warm periods (e.g., see 8-month lead forecasts in **Figure 3**), suggesting an issue with the bias correction. As mentioned earlier, anomalies are calculated relative to a 1982–2010 climatology but in fact biases change over time. The non-stationarity of CFSv2 biases was noted by Kumar et al. (2012), in particular with regards to an apparent shift to warmer biases around 1999. While this issue is not unique to CFSv2 (all models have state-dependent biases), the CFSv2 warm bias has increased relative to other models over time, especially since ~ 2007 (**Supplementary Figure 1**). Second, the CFS Reanalysis that is used to initialize CFSv2 forecasts had a prominent tropical Atlantic cold bias that developed in October 2013 and was addressed in March 2016. The cold Atlantic bias resulted in a persistent El Niño-like state, favoring warm anomalies in the northeast Pacific (NOAA/NCEP Climate Prediction Center, 2015, 2016a,b).

Northeast Pacific Spatial SST Anomalies and Forcing

To further explore and contextualize the CCS anomalies described in the previous section, we turn our attention to the spatial evolution of observed and forecast SSTa in the broader northeast Pacific, taking the years 2014, 2015, and 2016 in turn. We focus initially on the multi-model mean forecast, as forecasts for individual models differ quantitatively but display similar structure. We discuss observed anomalies and the ability of models to forecast them here, and in the discussion we link these findings to the mechanisms that may have imparted increased predictability to early 2014 and early 2016 relative to late 2014 and 2015.

In the observations, 2014 was characterized by an intense offshore warm anomaly evolving into an arc warming pattern with concomitant increases in CCS SSTa (**Figure 1**). As we have seen previously this anomalous 2014 warming occurred in two stages, one in early 2014 that was also seen in model forecasts and another in late summer/fall that was not. The early 2014 SSTa increase occurred by an expansion of the offshore warm

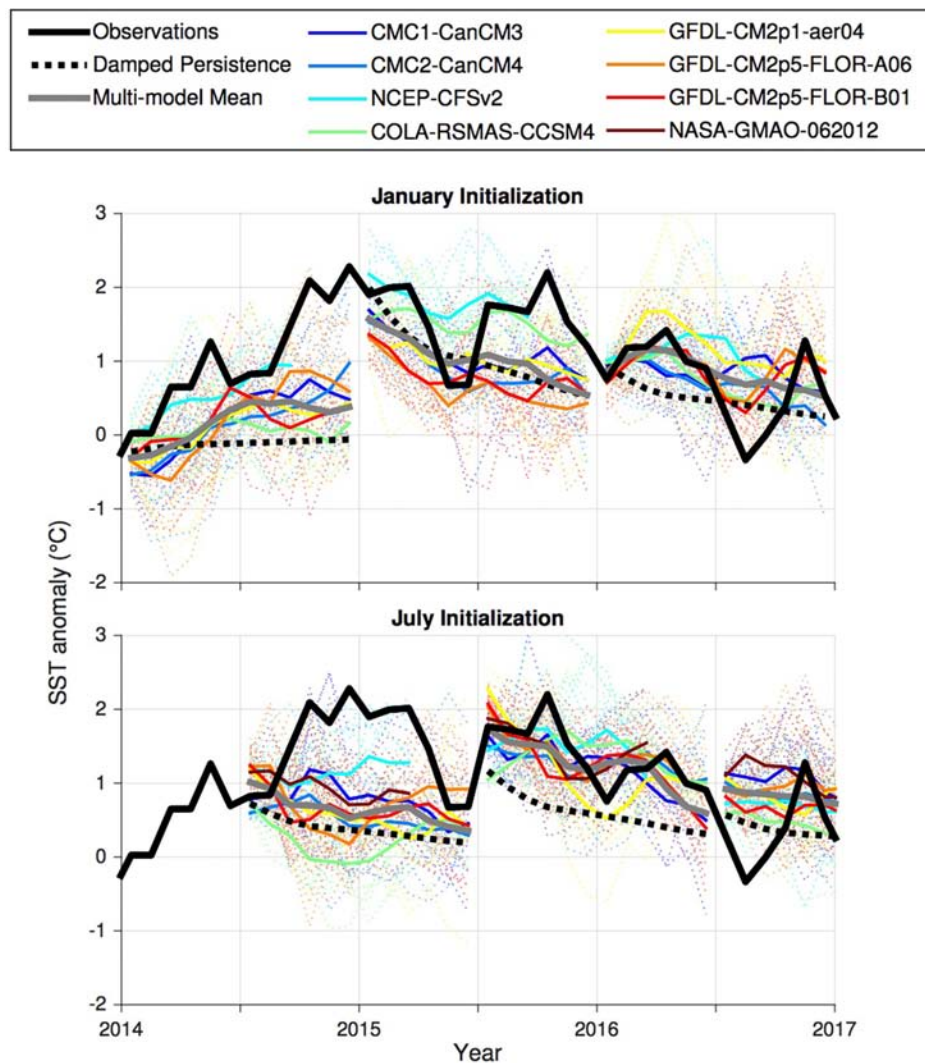


FIGURE 2 | Global climate forecasts for mean SSTa in the CCS, initialized in **(top)** January and **(bottom)** July of each year from 2013 to 2016. Thin dotted colored lines are individual ensemble members for each model while solid colored lines are model means. For each model, anomalies are calculated relative to the lead time- and initialization month-dependent climatology.

anomaly to the coast, which was forecast in the multi-model mean (**Figure 4**), albeit with a lag of several months relative to observations (May–June vs. March–April). Thus, while the formation of the Blob itself was not predictable (Hu et al., 2017), its subsequent influence on the CCS was somewhat predictable.

The SSTa increase of late 2014 had a very different character from that early in the year, as the spatial structure of northeast Pacific SSTa transitioned from a North Pacific Gyre Oscillation (NPGO)-like pattern with anomalies centered in the Gulf of Alaska to a Pacific Decadal Oscillation (PDO)-like arc pattern with warm anomalies along the North American coast and cold anomalies in the gyre (Di Lorenzo and Mantua, 2016). In contrast to the early part of the year, late 2014 was not characterized by clear forecast skill for the additional anomalous warming, though forecast anomalies from earlier 2014 persisted and provided model forecast skill superior to a damped persistence

forecast (**Figure 2**). Also notable in the spatial anomaly forecasts is that forecast SSTa are muted relative to observations; in the ensemble mean forecast biases from individual ensemble members cancel each other, reducing the ensemble mean forecast variance especially at longer leads (e.g., Doblas-Reyes et al., 2005).

In 2015, the CCS remained very warm with persistent SSTa near 2°C, interrupted only by a brief cooling in May–June that while dramatic in CCS time series (**Figure 2**) was a very localized event in the northeast Pacific (**Figure 5**) driven by an anomalously strong spring 2015 upwelling season (Peterson et al., 2017). Spatial correlations for both model and persistence forecasts were briefly reduced during this late spring/summer cooling before returning to relatively high levels ($r \approx 0.5$), supporting the notion that it was a brief interruption of a persistent warm period rather than a shift to a new and distinct warm event.

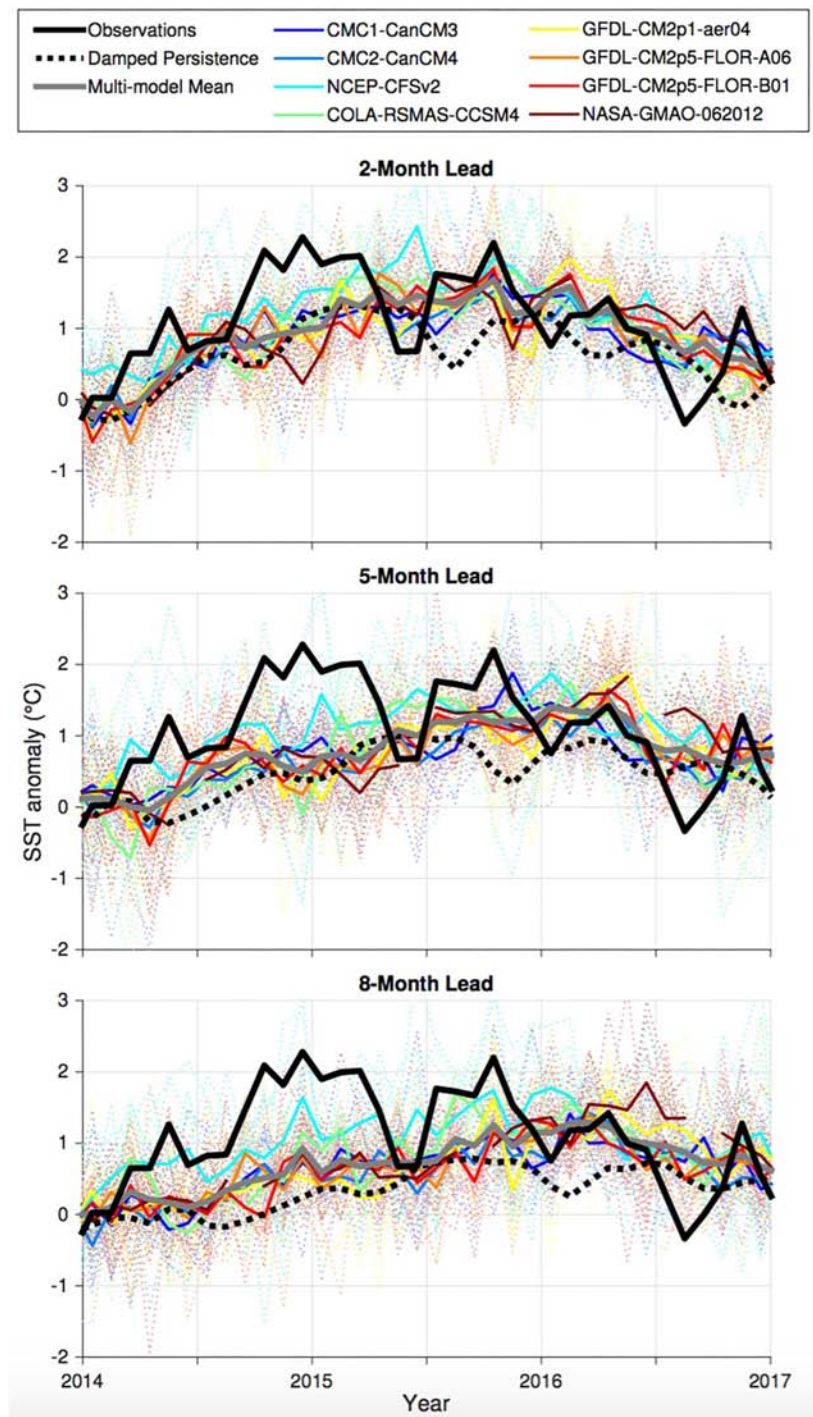


FIGURE 3 | Global climate forecasts for SSTa in the CCS at multiple lead times. Forecasts are initialized monthly. Lines are as in **Figure 2**.

Finally, by late 2015 the equatorial Pacific was experiencing by some metrics (e.g., NOAA's Oceanic Niño Index) one of the strongest El Niños on record. While its impact on the CCS was not as strong as expected based on tropical Pacific SSTa (Jacox et al., 2016), a moderate SSTa increase in spring 2016 was evident (**Figures 2, 6**). Model forecasts for this period were highly

accurate, and much better than damped persistence, for both the CCS averaged SSTa (**Figure 2**) and spatial SSTa (**Figure 6**).

In general, forecast errors for the mean CCS SSTa (**Figure 2**) mirror spatial anomaly correlations computed over the northeast Pacific (**Figure 7**). In other words, when forecast errors for the CCS are small, the structure of anomalies in the broader northeast

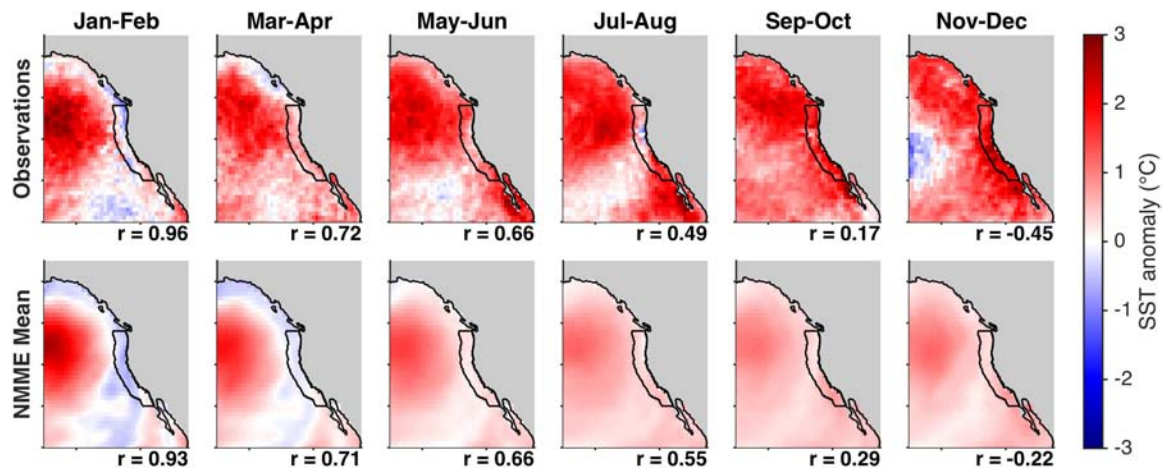


FIGURE 4 | (Top) Observed and **(bottom)** forecast SSTa for 2-month periods throughout 2014. Forecasts were initialized in January. Correlation coefficients in top panels are for persistence forecasts, correlation coefficients in bottom panels are for NMME multi-model mean forecasts. The CCS region is outlined in black.

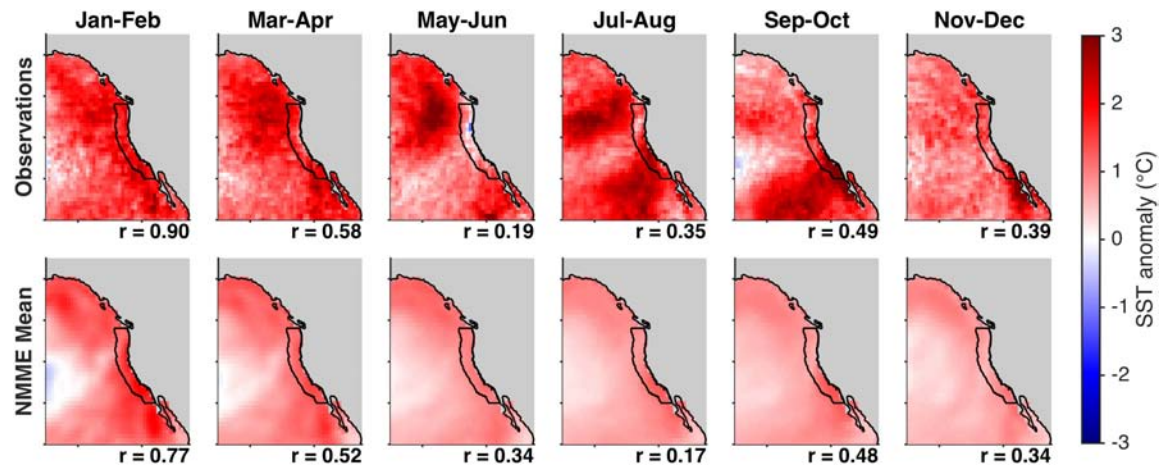


FIGURE 5 | As in this image, but for 2015.

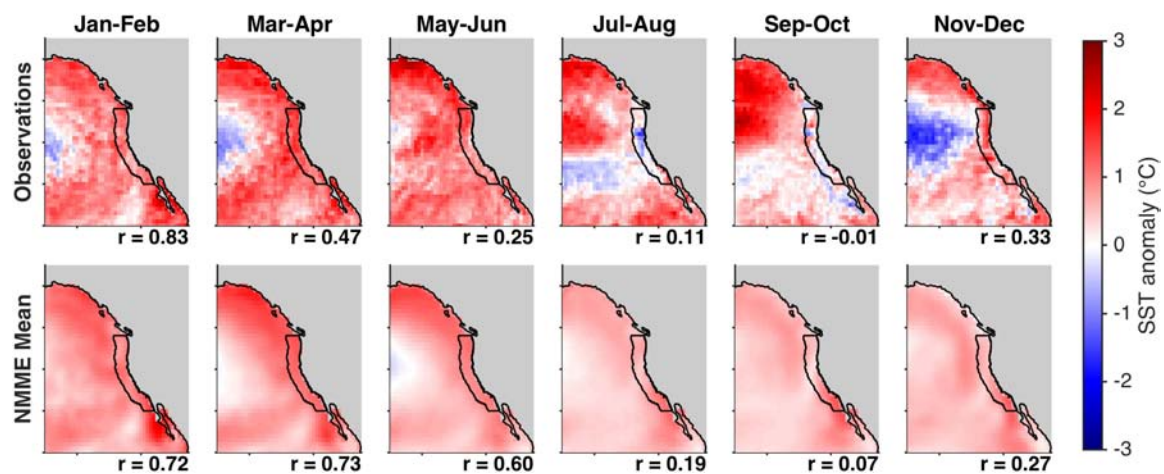


FIGURE 6 | As in Figure 5, but for 2016.

Pacific tends to also be skillfully forecast. Given that our CCS region occupies a relatively small fraction of the northeast Pacific, this result is not obvious. It suggests that when CCS forecasts are skillful, their skill derives from accurate representation of the large-scale dynamics.

A Large Ensemble of Forecasts

To this point we have focused our analysis on NMME multi-model mean forecasts or mean forecasts for individual climate models. Overall, ensemble mean forecasts outperformed damped persistence forecasts in the 2013–2016 period, and during the peak warm anomalies from mid-2014 to the end of 2015, 8-month lead multi-model mean forecasts outperformed damped persistence in 100% of months, with a substantially lower mean forecast error (0.8 vs. 1.2°C). However, since extreme events are by definition in the tails of probability distributions, large ensembles (50–100 members) may be required to forecast them (Doi et al., 2019). It is rare for a single modeling center to produce such an ensemble, but through the NMME we can obtain one. Combining ensemble members from each of the 8 models included in this study, we have a total of 85 ensemble members for each forecast initialization, which can be used to generate forecast plumes for the focal years of this study (Figure 8).

While model mean forecasts often evolve similarly in space and time (e.g., Supplementary Figure 2), individual ensemble members from a single model can differ dramatically (Supplementary Figure 3) such that the large ensemble forecast spread is regularly 3°C or more (Figure 8). While the multi-model ensemble mean forecast and the damped persistence forecast underestimated late 2014 and early 2015 SSTa by ~1.5 and 2°C, respectively, the observed extremes were still within the ensemble spread at 8-month lead (Figure 9). Thus, this

heatwave was forecast as an unlikely event, but not an impossible one. Furthermore, 8-month lead forecasts indicated elevated potential for extreme SSTa starting in mid-2014. The percentage of ensemble members forecasting SSTa greater than 2 standard deviations above the climatology ($SSTa \geq \sim 1.4^\circ\text{C}$) rose from the long term mean value of approximately 3% to over 10% by late 2014 and upwards of 30% for late 2015 – early 2016 (Figure 9). The only other time in the past 35 years when this extreme positive SSTa forecast probability exceeded 10% was in early 1998, following the peak of one of the strongest El Niños on record.

DISCUSSION

Forcing Mechanisms and Predictability of 2014–2016 Heatwave

In the previous section, we evaluated global climate forecast system predictions of the evolving 2014–2016 CCS warm anomalies. Here, we put those predictions, and their success or failure, in the context of the mechanisms driving the SST fluctuations.

Rapidly increasing SSTa in the CCS in 2014 appears to have been driven by the evolution of pre-existing warm anomalies offshore toward the coast, consistent with a lagged response of the CCS to Gulf of Alaska SSTa (Jacox et al., 2018). This period of warming was forecast by models with some skill, though slightly lagged and with reduced magnitude relative to observations. Based on a heat budget analysis of a regional ocean model, Chao et al. (2017) attributed the early 2014 upper ocean temperature increase in the central CCS to a combination of anomalous surface heat fluxes and oceanic influence from the west, and Zaba and Rudnick (2016) found anomalous surface heat flux to be a

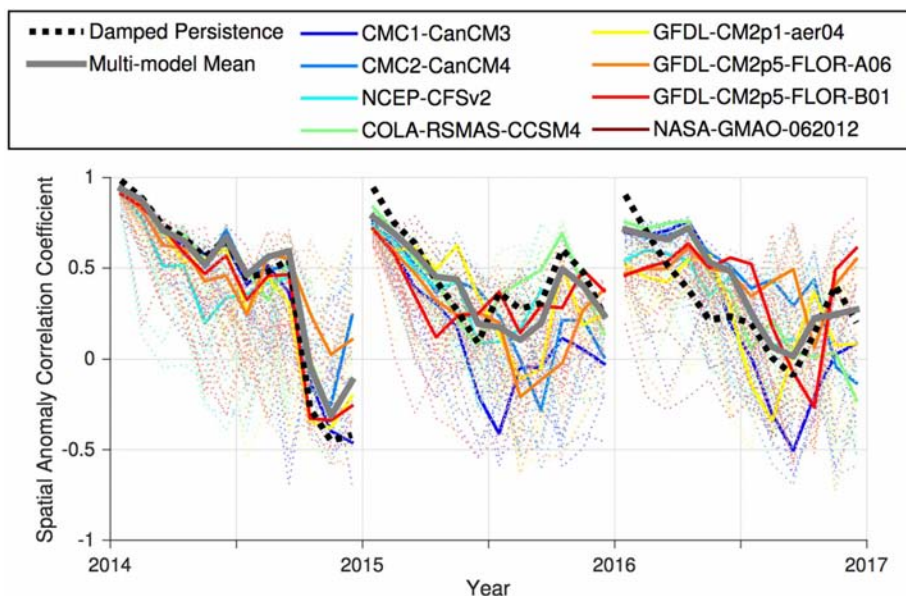
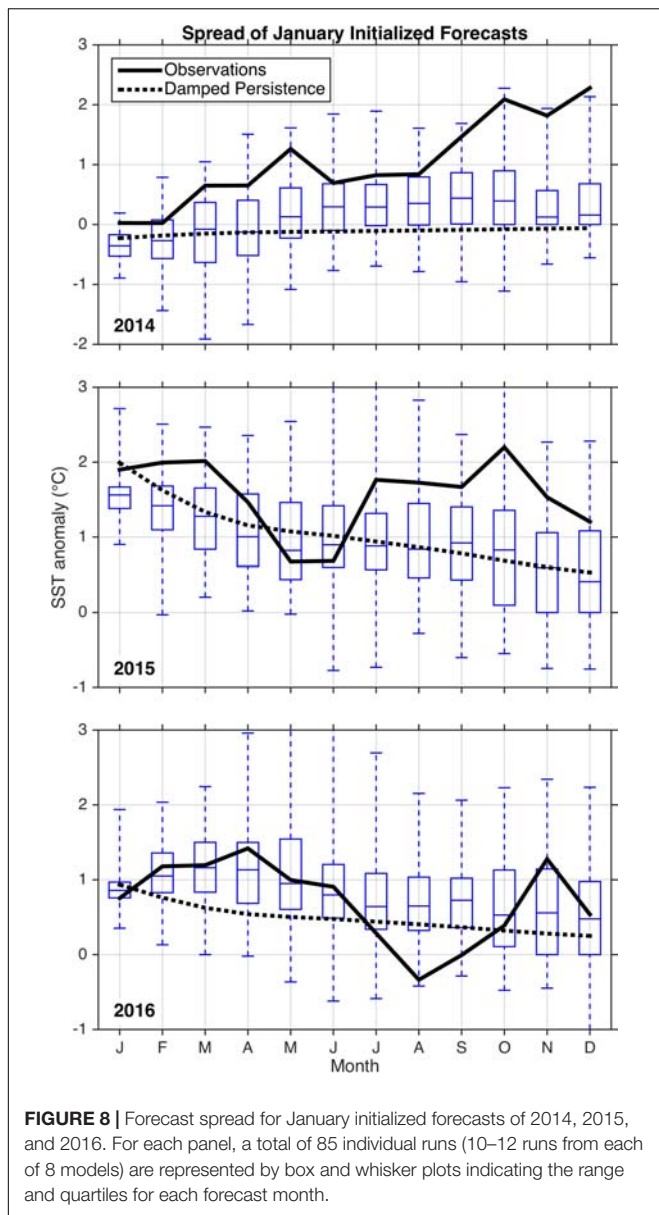


FIGURE 7 | Spatial anomaly correlation coefficients for January-initialized forecasts. At each lead time, anomaly correlation coefficients were calculated between forecast and observed SSTa for the area plotted in Figure 5 (150–105°W, 20–65°N). Lines are as in Figure 2.



dominant driver of anomalous warming in the southern CCS in the first half of 2014. Thus, a plausible explanation for forecast skill during this period is that the offshore anomalies present at initialization were conveyed to the CCS through the mean currents (i.e., eastward advection of offshore warm anomalies) and/or winds (i.e., westerlies transmitting anomalous surface heat fluxes after blowing over warm ocean anomalies upstream).

A second period of anomalous warming in late 2014 was not captured in model forecasts. During this period, the northeast Pacific SSTa pattern evolved from the “Blob” pattern with warm anomalies centered on the Gulf of Alaska to an arc pattern warming characteristic of the PDO. The positive PDO-like phase is typically characterized by anomalous northward winds and consequently reduced upwelling (or increased downwelling), which has been implicated in the anomalous CCS warming

during this period (Zaba and Rudnick, 2016; Chao et al., 2017; Jacox et al., 2018). However, wind-stress driven SST anomalies along the North American west coast tend to be forecast skillfully only when they are associated with moderate to strong ENSO events (Doi et al., 2015; Jacox et al., 2017), and the lack of forecast skill in late 2014 (Figures 2, 4) is consistent with the neutral or weakly positive ENSO state.

Warm anomalies persisted through much of 2015 with a brief but strong cooling in late spring/early summer due to anomalously strong coastal upwelling (Peterson et al., 2017), which was not predicted in model forecasts. Consistent with regional upwelling being the dominant influence in this period, a regional heat budget identified vertical entrainment as the primary driver of SSTa fluctuations during 2015 (Chao et al., 2017). Remote ocean influence from the developing 2015–2016 El Niño likely also influenced the CCS in fall 2015, especially in the south (Frischknecht et al., 2017), but does not appear to have generated any appreciable forecast skill. As for late-2014, the mid-2015 variability was driven primarily by wind stress anomalies not associated with an ENSO event, so it is unsurprising that it was not predicted in the global forecasts (Jacox et al., 2017).

After a reduction of SSTa in the last months of 2015, another warm period in early 2016 was forecast with impressive skill. This last SSTa increase has been attributed to the 2015–2016 El Niño event via coastal waves and potentially anomalous poleward advection from the south (Chao et al., 2017). Winds in winter 2015–2016 were anomalously upwelling favorable, in contrast to the canonical El Niño response (Jacox et al., 2016), so the atmospheric teleconnection associated with ENSO variability does not appear to have imparted predictability in this case. The fact that the predictable influence of the 2015–2016 El Niño appears to have come through the oceanic pathway suggests that global models contain some representation of ENSO-forced coastal propagation even though they are too coarse to resolve coastal waves and currents (Capotondi et al., 2005).

By analyzing the spatiotemporal evolution of SSTa in concert with published findings on the forcing of these anomalies, we have developed hypotheses for why different phases of the 2014–2016 CCS heatwave were or were not predictable. Our analysis has focused on SST primarily for practical reasons, as the suite of variables publicly available in NMME output for recent years does not include the comprehensive diagnostics required for a full heat budget. Further exploration of these hypotheses, using heat budgets calculated from oceanic and atmospheric fluxes in model forecasts, is needed.

Ensemble Forecasts of SST Extremes

Multi-model ensemble mean forecasts outperformed damped persistence forecasts for much of the study period in terms of both forecast error and spatial anomaly correlations. During the most extreme warm anomalies in 2014 and 2015, model forecasts were consistently better than damped persistence, which had ~50% higher mean forecast error. However, neither ensemble mean forecasts nor damped persistence forecasts predicted SSTa anywhere near those observed at their peak. We see two reasons for this discrepancy: first, the ensemble spread for individual forecasts tends to be quite large (Figure 8), such that bias

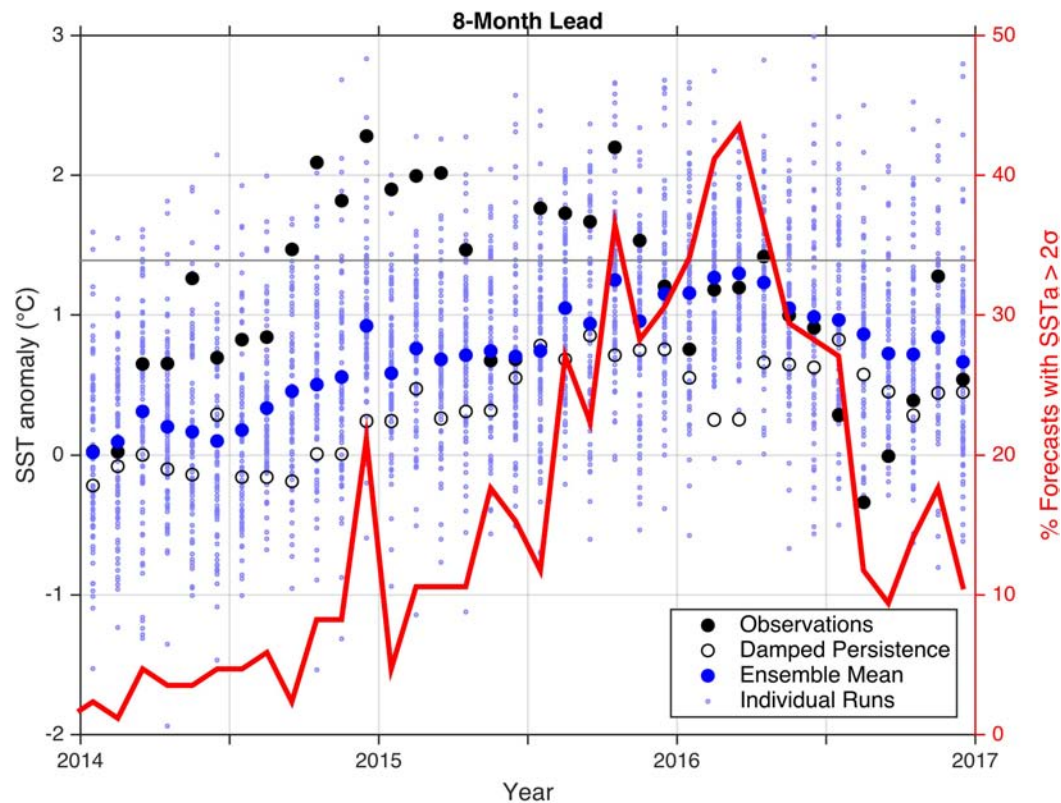


FIGURE 9 | Monthly initialized 8-month lead forecasts are shown for each of 85 ensemble members taken from 8 models (small blue markers), the multi-model ensemble mean (large blue markers), a damped persistence forecast (open black circles), and observations (filled black circles). The red line shows the percentage of ensemble members with forecast SSTa greater than 2σ ($\sim 1.39^\circ\text{C}$) for each forecast. The standard deviation (σ) was calculated from 1982 to 2017 observed SSTa and is marked by a thin gray line.

cancellation in the ensemble mean produces much reduced variance in forecasts relative to observations, especially at longer lead times (e.g., **Figures 4–6**). This reduced variance does not affect skill metrics based on correlation, but does impact the forecast error. One potential remedy is to scale the ensemble mean variance such that forecasts at each lead time maintain the same variance as that in the observations or the zero-lead forecasts (i.e., variance inflation; Doblas-Reyes et al., 2005). Second, an ensemble mean forecast that captures the observed magnitude of an extreme event requires that a large portion of individual ensemble members agrees on the extreme forecast, which in turn requires that its forcing be primarily deterministic and that model forecasts accurately represent that deterministic forcing. However, we know that internal variability can also strongly influence seasonal forecasts, leading to a wide range of forecast outcomes (**Figures 8, 9** and **Supplementary Figure 3**). Thus, a failed forecast could result either from unpredictable intrinsic variability or from the inability of a model forecast to capture a deterministic pathway (e.g., tropical-extratropical teleconnections proposed by Di Lorenzo and Mantua (2016) for the evolution of SSTa in 2015).

For both 2014 and 2016, the ratio of predictable components (Scaife and Smith, 2018) was greater than 1 (1.28 and 1.90, respectively), meaning that the correlation between the ensemble

mean forecast and observations ($r = 0.71$ and 0.63 , respectively) was stronger than the average correlation of the ensemble mean with individual ensemble members. Forecasts for these years were underconfident, as the ensemble mean forecast was better than what would be expected from the low model signal-to-noise ratio (Eade et al., 2014; Scaife and Smith, 2018). This is evidence of the “signal-to-noise paradox,” previously documented for ensemble climate predictions in the North Atlantic (Scaife and Smith, 2018). Scaife and Smith (2018) suggest that this underestimation of the signal-to-noise ratio in climate predictions may result from teleconnections, and their associated predictable signals, being too weak in climate models. Errors in the model signal-to-noise ratio can have a range of consequences that should be considered in forecast skill assessment, and post-processing techniques have been developed to correct for these errors (e.g., Eade et al., 2014).

Finally, rather than relying on ensemble mean forecasts to capture extremes, one can leverage the statistics of a large ensemble, which will contain members with low forecast error and high spatial correlations even when the ensemble mean predictions fail (**Figures 7–9** and **Supplementary Figures 2, 3**). Model ensembles have been shown to improve probabilistic skill scores relative to single model forecasts (Hagedorn et al., 2005), including for warm/neutral/cool SSTa terciles along North American coasts (Hervieux et al., 2017). Given that skillful

SSTa forecasts in the CCS appear to correspond to accurate representation of the broader-scale SSTa structure (i.e., low forecast errors in the CCS are associated with high spatial correlations in the northeast Pacific), one can speculate that the more skillful ensemble members are also predicting the mechanisms driving those anomalies more faithfully (i.e., they are right for the right reasons). However, such a hypothesis needs to be confirmed by comparing the heat budgets in successful and failed forecasts.

Regional Downscaling of Ocean Forecasts

One notable limitation of the climate forecast systems analyzed herein is their coarse resolution and resultant inability to resolve fine-scale ocean processes and features that are key to the functioning of the CCS and other systems. As a result, there are a number of ongoing efforts to improve regional forecasts through dynamical downscaling of global forecasts (e.g., Siedlecki et al., 2016). In such a configuration, output from global models such as those in the NMME are used as surface and lateral boundary conditions to regional ocean models that have 1–2 orders of magnitude higher resolution. Downscaled models have the advantage of being able to resolve important ocean dynamics that are sub-grid scale in global models (e.g., coastal upwelling, currents, eddies, and trapped waves). However, the downscaled model is ultimately dependent on the global model to impart forecast skill through surface or boundary forcing. For events where there is forecast skill derived from a clear deterministic pathway (e.g., surface fluxes and/or lateral advection in early 2014, poleward-propagating coastal trapped waves and/or anomalous advection in early 2016), a downscaled forecast or small ensemble of downscaled forecasts will better represent the fine scale impacts. On the other hand, for extreme events that result from unpredictable internal variability and can only be predicted in a probabilistic sense (e.g., wind driven SSTa variability in late 2014 and 2015), a downscaled ensemble of adequate size is currently computationally prohibitive and a large ensemble of global forecasts is the more appropriate tool (Doi et al., 2019).

CONCLUSION

An ongoing shift toward ecosystem-based management of the oceans (Levin et al., 2009; McLeod and Leslie, 2009) requires that information on the ocean state be accurate and readily available. The need for this information is even more pronounced in light of climate extremes that leave managers, fishers, and other stakeholders scrambling to adapt to rapid change. For one such extreme, the CCS marine heatwave of 2014–2016, we have outlined aspects of the ocean temperature evolution that were predictable in a deterministic sense, and others that were forecast with low probability in a large ensemble of seasonal forecasts. Incorporating ocean forecasts into management plans is a difficult task, complicated by inherent unpredictability in the climate system, an added layer

of uncertainty when translating physical changes to ecological impacts, and questions surrounding the decision making process (e.g., at what probability of an extreme event is a management action initiated?). However, to the extent that skillful forecasts of ocean conditions can improve decision making relative to that possible with ocean monitoring alone (Payne et al., 2017; Tommasi et al., 2017), our findings offer hope for more effective management when forecasted marine heatwaves ultimately do transpire.

DATA AVAILABILITY

The NMME System Phase II data (<https://www.earthsystemgrid.org/search.html?Project=NMME>) were obtained from <http://iri dl.ldeo.columbia.edu/SOURCES/.Models/.NMME/>. NOAA High Resolution SST data were provided by the NOAA/OAR/ESRL PSD, Boulder, CO, United States, from their website at <https://www.esrl.noaa.gov/psd/>.

AUTHOR CONTRIBUTIONS

DT conceived the study. MJ, DT, MA, and CS designed the analysis. MJ performed the analysis with the help from GH and drafted the manuscript. All authors contributed to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

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Factors Affecting the Recovery of Invertebrate Stocks From the 2011 Western Australian Extreme Marine Heatwave

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The extreme Western Australia 2011 marine heatwave had a lasting effect on the marine ecosystem and after 7 years, only parts of the ecosystem have showed good signs of recovery. After the heatwave, scallop fisheries in the Abrolhos Is. and Shark Bay were closed for 3-5 years, while the Shark Bay crab fishery was closed for 18 months; these fisheries at the center of the heatwave have shown some improvement due to better protection of spawning stock and improved environmental conditions. Also at the center of the heatwave, Roe's abalone suffered a catastrophic mortality and has not recovered as spawning stock remains very low. The Perth abalone stock which was outside the peak heatwave area had a major stock reduction but remained opened with reduced catches. The heatwave had a marked indirect effect on brown tiger prawns in Exmouth Gulf due to loss of seagrass habitat. The heatwave also resulted in a decline in western king prawn recruitment in Exmouth Gulf, to the north of heatwave center, but an improved recruitment in the cooler waters of Shark Bay. Western rock lobsters near the heatwave peak also appear to have been indirectly affected and have not recovered. Factors influencing the recovery rate from the heatwave appeared to be: species near their upper temperature range and/or sensitive to warming temperatures; spatial overlap between the warming event and species distribution; whether spawning stock was affected to the point of recruitment impairment; life-cycle duration of invertebrate (or habitat) species affected; and management intervention. This study provides a framework for managing the consequences of heatwaves on fisheries by highlighting the value of early identification of the event and its effect on fisheries and having flexible harvest strategies for early management intervention. This is particularly important as long-term increases in water temperatures will increase the frequency of marine heatwave events and the fisheries stocks would have less time for recovery.

Keywords: scallop, crab, prawn, abalone, rock lobster, pre-recruit, spawning stock, climate change

INTRODUCTION

Environmental factors are important drivers of fisheries recruitment variation and they have become increasingly important under climate change, with more frequent episodic extreme climatic events occurring such as marine heatwaves. Hobday et al. (2016a) define a heatwave event as a prolonged discrete warm-water event that can be described by its duration, intensity, rate of evolution and spatial extent. An extreme marine heatwave in the austral summer of 2010/2011 affected 2000 km of coastline in the mid-west of Western Australia (WA) with warming anomalies of 2–4°C (Pearce and Feng, 2013; Wernberg et al., 2013; Benthuyssen et al., 2014; **Figure 1A**). The marine heatwave was followed by 2 years of above-average summer water temperatures (**Figure 1A**). This region of WA is also a hotspot of long-term water temperature increases (Pearce and Feng, 2007), having been classified as one of the 24 global hotspots of temperature rise (Hobday and Pecl, 2013). Hobday et al. (2018) classified the 2011 WA event at their highest “Category IV level (extreme).” They also identified another heatwave in the same region in 1999, which was classified as Category III (severe).

The 2011 heatwave had some major short and long-term effects on the marine ecosystem such as a reduction in abundance of habitat-forming seaweeds, a subsequent shift in community structure and a southward distribution shift in tropical finfish communities (Wernberg et al., 2013; Lenanton et al., 2017). Seagrasses in Shark Bay (Fraser et al., 2014) and Exmouth Gulf were also significantly negatively affected by the heatwave (McMahon et al., 2017) with a 58% loss of the main seagrass species (*Amphibolis antarctica*) cover in Shark Bay (Thomson et al., 2015). Coral bleaching followed by high mortality was recorded in areas of Ningaloo and Abrolhos Is. (Depczynski et al., 2012). An assessment 4 years after the heatwave showed a 43% loss of kelp forests with a 100 km range contraction of extensive kelp forests, forcing a regime shift to seaweed turfs (Wernberg et al., 2016). They also saw temperate species replaced by seaweeds, invertebrates, corals, and fish characteristic of subtropical and tropical waters which altered key ecological processes. Smale et al. (2017) noted a major reduction of all benthic macroinvertebrates in Kalbarri near the center of the heatwave after 4 years. These ecological studies are valuable in providing an overview of the effect of the heatwave on the ecosystem, however, they may not be undertaken on a systematic basis in the long term compared to some fisheries surveys that occur annually to enable an assessment of the stock and the setting of management parameters (Caputi et al., 2014). Fisheries data can be valuable in understanding the effect of the heatwave on stocks and comparing it to the annual variation experienced prior to the heatwave under typical environmental variation and fishing intensities, and assessing the rate of recovery of the stocks after a heatwave event.

Off the WA coast, subtropical regions (including the lower west coast) are more susceptible to marine heatwaves during *La Niña* events and these have contributed to 1999 and 2011 events, whereas tropical regions are more susceptible to marine heatwaves during *El Niño* events (Zhang et al., 2017). Water

temperatures off the west coast of Australia have declined in subsequent years after the consecutive marine heatwave events during 2011–2013 (**Figures 1A, 2A**). Cooler water temperature anomalies have been observed off the lower west coast in the 2015/2016 summer (**Figures 1A, 2A**) during the onset of a strong *El Niño* event.

Western Australia is one of several regions affected by marine heatwaves in recent years (Hobday et al., 2016a) with south-east Australia being one of the latest regions affected in 2015/2016 (Oliver et al., 2017; Schaeffer and Roughan, 2017) with this event referred to as Tasman Sea, Australia 2015–Category II (strong) heatwave by Hobday et al. (2018). This latter event affected invertebrate fisheries of Pacific oysters and blacklip abalone, the aquaculture of Atlantic salmon, with intrusions of fish normally seen in warmer waters further north. Other events around the world in recent years include (a) the Mediterranean Sea 1999 event (Category I moderate) with a large-scale mass mortality of benthic species in the summer of 1999 (Cerrano et al., 2000) and also in 2003 (Category II strong) when macro-invertebrate species were affected (Garrahou et al., 2009); (b) the Northwest Atlantic 2012 event (Category II) resulting in a major impact on coastal ecosystems and economies, with a significant effect on the American lobster (Mills et al., 2013); (c) the Northeast Pacific blob 2015 event (Category III severe) resulted in an unprecedented warming event in 2014–2016 (Bond et al., 2015; Cavole et al., 2016) resulting in harmful algal bloom which caused the closure of valuable shellfish fisheries (Di Lorenzo and Mantua, 2016); and (d) declines in coral cover, due to coral bleaching were observed resulting from the Great Barrier Reef 2016 event (Category II) on the east coast of Australia due to extreme temperatures (Hughes et al., 2017). Some common features of many of these marine heatwave events appear to be a major effect on habitat structures (Wernberg et al., 2013) and sessile or slow-moving invertebrates and the movement of species from warmer waters into the affected area (Smale et al., 2019).

Under the present warming trend influenced by anthropogenic forcing, these extreme events are expected to become more frequent with an estimated increase in global average frequency and duration of 34 and 17%, respectively, since 1925 (Oliver et al., 2018). Frölicher and Laufkötter (2018) highlighted the large increase in marine heatwave events as a result of moderate long-term increase in mean sea surface temperature (SST) and Schlegel et al. (2017) identified the effect of aseasonal variability in wind and current patterns. Therefore it is important to assess the effects of these extreme events on the ecosystem and commercial and recreational fisheries stocks that are affected. As some parts of the ecosystem have not yet recovered to date or may be suffering a permanent change (Wernberg et al., 2016; Smale et al., 2017), the question remained as to whether the invertebrate fisheries stocks affected by the heatwave (Caputi et al., 2016) would ever fully recover given the very low abundance (99% decline in some cases) observed in the years after the heatwave.

There has been a high commercial cost to a number of invertebrate fisheries which have been affected by a series of low recruitment (Caputi et al., 2016). Therefore it is important

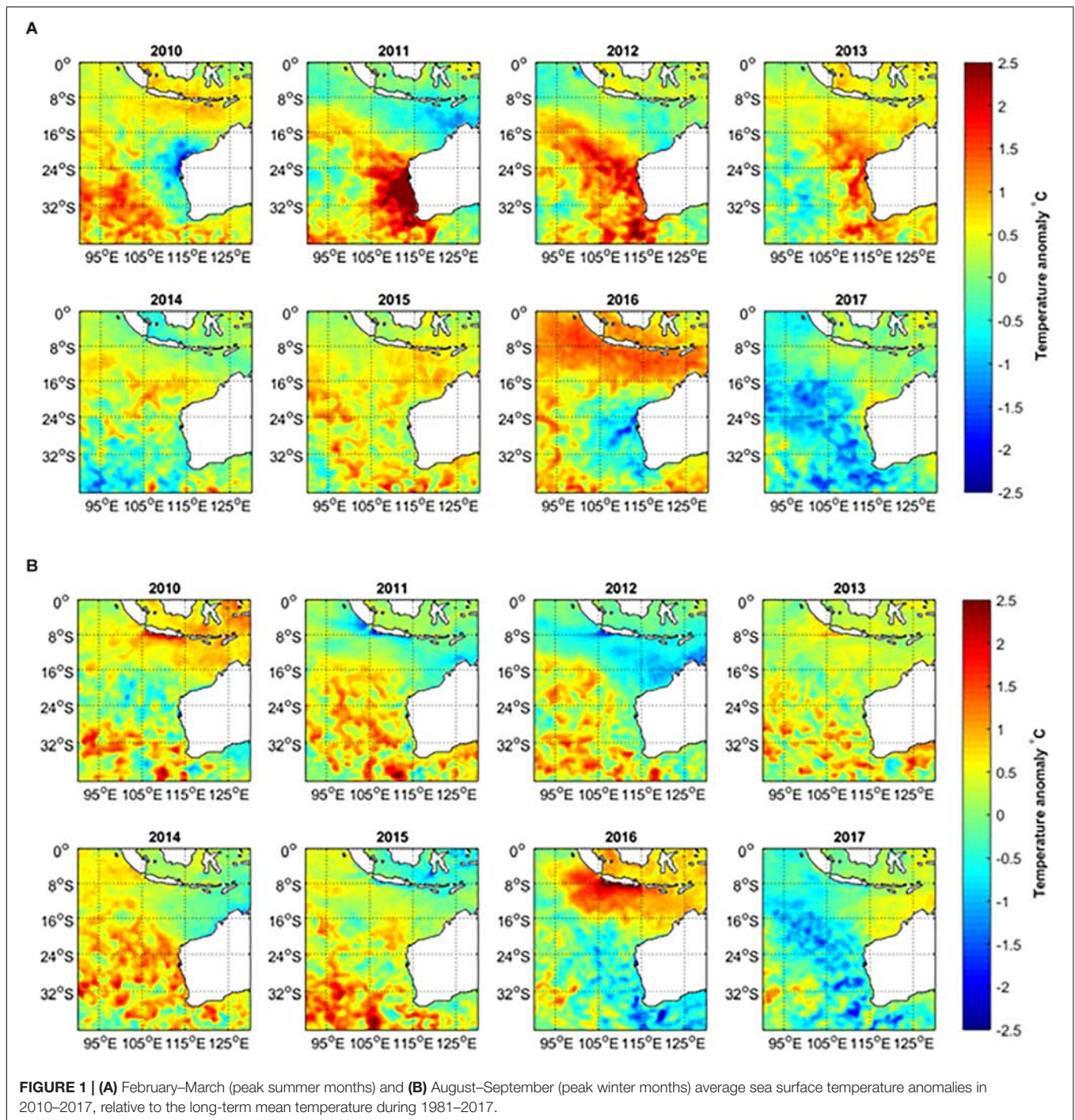


FIGURE 1 | (A) February–March (peak summer months) and **(B)** August–September (peak winter months) average sea surface temperature anomalies in 2010–2017, relative to the long-term mean temperature during 1981–2017.

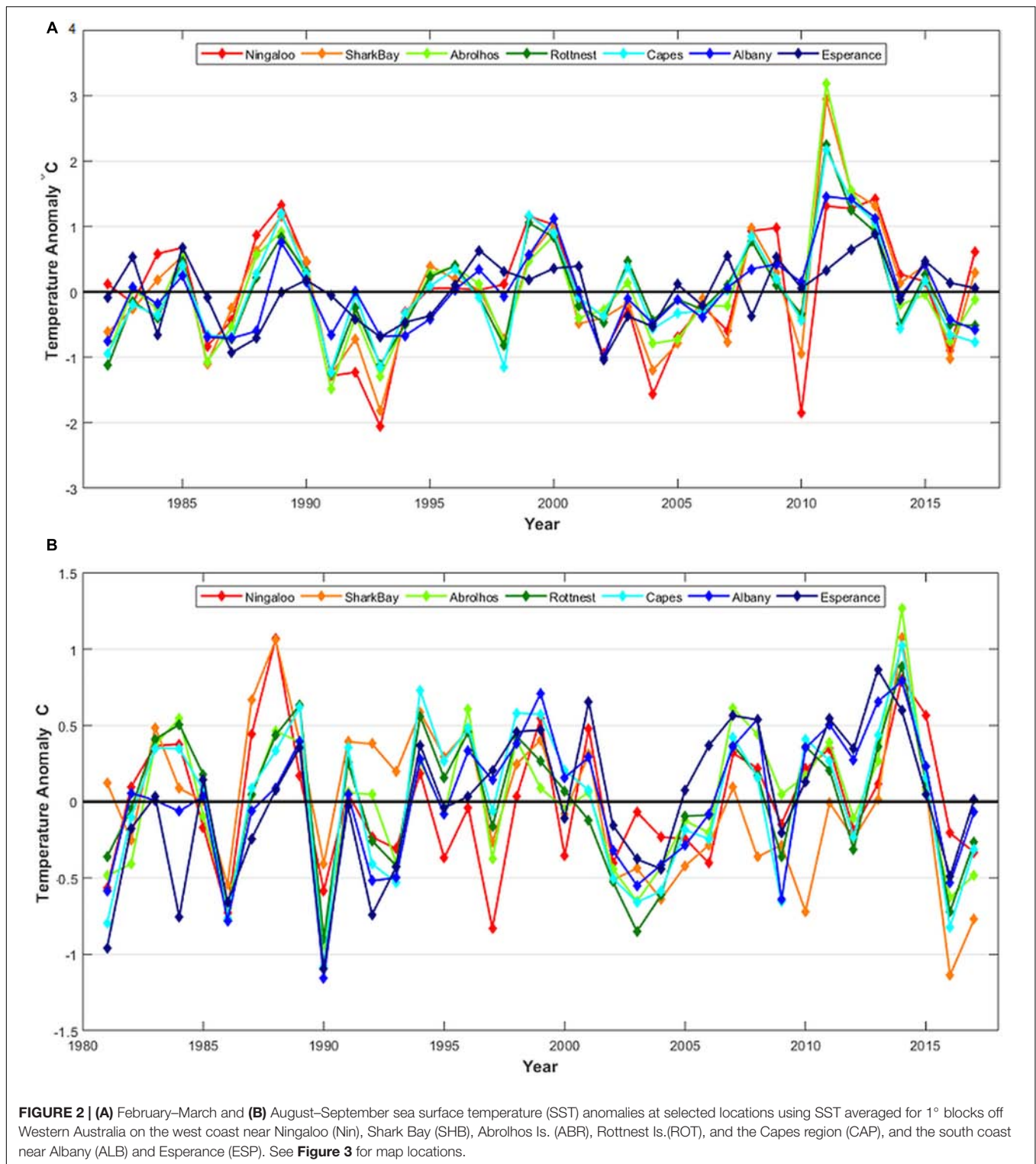
to examine how these stocks have fared in the 7 years since the heatwave, the extent of their recovery, and the reasons for the different timing of recovery. The invertebrate stocks examined include scallops, blue swimmer crabs, Roe's abalone, western king and brown tiger prawns and western rock lobsters (Figure 3). This study also provided a framework for assessment and management responses to marine heatwave impacts on fisheries in other regions by highlighting the value of early identification of the extreme event and its effect on

fishery stocks and having flexible harvest strategies for early management intervention.

MATERIALS AND METHODS

Marine Environment

The NOAA OIv2 SST data from 1981 to 2017 at 1/4 degree (~28 km) resolution (Reynolds et al., 2007) were used to calculate



monthly anomalies for each grid point relative to 1981–2017 and these are assessed for the austral summer (February–March) and winter (August–September). Smale and Wernberg (2009) have shown that satellite SST data can be reliably used to monitor water temperatures.

Effect of Heatwave on Invertebrate Stocks

The commercial and recreational invertebrate stocks selected for assessment of recovery from the heatwave event were those that overlapped the area of the heatwave and had been identified as

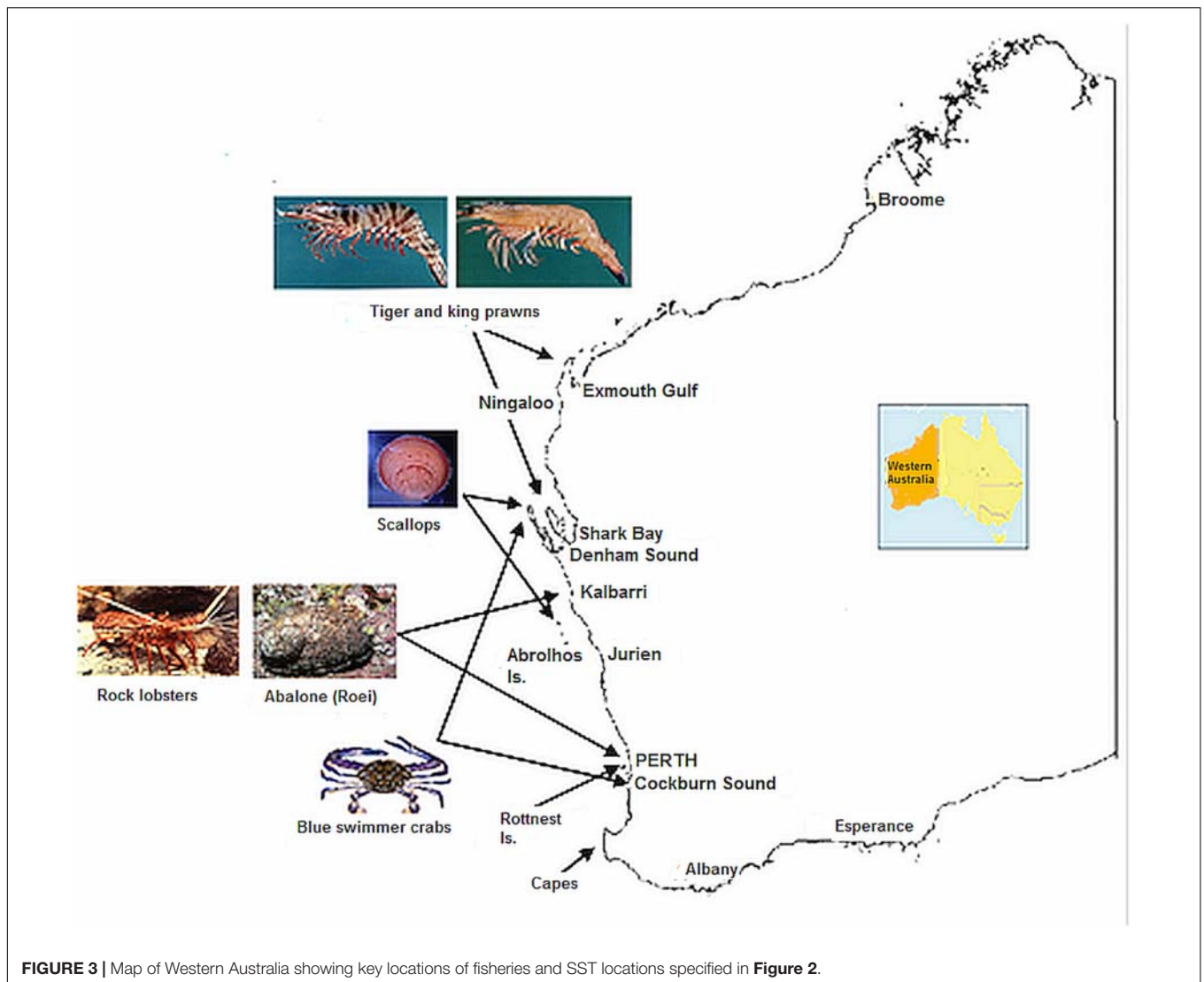


FIGURE 3 | Map of Western Australia showing key locations of fisheries and SST locations specified in **Figure 2**.

being affected by the heatwave (Caputi et al., 2016). The stocks examined with their annual fisheries recruitment abundance indices were: (a) Shark Bay crabs: annual November fishery-independent trawl survey legal-size abundance (Chandrapavan et al., 2018); (b) Shark Bay scallops: juvenile recruit (0+) and adult (1+) catch rates from the November trawl survey (Kangas et al., 2012); (c) Abrolhos Is. scallops: juvenile recruit catch rates (~1-year-old) in an annual November trawl survey; (d) Exmouth Gulf and Shark Bay: western king and brown tiger prawn: juvenile recruit (0+) trawl catch rates in March–April surveys (Kangas et al., 2015a,b); (e) Perth metropolitan area Roe’s abalone: dive survey abundance of 1+ juveniles in February–March (Hart et al., 2013, 2017); and (f) western rock lobster in the Kalbarri and Jurien region: fishery-independent puerulus (0+) monitoring and undersize (3 and 4+) abundance from commercial monitoring (de Lestang et al., 2016).

The effect of the heatwave on the recruitment abundance of the various invertebrate stocks is assessed by comparing the lowest (and highest) recruitment level post heatwave to

the average abundance in the 5 years (2006–2010) before the heatwave. The ratio of lowest (and highest) recruitment abundance post heatwave to the pre-heatwave average abundance is calculated as a measure of the maximum effect of the heatwave on the stocks and the level of recovery in the 7 years since the event.

For the western rock lobster fishery, the relationship between puerulus settlement and undersize abundance 3–4 years later for the period before the heatwave was used to project the expected undersize abundance post-heatwave to assess the effect of the heatwave during the puerulus to undersize (juvenile) phase of the life cycle.

The duration of the effect of the heatwave on the invertebrate stocks in Western Australia is classified as (1) short-term (<2 year) changes such as localized fish kills, increased or decreased recruitment abundance for 1–2 years; (2) longer-term (3–7 year) changes with “recovery” occurring after a few years; and (3) no recovery to date (> 7 years) with possible “permanent” changes on fisheries.

The factors examined which may have affected the rate of recovery include: (a) species near their upper temperature range; (b) species sensitivity to warming temperatures; (c) spatial overlap between the warming event and the species distribution; (d) whether spawning stock was affected to the point of recruitment impairment; (e) life-cycle duration of the invertebrate species affected; (f) changes to habitat/ecological structures and species' recruitment relationship with that structure; and (g) management action undertaken.

RESULTS

Marine Environment

The austral summer SSTs off the west coast of Australia highlighted the strength of the 2011 Western Australian marine heatwave (**Figures 1A, 2A**). Despite cooler summer ocean temperatures in 2010, as influenced by the 2009/2010 *El Niño* (**Figure 2A**), water temperatures were 2–3°C above the long-term bi-monthly average for all the west coast locations in summer 2010/2011, which represent the highest recorded (Hobday et al., 2016a). The elevated summer temperatures persisted into the 2011/2012 and 2012/2013 summers (**Figures 1A, 2A**). At the peak of the heatwave in February–March 2011, the entire region from the Abrolhos Islands to Exmouth experienced extremely high temperatures with warming anomalies of 2–4°C (Pearce and Feng, 2013). The heatwave expanded further into the South-East Indian Ocean, with temperature anomalies greater than 1°C observed as far as 100°E in the 2011/2012 summer (**Figure 1A**). From 2011 to 2013, winter temperatures along the west coast were close to average, although offshore waters generally experienced warmer temperatures with warming anomalies of 0.5–1°C. However, the 2014 winter temperatures also warmed up along most of the west coast, reaching 1–1.5°C anomalies at various locations (**Figures 1B, 2B**).

Shark Bay endured some extreme temperature fluctuations during 2010 and 2011 with SSTs being well-below average in the 2009/2010 summer and 2010 winter, but then changing to its highest SST during the 2010/2011 summer heatwave (**Figure 2**).

Summer SSTs declined from the peak in 2010/2011 and were close to average in 2013/2014 and 2014/2015 and then below average in 2015/2016 at a number of locations for the first time since 2010/2011 (**Figures 1A, 2A**). The cooler temperatures were influenced by one of the most severe *El Niño* events on record that lasted from early-2014 to mid-2016, dubbed the Godzilla-*El Niño*. This resulted in weaker Leeuwin Currents and cool SST anomalies off the lower west coast of Australia during 2015/2016, though with widespread warm anomalies in the tropical regions off the north coast of Australia (**Figure 1**; Benthuisen et al., 2018).

Shark Bay and Abrolhos Is. Scallops

The key scallop (*Ylistrum balloti*) trawl fisheries in Western Australia are based in Shark Bay which consists of two separate stocks, northern Shark Bay and Denham Sound (Kangas et al., 2012), and at the Abrolhos Islands. The annual trawl survey has been used for catch prediction in the following season for these fisheries (Joll and Caputi, 1995; Caputi et al., 2014).

Since 2015 these surveys have been used for the setting of the total allowable catch (TAC) in Shark Bay as the management of the fishery has moved from effort controls to individual transferable quota (ITQ).

Scallop recruitment abundance (and subsequent catch) fluctuates markedly between years and is strongly influenced by water temperature prior to and during the peak spawning period (e.g., $r = -0.46$, $p < 0.01$ for northern Shark Bay, $r = -0.39$, $p = 0.03$ for Denham Sound, and $r = -0.84$, $p < 0.001$ for Abrolhos Is. (Caputi et al., 2015). High water temperatures (associated with *La Niña* and strong Leeuwin Current) always result in poor recruitment (Joll and Caputi, 1995; Lenanton et al., 2009) while below-average temperatures are required for good recruitment although this is not always guaranteed (Caputi et al., 2016). Hence the effect of the 2011 heatwave and the subsequent years of above-average SST resulted in a series of record-low 0 + recruit abundances during 2011–2013 for both stocks in Shark Bay (**Figure 4**), particularly in northern Shark Bay which declined 2–3 orders of magnitude resulting in < 1% of the pre-heatwave abundance (**Table 1**). This resulted in early management intervention with industry's support that resulted in the Shark Bay scallop fishery being closed in 2012–2014 to maximize the protection of the spawning stock.

The series of years with low scallop recruitment abundance also meant that the spawning stock was reduced to historic low levels during 2012–2014 in both Shark Bay and the Abrolhos Islands and this is one of the key reasons that delayed the recovery of this stock (**Table 2**). Surveys of the Abrolhos Islands stock, for example, achieved an average catch rate of 0.4 scallops per nautical mile of trawling in 2012 and 2013 compared to 1000's of scallops per nautical mile before the heatwave (**Figure 5**). There were strong concerns at the time about the ability of these stocks to recover from these very low abundance levels, with the Abrolhos Islands remaining closed for 5 years between 2012 and 2016.

There have been previous periods of low scallop recruitment abundance in northern Shark Bay that were associated with periods of above-average SST such as the late 1980s and late 1990s (Joll and Caputi, 1995; Lenanton et al., 2009). However, the survey catch rate in these periods remained at 100's of scallops per nautical mile and were an order of magnitude higher than the survey catch rates experienced after the heatwave that declined to two scallops per nautical mile in the 2013 survey (**Figure 4A** and **Table 1**).

The stock-recruitment-environment relationship showed that the spawning stock from 2012 to 2014 was in a declining trend so that the 0 + recruitment abundances in these years were influenced by historic-low spawning stock as well as above-average SST (Caputi et al., 2016). Environmental conditions improved in 2014 with cooler SSTs (**Figure 2**) resulting in an improved recruitment abundance, particularly in Denham Sound, and a modest total allowable catch (TAC) was put in place for the Shark Bay fishery in 2015 as the fishery was moved from effort controls to quota management. The improved spawning stock for 2015 combined with cooler SSTs during the 2014/2015 summer resulted in an improved recruit 0 + abundance in the November 2015 survey (**Figure 4B**). Both stocks in Shark

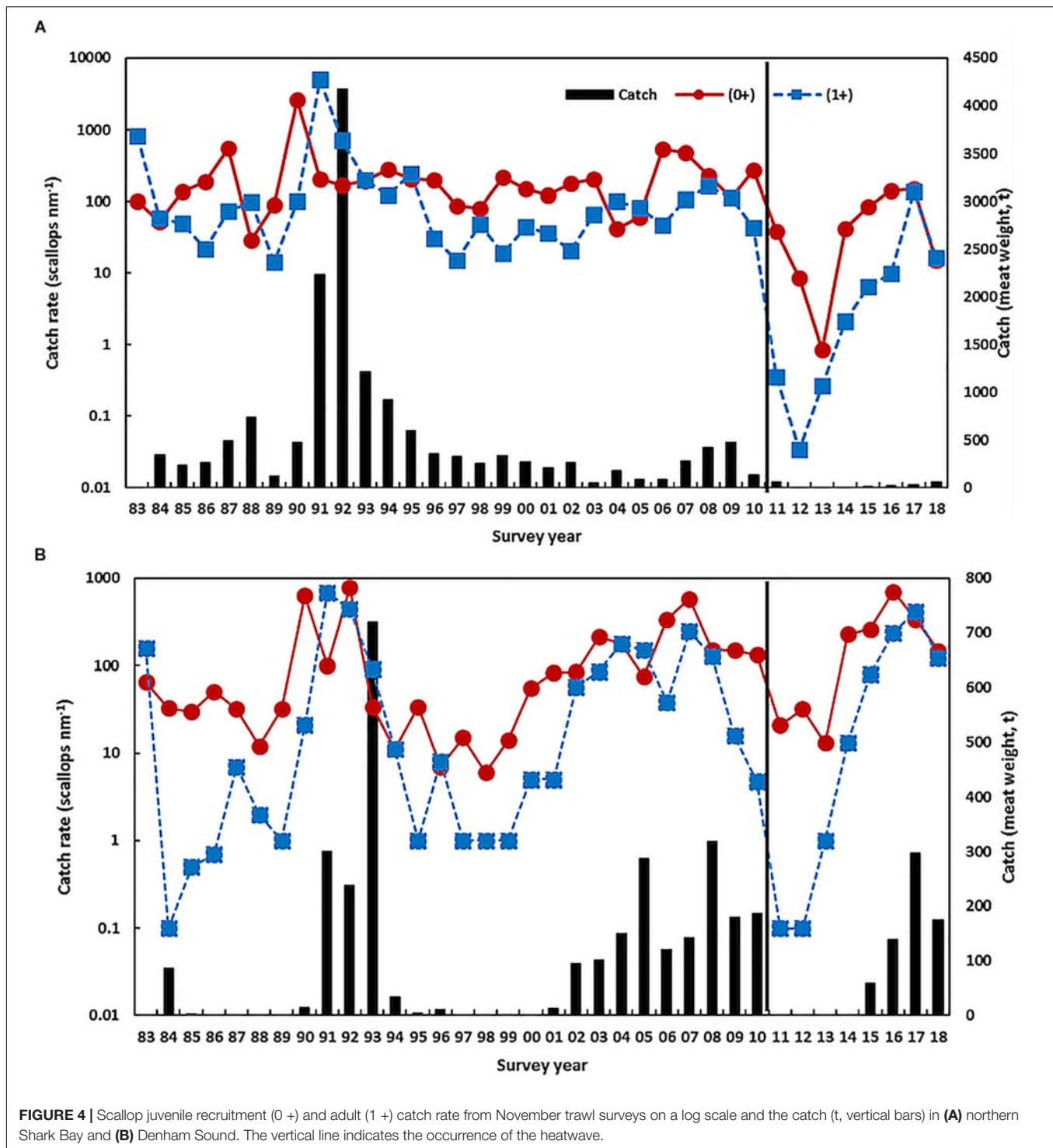


FIGURE 4 | Scallop juvenile recruitment (0 +) and adult (1 +) catch rate from November trawl surveys on a log scale and the catch (t, vertical bars) in **(A)** northern Shark Bay and **(B)** Denham Sound. The vertical line indicates the occurrence of the heatwave.

Bay showed continued improvement in 2016, with the total abundance returning within the pre-heatwave historic range in northern Shark Bay and particularly in Denham Sound which achieved its second highest recruitment in 34 years (**Figure 4** and **Table 1**). The Denham Sound stock is now assessed as recovered based on survey abundance. However, there are strong concerns about the productivity within northern Shark Bay with

the 2018 scallop survey abundance again declining to very low levels (**Figure 4A**).

The Abrolhos Islands scallop stock had a more protracted downturn compared to Shark Bay that commenced with poor recruitment of the 1 + scallops in the November 2011 survey and low recruitment abundance continuing for 5 years (**Figure 5**) with the fishery being closed during 2012–2016. This low

TABLE 1 | The effect of the marine heatwave (MHW) on the recruitment and the level of recovery after the heatwave are compared to the mean abundance indices in the 5 years before the heatwave.

Fishery	Age class	Mean abundance 5 y before MHW (SE)	Lowest abundance post MHW (year)	Ratio lowest abundance post MHW to before	Highest abundance post MHW (year)	Ratio highest abundance post MHW to before
Scallops Northern Shark Bay	0 +	667 (168)	2 (2013)	< 0.01	375 (2017)	0.56
Scallops Denham Sound	0 +	270 (86)	13 (2013)	0.05	704 (2016)	2.61
Scallops Abrolhos Is.	0/1 +	2301 (635)	< 1 (2012)	< 0.01	988 (2016)	0.43
Shark Bay crabs	1 +	741 (147)	15 (2011)	0.02	898 (2017)	1.21
Perth metro abalone	1 +	10.9 (1)	2.3 (2015)	0.21	5.1 (2017)	0.47
Kalbarri abalone	All			< 0.01		< 0.01
Tiger prawns Exmouth Gulf	0 +	54.5 (8.1)	21.5 (2012)	0.39	93.5 (2017)	1.72
King prawns Exmouth Gulf	0 +	50.3 (7.4)	23.1 (2014)	0.46	52.2 (2013)	1.04
Tiger prawns Shark Bay	0 +	48.4 (8.3)		NA	131.2 (2011)	2.71
King prawns Shark Bay	0 +	87.1 (16.4)		NA	175.8 (2011)	2.02
Kalbarri rock lobster	~4 +	1.01 (0.12)	0.05 (2014)	0.05	0.16 (2017)	0.16 (2017)

The ratios of the lowest and highest recruitment abundance index post heatwave to the pre-heatwave average abundance and the years of low and high post-heatwave abundances are indicated (NA, not applicable).

TABLE 2 | The factors affecting the level of recovery from the heatwave for the invertebrate stocks are compared.

Fishery	Age to legal size (y)	Stock Location relative to heatwave	Habitat affecting recovery	Spawning stock affecting recovery	Species upper end of SST range	Known effect of SST	Management response	Duration of recover
Scallops Northern Shark Bay	1	Near peak	No	Yes	Yes	—ve	Closed 4 y	Longer term
Scallops Denham Sound	1	Near peak	No	Yes	Yes	—ve	Closed 3 y	Longer term
Scallops Abrolhos Is.	1	Near peak	No	Yes	Yes	—ve	Closed 5 y	Longer term
Shark Bay crabs	1.5	Near peak	No	No	No	No	Closed 1.5 y	Short term
Perth metro abalone	5	Outside peak	No	Yes	No	No	Reduced TAC	Longer term
Kalbarri abalone	5	Near peak	Yes	Yes	Yes	No	Closed	No recovery
Tiger prawns Exmouth Gulf	0.5	Near peak	Yes	No	No	No	Reduced effort	Longer term
King prawns Exmouth Gulf	0.5	Near peak	No	No	No	No	Reduced effort	Longer term
Tiger prawns Shark Bay	0.5	Near peak	No	NA	No	No	None	Short term
King prawns Shark Bay	0.5	Near peak	No	NA	No	+ ve	None	Short term
Kalbarri Western rock lobster	5	Near peak	Yes	No	Yes	No	None	No recovery

They include the age to legal size, the location of the stock relative to the heatwave location, whether the habitat and spawning stock changes have affected the recovery, whether the stock is at the upper end of its SST range and whether there was a known relationship between SST and the recruitment abundance, management response and the duration of the heatwave effect.

recruitment resulted from the negative effect of a series of warm SSTs (Caputi et al., 2016) and the subsequent decline in spawning stock to very low levels that also slowed the recovery. The stock declined to less than 1% of its pre-heatwave abundance (Table 1 and Figure 5). There was a marked improvement in the recruitment abundance in 2016 to 25% of the pre-heatwave abundance (Table 1 and Figure 5) as a result of summer water temperatures returning to average conditions in 2014–2016 (Figure 2A). The improved 2016 survey recruitment abundance enabled a modest level of fishing in 2017 with 125 t of meat weight landed in the Abrolhos Islands fishery (Figure 5) which has remained under effort controls. The 2017 survey showed the distribution of recovery was spread wider than in 2016 which was concentrated in southern part of the fishery.

Shark Bay Crabs

The blue swimmer crab (*Portunus armatus*) stock in Shark Bay was at record-low levels in late 2011 after the summer

heatwave event with poor commercial trap catch rates and low fishery-independent trawl survey catch rates in November 2011 (Chandrapavan et al., in review) which showed that catch rates had declined to 2% of the pre-heatwave abundance (Table 1 and Figure 6). The fishery was closed for 18 months (April 2012 to October 2013) to protect the breeding stock and allow the stocks to recover. Additional trawl surveys were undertaken to monitor the status of the spawning stock and recruitment abundance to assess the stock recovery rate (Chandrapavan et al., 2018).

Caputi et al. (2016) identified a significant correlation between legal-size commercial catch rate and the SST in the summer period during the juvenile phase ($r = -0.76$, $p < 0.01$). The catch rates of legal crabs (1 + cohort) during the November survey were also negatively correlated ($r = -0.85$, $p < 0.01$) with SSTs during the previous summer (December–January) (Chandrapavan et al., in review). These assessments indicated that the cause of the low abundance in 2011/2012 was mainly due to the heatwave in the summer of 2010/2011. While there was a reduction in the

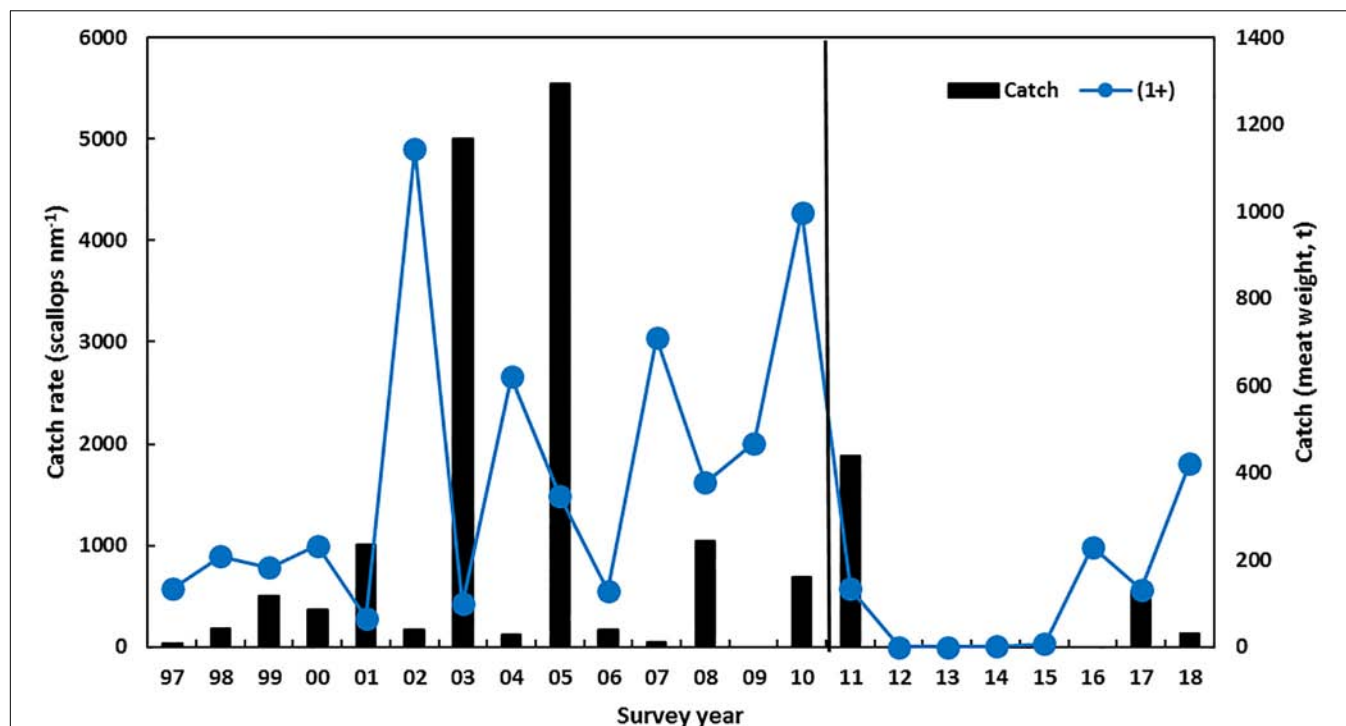


FIGURE 5 | Scallop recruitment catch rate (mainly 1-year-olds) in November trawl survey and the catch (meat weight t, vertical bars) in the Abrolhos Is. The vertical line indicates the occurrence of the heatwave.

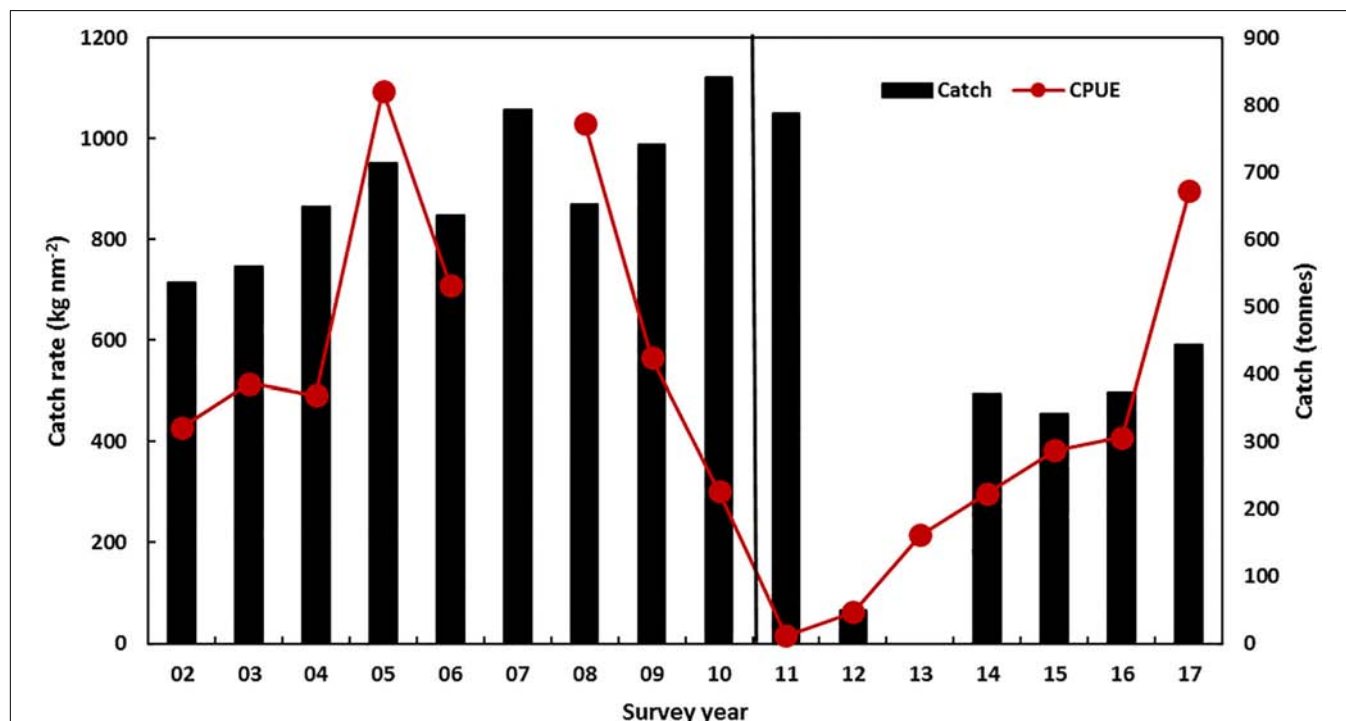


FIGURE 6 | November trawl survey standardized mean catch rate of legal-size blue swimmer crabs and the catch (t, vertical bars) in Shark Bay. No survey information was collected in 2007. The vertical line indicates the occurrence of the heatwave.

spawning stock in 2011 and 2012 to historic low levels, its effect on the recruitment is confounded by high summer SST in the same year. Fishery-independent surveys showed only a partial improvement in crab legal-size catch rate in 2013 (Figure 6) as the summer SST in 2011/2012 and 2012/2013 remained above-average, but lower than the peak in 2010/2011 (Figure 2). Therefore the fishery was opened in 2013/2014 with a nominal catch quota of 400 t that was much lower than the pre-heatwave catches of 700–800 t that were achieved with the fishery under effort controls with no TAC in place (Figure 6). Monitoring of the stock by fishery-independent surveys and commercial catch rates indicated a steady improvement over 2014–2017 in the crab stocks (Figure 6) and an increase in quota since the heatwave from 400 to 550 t for the 2017/2018 season with the fishery assessed as fully recovered with the legal-size abundance in 2017 being 21% higher than the pre-heatwave abundance (Table 1).

Perth Metropolitan Area and Mid-West Coast Roe's Abalone

The first major impact of the heatwave on invertebrate stocks was the catastrophic mortality of over 99% of Roe's abalone (*Haliotis roei*) in the mid-west region (Hart, 2014). This fish kill of Roe's abalone as well as other fish stocks probably occurred due to a combination of record-high water temperatures and very calm conditions in late February/early March 2011 (Pearce et al., 2011) which may have resulted in deoxygenation of the water. This mid-west stock is at the northern end of its latitudinal range where SSTs are typically warmer than the other locations where the stock occurs. For example, the mid-west would be warmer than the lower west coast by about 1–2°C and south coast by 2–3°C. It was also near the area where the heatwave was most intense (Figure 1A). The high mortality has affected the spawning stock and made the natural recovery of this stock problematic with no evidence of any stock recovery (Table 2). Therefore restocking is being evaluated based on translocation and the release of hatchery-grown abalone (Strain et al., 2019).

In the Perth metropolitan Roe's abalone fishery, which is south of the area where the heatwave peaked, major mortalities were not observed. However, there was a 30% drop in numbers of the sub-legal cohort growing into the legal-size class (Hart et al., 2018). The fishery has undergone a marked drop in commercial and recreational catches from 85 t in 2009 to 45 t in 2012 as a result of catch quota reductions to increase protection to the spawning stock. The Perth stock has also seen a reduction in 1 + juveniles to record-low levels during 2012–2016 to 21% of the pre-heatwave abundance from the annual dive survey (Figure 7 and Table 1). Record-low juvenile abundance was also observed within a marine protected area adjacent to the fishery (Figure 7) where no fishing occurred which indicated that environmental conditions were the primary cause of the low abundance after the heatwave. The spawning stock in this fishery has also moved to record-low levels since the heatwave and this may be contributing to the delay in the recovery of the juvenile abundance (Hart et al., 2018). There was an improvement in the 1 + juvenile abundance in 2017 (Figure 7) to 47% of the pre-heatwave abundance (Figure 7 and Table 1) which is probably due to the reduced SST

in 2015 (Figure 2). The low juvenile abundances may maintain legal-size catch rates at relatively low levels in the subsequent years (2018–2020) as these 1 + juveniles take about 4 years to reach legal size. However, the abundance of legal-size abalone is also negatively related by the water temperature during the juvenile to legal-size phase of the life cycle (Hart et al., 2018). Therefore the legal-size abundance will benefit from the cooler temperatures since 2015.

Exmouth Gulf and Shark Bay Brown Tiger and Western King Prawns

The brown tiger prawns (*Penaeus esculentus*) in Exmouth Gulf had an above-average recruitment abundance in March–April 2011 following the heatwave peak in February 2011 so that there did not appear to be any direct impact of the heatwave on the stocks. However, in 2012 there was a record-low recruitment abundance to 39% of the pre-heatwave abundance (Figure 8 and Table 1) and this appeared to be due to the heatwave causing the loss of seagrass/algal habitat in the nursery areas (McMahon et al., 2017). There was a moderate improvement in the brown tiger prawn recruitment abundance between 2013 and 2015 with a return to above-average recruitment abundance in 2016 and 2017 (Figure 8). This reflected the previous experience in 2000/2001 when a severe category-5 cyclone in 1999 caused significant physical damage to inshore nursery habitats (Loneragan et al., 2013) (also a strong *La Niña* in 1999/2000). The brown tiger prawn recruitment abundance slowly recovered between 2002 and 2003 (Figure 8) as the habitats recovered.

Conversely, there was a low recruitment abundance of western king prawns (*Penaeus latisulcatus*) in the surveys of March–April 2011 in Exmouth Gulf suggesting that the heatwave had a direct effect on recruitment (Figure 8). Caputi et al. (2016) showed that water temperature in November–December, during the juvenile phase prior to recruitment to the fishery, was negatively correlated to western king prawn recruitment in Exmouth Gulf ($r = -0.62$, $p < 0.05$). The extended period of below-average recruitment during 2014–2016 to 46% of the pre-heatwave abundance (Table 1) reflected the above-average SST experienced over this period and a modest improvement in the 2017 recruitment reflected the cooler SST (Figures 2, 8).

In contrast to Exmouth Gulf, the western king prawn stock in Shark Bay achieved the highest recruitment abundance in 2011 after the heatwave at twice the average pre-heatwave abundance (Table 1 and Figure 9). This is reflected by the positive relationships between the recruitment of western king and also brown tiger prawns with SST during the larval/juvenile phase, November–April ($r = 0.63$, $p = 0.02$, and $r = 0.83$, $p < 0.001$, respectively, Caputi et al., 2016). Similar positive relationships were previously identified for western king prawn catches (Caputi et al., 1996; Lenanton et al., 2009). The recruitment for both species returned to historical levels during the years following the heatwave (Figure 9).

Caputi et al. (2016) noted that SST in Shark Bay is generally about 2–3°C cooler than Exmouth Gulf. A comparison of the western king prawn recruitment abundance with SST during November–December in Shark Bay and Exmouth Gulf indicated

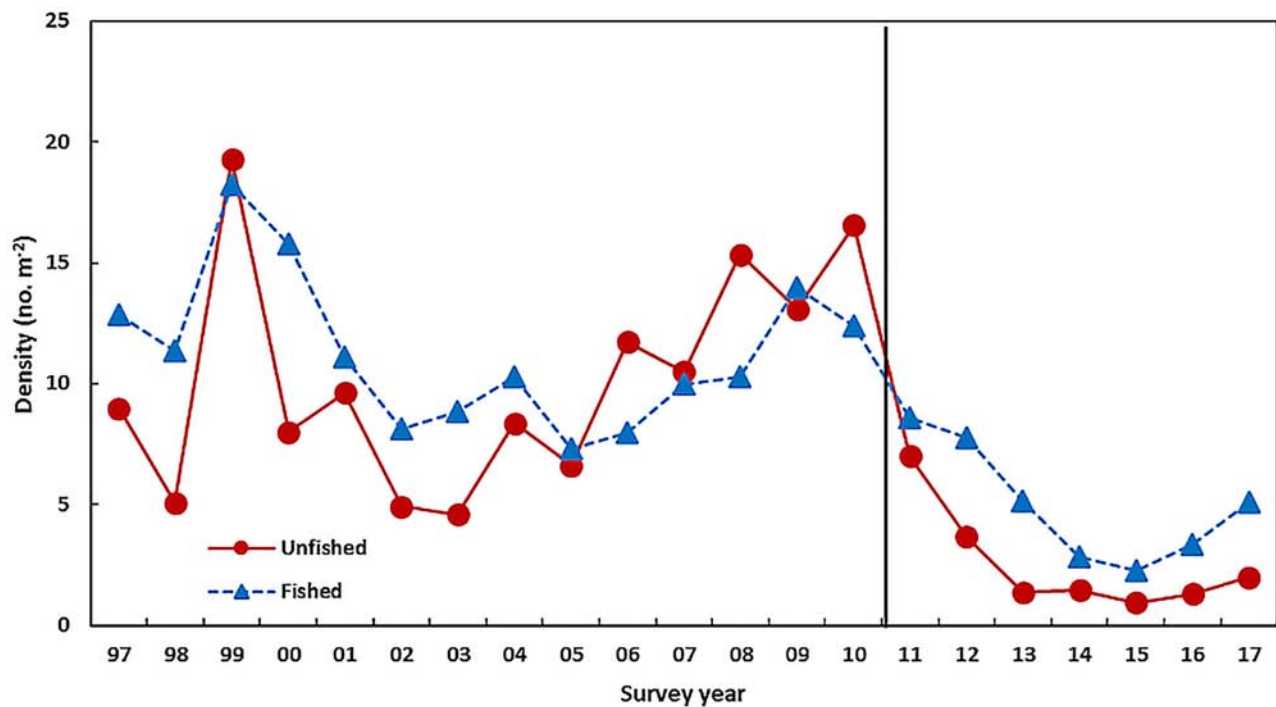


FIGURE 7 | The 1 + juvenile abundance from the Perth Roei abalone fishery-independent dive survey conducted in March each year averaged over a number of fished locations and an unfished area. The vertical line indicates the occurrence of the heatwave.

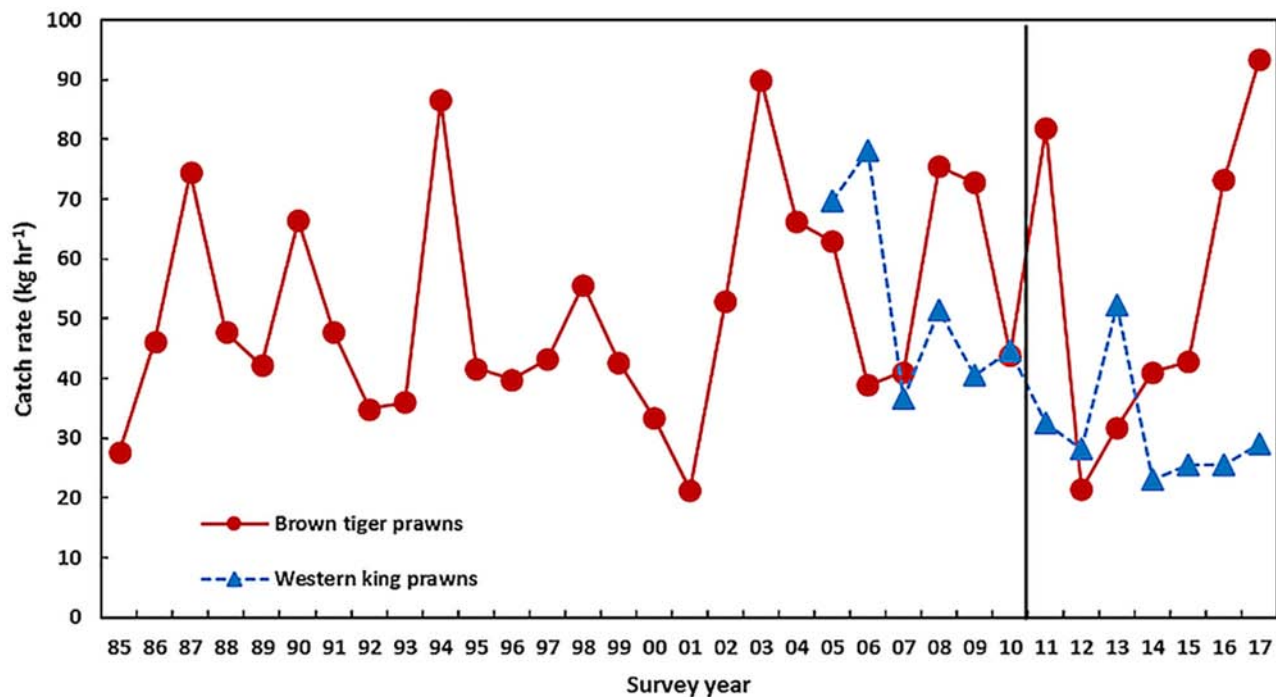
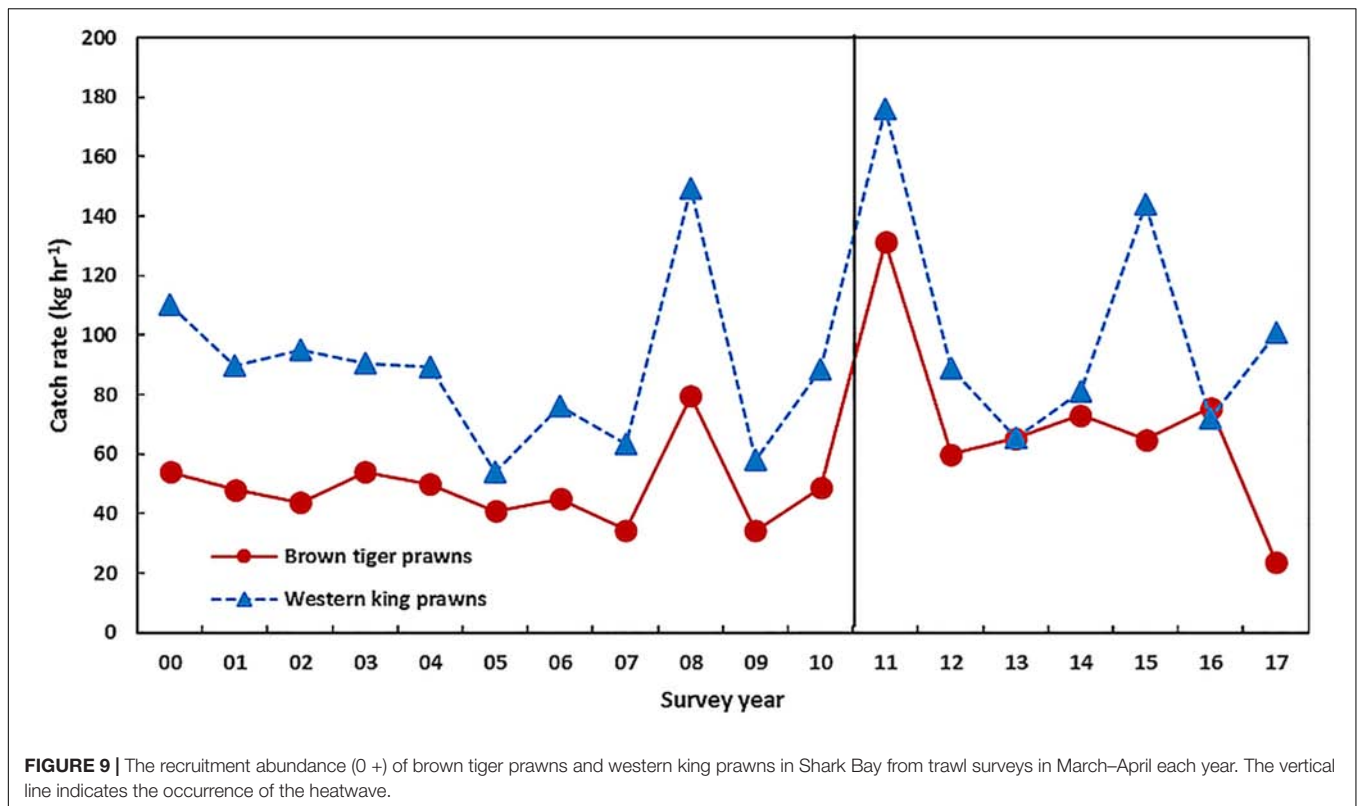


FIGURE 8 | The recruitment abundance (0 +) of brown tiger prawns and western king prawns in Exmouth Gulf from trawl surveys in March–April each year. The vertical line indicates the occurrence of the heatwave.



that the 2011 heatwave resulted in SST in Shark Bay reaching 24.5°C which resulted in the record-high recruitment abundance (Figure 10). In Exmouth Gulf good recruitment abundances have historically been achieved when the SST was 23.5–24.5°C in November–December, however, the heatwave resulted in SST reaching 27°C resulting in below-average recruitment (Figure 10). This indicated that the increase in SST during the 2011 heatwave in Shark Bay boosted the SST in November–December to an optimal range of about 23.5–24.5°C for the western king prawn. However, the increase in SST associated with the heatwave in Exmouth Gulf resulted in the SST moving well above the optimal range and hence a reduced recruitment abundance.

Western Rock Lobster

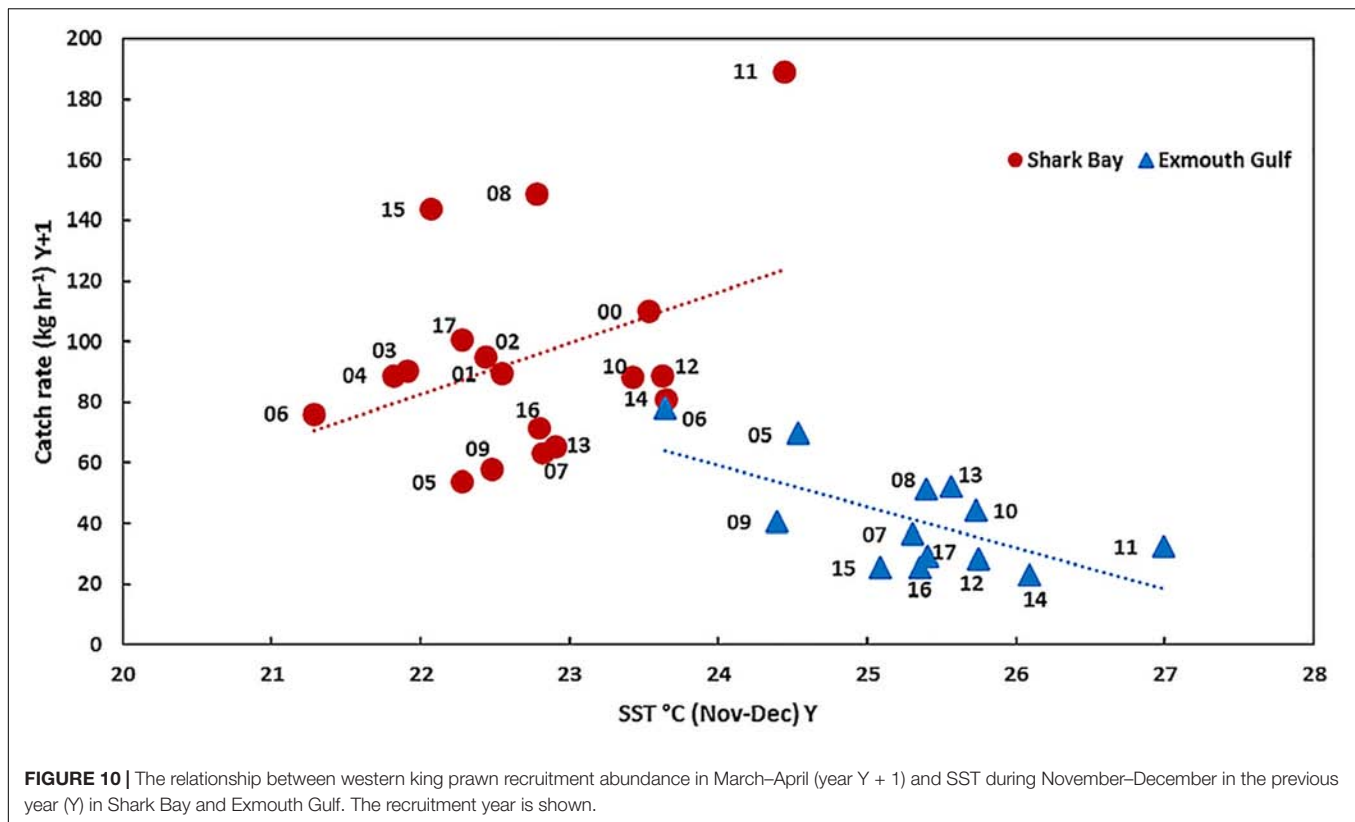
The western rock lobster (*Panulirus cygnus*) fishery operates on the lower west coast of WA and Kalbarri in the mid-west represents the northern part of the commercial fishery (Figure 3). The stock assessment of this valuable fishery (\$400 million) is supported by a long-term monitoring program that examines the stock abundance trend throughout its life cycle including the puerulus (post-larval) stage, undersize, legal size and spawning stock. The northern part of the stock in the Kalbarri region overlapped with the center of the heatwave event.

The puerulus settlement provides a reliable indicator of recruitment to the fishery 3–4 years later (de Lestang et al., 2009). The settlement was below average for an extended period (2006/2007 to 2012/2013) throughout the fishery with the lowest recorded settlement occurring in 2008/2009, well before the

heatwave event 2 years later and de Lestang et al. (2014) has assessed the factors contributing to this low settlement period. This low settlement resulted in a decline in undersize abundance during 2011 and 2012 (Figure 11). However, the abundance of undersize rock lobsters in Kalbarri has remained well below what would have been expected based on the puerulus settlement (Figure 11A). The abundance post heatwave in Kalbarri has been at 5–16% of the abundance prior to the heatwave and at about 14% of the predicted abundance based on the puerulus settlement (Table 1 and Figure 11A). This indicated that the survival and growth of the juvenile lobsters may have been affected by the changes in the habitat and prey availability (Smale et al., 2017) so that rock lobsters may have been indirectly affected by the heatwave with no sign of recovery evident after 7 years. The trend in undersize abundance for Jurien, which is south of the peak heatwave area, showed that there was a decline in the undersize abundance during 2011 and 2012 as a result of very low settlement in 2008/2009 (Figure 11B). However, the undersize abundance has recovered and is similar to what was expected from the puerulus settlement after the heatwave.

DISCUSSION

Marine heatwaves have received increased attention in recent years (Hobday et al., 2016a) and under the present warming trend influenced by anthropogenic forcing, these extreme events are expected to become more common (Oliver et al., 2017, 2018). Two features of many of these marine heatwave events



are firstly the negative effect on the habitat structures (Wernberg et al., 2013; Johnson and Holbrook, 2014) with 58% loss of the main seagrass species in Shark Bay (Thomson et al., 2015) and approx. 1,000 km² lost or severely impacted (Arias-Ortiz et al., 2018) from a total of 4,000 km² of seagrasses. Secondly there is generally the negative impact on sessile or slow moving invertebrates (Garrabou et al., 2009; Mills et al., 2013; Di Lorenzo and Mantua, 2016; Oliver et al., 2017; Smale et al., 2019). These features have also been prominent in the extreme 2011 Western Australian heatwave. Therefore, it was important to examine the rate of recovery of the invertebrate stocks affected and the reasons this varied between stocks. While there have been numerous studies on the marine heatwave impact on the marine ecosystem, there have been few studies of their overall effect on the commercial fisheries stocks. Fisheries provide an opportunity to assess the effect of an extreme event on interacting social-ecological systems (Pershing et al., 2015; Cavole et al., 2016). As many fish stocks are monitored annually, they provide a good indicator on the relative effect of the heatwave compared to the historic variations experienced under typical environmental variability.

The effect of the marine heatwave on the ecosystem produced some short-term changes (fish kills, extension of tropical fish distributions), as well as some longer-term changes such as loss of kelp forests in mid-west (Wernberg et al., 2016), loss of seagrass stocks in Shark Bay (Arias-Ortiz et al., 2018), loss of macro-invertebrates in Kalbarri (Smale et al., 2017) and the presence of rabbit fish in Cockburn Sound (Lenanton et al., 2017). As parts of

the coastal ecosystem appear to have not recovered after 7 years and may have undergone a “permanent” change, the question remained as to whether some of the commercial invertebrate stocks negatively affected by the heatwave would ever recover to pre-heatwave levels given the very low abundance observed for some stocks in the years after the heatwave. The duration of the effect of the heatwave on the invertebrate stocks and the factors contributing to recovery periods have been summarized in **Tables 1, 2**, respectively. This information provided a basis for assessing the different vulnerabilities of commercial invertebrate species to future heatwaves.

Short-Term Effects

There was an immediate short-term effect of localized fish kills of a number of fish and invertebrate species at the time of the peak heatwave (Pearce et al., 2011) that did not have a major effect on the stocks. The warmer temperatures appeared to have a short-term beneficial effect for the recruitment of the two short-lived prawn species in Shark Bay (**Figure 9**). The western king prawn stocks in Shark Bay, as well as the brown tiger prawn stocks, produced record-high recruitment in surveys after the heatwave.

Blue swimmer crabs occur over a wide latitudinal range (20–35°S) along the WA coastline. A short-term moderate increase in catches was observed on the south coast of WA after the heatwave which typically only occur for about 2 years after any period of above-average water temperatures (Chandrapavan et al., 2018). The cooler waters of this region represent the southern end of the crab's distribution. The blue swimmer crab fishery in Shark

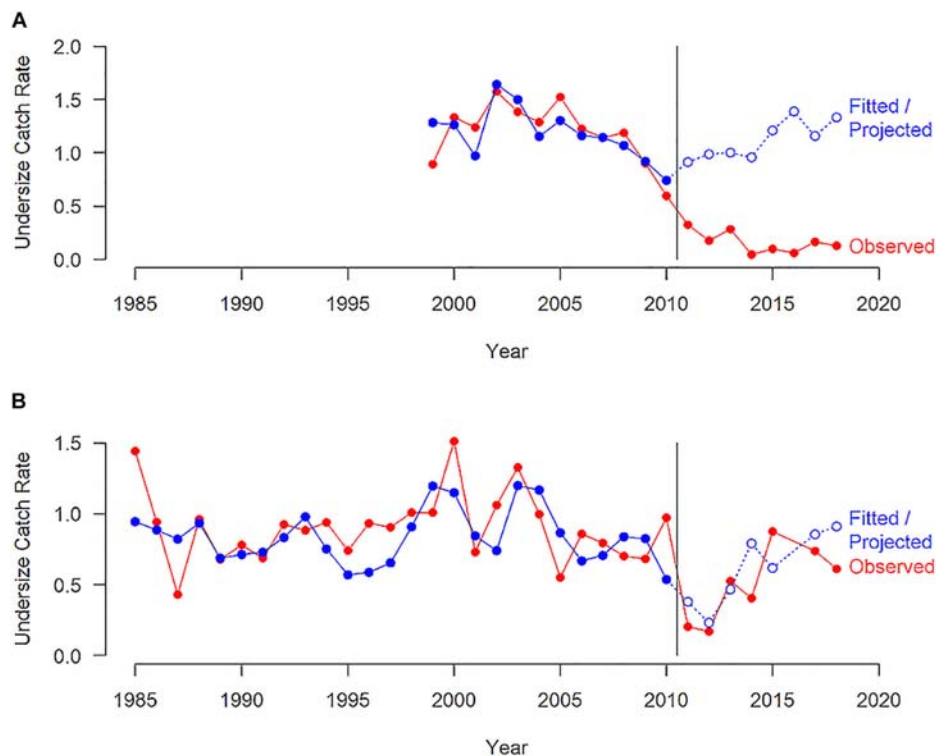


FIGURE 11 | The observed undersize catch rate from a commercial monitoring (number per pot lift) for western rock lobsters in the **(A)** Kalbarri and **(B)** Jurien region and the fitted undersize catch rate based on the relationship between undersize and puerulus settlement 3–4 years for the period prior to the heatwave and the projected undersize catch rates post heatwave. The vertical line indicates the occurrence of the heatwave.

Bay ($25\text{--}26^{\circ}\text{S}$) in the late 2000s had the highest catch of any crab fishery in Australia and therefore appeared to be situated in an ideal environmental location. However, this crab stock was negatively affected by the heatwave which resulted in poor recruitment and a fishery closure for 18 months. The recovery of the Shark Bay crab stock was relatively fast as the spawning stock did not appear to have been affected to the point that it inhibited the recovery of the stock. The fishery re-opened in late 2013 based on a weight-of-evidence approach to the assessment of the stock that included the survey catch rate of legal-size crabs being above the limit reference point in the draft harvest strategy. The stock was considered recovered in 2017 as the survey catch rate was within the target reference range.

Longer-Term Effects

The period for the recovery of the scallop stocks was longer (3–5 years) than for Shark Bay crabs, even though both species have relatively short life cycles of 2–3 years. Scallops in Shark Bay ($25\text{--}26^{\circ}\text{S}$) and Abrolhos Islands ($28\text{--}29^{\circ}\text{S}$) have historically been documented as having a strong negative response to above-average SST (Joll and Caputi, 1995; Lenanton et al., 2009) and these stocks occurred within the peak heatwave area. Therefore, it was expected that they would undergo a major decline in recruitment abundance (Figures 4, 5). The series of low recruitment abundances resulted in the spawning stock being affected to the point that it impaired recruitment and this

increased the time for recovery. The fisheries were closed for 3–5 years and the Denham Sound and Abrolhos Islands stocks are now assessed as recovered as the survey catch rates are above the proposed threshold reference levels and hence within the target area of the draft harvest strategy. Since reopening, the commercial catch from these stocks were commensurate to the pre-recruit survey abundance. However, the northern Shark Bay catch was well below expectation which indicates that this part of the fishery is not fully recovered at this stage. Scallop fisheries are widely known for their high variability in recruitment abundance with environmental factors often identified as influencing recruitment abundance (Hancock, 1973; Joll and Caputi, 1995). The scallop stocks on the east coast of Australia have recently shown a major downturn with near record-low catches in 2014 and 2015 and a spawning biomass as low as 5–6% of the unfished level (Kangas and Zeller, 2018). Environmental influences have been assessed as affecting this stock including water temperature. Management measures have been implemented to assist in recovery of the east coast stock but no recovery is evident to date.

The Roe's abalone stock in the Perth metropolitan area (32°S) is centrally located within its spatial distribution range ($27\text{--}35^{\circ}\text{S}$) and was the only stock outside the peak area of the warming event that experienced a marked negative effect. The stock is undergoing a relatively slow recovery as its spawning stock declined to record-low levels (Hart et al., 2018). The

fishery has undergone a major downturn for over 6 years, and while a complete closure of the fishery may have resulted in a faster recovery time, it was assessed that the stock could recover while operating at lower catch levels during this period of lower abundance. The juvenile 1 + recruitment improved in 2017 which provided an important indicator that the recovery of the stocks was underway. However, the recovery of the legal-size abundance may take longer as it is dependent on the juvenile abundance 4 years previously and the environmental conditions during the juvenile to legal-size phase. Declines in abalone stocks are common around the world as they are vulnerable to overfishing but stocks in Australia have generally fared better because of the management systems such as individual transferable quotas (ITQ) and responsive harvest strategies (Mayfield et al., 2012).

Although the heatwave did not directly impact brown tiger prawns in Exmouth Gulf this stock took about 4 years to recover from lower recruitment levels as it was dependent on the rate of recovery of the inshore nursery habitat. This was similar to the previous experience of habitat destruction due to a cyclone in 1999 (Loneragan et al., 2013). There was, however, no indication of the indirect effect on the habitat for western king prawns as the two species have different habitat preferences with juvenile western king prawns preferring a sandy/muddy habitat (Penn, 1984; Kangas and Jackson, 1998).

No Recovery

The Roe's abalone stock in Kalbarri (27°40'S) is near the northern edge of its spatial distribution range in WA and located near the center of the warming event which peaked over 24–31°S (Figure 1) and hence suffered over 99% mortality. The stock may prove to be an example of a “permanent change” as there appears no sign of recovery after 7 years. The natural abundance remains at very low levels and monitoring of the research translocation and restocking of juvenile abalone will continue to assess whether this is a viable approach to aid in the recovery. The effect on the abalone stocks reflected that observed by Smale et al. (2017) who demonstrated that the marine heatwave significantly altered the composition of the benthic macro-invertebrate assemblage on subtidal reefs in southwest Australia with the magnitude of the impact inversely related to latitude, i.e., the warmest locations were the hardest hit. The western rock lobster stocks in Kalbarri are also in the northern part of the commercial fishery and their undersize abundance also showed no signs of recovery.

Plagányi et al. (2011) highlighted the importance of an adaptive management response that permits rapid response to short-term changes. Hobday et al. (2016b) demonstrated the value of seasonal climate forecasts that provided some insights into upcoming environmental conditions and improved decision making. They also noted that the effective use of these forecasts required responsive management with strategies that can be implemented on the basis of the forecasts. Similarly, Mills et al. (2017) developed a forecast system of the start of the period of high landings for the Maine lobster fishery. This was in response to disruption caused to fishery by the early onset of lobster

landings, and subsequent price collapse, due to the effect the 2012 marine heatwave.

The early detection of the heatwave event in WA and the monitoring of the immediate effects on the ecosystem as well as a qualitative assessment of the likely impacts on the fisheries stocks (Pearce et al., 2011) provided the basis for early management intervention. This highlighted the value of integrated monitoring framework like that developed in Australia through the Integrated Marine Observing System (IMOS)¹, to enable early detection of climate extreme events, particularly marine heatwaves. A key factor to enable fisheries to recover quickly after extreme events was the early detection of the effect of the heatwave on invertebrate stocks. This was achieved from pre-recruit surveys that are conducted annually on the key prawn, scallop, abalone, crab and western rock lobster stocks in WA that are reliable indicators of the future recruitment to the fishery and catches (Caputi et al., 2014). These proved valuable in the early detection of the effect of the heatwave on the stocks (Caputi et al., 2016) which enabled early management intervention based on harvest strategies that were responsive to changes in abundance (Department of Fisheries, 2015). The surveys have also been valuable in the early detection of the recovery that has allowed fishing to recommence as soon as the recovery was evident with catches increasing as the stocks moved to full recovery. This was particularly important for the fisheries that had been shut for 1.5 to 5 years. The lessons learnt here have wide application to other fisheries in other regions affected by extreme events and highlighted the valuable role fisheries monitoring and stock assessments and environmental monitoring can play in understanding the effect of extreme events on ecosystems. In particular, they highlight the importance of adopting fishery-independent surveys of pre-recruit abundance of stocks to enable pro-active management response on changes in stock abundance as a result of climate change related extreme events.

Globally, 87% of currently occurring marine heatwaves can be attributed to global warming primarily driven by anthropogenic emissions of greenhouse gasses (Frölicher et al., 2018). Moreover, it is expected that with the continuing warming of the global ocean, the marine heatwave events will occur more often and be more intense under the future warm climate. Global model projections show that the current carbon emissions will result in an average increase in the probability of extreme marine heatwaves in the global ocean by a factor of 3 by the mid-century (Frölicher et al., 2018), which may significantly reduce the recovery time for the marine species after the impacts of a strong marine heatwave.

The 2011 WA marine heatwave was associated with a strong La Niña event in the Pacific (Feng et al., 2013). Future climate projections suggest that extreme La Niña events may become more frequent under a warm climate (Cai et al., 2015). Thus, there may be increased likelihood of occurrences of extreme marine heatwaves off WA compared to the global average. In addition, occurrences of the marine heatwaves off the WA coast

¹<http://imos.org.au>

can also be triggered or amplified by the local air-sea coupling (Kataoka et al., 2014; Marshall et al., 2015). Future expansion of the tropical warm pool along the WA coast may induce deep convection and enhance the air-sea coupling in the region (Doi et al., 2015). Holbrook et al. (2019) identified important local processes and large scale climate modes that are associated with marine heatwave occurrences in their assessment of 22 case-study regions. Improved oceanographic monitoring and high resolution ocean-atmosphere coupled models are needed to capture the regional processes, to properly assess the marine heatwave risks off the WA coast, as these risks may be graver than the current climate model predictions.

DATA AVAILABILITY

The datasets for this manuscript are not publicly available because of confidentiality restrictions under the Fisheries Act. Requests to access the datasets should be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

NC wrote the first draft of the manuscript. All authors wrote the sections of the manuscript, contributed to the manuscript

revision, and read and approved the submitted version. MK, AC, AH, MF, MM, and SdL contributed to the figures.

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Marine Heatwave Hotspots in Coral Reef Environments: Physical Drivers, Ecophysiological Outcomes, and Impact Upon Structural Complexity

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A changing climate is driving increasingly common and prolonged marine heatwaves (MHWs) and these extreme events have now been widely documented to severely impact marine ecosystems globally. However, MHWs have rarely been considered when examining temperature-induced degradation of coral reef ecosystems. Here we consider extreme, localized thermal anomalies, nested within broader increases in sea surface temperature, which fulfill the definitive criteria for MHWs. These acute and intense events, referred to here as MHW hotspots, are not always well represented in the current framework used to describe coral bleaching, but do have distinct ecological outcomes, including widespread bleaching, and rapid mass mortality of putatively thermally tolerant coral species. The physical drivers of these localized hotspots are discussed here, and in doing so we present a comprehensive theoretical framework that links the biological responses of the coral photo-endosymbiotic organism to extreme thermal stress and ecological changes on reefs as a consequence of MHW hotspots. We describe how the rapid onset of high temperatures drives immediate heat-stress induced cellular damage, overwhelming mechanisms that would otherwise mitigate the impact of gradually accumulated thermal stress. The warm environment, and increased light penetration of the coral skeleton due to the loss of coral tissues, coupled with coral tissue decay support rapid microbial growth in the skeletal microenvironment, resulting in the widely unrecognized consequence of rapid decay, and degeneration of the coral skeletons. This accelerated degeneration of coral skeletons on a reef scale hinder the recovery of coral populations and increase the likelihood of phase shifts toward algal dominance. We suggest that MHW hotspots, through driving rapid heat-induced mortality, compromise reefs' structural frameworks to the detriment of long term recovery. We propose that MHW hotspots be considered as a distinct class of thermal stress events in coral reefs, and that the current framework used to describe coral bleaching and mass mortality be expanded to include these. We urge further research into how coral mortality affects bioerosion by coral endoliths.

Keywords: marine heatwaves, mass mortality, bioerosion, endolithic microbes, coral bleaching, phase shifts

CORAL BLEACHING AND THE EMERGENCE OF MARINE HEATWAVES

It has now been well established that warming oceans compromise the symbiotic relationship that hard corals share with single-celled dinoflagellates known as zooxanthellae (Symbiodiniaceae, Suessiales) (Muscattine and Porter, 1977; LaJeunesse et al., 2018). Normally, the zooxanthellae that reside within corals' gastrodermal tissue fix carbon through photosynthesis and thereby support the growth and survival of tropical corals (Muscattine and Porter, 1977). The sugars and other organics produced through photosynthesis are translocated to the coral host, meeting its metabolic requirements in the nutrient-poor waters that most corals inhabit (Muscattine and Porter, 1977; Yellowlees et al., 2008). However, when the temperature of the surrounding seawater increases beyond what can be tolerated by the coral host and/or algal symbiont, cellular dysfunction disrupts this symbiosis (Hoegh-Guldberg, 1999). As the partnership breaks down, the coral colony goes white, due to a loss of symbionts and/or a degradation of their pigments which leaves the coral skeleton visible through the now transparent, and symbiont-depleted host tissues (Hoegh-Guldberg, 1999). This phenomenon is therefore known as coral bleaching (Table 1) and generally reduces the survivorship of corals during times of environmental stress (Grottoli et al., 2006; Anthony et al., 2009).

In the last 20 years, the prevalence and intensity of mass coral bleaching events triggered by anomalously warm SSTs has increased (Heron et al., 2016; Frolicher and Laufkotter, 2018; Hughes et al., 2018a). For example, on the GBR mass coral bleaching was observed in 1998, 2002, and 2015–2017 (Berkelmans et al., 2004; Heron et al., 2016; Hughes et al., 2017). Comparisons of the 1998, 2002, and 2015–2017 bleaching events highlighted the unprecedented scale and severity of the most recent event which affected nearly two-thirds of the 2,300 km long system (Hughes et al., 2017). This was driven by an increase in the relative proportion of individual reefs experiencing severe thermal stress (Hughes et al., 2017). These observations are reflective of the global trend in the intensity of coral bleaching events throughout the Anthropocene (Hughes et al., 2018a). The intensity and frequency of marine heatwaves (MHWs) in the same time period has also increased (Oliver et al., 2018). MHWs have recently been defined as a period in which the water temperature is above the 90th percentile for that area's historical conditions for five or more days, where the climatological threshold is a time-of-year dependent 11-day shifting window (Hobday et al., 2016). MHWs represent the most extreme and "rare" incidences of thermal stress relative to a season-dependent historical baseline (Hobday et al., 2016). However, this definition has only recently been applied, for the first time, to the study of coral bleaching events (Smale et al., 2019) though this considered the annual accumulation of MHW days rather than individual events.

For over two decades, the degree heating week (DHW) product of the NOAA Coral Reef Watch (Liu et al., 2017) has been the standard metric for measuring, comparing and predicting accumulated heat stress, referenced to the historically warmest time of the year ("summertime") in coral

reef environments. DHWs represent the duration of thermal anomalies experienced by corals, accumulated across a three month period (Liu et al., 2005). In this instance, positive temperature anomalies are calculated above the maximum of the monthly mean (MMM) threshold, which is the temperature of the climatologically warmest month for an area (Heron et al., 2014; Liu et al., 2017). When DHW values reach 4°C-weeks, coral reefs are predicted to experience mild bleaching, while greater than 8°C-weeks has been associated with severe bleaching and widespread mortality (Liu et al., 2005). DHWs allow for the broad tracking of the accumulation of heat in a water body over a relatively long time frame and can be used to infer some physiological heat stress responses (Liu et al., 2005).

The degree heating week approach, while powerful, has not always detected intense, acute events that are able to cause significant coral bleaching, particularly those that are spatially restricted (Weeks et al., 2008; Bainbridge, 2017; DeCarlo et al., 2017). For example, intense heating in the southern GBR in 2006 caused bleaching in more than 90% of surveyed corals in the Keppel Islands (Weeks et al., 2008) but was insufficient to trigger alerts when relying solely upon the DHW approach due to ocean heating occurring earlier than usual outside of the summer season. Likewise, extreme heating in 2015 on the Dongsha Atoll drove temperatures to 6°C above the climatological mean and the mass mortality of 40% of the local coral population was observed (DeCarlo et al., 2017). The short-lived and localized nature of the heating meant large-scale satellite monitoring did not capture the event and alert systems failed due to a reliance on accumulation of heat over extended periods, which did not occur. In this case the rapid onset of warming within less than a week and persistence of these high temperatures for more than 5 days (DeCarlo et al., 2017) would qualify the event as a MHW (Hobday et al., 2016). Similarly, the peak of thermal stress on Thursday Island during the 2016 mass bleaching event was not accurately represented when using traditional remote sensing techniques (Bainbridge, 2017). Temperatures increased from the climatological baseline to well above the 99th percentile within less than a month, and this persisted for 11 days (Bainbridge, 2017), qualifying the event as a strong MHW (Hobday et al., 2018). While the accumulated thermal stress in this area eventually peaked at 14°C-weeks in mid-May, this was almost 2 months after the occurrence of the majority of mass mortality (Great Barrier Reef Marine Park Authority, 2016; Hoogenboom et al., 2017; Hughes et al., 2017).

Marine heatwaves do not always translate into a meaningful value for DHWs, and this is particularly relevant when predicting the ecological and physiological outcomes of these events. During the 2011 massive thermal anomaly off the coast of Western Australia, $\geq 16^\circ\text{C}$ -weeks was recorded across approximately 1200 km along the coast (Moore et al., 2012). The most intense heating, around the Houtman Abrolhos Islands, was also represented by a 95-day MHW (Hobday et al., 2016) and triggered mass coral bleaching (Smale and Wernberg, 2012). Here, a new "extreme" category of DHWs might complement the existing "mild" and "severe" thresholds and serve to represent MHWs. However, acute and intense summertime MHWs can occur independently of high corresponding DHW values. For

TABLE 1 | Common and key terms, and their definitions, used in this review.

Term	Definition	Source
Acclimatization	The behavioral or physiological changes of an organism to increase the endurance of or reduce the source of cellular stress arising from changes in the environment	Bowler, 2005
Antioxidants	A class of enzymes or compounds that scavenge reactive oxygen species (see below) and so prevent cellular oxidative stress. The following are commonly studied in the context of coral bleaching: superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX), catalase (CAT), and dimethyl sulfoxide (DMSO)	Krueger et al., 2014, 2015; Roberty et al., 2015; Gardner et al., 2017
Coral bleaching	The disassociation between corals and their colored endosymbiotic algae due to cellular stress, resulting in a characteristic white appearance. Commonly a result of thermal stress. When this is driven by light stress only, it is referred to as photo-bleaching	Lesser, 1997
Degree heating weeks	A measure of heat stress combining the effects of magnitude and duration of SST that exceeds the expected summertime conditions (MMM), accumulated across a rolling 12-week period	Liu et al., 2005
Endolithic microborers	Microbial, boring organisms living within rocks, shells, and coral skeletons	Tribollet, 2008b
Marine heatwaves (MHWs)	A period of ≥ 5 days wherein the temperature is above the 90th percentile of historically observed values for that location for that time of year	Hobday et al., 2016
MHW hotspots	Localized thermal extremes nested within regional SST anomalies that are not accurately represented using the DHW framework, but fulfil the above criteria for an MHW	This review
Mass mortality	An ill-defined term. Previously used to described mortality prevalence of greater than 30%	Hughes et al., 2017
Maximum of the monthly mean (MMM)	The location-specific SST representative of expected summertime conditions, determined as the warmest monthly climatological SST with a baseline period in the late 1980s	Liu et al., 2014
Microbioerosion (corals)	Chemical dissolution of aragonite skeleton by endolithic microborers	Tribollet, 2008b
Phase shift	Shifts between alternative stable states of an ecosystem. In coral reefs, this is typically between coral- and algal-dominated benthos	Idjadi et al., 2006
Reactive oxygen species (ROS)	Oxygen radicals produced as by-products of photosynthesis and respiration, with the potential to damage lipids, proteins and DNA: superoxide (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and hydroxyl (OH^-)	Murphy, 2009
Sea surface temperature (SST) anomalies	The variation in SST from what is expected to occur at each location at the specific time of year. Expected values are typically defined using a long-term climatology	Liu et al., 2005

example, at the peak of the MHW on Thursday Island in 2016 the corresponding DHW value was approximately six (Bainbridge, 2017). In the same study, water temperatures around Lizard Island were recorded as increasing to around the 95th climatological percentile, where they remained for 9 days (Bainbridge, 2017). A corresponding DHW value of 4°C -weeks would predict mild coral bleaching, in stark contrast to the observed extent and severity of coral bleaching and mortality around Lizard Island (Hoogenboom et al., 2017; Hughes et al., 2017). Using the online Marine Heatwave Tracker¹ (Schlegel, 2018), this same event is categorized as a “II Strong” MHW using the classification system proposed by Hobday et al. (2018).

In addition to the improved detection of short-lived, intense thermal anomalies, the application of the MHW criteria also allows us to consider thermal stress outside of summer months. As the accumulation of DHWs is based on the exceedance of summertime maxima, this limits application to this season. Yet there is evidence that thermal stress outside of this period can have significant impacts on marine environments and are captured using season-dependent shifting climatological baselines (Weeks et al., 2008; Hobday et al., 2016, 2018). But while it is known that cold temperatures can lead to cold water coral bleaching (Hoegh-Guldberg and Fine, 2004; Lirman et al., 2011), as yet we have little information on the effects of positive winter anomalies on corals. Berkelmans and Willis (1999) examined

seasonal changes in bleaching thresholds for the coral *Pocillopora damicornis* and found the thresholds decreased by only 1°C from summer to winter, suggesting that seasonal acclimatization may not reduce thresholds to such an extent that winter bleaching will occur during a winter MHW. There is, however, evidence that water temperatures in the winter can affect coral disease progression and susceptibility. Sato et al. (2009) identified a correlation between lower winter temperatures and the lower infectivity and progression in black band disease while a large scale temporal analysis by Heron et al. (2010) found that mild winters (i.e., neither anomalously hot or cold) frequently preceded outbreaks of coral white syndrome in the following year. The observation that disease outbreaks did not generally follow warmer winters suggest that winter MHWs have the capacity to significantly influence coral physiology in the long term. This is an important area for future exploration given that coral tissue biomass is higher in the winter and early spring (Fitt et al., 2000) and influences coral bleaching responses (Fitt et al., 2009). These periods are likely important for resource provisioning leading into coral spawning and summertime.

Examining thermal stress in coral reef environments using a MHW approach can therefore add a new dimension to how we understand, detect and measure coral bleaching and mortality events to the benefit of our present alert systems. The cases outlined here demonstrate firstly that extreme and small scale coral bleaching and mortality events, which do not accumulate DHWs above thresholds needed to trigger alerts, can be identified

¹<http://www.marineheatwaves.org/tracker>

using MHW criteria. When used in conjunction with DHWs, this may improve our ability to predict fine scale ecological patterns during mass coral bleaching events. Secondly, that mismatches between low DHW values and severe ecological degradation can be reconciled by applying MHW criteria in explaining causative factors of mass coral mortality. This evidence provides a means to improve the accuracy of our predictions of the responses of reef communities when these values are considered alongside an understanding of the biological responses to the thermal conditions. It is important to consider MHWs as acute, intense events disparate from those characterized by chronic heat accumulation, and independent of the existing DHW scale. As summertime MHWs are often nested within broader thermal anomalies, the term “MHW hotspots” as used in this

review represents the most extreme patches of thermal stress, and the distinct ecological and physiological responses that occur within these.

THE EVOLUTION OF MHW HOTSPOTS

Marine heatwaves hotspots are often the result of combined regional heating and local weather patterns, which interact to promote the rapid accumulation of heat (Skirving et al., 2006; MacKellar and McGowan, 2010; Wernberg et al., 2012; Bainbridge, 2017; DeCarlo et al., 2017). Abiotic factors that influence these events include tidal cycles, calm winds, clear skies and low water flow, which act to amplify regional thermal stress

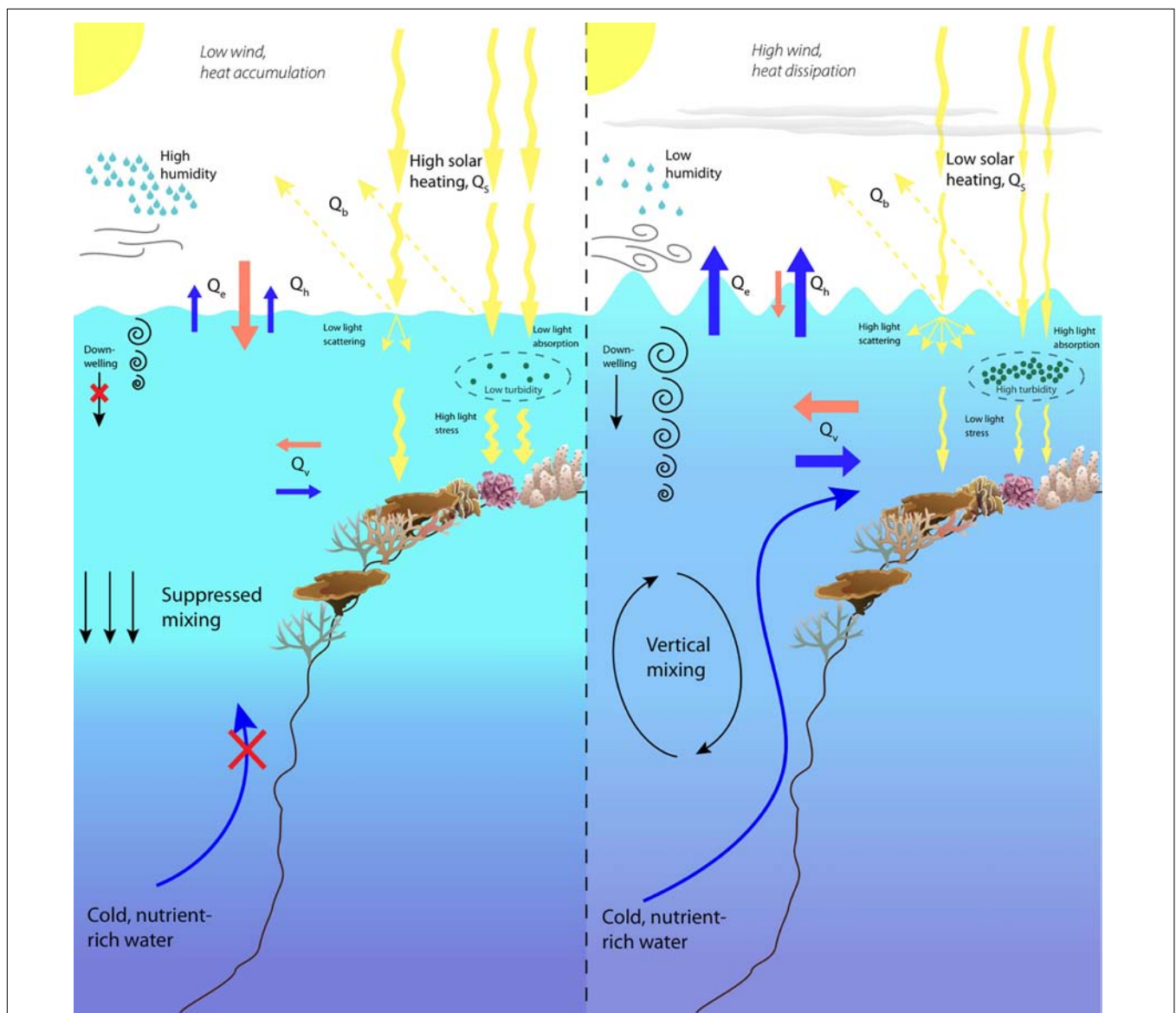


FIGURE 1 | Conceptual diagram illustrating the confluence of environmental conditions that drive the rapid and intense heating in reef environments. Coral colony graphics courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science.

on the scale of individual reefs (**Figure 1**; Skirving et al., 2006; MacKellar and McGowan, 2010; Baird et al., 2017; Raymundo et al., 2017; Burt et al., 2019). Potentially the most commonly cited driver of thermal extremes in coral reef environments is a drop in wind speed (Baird et al., 2009; Bainbridge, 2017; Burt et al., 2019). Wind influences most components of the oceanic heat budget (**Figure 1**; Talley et al., 2011; Lowe and Falter, 2014), in part through how it affects currents and wave action (Davis et al., 2011; MacKellar et al., 2013). However, these latter factors are not always forced by local wind patterns and can have distinct effects upon heat accumulation and physiological responses (Nakamura, 2010; Lentz et al., 2016). There is therefore often a mismatch between the scale of a MHW hotspot and the resolution of available satellite imagery, due to the influence of these abiotic factors at the reef-scale. The confluence of these physical drivers is physiologically significant for reef corals and determines the severity of the bleaching process. High insolation maximizes the heat and light stress experienced by corals, which act synergistically to drive and exacerbate coral bleaching and mass mortality in time frames directly related to the intensity of environmental stress (Jones et al., 1998; Lesser and Farrell, 2004; Skirving et al., 2017).

The highest potential for heat loss from a water body results from evaporative cooling i.e., latent heat flux (Q_e) (**Figure 1**; Talley et al., 2011). Weller et al. (2008) attributed coral bleaching on the GBR in 2001/2002 primarily to low wind and resultant low evaporation. Indeed, evaporative cooling has been shown to be strongly coupled to wind speed because of how this affects the air-sea temperature difference (Wu et al., 2007; MacKellar and McGowan, 2010; MacKellar et al., 2013; DeCarlo et al., 2017). When wind speeds drop to negligible levels, evaporation quickly leads to high humidity at the air-sea interface which reduces the potential for further evaporative cooling (Wu et al., 2007; Weller et al., 2008; MacKellar and McGowan, 2010). Additionally, this increases the air's heat capacity and promotes air-to-sea heat transfer through sensible heat flux (Q_h) (**Figure 1**; Weller et al., 2008; DeCarlo et al., 2017). Reductions in wind speed often precede increases in SSTs and a number of case studies have identified a reduction in wind speed with subsequent increases in humidity and heat accumulation. Two small scale bleaching events, at Lee Stocking Island in 1990 (Smith, 2001) and on the sub-tropical Heron Reef in 2009 (MacKellar and McGowan, 2010), linked a drop in wind speed below 3 ms^{-1} to an increase in humidity and reduction in evaporative cooling. In the case of the latter, the daytime maximum temperature increased to $>34^\circ\text{C}$ in a matter of days and caused short term coral bleaching (MacKellar and McGowan, 2010). Similarly, the most extreme temperatures recorded at a depth of 6.5 m by Burt et al. (2019), in the southern Arabian Gulf, were strongly correlated with wind speeds below a local threshold of 4 ms^{-1} . These values, as well as that identified by Bainbridge (2017) (2.8 ms^{-1}), lend credence to the threshold chosen by NOAA (3 ms^{-1}) in defining doldrum-like winds in relation to coral bleaching (Liu et al., 2012).

On a larger scale, a reduction in wind speed was linked to widespread warming during the 2001/2002 mass bleaching event on the GBR (Weller et al., 2008) and the 2015 thermal anomaly in the South China Sea that underpinned the mass mortality

event on the Dongsha Atoll (DeCarlo et al., 2017). These studies also identified increased air-to-sea sensible heat flux resulting from increases in humidity. In the converse scenario, strong winds promote cooling and are able to reduce temperatures by several degrees, especially at night (MacKellar et al., 2013). This is thought to be an important cellular recovery period after damage sustained by daytime maxima (Roberty et al., 2015). Thus, negligible wind speeds and associated rapid heat accumulation not only increases daytime heat stress but also possibly reduces the potential for night-time recovery.

Accompanying doldrum-like wind speeds is a reduction in sea surface turbulence which would otherwise promote cooling. A flat ocean surface acts as a viscous boundary layer at the air-sea interface and significantly limits sea-to-air heat flux (Moum and Smyth, 2001; Grant and Belcher, 2011). This promotes the accumulation of heat in surface waters and thermal stratification in the water column (Van Hooideonk et al., 2013; Lowe and Falter, 2014; Zhang et al., 2016). Exacerbating this effect, flat seas generate little to no downwelling (Moum and Smyth, 2001). In contrast, strong winds generate shear-induced turbulence at the air-sea interface which leads to small pockets of cool water that sink down through the upper layer (Moum and Smyth, 2001; Grant and Belcher, 2011). This downwelling destabilizes a stratified water column and aids in distributing heat from insolation away from surface waters (**Figure 1**; Moum and Smyth, 2001; Lowe and Falter, 2014). A lack of wind-generated wave action therefore promotes a positive feedback loop in which heat accumulation stabilizes thermal strata which in turn allows for a greater heat load in surface waters (**Figure 1**). Oceanic swell can generate wave-related surface cooling independent of wind conditions; however, the rapid dissipation of wave energy by fore reef environments limits the spatial extent of this mechanism (Lowe and Falter, 2014). Wind-driven turbulence, on the other hand, can extend into reef lagoons, and cause significant cooling by vertical mixing (MacKellar et al., 2013).

A lack of wind forcing and wave action often results in low levels of water circulation and heat exchange with the open ocean (Davis et al., 2011; Lentz et al., 2016; DeCarlo et al., 2017). Advection (i.e., horizontal water movement, Q_v), or a lack thereof, has been proposed as a key determinant of the accumulation of heat on coral reefs (**Figure 1**; MacKellar et al., 2013; Lowe and Falter, 2014). Flushing reefs with cool water from deeper surroundings can lower daytime maximum temperatures and reduce diurnal variation (Davis et al., 2011; MacKellar et al., 2013; DeCarlo et al., 2017). Additionally, currents have been shown to promote vertical mixing independent of wave-driven down-flow (DiMassa et al., 2010). Circulation is controlled by surface wind-driven currents (Lowe and Falter, 2014), waves (Lentz et al., 2016), and tidal cycles (MacKellar et al., 2013). The more sheltered the reef environment, the more dependent it is upon circulation driven by wind and wind-generated waves (Davis et al., 2011; Lentz et al., 2016). In MHW hotspots, the lack of wind and waves therefore limits circulation and advective cooling (DeCarlo et al., 2017; Van Wynsberge et al., 2017). As a result, water has high residency time, pools over the reef and heats up rapidly (DeCarlo et al., 2017; Van Wynsberge et al., 2017). Tidal flushing can, in some cases, offset heat

accumulation considerably (MacKellar and McGowan, 2010; Lowe and Falter, 2014) while neap tides and weak intertidal currents have been identified as causal factors for intense heating (DeCarlo et al., 2017). Conversely, mass mortality has also been associated with large spring tides during regional low-stand periods that drove increased subaerial exposure (Raymundo et al., 2017). Therefore, the effect of tidal cycles on coral bleaching and mortality is likely to be highly dependent upon a reef's bathymetry and tidal range.

Doldrum-like winds and the associated physical outcomes are often representative of broad areas of high atmospheric pressure (MacKellar and McGowan, 2010; Bainbridge, 2017; Couch et al., 2017). The consequence is increased solar irradiance (Q_s) (Figure 1), which is the primary source of heat input on coral reefs, and has been linked to the rapid onset of thermal stress (Davis et al., 2011; MacKellar et al., 2013; DeCarlo et al., 2017). High irradiance is also a primary source of stress as it drives oxidative stress in symbiotic algae through the production of reactive oxygen species (ROS) (Jones et al., 1998; Hoegh-Guldberg, 1999; Krug et al., 2013). The effect of high cloud cover in reducing coral bleaching intensity is well documented (Berkelmans et al., 2004; Zelinka and Hartmann, 2010; Hughes et al., 2017), particularly when tropical cyclones pass over coral reefs, and simultaneously cool surface waters through wind exposure (Manzello et al., 2007; Carrigan and Puotinen, 2011). Water column stratification can increase light stress by reducing light attenuation of suspended particulates (through absorption and/or backscatter) in the surface layers (Manzello et al., 2004; Zepp et al., 2008). The opposite effect (i.e., suspended particulates reducing light stress) is apparent when we observe high coral bleaching tolerance on turbid inshore reefs compared to offshore reefs with high water clarity (Morgan et al., 2017). Additionally, flat seas minimize light scattering through surface turbulence and so maximize the intensity of light experience by corals and their symbionts. Combined with the high accumulation of heat, increased light is able to rapidly overcome corals' mechanisms of physiological resilience in short time frames.

ECOLOGICAL CONSEQUENCES OF MHW HOTSPOTS

The impact of MHW hotspots on coral populations can be ecologically distinct from what is understood of traditional bleaching events. The first compelling evidence for MHW hotspots leading to distinct ecological outcomes, is that they cause widespread bleaching and mortality in corals that would normally be categorized as thermally tolerant "winners" during milder events (Loya et al., 2001; Hoogenboom et al., 2017; Hughes et al., 2018b). In their study of the Dongsha Atoll, DeCarlo et al. (2017) used coral cores of a thermally tolerant *Porites* sp. to examine historical bleaching in the reef lagoon. In the previous 100 years, no more than 50% of the population had bleached during any one event (DeCarlo et al., 2017). In contrast, 100% of this species bleached during the acute 2015 event where temperatures peaked at 6°C over the climatological mean (DeCarlo et al., 2017). In a similar case, Hoogenboom

et al. (2017) examined the responses of Acroporids during the extreme 2016 anomaly on Lizard Island. The authors highlighted how species that exhibited high thermal tolerance during previous mass bleaching events on the GBR in 1998 and 2002 experienced widespread and indiscriminate bleaching in mid-to-late March (Hoogenboom et al., 2017). This coincided with the temperatures spiking above the 95th climatological percentile (Bainbridge, 2017). The ability for extreme, acute thermal stress to overcome the protective mechanisms of otherwise heat tolerant species was also evident in regions where corals have adapted to naturally extreme environments. Corals in the Arabian Gulf have some of the highest bleaching thresholds, partly due to the selective pressure of maximum summer temperatures exceeding 34°C annually (Riegl et al., 2011). Between August and September 2017, these thermally tolerant coral populations experienced mass bleaching and mortality following up to 20 consecutive days above their lethal threshold of 35.5°C, less than two degrees Celsius above the climatological summertime maximum (Shuail et al., 2016; Burt et al., 2019). Even in the context of this naturally warm environment, the non-selective bleaching of thermally tolerant coral populations was considered unusual and extreme (Burt et al., 2019). Similarly, during the 2014–2017 global coral bleaching event (Eakin et al., 2017), mass bleaching of thermally tolerant corals in the southern Kimberley region of northwestern Australia was observed (Le Nohaïc et al., 2017). This population is considered to be relatively resistant to climatic extremes (Schoepf et al., 2015) and indeed this was the first recorded instance of coral bleaching at these extreme, inshore reefs (Gilmour et al., 2019). However, while heat stress of 11.4°C-weeks drove this extreme response, further north reefs exposed to 14.8°C-weeks showed little to no bleaching (Gilmour et al., 2019). This supports the notion that DHWs are not accurately predicting ecological responses during these extreme events.

Finally, the rate of heating during a MHW hotspot can drive uncharacteristically rapid onset of bleaching and mortality. For example, water temperatures in the Keppel Islands, 2006, reached summertime maxima in December as opposed to February which would normally be the result of long-term accumulation of heat (Weeks et al., 2008). By mid-January, between 77 and 95% of coral colonies exhibited bleaching (Diaz-Pulido et al., 2009) due to both the rate and seasonal timing of heat accumulation (Weeks et al., 2008). During the 2016 event on Lizard Island, healthy coral-dominated reefs transitioned through mass bleaching and mortality to algal-domination in approximately 6 weeks (Hoogenboom et al., 2017; Hughes et al., 2017). This timeline is remarkably similar to that recorded on the Dongsha Atoll, where mass mortality occurred in less than 6 weeks (DeCarlo et al., 2017). The accelerated rate of mortality associated with the rapid accumulation of heat is further exemplified by observations of coral mortality in Iriomote 2 weeks after the initial onset of thermal stress driven primarily by doldrum-like wind speeds (Baird et al., 2017). These timescales are in contrast to normal bleaching events, where coral bleaching typically occurs following several months of heat stress (Weeks et al., 2008; Liu et al., 2014). In the most extreme examples, this accelerated heating can even

lead to coral mortality without prior bleaching as observed on the GBR in 2016 (Hughes et al., 2017). This is likely a combined result of increased heat damage to coral host cells and higher *in situ* degradation of symbionts observed during extreme thermal stress (Strychar et al., 2004; Strychar and Sammarco, 2009).

These ecological observations of MHW hotspots overcoming thermal tolerance and causing mass bleaching and/or mortality in short time frames indicates that mechanisms usually associated

with coral acclimatization or resistance to high temperatures are being overcome during these extreme events. Typical coral bleaching events often result in the emergence of thermally tolerant “winners” and thermally susceptible “losers” within a coral reef community (Loya et al., 2001), selecting for those most thermally tolerant coral species (see **Table 2**). When subjected to extreme MHW hotspots however, the interspecific differences in coral thermal tolerance that underpin this paradigm appear

TABLE 2 | Examples of coral genera and species reported to have high or low thermal tolerance.

GENUS		SPECIES			
Genus	Tolerance	Species	Tolerance	Location	Source
<i>Acropora</i> spp.	Low	<i>A. digitifera</i>	Low	Okinawa, Japan	Loya et al., 2001; Van Woesik et al., 2004
		<i>A. gemmifera</i>	Low	Okinawa, Japan	Van Woesik et al., 2004
		<i>A. hyacinthus</i>	Low	GBR, Aust.	Baird and Marshall, 2002
		<i>A. millepora</i>	Low	GBR, Aust.	Baird and Marshall, 2002; Berkelmans and Van Oppen, 2006
		<i>A. tenuis</i>	High	GBR, Aust.	Camp et al., 2018
		<i>Acropora</i> sp.	Low	Mombasa, Kenya	McClanahan et al., 2004
<i>Agaricia</i> spp.	Low		High	GBR, Aust.	
		<i>A. agaricites</i>	High	Jamaica, Caribbean	Fitt and Warner, 1995
		<i>A. lamarcki</i>	Low		
<i>Favites</i> spp.	High	<i>F. halicora</i>	High	Okinawa, Japan	Loya et al., 2001
<i>Goniastrea</i> spp.	Low	<i>G. aspera</i>	High	Okinawa, Japan; Phuket, Thailand	Loya et al., 2001; Brown et al., 2014
		<i>G. pectinata</i>	High	Okinawa, Japan	Loya et al., 2001
<i>Leptastrea</i> spp.	High	<i>L. purpurea</i>	High	Okinawa, Japan	Loya et al., 2001
		<i>L. transversa</i>	High	Okinawa, Japan	Loya et al., 2001
<i>Montastrea</i> spp.	High	<i>M. annularis</i>	Low	Jamaica, Caribbean	Fitt and Warner, 1995
		(<i>Orbicella annularis</i>)			
<i>Montipora</i> spp.	Low	<i>M. cavernosa</i>	High		
		<i>M. aequituberculata</i>	Low	Okinawa, Japan	Loya et al., 2001
<i>Pavona</i> spp.	Low	<i>M. digitata</i>	High	GBR, Aust.	Nitschke et al., 2018
		<i>P. minuta</i>	High	Okinawa, Japan	Van Woesik et al., 2004
		<i>P. varians</i>			
<i>Platygyra</i> spp.	Low	<i>P. clavus</i>	Low	Phuket, Thailand	Phongsuwan and Chansang, 2012
		<i>P. daedalea</i>	High	GBR, Australia	Baird and Marshall, 2002
		<i>P. ryukuensis</i>	High	Okinawa, Japan	Loya et al., 2001
<i>Pocillopora</i> spp.	Low	<i>P. damicornis</i>	Low	Okinawa, Japan	Loya et al., 2001
			High	Eilat, Red Sea	Grottoli et al., 2017
		<i>P. verrucosa</i>	High	Okinawa, Japan	Van Woesik et al., 2004
<i>Porites</i> spp.	High	<i>P. attenuata</i>	Low	Okinawa, Japan	Loya et al., 2001
		<i>P. cylindrica</i>	Low		
			High		Loya et al., 2001
			High		Van Woesik et al., 2004
		<i>P. lutea</i>	High	Phuket, Thailand	Brown et al., 2014
		<i>P. nigriscens</i>	Low	Okinawa, Japan	Loya et al., 2001
<i>Stylophora</i> spp.	Low	<i>Porites</i> sp.	Low	Mombasa, Kenya	McClanahan et al., 2004
			High	GBR, Aust.	
		<i>S. pistillata</i>	Low	Okinawa, Japan	Loya et al., 2001
			High	Gulf of Aqaba, Red Sea	Krueger et al., 2017

Genera-specific susceptibilities were defined according to the meta-analysis performed by Swain et al. (2016). The threshold used to distinguish high and low thermal tolerance was set at the total sample median (23.17) of the Bleaching Response Indices calculated for the 374 taxa used in Swain et al. (2016). Individual species' susceptibility is commonly defined by each taxon's response to a natural bleaching event, and so is relative to the total community response to said event. Thermal tolerance is influenced by location and environmental history, but shows taxon-specific consistency across locations (McClanahan et al., 2004; Swain et al., 2016).

to be less important in shaping community responses, given the extensive bleaching and mortality observed in putatively tolerant coral species.

CORAL THERMAL STRESS RESPONSES AND MHWS

Thermal stress events have a variety of impacts on the coral photo-endosymbiotic organism. These range from sub-lethal effects, which may reduce fitness, to mortality that is most often associated with starvation due to the breakdown of the coral-algal symbiosis (Hoegh-Guldberg, 1999; Anthony et al., 2009; **Tables 1, 3**). Coral species are generally described in categories of thermal stress susceptibility, ranging from slow growing species with massive growth forms, such as *Porites* spp., which have high tolerance to thermal stress to fast growing branched species, such as *Acropora* spp., which are considered to have low tolerance (**Table 2**). The thermal tolerance of a species in a specific coral reef location is determined by a complex interplay of factors. While there is some consistency over large spatial scales (**Table 2**), the current and historical environmental conditions at a particular reef drive intraspecific physiological and morphological differences. These include: characteristics of the corals growth form and skeletal phenotype (massive vs. branching morphology) (Loya et al., 2001); capacity for and extent of heterotrophic feeding (Grottoli et al., 2006); dominant symbiont type (e.g., thermally tolerant clade D vs. susceptible symbiont clade C) (Berkelmans and Van Oppen, 2006); acclimatization potential (Gates and Edmunds, 1999); and adaptive tolerance to thermal stress (Coles and Brown, 2003). There is a spectrum of traditional responses by the coral animal to thermal stress, ranging from short-lived photobleaching, where photosynthetic efficiency is reduced often accompanied by a

reduction in photosynthetic pigments, and through to mortality of the host animal from starvation (**Table 3**). This spectrum has been used to model the future characteristics of reefs under climate change scenarios under the assumption that, in general, as thermal stress accumulates within an event corals progress through each stage of this scale at different rates reflective of the animals' resilience and the severity of the stress (Donner et al., 2005). This is generally consistent across different bleaching events, although there are exceptions and there is mounting evidence that animals' resilience can be altered within one generation due to acclimatization (Coles and Brown, 2003). However, under conditions concomitant with a MHW hotspot, this progression of the thermal bleaching response is no longer evident. Instead, the responses typical of acclimatization (see **Table 4**) are absent, corals exhibit signs of direct heat damage and mortality can happen in a matter of days (Leggat et al., 2019), potentially without prior bleaching (Hughes et al., 2017). This is due to the intensity of these thermal stress events overwhelming corals' ability to cope in the short term, bypassing the meta-organism's bleaching process and instead resulting in heat-induced mortality of the coral animal. This is a distinct physiological outcome of extreme thermal stress compared to how we traditionally consider bleaching-induced mortality (i.e., the progressive breakdown of symbiosis leading to mortality from starvation).

While both the coral host and its symbiont are physiologically challenged by the temperature stress associated with historical coral bleaching events (Baird et al., 2009), the symbiont has been considered as the more thermally sensitive partner in the symbiosis (Jones et al., 1998; Hoegh-Guldberg, 1999; Krug et al., 2013). This widely accepted understanding of coral bleaching has driven substantial research into determining the mechanisms underpinning damage to the endosymbiotic photosystems, a process generally described as photo-bleaching

TABLE 3 | The range of ecological and physiological responses of corals to varying degrees of environmental stress.

	Healthy	Photo-bleaching	Traditional thermal bleaching, mild (i.e., DHW > 4)	Traditional thermal bleaching, severe (i.e., DHW > 8)	Summertime marine heatwave, heat damage
Damage to photosynthetic pigments	×	✓	✓	✓	✓
Reduction in symbiont density	×	×	✓	✓	✓ Highest
Whole colony bleaching (>50% reduced symbiont density)	×	×	✓	✓	✓
Tissue damage	× Polyps intact	× Polyps intact	× Polyps intact	✓ Polyps possibly damaged	✓ Polyps degraded
Cell death	×	×	✓ Minimal	✓ Widespread apoptosis, starvation	✓ Widespread necrosis, may precede whitening
Colony recovery	N/A	✓ Fastest	✓	✓ Slowest, tissue re-modeling	×
Mass mortality	×	×	×	✓ Gradual, across months	✓ Highest, rapid, within weeks
Reef recovery	N/A	N/A	✓	✓ Survival and re-growth	✓ Slowest Recruitment

TABLE 4 | Demonstrated acclamatory responses of coral host and/or symbiotic algal cells to thermal stress.

Cellular component	Acclamatory response	Source
Heat shock proteins (HSPs)	Increased production and activity of molecular chaperones Hsp 60, 70, and 90 to ensure correct digestion of degraded proteins and folding of new proteins within the Endoplasmic Reticulum. Core component of the Unfolded Protein Response	Leggat et al., 2011; Rosic et al., 2011; Seveso et al., 2014, 2016
Enzymatic antioxidants	Increased production and activity of SOD, APX, CAT, GR, and DMSO (see Table 1) in order to counter the accumulation of oxygen radicals and prevent cellular damage	Krueger et al., 2014, 2015; Roberty et al., 2015; Gardner et al., 2017
Non-enzymatic antioxidants	Increased genetic expression of cytochrome P450 and heat shock proteins, with putative antioxidant properties	Rosic et al., 2010
D1 repair and de novo synthesis (symbiont)	Increased <i>in situ</i> repair and <i>de novo</i> synthesis of D1 reaction centre proteins that are damaged during photoinhibition by combined high light and high temperature	Takahashi et al., 2008, 2009, 2013; Hill et al., 2011
Lipid membrane composition	Composition shift toward higher saturation of Polyunsaturated Fatty Acids (PUFAs) in the lipid membrane, to increase resistance to oxidative stress	Tchernov et al., 2004
Photoprotective proteins and MAAs	Higher bio-synthesis of mycosporine-like amino acids (MAAs) and photoprotective proteins in both coral host and algal symbiont	Dove, 2004; Banaszak et al., 2006; Dove and Hoegh-Guldberg, 2006; Rosic and Dove, 2011
Non-photochemical quenching (symbiont)	More de-epoxidation of xanthophyll pigments in order to dissipate excess excitation energy	Hill et al., 2005; Middlebrook et al., 2010
Unfolded protein response	Generalized response to the accumulation of degraded proteins. Acts to slow and minimize errors in protein synthesis	Walter and Ron, 2011; Ruiz-Jones and Palumbi, 2017; Traylor-Knowles et al., 2017

See **Table 1** for antioxidant abbreviations.

or light stress-induced symbiosis breakdown. The prevailing theory around the primary cause of coral bleaching is the production of ROS following heat induced impairment to photosynthesis within the symbiont (**Table 1**; Jones et al., 1998; Takahashi et al., 2009), although mitochondrial damage in both host and symbiont has also been implicated (Dunn et al., 2012). ROS are natural products of the series of redox reactions that form electron transport chains in both photosynthesis and respiration (Eberhard et al., 2008; Murphy, 2009). There are numerous ROS species generated through multiple molecular pathways that have the potential to disrupt cellular homeostasis through the oxidation of lipids, proteins and DNA (**Table 1**; Lesser, 1997; Jones et al., 1998). As such, cells have evolved natural antioxidant mechanisms to neutralize ROS and prevent oxidative stress (see **Table 4**). For example, during thermal stress, there is an increased production and activity of antioxidants in the symbiotic algae, in response to the accumulation of ROS that arises from the disruption to electron transport (Krueger et al., 2014, 2015; Roberty et al., 2015).

Increased temperature is also characterized by higher frequencies of apoptosis (cell death) and the upregulation of cellular apoptotic pathways in the coral animal. Apoptosis is a highly conserved evolutionary response (Quistad et al., 2014; Moya et al., 2016) that has evolved to remove damaged cells and prevent the further damage (Elmore, 2007). This is in contrast to uncontrolled cell necrosis in which cells degrade, swell and burst, to the detriment of neighboring cells (Elmore, 2007). Apoptosis has been observed to occur in both coral and algal cells during the very early stages of thermal stress (Dunn et al., 2004; Ainsworth et al., 2008, 2011; Strychar and Sammarco, 2009) and initially is localized to the gastrodermal cells that contain symbionts, suggesting that this is triggered through the initial photo-bleaching stage of the bleaching

process (Ainsworth et al., 2008, 2011). While apoptosis is a stress response to cellular damage that results in the removal of host cells, this process increases the potential of the individual coral colony to survive by maximizing resources for the surviving cells and removing sources of ROS (Ainsworth et al., 2011; Tchernov et al., 2011; Kvitt et al., 2016).

Upregulation of antioxidants, the apoptotic pathway and other stress responses, such as increased heat shock protein production for protein repair and replacement (**Table 4**; Walter and Ron, 2011; Seveso et al., 2014; Ruiz-Jones and Palumbi, 2017), are evolutionary mechanisms designed to increased colony survival during thermal stress. Together with species-specific characteristics, such as tissue thickness, skeletal morphology and feeding behavior, these mechanisms drive interspecific variability in coral stress responses (through acclimatization) as heat stress accumulates. Therefore, in canonical bleaching events where summertime thermal stress drives coral bleaching after several weeks to months, the meta-organism's thermal tolerance is directly determined by the cellular processes and species-specific traits that underpin inherent thermal tolerance and the potential for the induction of further protective mechanisms (i.e., acclimatization) (Coles and Brown, 2003; Bowler, 2005). These processes ultimately drive differential interspecific responses to thermal stress and thus determine how coral communities are affected by coral bleaching events. Under the extreme conditions of summertime MHW hotspots, this relationship between temperature stress and bleaching susceptibility becomes less clear as the severity undermines the capacity for acclimatization. When exposed to sufficiently large and rapid onset temperature anomalies, the induction of acclamatory mechanisms is bypassed or impaired and inherent thermal tolerance is overwhelmed. The hosts' molecular and cellular responses to damage are either inhibited or insufficient to repair the extent of damage as it

occurs within the cells. For example, a uniformly sharp decline in the activity of the antioxidant enzymes, glutathione reductase (GR) and superoxide dismutase (SOD), was described following exposure of zooxanthellae to 33°C for 6 days, irrespective of whether the symbiont was considered thermally tolerant or susceptible (Krueger et al., 2014). A similar thermal exposure (33.5°C for 6 days) of the zooxanthellate sea anemone *Aiptasia* also resulted in a reduced frequency of apoptosis but more frequent necrosis in both host and symbiont (Dunn et al., 2004). In the coral *Seriatopora caliendrum*, a collapse in the activity of heat shock protein 60 was seen in just 18 h after a sudden temperature increase to 33°C (Seveso et al., 2016). This inhibition of the apoptotic protective mechanism, in conjunction with reduced antioxidation and cellular repair, indicates damage to, or overwhelming of, cellular acclimatory mechanisms and the rapid coral mortality of species with both high and low tolerance indicates a failure of protective mechanisms to safeguard the animal against heat-induced cell death. This scenario has recently been observed in a number of locations where coral mortality during extreme thermal stress is unrelated to historical community responses (Schoepf et al., 2015; Baird et al., 2017; DeCarlo et al., 2017; Hoogenboom et al., 2017; Le Nohaïc et al., 2017). This evidence demonstrates that under severe and rapid heating associated with MHW hotspots, the response of the coral animal is distinct from how we currently define coral bleaching and associated mortality.

POST-MORTALITY PROCESSES FOLLOWING MHWs

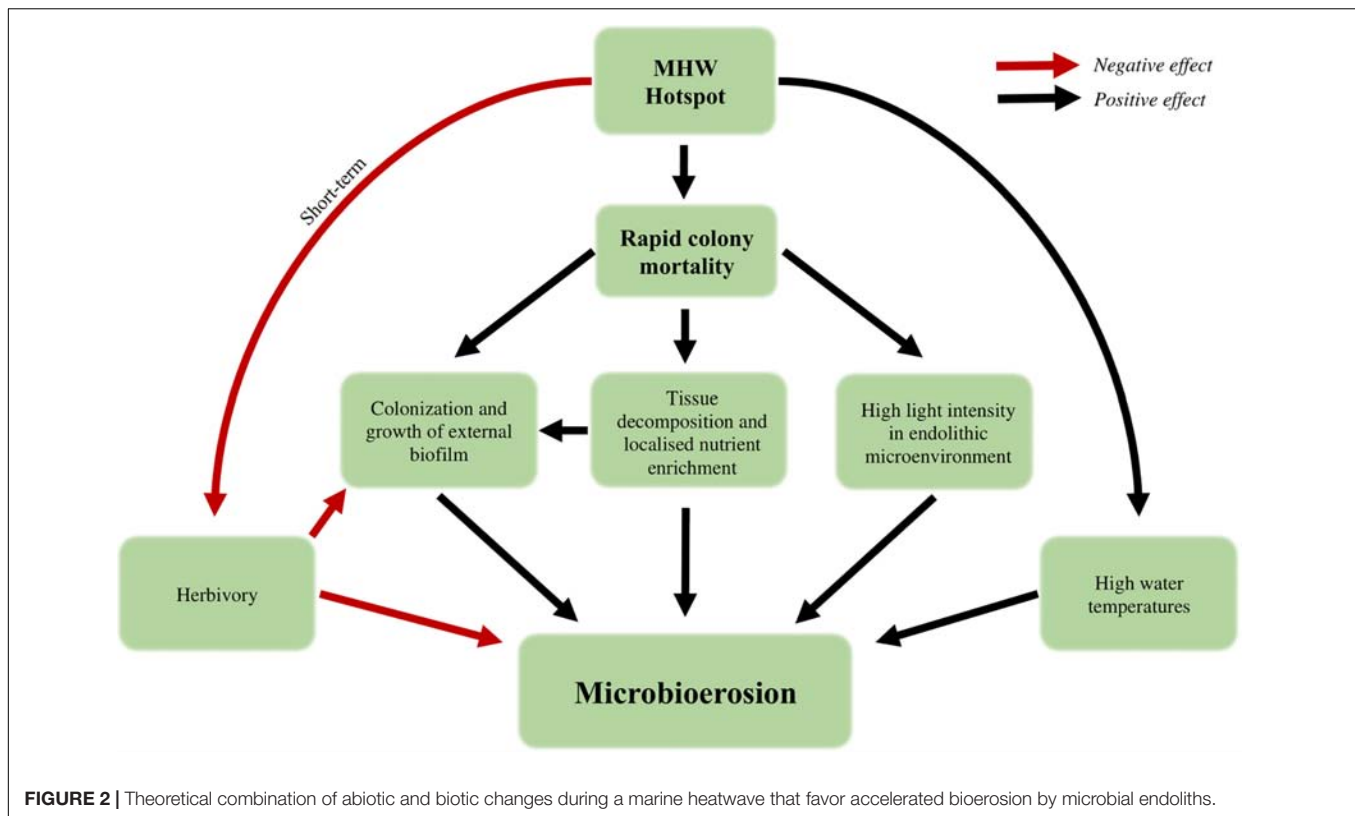
Given that rapid and extensive cell (and thus colony) mortality is a direct consequence of extreme thermal stress and occurs in a distinct fashion, this suggests that post-mortality processes on coral colonies may also be distinct. This is especially the case when thermal stress conditions persist after rapid coral

mortality, which is likely given the short time frames in which MHW hotspots can drive ecological degradation. Recent evidence presented by Leggat et al. (2019) demonstrates that extreme, rapid onset thermal stress, and the associated heat-induced mortality, together with local oceanographic conditions (doldrums, low water flow, and high light intensity) promote rapid microbial bioerosion of coral skeletons by phototrophic microbes, resulting in a degradation of reef structural frameworks at rates hereto unprecedented (Table 5). The cause is the microbial bloom formation of endolithic microborers, which reside within the skeletons of living corals skeleton and colonize newly exposed substrates (i.e., recently dead corals). This study represents the first time that the effect of coral mortality and thermal stress upon microbial bioerosion has been investigated, and suggests that MHW hotspots have an effect upon the physical reef structure, as well as the biological community.

Endolithic phototrophic microbes are arguably the second most significant bioeroders on coral reefs, after parrotfish (Carreiro-Silva et al., 2005; Perry et al., 2014). Knowledge of this microbial community is extremely limited, but it is already recognized as able to undermine structural stability over longer time frames (Tribollet, 2008a; Tribollet and Golubic, 2011; Silbiger et al., 2015; Couch et al., 2017) and is considered an important driver of reef-wide shifts toward net erosion (Perry and Morgan, 2017). The evidence presented by Leggat et al. (2019) changes how we currently understand the short- and long-term consequences of thermal stress on a reef, though the processes underlying this outcome remain to be elucidated (Figure 2). Studies over longer time frames have shown that increased light, temperature, $p\text{CO}_2$ and nutrient load accelerate rates of microbial bioerosion (Tribollet and Golubic, 2005; Carreiro-Silva et al., 2009; Tribollet et al., 2009; Reyes-Nivia et al., 2013), through promoting the growth of primarily endolithic eukaryotic algae. The rapid mortality during a MHW hotspot represents a rapid shift in conditions within the otherwise stable endolithic

TABLE 5 | Maximum rates of microbioreosion reported in the literature, in different substrates and under a variety of environmental or experimental conditions (Leggat et al., 2019).

Substrate	Environmental conditions	Rate (g $\text{CaCO}_3 \text{ m}^{-2} \text{ month}^{-1}$)	Source
Mollusc sediment	Ambient, reef lagoon	29.2	Tudhope and Risk, 1985
Mollusc shell (<i>Strombus gigas</i>)	Experimental inorganic nutrient enrichment, <i>in situ</i>	37.6	Carreiro-Silva et al., 2005
Mollusc shell (<i>Strombus gigas</i>)	Experimental inorganic nutrient enrichment, <i>in situ</i>	33.2	Carreiro-Silva et al., 2009
Mollusc shell (<i>Strombus gigas</i>)	Experimental inorganic nutrient enrichment, <i>in situ</i>	49.4	Carreiro-Silva et al., 2012
Mollusc shell (<i>Tricadna</i> sp.)	Inshore reef subject to terrestrial discharge (river)	11.4	Mwachireya et al., 2018
Coral block (<i>Porites</i> sp.)	Volcanically acidified reef ($p\text{CO}_2 = 502 \mu\text{atm}$)	126.6	Enochs et al., 2016
Coral block (<i>Porites</i> sp.)	Oligotrophic offshore reef (Osprey Reef)	111.7	Tribollet et al., 2002
Coral block (<i>Porites</i> sp.)	Oligotrophic offshore reef (Osprey Reef)	112.5	Tribollet, 2008a
Coral block (<i>Porites</i> sp.)	Experimental $p\text{CO}_2$ increase, <i>ex situ</i> ($p\text{CO}_2 = 750 \mu\text{atm}$)	39.0	Tribollet et al., 2009
Coral block (<i>Porites</i> sp.)	Oligotrophic offshore reef (Osprey Reef)	116.7	Tribollet and Golubic, 2005
Micritic limestone	Ambient, reef lagoon	43.3	Vogel et al., 2000
Coral block (<i>Porites cylindrica</i>)	Experimental $p\text{CO}_2$ + temperature increase, <i>ex situ</i> ($p\text{CO}_2 = 1010 \mu\text{atm}$; temp = control + 4°C)	239.6	Reyes-Nivia et al., 2013
Coral colony fragment (<i>Acropora aspera</i>)	Experimental, marine heatwave induced mortality (DHW > 8)	1584	Leggat et al., 2019



microenvironment, changes to which the resident microbes can rapidly acclimatize (Fine et al., 2004, 2005). Increased light intensity, due to the loss of coral symbionts that otherwise attenuate incoming irradiance, high water temperatures that drive faster metabolism and growth, and a higher availability of nitrogen through rapid tissue decomposition that supports greater biomass, are all likely to play roles in driving increased microbial bioerosion (Figure 2).

While there is evidence of MHW hotspots accelerating microbioerosion, and a theoretical framework to support this, what remains unclear is how microbioerosion is influenced by less severe and/or rapid coral bleaching and mortality events. During a canonical coral bleaching/mortality event, ecological degradation evolves over a longer time frame compared to MHW hotspot driven mass mortality as described above. This has a number of possible implications for the process of microbioerosion. Firstly, as coral mortality and the subsequent bloom formation of phototrophic microbes is spatially more patchy, these patches of algal overgrowth can more easily be grazed down by reef herbivores. On the other hand, if a large population of corals dies within a very short time frame then the ensuing growth of microbial algae over a large area could exceed rates of herbivory. This is especially true of endolithic algae already living within coral skeletons (as opposed to colonizers) that only excavating herbivores, such as parrotfish, are able to graze upon (Clements et al., 2017).

Secondly, given that canonical coral mortality events tend to occur toward the end of the summer season after months of heat accumulation and stress, algal microborers are exposed to warm,

bright summer conditions for less time before the season ends. In contrast, if a MHW hotspot causes mass mortality in the early summer months [e.g., Weeks et al. (2008)] then microborers have a full summer of ideal conditions for growth and bioerosion. We emphasize here that the accelerated microbioerosion associated with MHW hotspots is, as we currently understand it, an acute effect. It is unknown whether these accelerated rates persist in the long term, though the effects of rapid degradation in reducing structural complexity are likely to persist given that this physical characteristic of coral reefs is otherwise relatively stable over time (Graham et al., 2015).

Finally, the extremity of physical conditions during MHW hotspots that drive rapid ecological degradation would increase the metabolism and growth of phototrophic microbes more so than the comparatively milder conditions of canonical coral mortality events. Together, these characteristics of MHW hotspot driven mass mortality suggest that rapid erosion of the physical reef framework is likely to be a product of extreme thermal stress events, but further research into the effects of thermal stress and coral mortality upon microbial bioerosion is needed to support this.

Given the negative effect of MHW hotspots upon reef structural complexity, we can expect this acute process to affect the long term recovery of affected coral reefs. In our current understanding of coral bleaching events, the recovery of surviving bleached corals depends on the replenishment of symbionts within the intact host, and the re-growth and propagation of these “winners” drives reef-scale recovery. Following events resulting in mass mortality, reef recovery

depends upon successful larval recruitment (Idjadi et al., 2006; Gilmour et al., 2013; Hock et al., 2017), and the suppression of algal competition (Edmunds and Carpenter, 2001; Bellwood et al., 2006; Hock et al., 2017). These factors together influence the likelihood of an ecosystem-wide phase shift (Table 1) toward an algal reef and an alteration to ecosystem function (Graham et al., 2011, 2015; Stuart-Smith et al., 2018).

An important component of both successful recruitment and the suppression of algal competition is the structural complexity of the reef (Vergés et al., 2011; Coker et al., 2012; Harris et al., 2018). For example, topographic complexity has been shown to support higher abundances of settled larvae by presenting more opportunity for refuge from predation (Coker et al., 2012; Graham and Nash, 2013; Rogers et al., 2014). Similarly, herbivory is a core driver of reef recovery (Bellwood et al., 2006; Graham et al., 2011) and is promoted by structural complexity (Vergés et al., 2011). Indeed, a loss of structural complexity can effectively predict the probability of a coral-algal phase shift following mass mortality (Graham et al., 2015), as well as the long term recovery trajectory of coral populations (Robinson et al., 2019a) in part due to concurrent changes in the composition of fish communities (Graham et al., 2015; Robinson et al., 2019b) and the level of larval recruitment (Gilmour et al., 2013; Graham et al., 2015).

The effect of MHW hotspots upon herbivore biomass and abundance likely depends upon the examined functional group and the time frame during which we consider changes. In the short term, MHWs have been observed to result in the mass mortality of benthic herbivores, which can be significant grazers of turf and macroalgae (Garrahou et al., 2009; Wernberg et al., 2012). A key example of this is the 2011 MHW in Western Australia which caused, in one location, 99% mortality in a herbivorous benthic gastropod (Smale et al., 2017). Herbivorous fish often increase in abundance in the months and years following thermal stress events (Garrahou et al., 2009; Wernberg et al., 2012). However, given the short time frames in which algal overgrowth and coral-algal phase shifts are occurring during MHW hotspots (<2 months) (DeCarlo et al., 2017; Hughes et al., 2017), this effect is either delayed with respect to the phototrophic microbial bloom or insufficient to prevent rapid phase shifts. In fact, in the long term, overall bioerosion may increase in the months following a MHW hotspot due to a higher relative and absolute abundance of excavating fish herbivores (Pratchett et al., 2008; Stuart-Smith et al., 2018) which can be the biggest source of bioerosion in reef environments (Carreiro-Silva et al., 2005; Perry et al., 2014). The three-way interaction between herbivory, microbioerosion and MHW hotspots needs further investigation but we hypothesize that short-term increases in microbioerosion may then be followed by higher macrobioerosion by excavating fish. While a number

of questions remain to be resolved regarding this process, these studies highlight the potential for MHW hotspots to impair long term recovery by leading to a rapid degradation of structural complexity (Figure 2).

CONCLUSION

Our current understanding of the responses of corals to thermal stress, and our predictions of how they will respond in the future are based upon historic bleaching events under which coral and reef degradation is progressive as stress accumulates. However, the emergence of summertime MHW hotspots, the extreme nature of which have no historical counterparts, fundamentally changes how we understand the consequences of climate change in regards to corals reefs worldwide. They result in distinct molecular, cellular and microbial responses, and drive rapid large-scale coral mortality and decay in atypical timeframes. These devastating impacts are occurring irrespective of historical temperature and bleaching regimes, and the long-term ecological consequences of these large-scale mortality events are only now being documented. As such we propose that acute, intense summertime MHW hotspots need to be recognized as a new category of thermal stress event in coral reefs, distinct from the canonical DHW scale that has historically been used to describe bleaching-induced mortality in recent decades.

AUTHOR CONTRIBUTIONS

AF, TA, SF, and WL developed the concept for the manuscript. AF wrote the original draft of the review which was edited and expanded upon by TA, SF, and WL.

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The Decline and Recovery of a Crab Population From an Extreme Marine Heatwave and a Changing Climate

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Driven by a very strong La Niña event and a record strength Leeuwin Current, the 2011 Western Australian marine heatwave (MHW) raised sea surface temperatures (SSTs) along the Western Australian coastline by up to 5°C between November 2010 and March 2011. This single thermal perturbation led to several mortality events and recruitment impairment of commercially important species including Australia's single highest producing blue swimmer crab (*Portunus armatus*) fishery in Shark Bay. Monthly catch landings dramatically declined from 166 t in April 2011 to <10 t by December 2011 promoting a fishery closure in 2012 to allow for stock recovery. Examination of stock-environment relationships critical to the recruitment of blue swimmer crabs living toward their thermal maxima, showed juvenile *P. armatus* to be most susceptible to heat stress when mean water temperatures between December and January were >24°C, and detrimental when they exceed 26°C as was the case during the 2011 MHW when SSTs reached 29°C inside Shark Bay. Partial recovery of the crab stock 18 months after the MHW was strongly associated with mean summer temperatures returning below 24°C. Together with a change in management to a quota system, the fishery returned to full recovery status in 2018 with sustainable catch levels of up to 550 t. Long term productivity of this fishery is now at high risk from climate change impacts with shifts in winter water temperatures being cooler by 2°C and occurring earlier by few months inside the Bay. This cooling trend appears to be impacting the spawning period with the timing of peak recruitment also occurring earlier, shifting from February to November. The impacts of the 2011 MHW highlighted the risk to stock sustainability through external drivers such as climate change that was previously poorly understood. The south-west region of Western Australia is considered a climate change hotspot with water temperatures rising at rates above global trends and at increased risk from further MHWs. Therefore, responding to climate change is now about managing risks to achieve a balance between fisheries sustainability and economic viability. Increased stock monitoring now provides biomass measures 12 months prior to the fishing season, a form of stock forecasting that stakeholders can utilize to better manage their fishing business and minimize economic loss. Development of a flexible harvest strategy is also underway which responds to recruitment variation and climate extremes.

Keywords: Shark Bay, Western Australia, 2011 marine heatwave, crab fishery, stock decline, climate change

INTRODUCTION

Effective fisheries management strives to maintain long-term sustainability of the resource, maximize the economic and social value of a fishery, and minimize ecosystem impacts of its practices (Caddy and Cochrane, 2001). This balancing act is often confounded by recruitment variability which typically requires reduction in harvest levels in response to low stock biomass, and vice versa, so as to avoid recruitment overfishing. However, as climate change creates conditions that are increasingly outside the dimensions of historical experiences, the risks increase, and maintaining stable productivity may no longer be a realistic objective, particularly for species at their distributional range limits. Symptomatic of a warming climate is the increasing frequency of extreme events such as marine heatwaves (MHWs) (Bond et al., 2015; Benthuisen et al., 2018; Oliver et al., 2018), which are “prolonged discrete anomalously warm water events” (Hobday et al., 2016) of varying duration, intensity, and spatial extent that can cause devastating impacts on fisheries and ecosystems including the social and economic regimes they support (Wernberg et al., 2013; Fraser et al., 2014; Caputi et al., 2016; Le Nohaïc et al., 2017; Arias-Ortiz et al., 2018; Smale et al., 2019).

The Western Australian 2011 MHW is currently the only Category IV (extreme) MHW (Hobday et al., 2018) recorded which occurred during the austral summer of 2010/11 for 66 days between November 2010 and March 2011. Nearshore water temperatures along the 200 km of the mid-west coast of Western Australia rose 2–3°C higher than historical temperatures and up to 5°C higher in some coastal regional areas (Feng et al., 2013). The 2011 MHW occurred as a result of the alignment of inter-seasonal and inter-decadal processes, where an extremely strong La Niña event over the summer months was accompanied by an unseasonal early surge of a very strong Leeuwin Current accompanied by unusually high atmospheric heat input into the ocean (Feng et al., 2013; Pearce and Feng, 2013). During the 2011 MHW, reports of species range extensions (north to south), fish kills of finfish and invertebrates, coral bleaching, and seagrass die-offs were widespread (Pearce et al., 2011; Abdo et al., 2012; Wernberg et al., 2013; Caputi et al., 2014; Lenanton et al., 2017; Smale et al., 2017). In the months following the MHW, impacts on early recruitment processes were amongst the less visible impacts that were being detected from monitoring surveys and commercial fishing data. This was the case for the Shark Bay blue swimmer crab (*Portunus armatus*) resource, one of 14 managed blue swimmer crab stocks that contribute to Australia’s fisheries economy (Johnston et al., 2018) and nationally the most popular recreationally caught invertebrate species (Ryan et al., 2017; Chandrapavan, 2018).

The Shark Bay crab resource is harvested commercially by both trap and trawl fishing sectors, and during the 2010/11 season it was Australia’s single highest producing (787 t) blue swimmer crab fishery with an estimated value of \$4 million (Harris et al., 2014). By the end of 2011, the stock status dramatically shifted to being severely depleted with unprecedented low biomass levels across the Bay leaving everyone wondering what went wrong (Pearce et al., 2011). Management measures

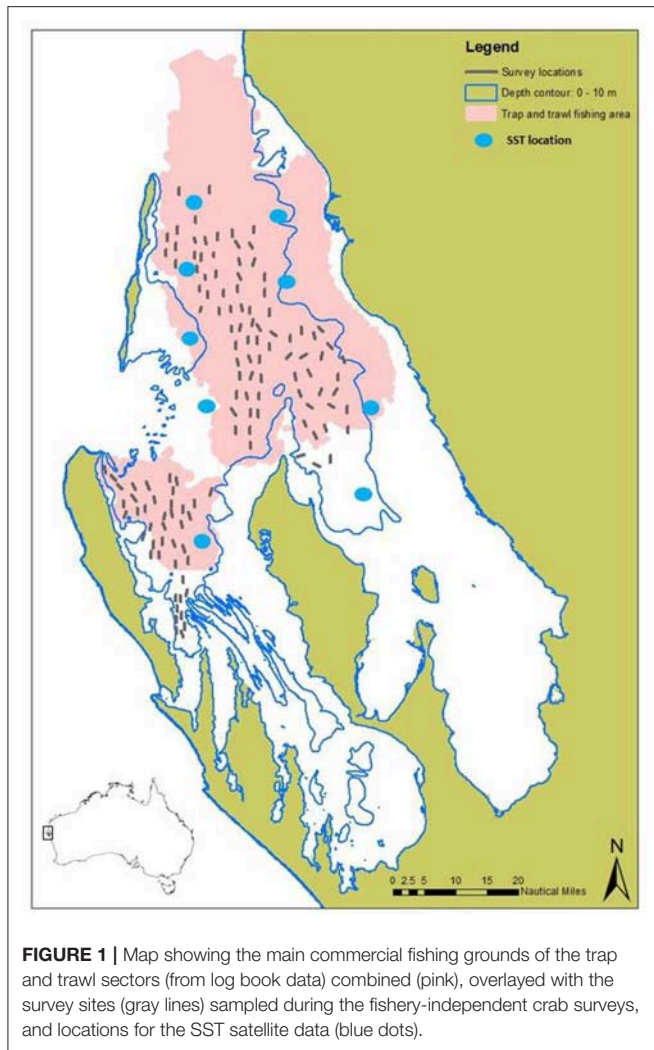
were taken in consultation with industry to cease commercial fishing and intensive stock monitoring and research began into understanding environmental drivers of crab recruitment in Shark Bay and the impacts from the 2011 MHW (Chandrapavan et al., 2018). The socio-economic impact to the region and communities supporting fishing operations was also high (Daley and van Putten, 2018), especially since the Shark Bay scallop fishery also closed at this time due to significant stock decline as a result of the MHW (Caputi et al., 2015a). Crab fishers were under considerable stress from the uncertainty regarding stock recovery potential and future productivity. Shark Bay is a World Heritage area whose economy is derived from eco-tourism, fisheries and agriculture. The regional community is familiar with seasonal environmental cycles and episodic flooding events, however, the concept of an extreme marine heatwave was fairly novel, even to the wider scientific community trying to understand this phenomenon. Following the decline in crab abundance, fisheries managers and industry stakeholders identified the need for predictive tools for better stock forecasting so they can better manage the fishery and their fishing business to minimize economic loss. To facilitate this process, an understanding of how stocks were impacted by local-scale climate shifts was recognized as a high priority to better inform future harvest strategies.

This study describes the decline and recovery of the Shark Bay blue swimmer crab population as one example of stock resilience to the 2011 MHW and ongoing climate variability. Caputi et al. (2016) first identified a negative relationship between commercial catch rates and the previous summer water temperatures in the years leading up to and including the stock decline in 2012. We build on this study by examining all post recovery years up to 2018 using fishery-independent survey data to hypothesize that the 2011 MHW caused a significant thermal disruption to the recruitment dynamics of *P. armatus* in Shark Bay. To test this hypothesis, we examined sea surface temperature (SST) data together with long-term fishery-independent survey biomass indices to identify key periods when water temperatures impacted negatively on recruitment processes. In doing so we discuss how ongoing climate shifts inside Shark Bay are likely to impact future productivity of *P. armatus* which historically been at an optimum temperature range.

MATERIALS AND METHODS

Study Area

Shark Bay is the largest marine embayment in Australia and received a UNESCO World Heritage status in 1991 for its unique marine and terrestrial ecosystems that include extensive and diverse seagrass meadows, examples of Earth’s evolutionary history in the form of stromatolites and microbial mats, steep salinity gradients forming three biotic zones and a range of endemic and endangered flora and fauna (NESP, 2018). It is an inverse estuary covering an area of ~13 000 km², with a semi-arid climate with limited exchange of oceanic water, minimal freshwater input and high evaporation rates (Francesconi and Clayton, 1996; Burling et al., 2003; **Figure 1**). Water temperatures are typically between 23 and 26°C during the austral summer months, January to March, and dominated by strong southerly



wind conditions creating greater mixing between the cool dense, saltier bottom layer and the warmer, oceanic upper layer in the water column (Nahas et al., 2005). Water temperatures begin to cool from April with winter typically between August to September (20–22°C) when weaker winds create pleasant conditions for the peak tourist season. During autumn/winter the Bay can experience the intrusion of warmer waters of the southward flowing Leeuwin Current at the channel entrances which can influence greater flushing rates from the Bay (Hetzl et al., 2015). This seasonal pattern in climate and circulation is considered “typical” in comparison to the events during the summer of 2010/11 and thereafter.

Biological Data

P. armatus has a large geographical distribution range from tropical (Queensland) to temperate latitudes around Australia (South Australia) with Western Australia having a number of managed stocks along its coastline (Johnston et al., 2018). It is a short-lived (2–3 years), fast-growing and highly fecund tropical

species (de Lestang et al., 2003; Harris et al., 2014), and typically in Shark Bay, low level spawning activity is observed all year with increased spawning activity during the cooler months of the year July to October (Chandrapavan et al., 2018) when more stable wind conditions are likely to be favorable for larval retention (Kangas et al., 2012). Recruits of 0+ age cohort of crabs [<100 mm carapace width (CW)] first settle among shallower seagrass habitats of the Bay for greater protection where they rapidly molt and grow over the spring/summer months and are first detected on the deeper trawl grounds from 50 mm CW onwards around February. Females reach maturity around 110 mm CW and enter their first breeding season producing up to 1.3 million eggs per/batch (for a 150 mm CW female) and can produce multiple batches within a breeding season (Chandrapavan et al., 2018). The 12-month commercial fishing season for crabs begins in November and fishers target larger adult crabs ≥ 135 mm CW (~ 18 months old).

Commercial catch and effort data since 1989 have been provided by fishers through a combination of log book and catch disposal records for unloaded catch. Since the trawl sector is a multi-species fishery, directed effort cannot be attributed to crabs, therefore monthly catch rate data is only available for the trap sector. Since 2002, information relating to crab abundance has been collected as part of the annual fishery-independent (standardized scientific survey at sea not affected by changes in fishing efficiency) scallop trawl survey program, where crab catch rates (kg/nm^2) (kg per nautical mile² trawled), size composition (CW), sex and breeding condition are recorded (Chandrapavan et al., 2018). This survey is undertaken in November each year and consists of up to 82 sampling sites across central Shark Bay and Denham Sound (Western Gulf) regions (Figure 1). Following the 2011 MHW, an expanded stock monitoring program was established for blue swimmer crabs where additional sites and sampling months (February and June) were included to better capture peak recruitment and peak spawning biomass levels. The timing of these surveys during peak summer and winter periods also allows for more informative assessments of summer and winter environmental conditions on stock recovery.

Temperature Effect on Crab Stock

Satellite-derived continuous daily sea surface temperatures (SSTs) were obtained from the NOAA OIv2 dataset (NOAA, 2019) from 1982 onwards at $\frac{1}{4}$ degree (~ 28 km) resolution at nine sites (Figure 1) across the varying depths inside Shark Bay. Daily SST data were used to calculate monthly mean SSTs and characterize trends and anomalies inside Shark Bay. Standardization of survey catch rates (weighted by area trawled) were calculated assuming that the densities of crabs among the individual trawl shots have a delta-lognormal distribution (see details in Chandrapavan et al., 2018).

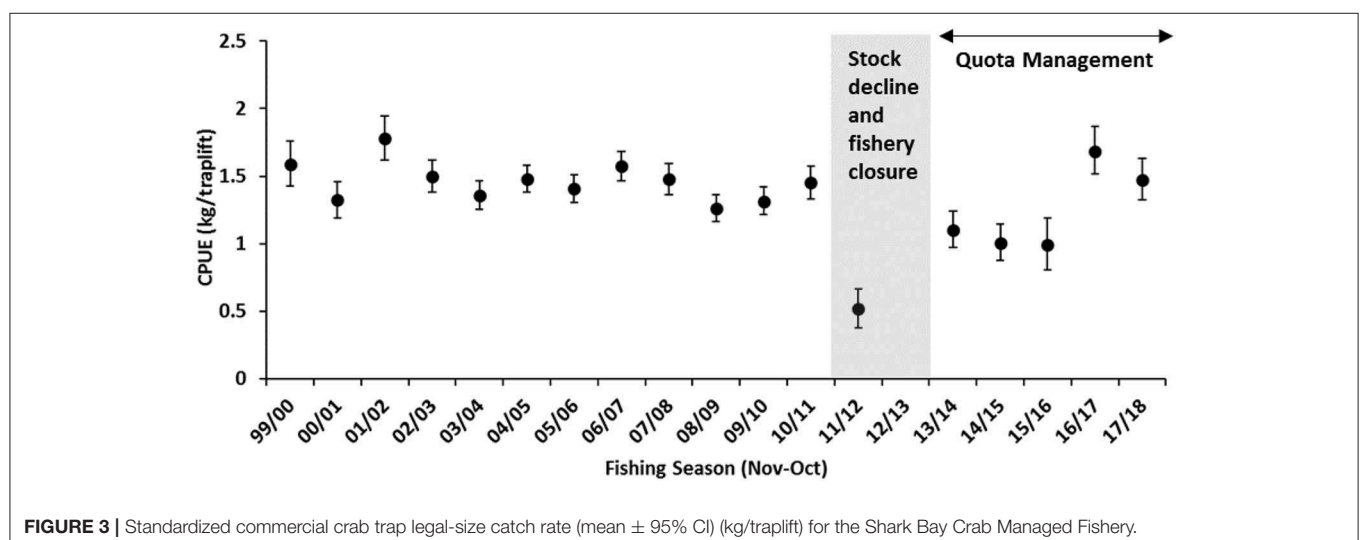
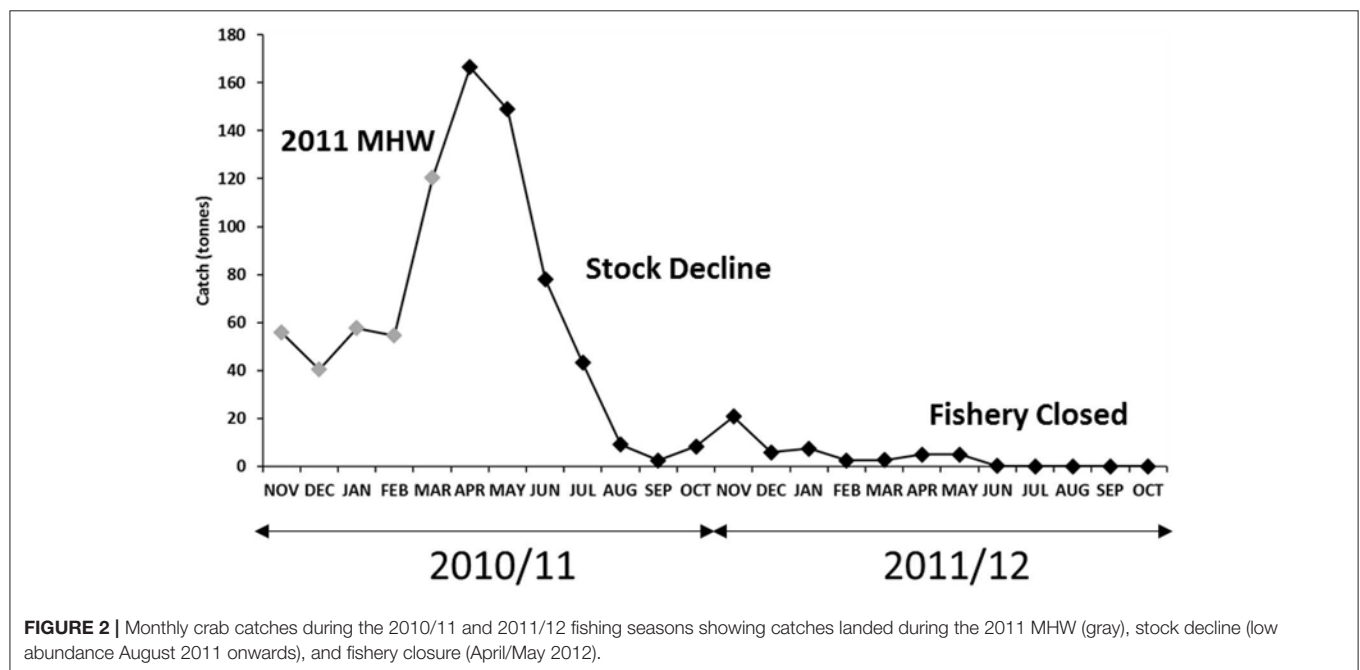
We examined the relationship between fishery-independent survey catch rates of legal (crabs ≥ 135 mm CW), spawning (all females ≥ 110 CW), immature juvenile (males <100 mm, females <110 mm CW) crabs with SST data. The annual November survey is the longest time-series of fishery-independent survey of crab data available and even though it is not representative

of peak spawning and recruitment, the biomass is proportional to the overall annual stock levels (Chandrapavan et al., 2018). The cohort of legal-sized (1+) crabs entering the fishery in November every year would have been juveniles (0+) during the previous summer. Correlations of standardized survey catch rates of legal-size and juvenile crabs between 2002 and 2018 with mean monthly SSTs during previous months was determined using Pearson's correlation coefficients (r). If any significant periods were identified for recruitment, this was used to explore a preliminary stock-recruitment relationship using the peak spawning catch rate of crabs from the June survey and peak juvenile recruitment catch rate from the February survey. All analyses were done using R (version 3.0.2; R Core Team, 2013).

RESULTS

Stock Decline

The 2010/11 commercial crab season began in November 2010 with average crab landings by the trap sector, which gradually increased to above-average landings once the trawl sector started fishing from March 2011 onwards. Adverse impacts from the MHW was not immediately identified. In August 2011, almost 6 months post MHW, monthly commercial catch from both the trap and trawl fleets and trap catch rates declined to historically low levels (<10 t) for this time of year (Figure 2), although catches usually decline progressively toward the end of fishing season. When the 2011/12 fishing season began in November 2011, a marked shift in crab distribution patterns and biomass



was observed by trap fishers when their catch rates declined to a record-low ~ 0.5 kg/traplift and < 5 t overall had been landed by February 2012 (Figure 3).

The November 2011 trawl survey confirmed the unprecedented stock decline in the Bay where the survey CPUE of all crabs dropped from an average of 1,345 to 41 kg/nm² (Figure 4A), and spawning and legal-sized

crabs were at historically record-low biomass levels of 3–6 kg/nm² (Figures 4B,C). While juvenile abundance was also relatively low (Figure 4D), the November survey was not an optimal time to measure the abundance of new recruits. Management measures were taken to cease commercial fishing in April 2012 to allow the surviving stock to recover and rebuild.

Environmental Conditions and Stock Recovery

Typically (mean SST between 1981 and 2009), the coolest winter period inside Shark Bay has been August to October with a SST range of 20.5–21.5°C, and the warmest summer period as February to April with a SST range of 24–25 °C (Figure 5A). During 2010, SSTs were cooler than the average between February and September, lowest during July 2010 at 20.0°C. From September 2010 onwards, mean monthly SSTs rapidly increased to above-average temperatures peaking during February 2011 at $\sim 29^\circ\text{C}$. Shallower regions of the Bay experienced above-average temperatures of up to 5°C while the central deeper Bay regions experienced up to 3°C above-average temperatures. The 2011 MHW was part of the 2010–12 La Niña event which consisted of two peaks in La Niña strength over successive summers (BOM, 2019a). The 2011/12 peak was weaker, but still of moderate strength, and led to SSTs up to 2°C warmer inside Shark Bay (Figure 5B).

Following the 2012/13 summer, February and June 2013 surveys delivered the first positive indication of sustained stock recovery with peak recruitment levels of 991 kg/nm² and spawning levels of 1,789 kg/nm². Through industry consultation, a limited commercial fishing trial was undertaken during July 2013 to assess the feasibility of reopening the fishery. The trial was deemed successful with commercial catch rates reflecting those of pre-MHW years and provided confidence to resume commercial operations. Prior to the stock decline, the fishery was in the process of transitioning to a quota management system as a measure to reduce fishing pressure and to resolve resource allocation issues between trap and trawl sectors (Chandrapavan et al., 2018). Implementing the quota system as part of the stock rebuilding strategy was a timely regulatory action that was key to managing harvest levels without impeding stock recovery. After extensive consultation with stakeholders, an initial quota of 200 t was set for the 2013/14 season, but later revised to 400 t after a mid-season review of commercial catch rates and additional survey information indicated moderate sustainability risk of this increase to the recovering stock. Increasing levels of recruitment and spawning biomass were observed during 2015, 2016, and 2017 with biomass levels slowly returning to historical (pre-MHW) ranges (Figure 4). Landings also increased from 341 to 516 t under quota limits of 400 t (2014/15 to 2016/17) to 550 t (2017/18) (Figure 6).

Stock-Environment Relationships

Correlation analyses identified (log-transformed) survey catch rates of legal crabs (1+ cohort) during November (year y) being negatively correlated with SSTs during the previous summer

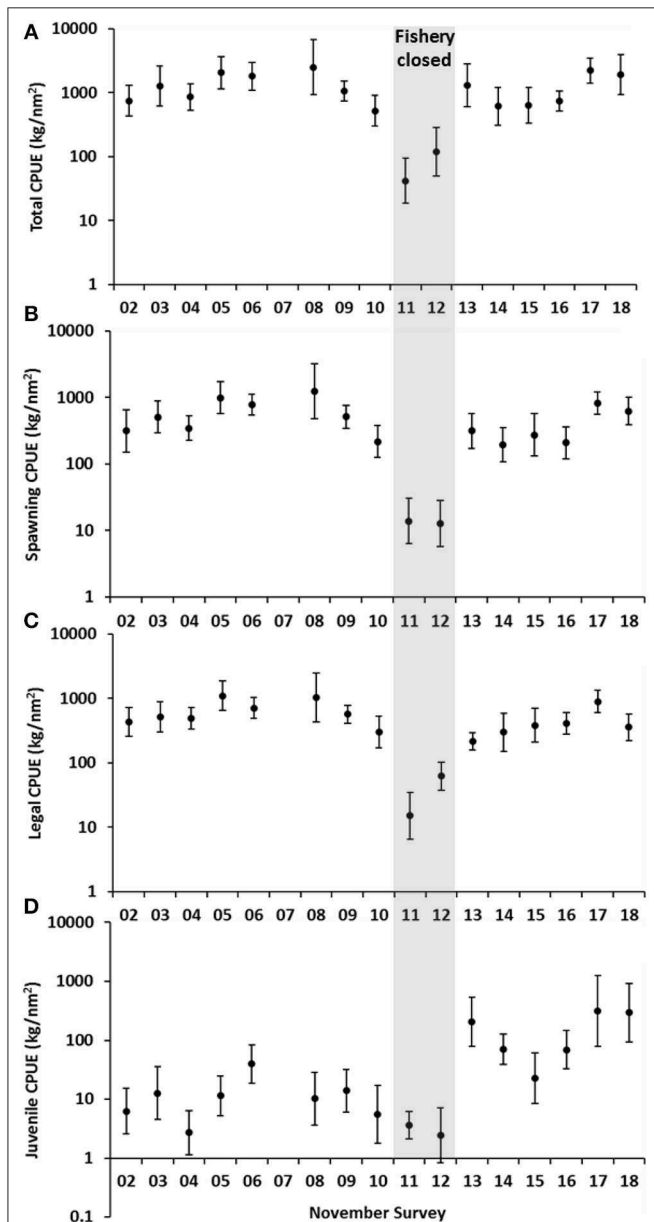


FIGURE 4 | Annual November fishery-independent survey catch rates (standardized mean $\pm$ 95% CI) presented on a log scale (A) total (all crabs) biomass levels (B) spawning (all females ≥ 110 mm CW) (C) legal (all crabs ≥ 135 mm CW) and (D) juvenile (females < 110 mm CW, males < 100 mm CW). Catch rates prior to 2011 represents fishery operating under input management system, 2011–2012 represents stock decline and recovery period, 2013–2018 represents recovery under a quota management system.

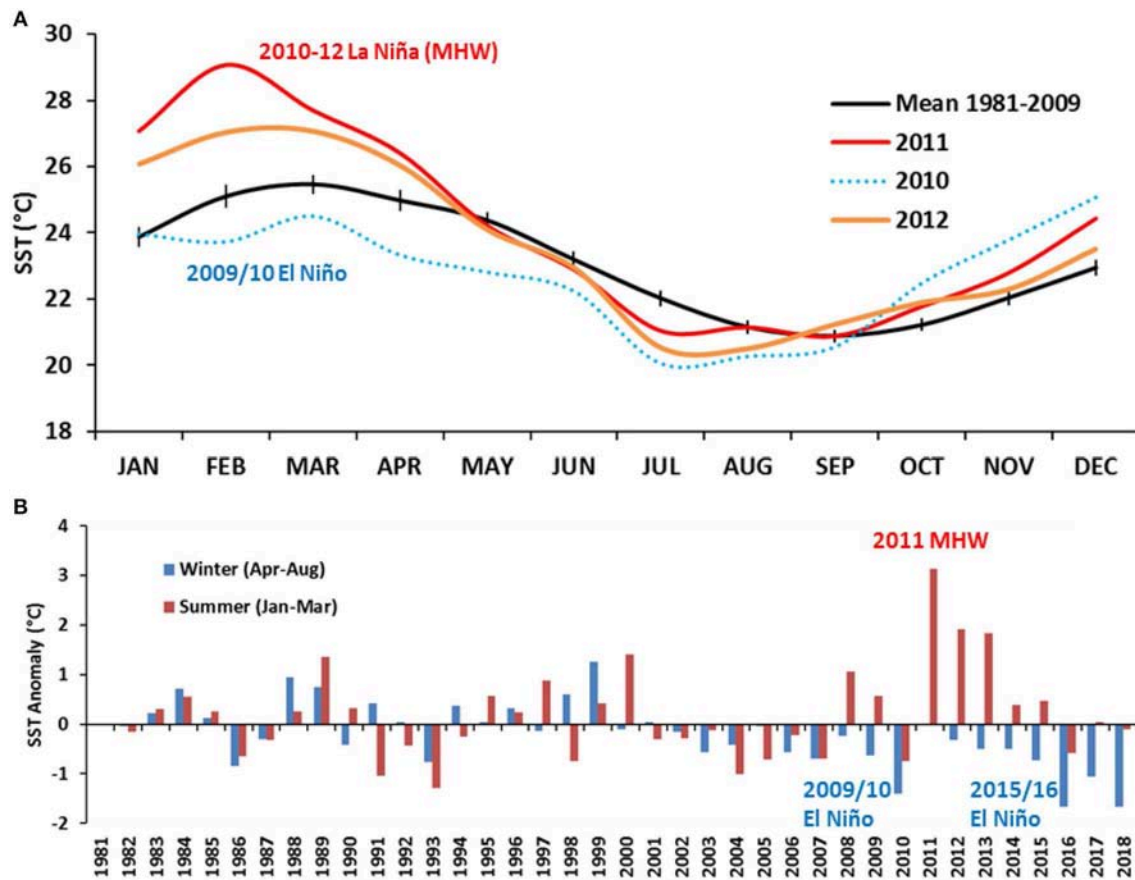


FIGURE 5 | (A) Comparison of the historical (pre-heatwave) mean monthly SST [mean ($\pm 95\%$ CI) (1981–2009) and the mean monthly SST between 2010 and 2012 showing a combination of the 2009/10 El Niño phase transitioning to the 2011 MHW as part of the 2010–12 La Niña phase. **(B)** Mean winter (April to August—blue) and summer (January to March—red) SST anomalies for Shark Bay region from 1982 to 2018, calculated against the 1982–2009 means (representing pre-heatwave years).

months December to January ($y-1/y$). The regression analysis provided a significant model fit of $r^2 = 0.73$ ($p < 0.01$) (Figure 7).

$$\ln \text{ Legal } (1+) \text{ CPUE}_{(y)} = -0.93 \text{ SST (Dec-Jan)}_{(y-1/y)} + 27.88$$

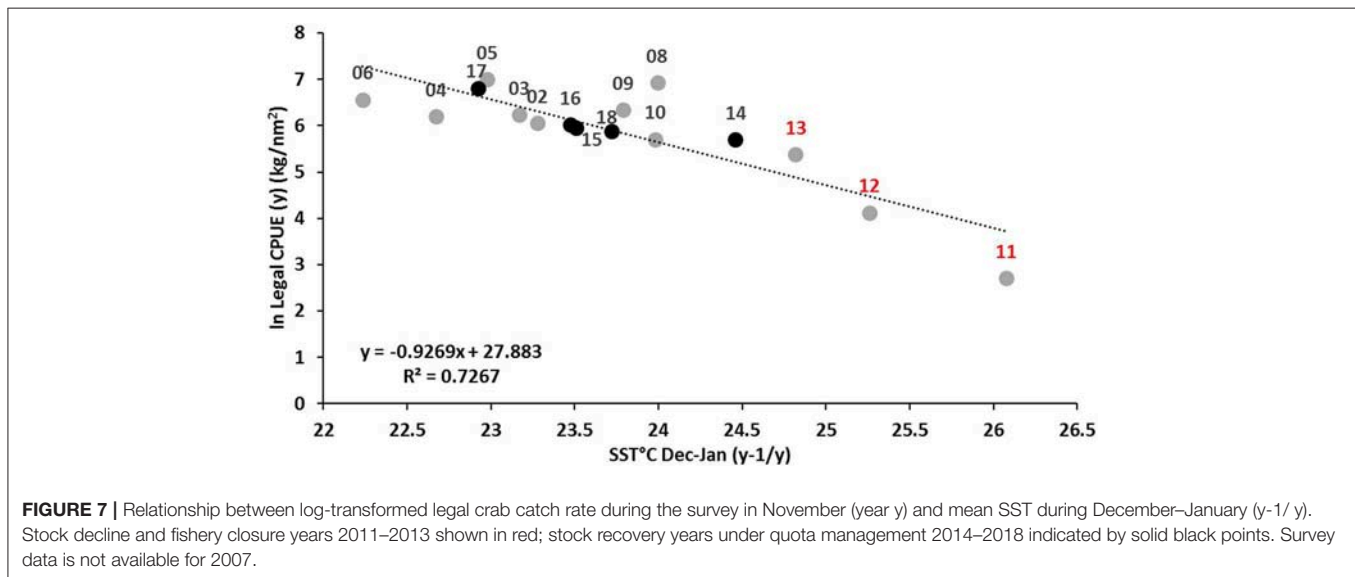
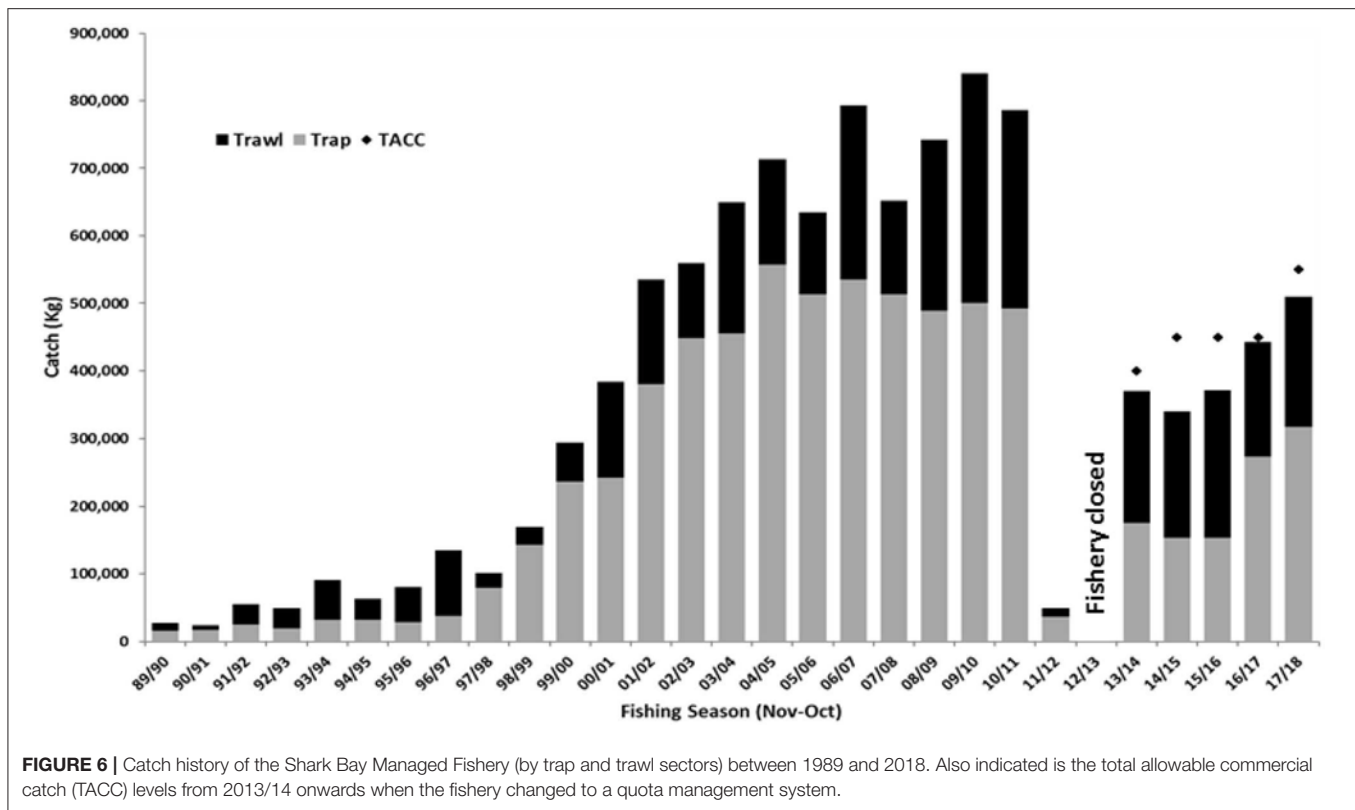
The relationship suggests that achieving above-average recruitment requires cooler summer temperatures $\leq 24^\circ\text{C}$ which are likely to produce higher catch rates ($> \ln 5.5$ or $> 245 \text{ kg/nm}^2$) of legal crabs in the following summer when they start to recruit into the fishery (and the reason the quota fishing season is set from November to October). Stock decline during 2011 is clearly associated with the highest mean SST (Dec-Jan) of 26.1°C , followed by progressive decreases in mean temperatures during 2012 and 2013 as SSTs fell toward 24°C allowing the stock to rebuild in the absence of fishing pressure. Legal crab CPUE in the fishery-independent survey increased slightly during 2014 with a cooler mean summer SST of 24.5°C , although this catch rate had been impacted by resumed fishing removing 371 t of crabs during the 2013/14 season. Since 2015, summer (Dec-Jan) SSTs have been cooler than the historical average (Figure 5B) and below 24°C allowing recruitment to return back

within the historical range (Figure 7) under catch levels of up to 518 t.

The other significant environmental relationship relating to recruitment was that between juvenile (0+) recruitment levels during November (y) and mean SSTs during the preceding winter months of June and July (y). The regression analysis provided a significant model fit of $r^2 = 0.57$ ($p < 0.01$) (Figure 8).

$$\ln \text{ Juvenile } (0+) \text{ CPUE}_{(y)} = -1.71 \text{ SST (Jun-July)}_{(y)} + 40.45$$

This relationship suggests higher catch rates ($> \log 3$ or $> 20 \text{ kg/nm}^2$) of juvenile crabs in November are associated with winter SSTs $\leq 21.5^\circ\text{C}$ and low to below average catch rates with winter SSTs $> 21.5^\circ\text{C}$. Interestingly, all the winters that were colder than 21.5°C were between 2013 and 2018, post- 2011 MHW years, while the warmer winter seasons were all associated with pre-MHW years. This has resulted in an increase in the average juvenile catch rates from 11 kg/nm^2 before 2013 to 163 kg/nm^2 since 2014. As the peak recruitment is considered to occur around February, this relationship may not represent environmental effect on juvenile recruitment abundance. The



relationship probably reflects the effect of the environment on the earlier onset of juveniles present in the November surveys in recent years. Data from 2010 to 2012 were omitted from this analysis as they may have been confounded by unknown level of mortality during the 2011 MHW and subsequent low spawning stock levels during 2012. Since 2011, there has been a notable shift in the winter period in Shark Bay with the coolest SSTs occurring earlier, between June and July and also on average

being cooler by $\sim 2^{\circ}\text{C}$ (Figure 5A). In fact, winter SST anomalies Shark Bay, April to August, have been cooler than the average since 2002, with record-low winter SSTs during 2010, 2016, and 2018 (Figure 5B).

A preliminary examination of the stock-recruitment relationship was attempted using juvenile recruitment during February (y) with peak spawning catch rate during June ($y-1$). This analysis provided a significant model fit of $r^2 = 0.85$ ($p <$

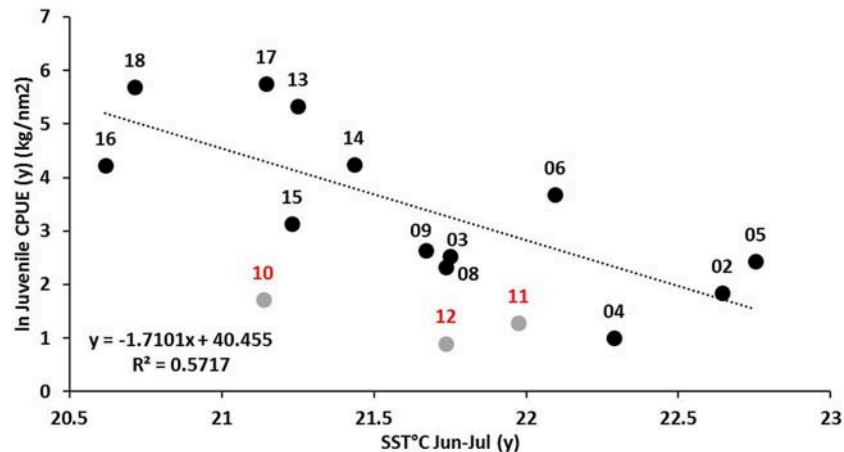


FIGURE 8 | Relationship between log transformed juvenile crab catch rate during November (y) and mean SST during May-July (y) for all years 2002–2018 excluding 2010–2012 as they were affected by 2011 MHW and subsequent low spawning stock levels. Survey data is not available for 2007.

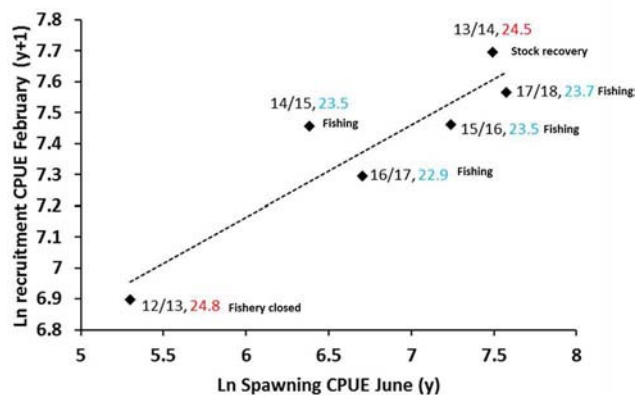


FIGURE 9 | Preliminary stock-recruitment relationship for the Shark Bay crab stock based on peak spawning (all females ≥ 110 mm CW) biomass during the June survey (t) and peak recruitment (females < 110 mm, males < 105 mm CW) biomass during the following February survey (y+1). Labels refer to year of spawning/year of recruitment, mean summer SST (Dec–Jan) (y/y+1) $\geq 24^\circ\text{C}$ in red and $< 24^\circ\text{C}$ in blue and fishery status.

0.05) showing spawning stock as the major driver of recruitment variability since 2012 (Figure 9).

$$\begin{aligned} \text{Ln Recruitment (0+) (Feb)}_{(y+1)} \\ = 0.3 \text{ Ln Spawning (Jun)}_{(y)} + 5.4 \end{aligned}$$

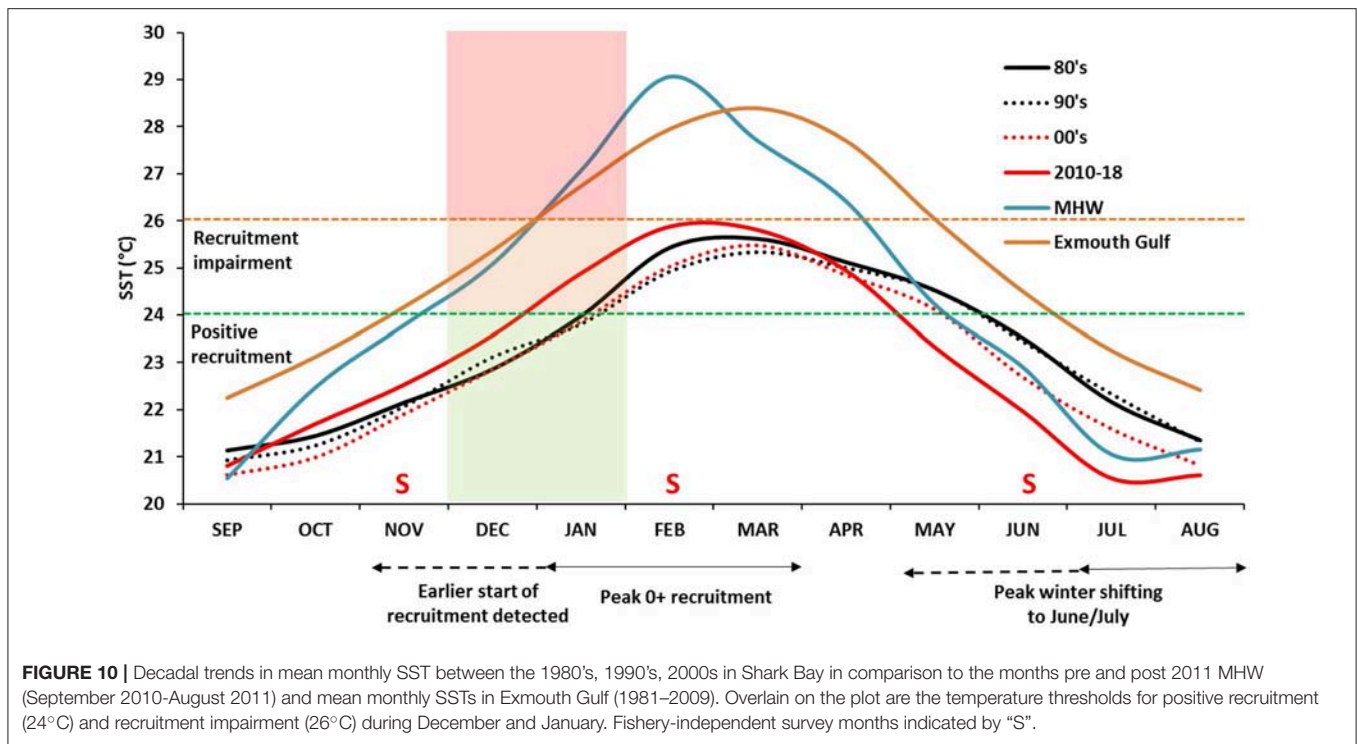
The model outcomes are not surprising for the 7 years of stock rebuilding since the 2011 MHW where summer SSTs have not been highly variable and harvest levels have been restricted. The low recruitment in 2012/13 is likely due to a combination of low spawning stock abundance and the warmer than average summer temperatures. The large increase in recruitment from 2012/13 to 2013/14 was a period of no fishing in conjunction with summer temperatures dropping toward 24°C . Since the resumption of fishing, spawning stock and recruitment levels have improved and have been maintained during successive years

of cooler summer SSTs but also through setting the harvest levels (quota) such that recruitment overfishing is avoided.

DISCUSSION

A significant decline in overall stock abundance of blue swimmer crabs 6–12 months after the 2011 MHW and partial recovery within 18 months (a single generation time for *P. armatus*) demonstrated both vulnerability and resilience of the Shark Bay crab population to acute and moderate temperature shifts. This study has identified two significant stock-environment relationships critical to the recruitment processes of blue swimmer crabs that will continue to impact the long-term productivity of this fishery, particularly as their environment shifts toward suboptimal conditions.

Our study infers juvenile (5–8 month old) *P. armatus* in Shark Bay to be most susceptible to heat stress when mean water temperatures between December and January are $> 24^\circ\text{C}$, and detrimental when they exceeded 26°C (Figure 7). During the 2011 MHW, mean SSTs were higher than 24°C from November through to May with peak SSTs up to 29°C (Figure 10). Prolonged and sustained high water temperatures without reprieve across the whole Bay region would have escalated thermal stress levels beyond physiological repair leading to mortality. Dead crabs were not observed directly during the heatwave period and good catch rates were maintained for a few months after the heatwave. However, fish kills of Pink Snapper (*Chrysophrys auratus*) in Shark Bay and other invertebrate species such as lobsters and abalone along the WA coastline during the MHW (Pearce et al., 2011) from (assumed) similar physiological stress responses. During the post-heatwave years, *P. armatus* recruitment levels have increased as the mean December–January temperatures returned and remained below the thermal threshold temperature of 24°C . Therefore, summer water temperature does appear to be a significant driver of recruitment in Shark Bay. The preliminary stock-recruitment relationship during the stock recovery years since the MHW,



show spawning stock in 2012 appears to be the major driver of the 2013 recruitment. This analysis is based on a very short time series and a return to warmer summer SSTs will test this relationship into the future as more years of data become available. We believe a combination of favorable summer water temperatures for recruitment and a change to quota management allowing greater protection of the spawning stock has together recovered the crab stock back to sustainable levels after the MHW.

Many crustaceans including crabs respond to variation in water temperatures through changes to molt timing and frequency, growth rates, size at maturity, spawning period, larval development, and survival (Green et al., 2014). When these shifts reach their thermal thresholds it will ultimately limit productivity as one or more environmental conditions compromise reproductive success. In Shark Bay, decadal trends in monthly SSTs are showing an increase of summer temperatures from the 1980s to recent years. The mean January SST has increased from around 24°C during the 1980's, 1990's, 2000s to 24.8°C since 2010 as a result of the MWH and following two warm summers (Figure 10). It is therefore important to monitor and understand the trends in these summer temperatures as they can have major effect on crab recruitment. The current summer SSTs inside Exmouth Gulf, the next largest embayment 400 km north of Shark Bay, are similar to that experienced during the MWH in Shark Bay. Blue swimmer crabs are incidentally retained by the trawl fishery in Exmouth Gulf and constitute a minor trap fishery (Johnston et al., 2018) along the northern Western Australian coastline. Annual catches are highly variable and generally <50 t and reflect the reduced performance

of this species at higher latitudes and water temperatures above the critical thermal tolerance range for juvenile *P. armatus*. We hypothesize that if there is greater warming of summer months in Shark Bay into the future, it will gradually alter the success of the protracted spawning period to one more restricted toward those months conducive for larval survival and settlement.

Shark Bay is currently also experiencing greater magnitude of annual temperature variation (difference between maximum and minimum SST) of 6°C in the past decade compared with 4.8°C during the 1980's. A warming summer trend is partly responsible for this variation, however it seems to be also driven by winter water temperatures cooling at a faster rate between April and September. The mean temperature minima is shifting forward to June/July from August/September (Figure 10) and this cooling phenomenon is restricted to waters inside the Bay. Cooler than average SSTs are usually associated with strong El Niño events such as during 2009 and 2016 (Figure 5B), however both 2017 and 2018 were neutral ENSO years where winter SSTs were 1–2°C below average temperatures. Recent investigations reveal Shark Bay (and likely Exmouth Gulf) as being sensitive to the shifts and position of the subtropical ridge (STR), a band of high pressure systems which is positioned over Shark Bay during winter and moves further south during summer (BOM, 2019b). Global climate change is now causing the shift in the STR to be further south allowing stronger easterly winds to dominate. Stronger winds cause greater heat loss to the atmosphere thus cooling the inner waters of Shark Bay during winter (Hetzel, 2018).

In Shark Bay, peak juvenile (<100 mm CW) recruitment over the summer months largely arises due to winter water temperatures between 20 and 22°C as being optimal for spawning

(Chandrapavan, 2018). Prior to 2011, peak spawning was likely around August–September, and therefore juvenile crabs were not generally sampled during the November survey as they were too small to have moved out on to the central Bay region from the inshore seagrass habitats. Currently, the peak winter temperature range is occurring 2 months earlier during June–July (**Figure 10**) while concurrently higher catch rate of juvenile abundance during November surveys are also being observed. The negative relationship with juvenile recruitment during November and SSTs during June–July supports our hypothesis that a forward shift in the peak spawning is occurring, allowing crabs to take advantage of optimal temperatures earlier (**Figure 10**) resulting in an earlier observation of juveniles in the November survey since 2013 (**Figure 8**).

Ongoing climate change is expected to continue to alter crab recruitment patterns and timing of spawning given organisms generally evolve to coincide reproduction with food availability for survival and development of the offspring (Green et al., 2014). While acute cold stress events such as cold spells and cold snaps are known to occur due to climate variability (Schlegel et al., 2017), the observed long-term climate change driven cooling pattern as observed inside Shark Bay may be unique to this region of Western Australia with the phenomenon also occurring inside Exmouth Gulf. What remains unclear is the impact of temperatures cooler than 20°C on larval development and survival, which the Bay has not experienced in the past but is occurring at greater frequency since 2014. Climate models are also predicting a long-term southward shift of the STR, therefore Shark Bay may experience colder SSTs and greater wind intensity which will certainly impact the overall circulation and flushing of the Bay thus affecting overall larval dispersal and recruitment processes inside the Bay (Hetzel, 2018). Furthermore, climate change is also likely to alter primary productivity and overall trophic structures of the system either through discrete events or gradual ecological changes (Wernberg et al., 2013). Approximately 36% of the seagrass habitat was severely damaged or lost following the 2011 MHW (Arias-Ortiz et al., 2018) and this may have contributed to the recruitment decline of *P. armatus*. However, the remaining seagrass habitat appears to be sufficient to support the recovery of the crab stock in the subsequent years despite little recovery in the seagrass habitat. Further research is required to fully understand the changes in oceanography-habitat-species interactions that are likely to occur with changes in climate and hydrodynamics of the Bay.

In trying to project the productivity of the Shark Bay crab resource forward, it is clear that the role of climate in determining recruitment success adds significant uncertainty and risk to estimates of future yields. One of the key lessons learned from the rebuilding of the Shark Bay crab population was the importance of environmental and stock monitoring programs that are able to capture changes in stock abundance with changes in the environment. Targeted surveys around peak recruitment and spawning during summer and winter months allows for biomass indices of future harvest to be assessed precisely but more importantly provides early detection of any impacts from environmental perturbations. Hence an accurate assessment of stock status and harvest levels is currently

based on a risk-based weight of evidence approach (Department of Fisheries, 2015), utilizing a range of survey indices, environmental and climate data, biomass dynamics modeling and validation using commercial performance indicators. This information is assessed to set appropriate harvest levels 6 months prior to a fishing season and is re-assessed mid-season to allow for harvest levels to be adjusted (higher or lower) in accordance with the control rules governing the harvest strategy. Early detection of any impacts on the stocks through monitoring the pre-recruit abundance thus allows for more timely decision making for both the protection of the stock and to inform industry.

No La Niña events have occurred in years since the 2010–12 event which occurred unseasonably over the summer months. Previously, the “Western Australia 1999 MHW (Category 3)” occurred during the autumn/winter months (Hobday et al., 2018) with no known documented impacts and was primarily considered to be a warmer than average winter period due to the accompanying strong La Niña event. The Bureau of Meteorology (BOM, 2019c) provides ENSO forecasting which is regularly reviewed prior to and during the crab fishing season in Shark Bay. Therefore, with further development of stock-recruitment-environment models, the capacity to act early to reduce fishing pressure ahead of catastrophic events is now possible.

CONCLUSION

The south-west coast of Western Australia, with Shark Bay at its northern range, is identified as one of 24 global marine hot-spots thus increasing the likelihood and frequency of extreme events (Hobday and Pecl, 2013; Hallett et al., 2018). The 2011 MHW highlighted the risk of climate variability to crab (and other fish) stocks from a single climatic perturbation. Its impact on the Shark Bay crab fishery and industry was devastating. Rapid rebuilding has occurred through a combination of return to ideal environmental conditions, increased monitoring of stock abundance and environmental factors, adaptive management actions combined with industry cooperation. Using these learnings, consideration of environmental parameters is currently being incorporated into the fishery's harvest strategy.

The “typical” climate and circulation processes characteristic of Shark Bay are changing as shifts in seasonal temperatures and wind patterns are creating “atypical” environmental conditions. The cooling phenomenon inside Shark Bay further highlights the importance of considering climate shifts and impacts at a local scale irrespective of global or national climate model projections. Risk assessments of Western Australian fishery resources identified blue swimmer crabs as at the highest risk level to climate change impacts (Caputi et al., 2015b). More recently, a climate change vulnerability index developed for assessing climate change impacts across World Heritage Sites ranked Shark Bay at “High Risk” (NESP, 2018). This assessment considered multiple stressors due to climate change on both the terrestrial and marine ecosystems highlighting the need for urgent action. Adapting to this new reality will be an evolving and challenging process. Fishing industries need to find ways to remain profitable and competitive within a changing climate, while fisheries regulatory bodies need to provide flexible and

adaptive management frameworks to support sustainability, deal with uncertainty and respond to climate change.

DATA AVAILABILITY

The datasets for this manuscript are not publically available because of confidentiality restrictions under the Fisheries Act. Requests to access the datasets should be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

AC and MK designed the study. AC collected some of the data, processed and analyzed the datasets, and worked

on interpretations of the results with NC. AC wrote the manuscript. MK and NC contributed to the text by reviewing and writing.

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Extreme Marine Heatwaves Alter Kelp Forest Community Near Its Equatorward Distribution Limit

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Climate change is increasing the frequency and severity of marine heatwaves. A recent extreme warming event (2014–2016) of unprecedented magnitude and duration in the California Current System allowed us to evaluate the response of the kelp forest community near its southern (warm) distribution limit. We obtained sea surface temperatures for the northern Pacific of Baja California, Mexico, and collected kelp forest community data at three islands, before and after the warming event. The warming was the most intense and persistent event observed to date, with low-pass anomalies 1°C warmer than the previous extremes during the 1982–1984 and 1997–1998 El Niños. The period between 2014 and 2017 accounted for ~50% of marine heatwaves days in the past 37 years, with the highest maximum temperature intensities peaking at 5.9°C above average temperatures for the period. We found significant declines in the number of *Macrocystis pyrifera* individuals, except at the northernmost island, and corresponding declines in the number of fronds per kelp individual. We also found significant changes in the community structure associated with the kelp beds: half of the fish and invertebrate species disappeared after the marine heatwaves, species with warmer affinities appeared or increased their abundance, and introduced algae, previously absent, appeared at all islands. Changes in subcanopy and understory algal assemblages were also evident; however, the response varied among islands. These results suggest that the effect of global warming can be more apparent in sensitive species, such as sessile invertebrates, and that warming-related impacts have the potential to facilitate the establishment of tropical and invasive species.

Keywords: kelp forest, extreme warming event, marine heatwaves, community structure, tropicalization, trailing edge

INTRODUCTION

Climate change is predicted to increase the frequency and severity of extreme climatic events (Solomon et al., 2007; Perkins et al., 2012; Sydeman et al., 2013; Frölicher et al., 2018) such as marine heatwaves (MHWs) (Hobday et al., 2016), which are impacting coastal marine ecosystems worldwide (Garrahou et al., 2009; Marba and Duarte, 2010; Smale and Wernberg, 2013; Wernberg et al., 2013, 2016; Cavole et al., 2016; Hughes T. P. et al., 2017; Oliver et al., 2017; Smale et al., 2019), as well as the human populations that depend on them (McCarthy et al., 2001; Harley et al., 2006). In the past decades, MHWs have already increased in frequency and severity, with a global average of 50% more MHW days registered per year (Frölicher et al., 2018; Oliver et al., 2018). Temperate foundation (habitat-forming) species, are reported to be sensitive to MHWs (Wernberg et al., 2019), especially to warmer water temperatures and to decreases in nutrient availability due to thermal stratification or to a weakening of coastal upwelling (Carr and Reed, 2015; Schiel and Foster, 2015). They are particularly susceptible to MHWs when located close to their equatorward (warm) range edges (Smale et al., 2019). Changes in the abundance and distribution of these foundation species could have consequences for the structure and function of the entire ecosystem (Harley et al., 2012; Schiel and Foster, 2015; Smale et al., 2019).

The temperate ecosystems of the California Current System (CCS) were recently exposed to a sustained and intense warming event. It began in November 2013 in the Gulf of Alaska (Gentemann et al., 2017), with positive (warm) sea surface temperature anomalies (SSTAs) in the upper ocean layer (~100 m). By May 2014, it spread south to the coasts of Baja California, lasting until April 2015 (Di Lorenzo and Mantua, 2016). Nicknamed the “Blob,” temperature anomalies exceeded 3°C above previous climate records (Bond et al., 2015; Di Lorenzo and Mantua, 2016). Severe El Niño Southern Oscillation (Jaxco et al., 2016) (nicknamed Godzilla) conditions (SSTAs of ~2.3°C, as measured by el Niño 3.4 index) followed this event, extending the warming in Baja California until the end of 2016 (Di Lorenzo and Mantua, 2016; Jaxco et al., 2016). Reports of biological changes across the entire food web of the CCS (Cavole et al., 2016; Sanford et al., 2019) followed these extreme conditions. However, limited knowledge exists regarding the corresponding responses of temperate coastal ecosystems.

Kelp forest ecosystems in the northeastern Pacific Ocean are distributed along the coasts of the CCS, from Alaska, United States, to their southern distribution limit in Baja California, Mexico (Graham et al., 2007; Carr and Reed, 2015; Schiel and Foster, 2015). The giant kelp, *Macrocystis pyrifera*, one of the foundation species in kelp forests of this region, creates a three-dimensional biogenic marine habitat that sustains diverse biological assemblages, and provides valuable ecosystem services (Foster and Schiel, 1985; Costanza et al., 1997; Carr and Reed, 2015). The occurrence of periodic warm oceanographic events, such as El Niño, which tend to generate warm and nutrient-poor environmental conditions, as well as episodic strong storms that dislodge *M. pyrifera* individuals (Dayton, 1985; Foster and Schiel, 1985; Byrnes et al., 2011), can cause the decrease or

loss of *M. pyrifera* forests (Dayton and Tegner, 1984; Foster and Schiel, 1985; Zimmerman and Robertson, 1985; Edwards, 2004), and alter the structure of entire communities (Dayton and Tegner, 1984; Dayton et al., 1984, 1992; Tegner and Dayton, 1987; Schiel and Foster, 2015).

Kelp forest ecosystems located near temperate-subtropical transition zones, where conditions are more variable and extreme, are more vulnerable to warming events than those found at higher latitudes (Steneck et al., 2002; Edwards, 2004; Edwards and Estes, 2006; Johnson et al., 2011; Wernberg et al., 2013, 2016; Vergés et al., 2014). During El Niño 1997–1998, in the CCS, almost all of Baja California's *M. pyrifera* forests disappeared, and while heavy losses were reported for central California, only minor impacts were observed for northern California (Edwards, 2004; Edwards and Estes, 2006). *M. pyrifera* forests are resilient to disturbance and quickly recover after catastrophic events due to their rapid responses to changes in nutrient supply, short lifespans, rapid growth rates, constant spore production, and propensity to generate a bank of microscopic stages that endure stressful conditions (Dayton et al., 1992; Reed et al., 1996; Lada et al., 1999; Filbee-Dexter and Scheibling, 2014). Also, during El Niño 1997–1998, recovery rates for *M. pyrifera* were slower in Baja California than in central and northern California (Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006). The secular trend toward increasing temperatures might be challenging the capacity of *M. pyrifera* forests to recover near their southern (warm) limit in the CCS. This notion is supported by observations that their historical southern distribution edge has already suffered considerable poleward range contraction (Hernandez-Carmona et al., 2000), and that they might continue to contract poleward due to climate change.

Long-term, large-scale monitoring programs have proven to be extremely valuable to understand the response of complex marine ecosystems to extreme environmental changes (Hughes B. B. et al., 2017). But the high cost of collecting ecological data is shifting research efforts toward studies of sentinel species for climate change (early indicators of climate change), such as *M. pyrifera* (Krumhansl et al., 2016; Reed et al., 2016). It is particularly valuable to monitor such species when located in sentinel areas for climate change, that is regions such as Baja California, where ocean surface temperatures have changed rapidly, and are projected to continue to do so (Hobday and Pecl, 2014). Despite the sensitivity of Baja California's kelp forest to warming events (Hernández Carmona, 1988; Lada et al., 1999; Hernandez-Carmona et al., 2001; Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006; Torres-Moye et al., 2013; Beas-Luna and Lada et al., 2014; Woodson et al., 2018), they have received far less attention than those further north (Ramírez-Valdez et al., 2017). Moreover, given the relevance of kelp forests near the southern end of their distributional range, understanding changes associated with an extreme environmental event might provide insights into how climate change will alter kelp forest ecosystems in the CCS.

Islands are vulnerable environments, where isolation can preclude recovery after an extreme event due to restricted adult migration, and larval input (Johnson and Black, 2006; Bell, 2008), making them good candidate sites in which to

study ecosystem responses to MHWs. In December 2016, the Mexican government declared all Islands in the Pacific Coast of Baja California as a biosphere reserve. This action made them priority areas for conservation in the region, raising the need to understand the consequences of extreme events, which can endanger ongoing protection efforts in these vulnerable marine ecosystems.

The goal of this study is to provide a comprehensive report on the ecological impacts of the 2014–2016 warming event in the southern kelp forest communities of the CCS. We selected three islands, separated from each other at roughly 125 km intervals, to represent a latitudinal gradient off the coast of Baja California, and documented changes in community attributes from before to after the MHWs. We hypothesized that *M. pyrifera* kelp forests would suffer greatest impacts from the MHWs at the southernmost locations, since these are closer to the warm edge of their distribution limit, and that these changes would be reflected in the assemblage structure of invertebrates, fish, and algae.

MATERIALS AND METHODS

Study Sites

Our study sites encompass three inhabited islands that are part of the Baja California Pacific Islands biosphere reserve in Mexico: Isla Todos Santos (ITS), Isla San Martin (ISM), and Isla San Jeronimo (ISJ) (**Figure 1**). Located in the CCS, these islands stretch along a 250 km latitudinal gradient (29.8°–31.8°N) near the southern biogeographic distribution limit of boreal populations of *M. pyrifera*. They are internationally recognized for their high diversity, the abundance of their flora and fauna, the relative natural integrity of their ecosystems, and their high levels of endemism (Samaniego-Herrera et al., 2007). The marine areas adjacent to these islands, support various fisheries, most of them targeting species dependent on *M. pyrifera* as a source of food and habitat (Montaño-Moctezuma et al., 2014).

Sea Surface Temperature

We obtained satellite-derived data of sea surface temperature by using the GHRST Level 4 AVHRR Optimally Interpolated Global Blended Sea Surface Temperature Analysis (GDS version 2), from the National Centers for Environmental Information (2016), available at the physical oceanography distributed active archive center (PODAAC) of the NASA Jet Propulsion Laboratory (Last access: 2019-01-19). Daily sea surface temperature data are available at a 0.25° spatial resolution for 37 years (from September 1981 to present) (Reynolds et al., 2007; Banzon et al., 2016). To have a historical perspective of the strength of the 2014–2016 warming event, we calculated sea surface temperature anomalies for each 0.25° grid cell by subtracting the 1982–2018 local mean. We used a Fourier low-pass filter to show the contribution of interannual (basin-scale) processes (e.g., El Niño and the Blob) by removing signals with periods shorter than 18 months (cut off frequency), retaining inter-annual variability.

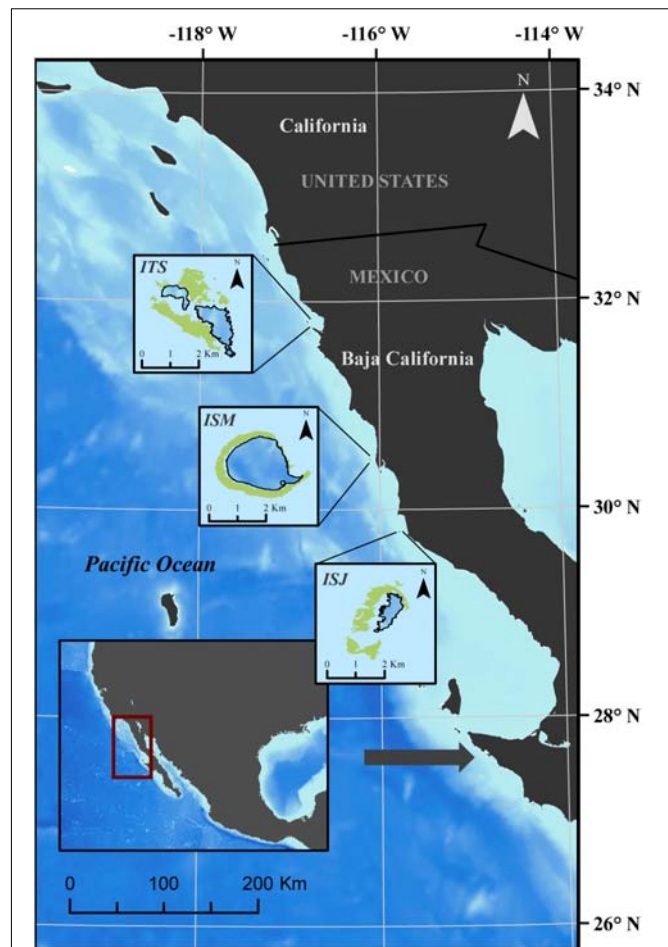


FIGURE 1 | Location of Isla Todos Santos (ITS), Isla San Martin (ISM), and Isla San Jeronimo (ISJ) in Baja California, Mexico. Green polygons in the insets represent *M. pyrifera* beds at the three islands. The dark arrow in the main figure shows the southern distribution limit of *M. pyrifera* in the CCS.

MHWs

We identified MHWs, defined by Hobday et al. (2016) as discrete prolonged anomalously warm-water events in a location, using the same daily sea surface temperature database for the 1982–2018 period. As with other studies of MHWs, we focused on upper percentiles of SSTAs, rather than on absolute SSTs. This approach accounts for the likelihood that marine populations are adapted to local temperature conditions, with anomalies indicating deviation from normal conditions that might elicit location-specific responses to thermal stress. We used the Matlab toolbox (Zhao and Marin, 2019) to identify periods of time where temperatures were above the 90th percentile threshold relative to the climatology (seasonally varying mean), and with a duration of at least 5 days. We identified the start and end dates and calculated the duration and intensity for each MHW event.

Biological Monitoring

We collected ecological data from the three islands. At each island, two sampling sites were selected (i.e., northern and

southern sites). Within each of these sites, we used underwater survey techniques (depth ranges of 10–15 m) to characterize the assemblages of invertebrates, fish, and algae at three transects. Data were collected by experienced, trained divers to ensure constancy in survey methods, and species lists compiled over the years. We estimated abundance of *M. pyrifera* and fish *in situ* by census transects and assessed abundance of invertebrates and algae by analyzing video transects. To corroborate the results of the *in situ* estimate of *M. pyrifera* abundance and better understand the effects of the MHWs, we estimated kelp biomass using remote-sensed Landsat imagery. We conducted the field surveys in late autumn 2013 and 2016, but due to bad weather in 2016, we had to extend the field work to early winter 2017 (henceforth “2016”).

Census Transects

For each island and year, we conducted three fish transects of 30 m × 2 m (60 m²) at each sampling site (six transects in total). Divers recorded identity and abundance of fish species along each transect. To assess the importance of the MHWs for fish species with different thermal affinities, we classified fish species from north to south, based on the centroid of their latitudinal distribution (FishBase). We evaluated the density of *M. pyrifera* by counting all the individuals (sporophytes), taller than 1 m, and the number of fronds (also known as stipes) per individual (measured above the holdfast), reporting the number of individuals per unit area. In 2013, we counted the number of *M. pyrifera* fronds along the transects in a sub-sample of randomly picked 9 individuals: three at the beginning of the transect (0–10 m), three at 10–20 m, and three at 20–30 m. In 2016, we counted the fronds for all *M. pyrifera* individuals found along the transect.

Video Transects

For each island and year, we conducted three video transects at each sampling site (six transects in total). In 2013, the transects were 10 m × 1.5 m (15 m²), while in 2016 they were 20 m × 2 m (40 m²). We analyzed each video transect to estimate the number of individuals of all invertebrate species. We grouped algae into subcanopy, introduced and understory species, and reported as numbers of individuals per square meter for the subcanopy and introduced species (to account for different sampled areas). We grouped understory algae into coralline crustose, coralline articulated, red crustose, red branch, and brown algae and estimated per cent cover of each group by using the ImageJ software (Schneider et al., 2012). For this group, we manually captured images from the video transects in VLC Media Player software and improved if necessary with Microsoft Office Picture Manager 2010. Then we estimated the total area of each picture based on an object of known size. Finally, we manually selected the area covered by each algal group, and the software calculated the total area for each group as a percentage cover.

Satellite Images

We used multispectral Landsat imagery to estimate *M. pyrifera* canopy biomass at 30-m resolution for a 10-year period (from January 1, 2009 to December 31, 2018) following

Cavanaugh et al. (2011). We analyzed each atmospherically corrected Landsat image using multiple endmember spectral unmixing (MESMA) (Roberts et al., 1998). This analysis enables estimates of kelp canopy area and biomass using observed relationships between MESMA-derived canopy fractions and diver-measured canopy biomass (Cavanaugh et al., 2011). These relationships were developed using data from the Santa Barbara Channel. There are 2 Landsat “scenes” that cover our study sites, and each scene has about 60 images between 1984–present, allowing us to determine seasonal canopy biomass for each 30 m × 30 m pixel.

Statistical Analysis

For all analyses comparing data collected before and after the MHWs, we used the parallel approach of modeling the response as a function of the crossed fixed factors Island (three levels: ITS, ISM, and ISJ) and Time (two levels: Before and After). In each instance, we assumed the six replicates taken at each time at each island (three replicates taken from two sites at each island) to comprise an independent, representative sample for that island. For univariate counts, we fit generalized linear models (GLMs) with Poisson errors, and simplified these based on standard log-likelihood ratio tests. For these models, we assessed approximate significance of pair-wise differences based on 95% confidence intervals. For multivariate responses, we used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) in the R package *vegan* (Oksanen et al., 2013) on the basis of Bray-Curtis distance matrices derived from square-root transformed data, and used non-Metric Multidimensional Scaling (nMDS) to visualize multivariate patterns in community structure. Where *post hoc* tests were required, we employed pairwise PERMANOVAs, with false-discovery-rate adjustment for multiple tests (Benjamini and Hochberg, 1995), using functions in the R package *RVAideMemoire* (Hervé, 2018). We used Dufrene-Legendre Indicator Species Analysis (Dufrene and Legendre, 1997) to distinguish which species were contributing to significant clusters identified by these *post hoc* tests, using functions from the R Package *labdsv* (Roberts, 2018).

The time series of Landsat estimates of kelp biomass were the only long-term data available to explore whether observations from the period after the MHWs were beyond the bounds of natural variation for the period before the MHWs. We could not use standard linear modeling approaches in this instance, because observations would be expected to contain significant temporal autocorrelation, violating assumptions of independence. We therefore used automatic algorithms from the R package *tsoutliers* (López-de-Lacalle, 2019) to detect outliers from ARIMA (0,1,1) time series fitted to the log₁₀(x + 1)-transformed data from each island. This approach has the advantage over a random walk model of smoothing the fit using an exponentially weighted moving average of preceding values, rather than placing excessive emphasis on the most recent observation. Outliers detected in this way can be assumed to arise from a process not inherent to that which generated the other observations in the time series (i.e., they are outside the natural variation associated with the time series).

We programmed all analyses in R version 3.5.2 (R Core Team, 2013), setting $\alpha = 0.05$.

RESULTS

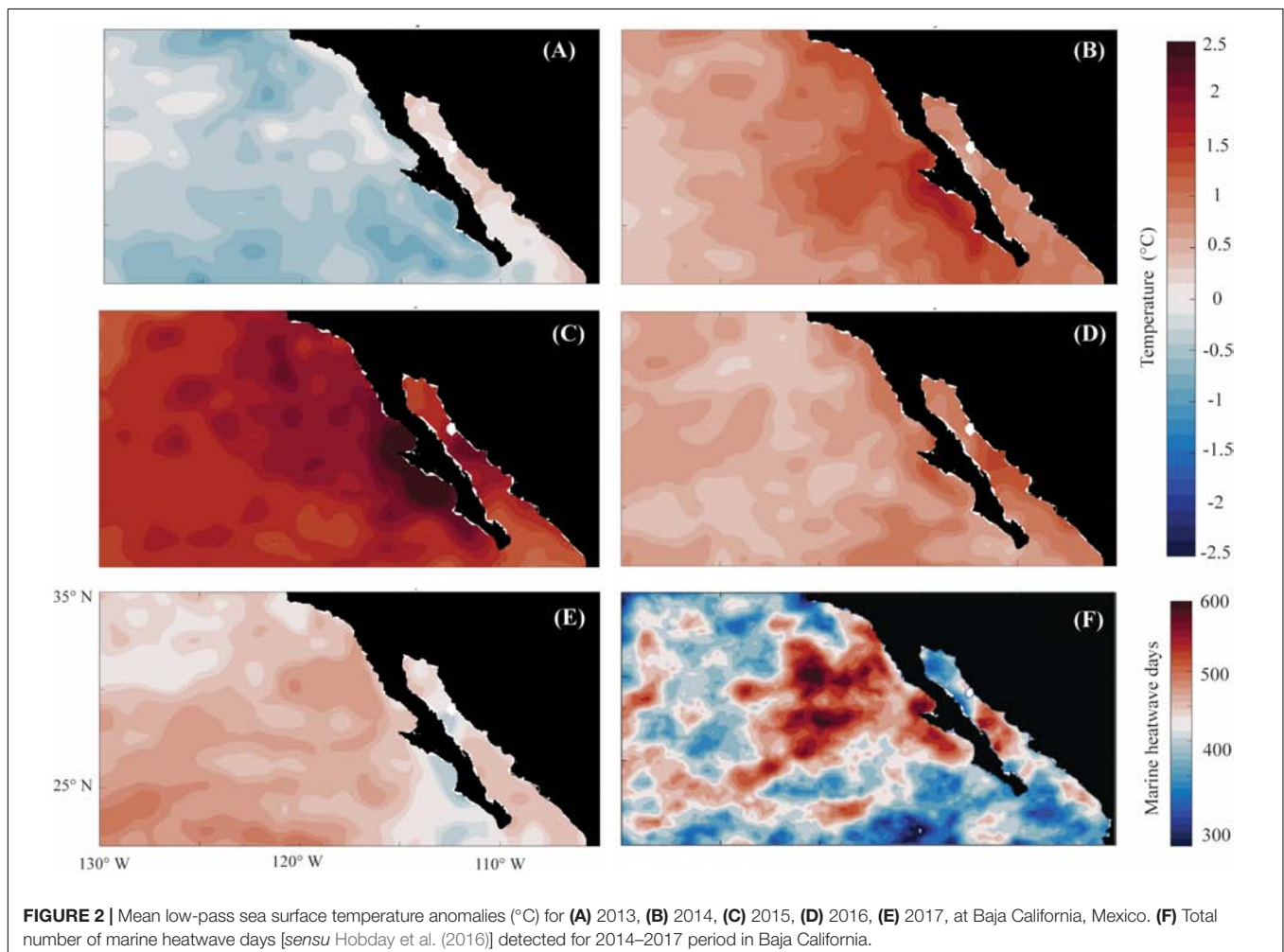
Sea Surface Temperature Changes

Along the Baja California coast, 2013 was in a slightly cold stage, with negative (cold) anomalies and no evidence of the “Blob” (Figure 2A), until 2014, when the warming event became evident (Figure 2B). By 2015, the additional El Niño effect boosted the warm anomalies and extended their distribution offshore and along the coastal waters of Baja California (Figure 2C). Toward the end of 2016, this effect had weakened (Figure 2D), but warm water anomalies remained throughout 2017 (Figure 2E and Supplementary Figure S1). After removing the annual cycle, the average low-pass anomalies were more than 1°C warmer than the extreme El Niño 1982–1984 and 1997–1998 events (Supplementary Figure S1). The 2014–2016 warm-event anomaly registered on the three islands was the largest in extent and most prolonged in duration observed to date, with SSTAs slightly lower at

the northernmost site (ITS) than the southernmost sites (ISM and ISJ), with anomalous temperatures peaking on summer 2015 at 2.15, 2.32, and 2.39°C above average, respectively (Supplementary Figure S1).

Marine Heatwaves

Around 50% of the identified MHW days between 1982–2017 registered at the three study sites occurred during 2014–2017 (Figure 2F and Supplementary Figure S3A). The period 2014–2015 accounted for 545 MHW days at ITS (58%), 466 at ISM (51%), and 476 at ISJ (53%) (Figures 3A,C). The year with the highest number of MHW days registered was in 2015 for ITS (261 days), ISM (242 days) and ISJ (256 days) (Figures 3A,C). For ITS, the longest continuous MHW comprised 152 days, lasting from November 2014 until late April 2015, while ISM and ISJ registered events lasting 123 and 124 consecutive MHW days, respectively, between late August and late December 2015 (Supplementary Tables S1–S3). In autumn 2015, the highest maximum temperature during a MHW were identified for the three islands, peaking at 5.6, 5.9, and 5.7°C, respectively (Figures 3A,B and Supplementary Tables S1–S3). These values are higher than the maximum registered during previous strong



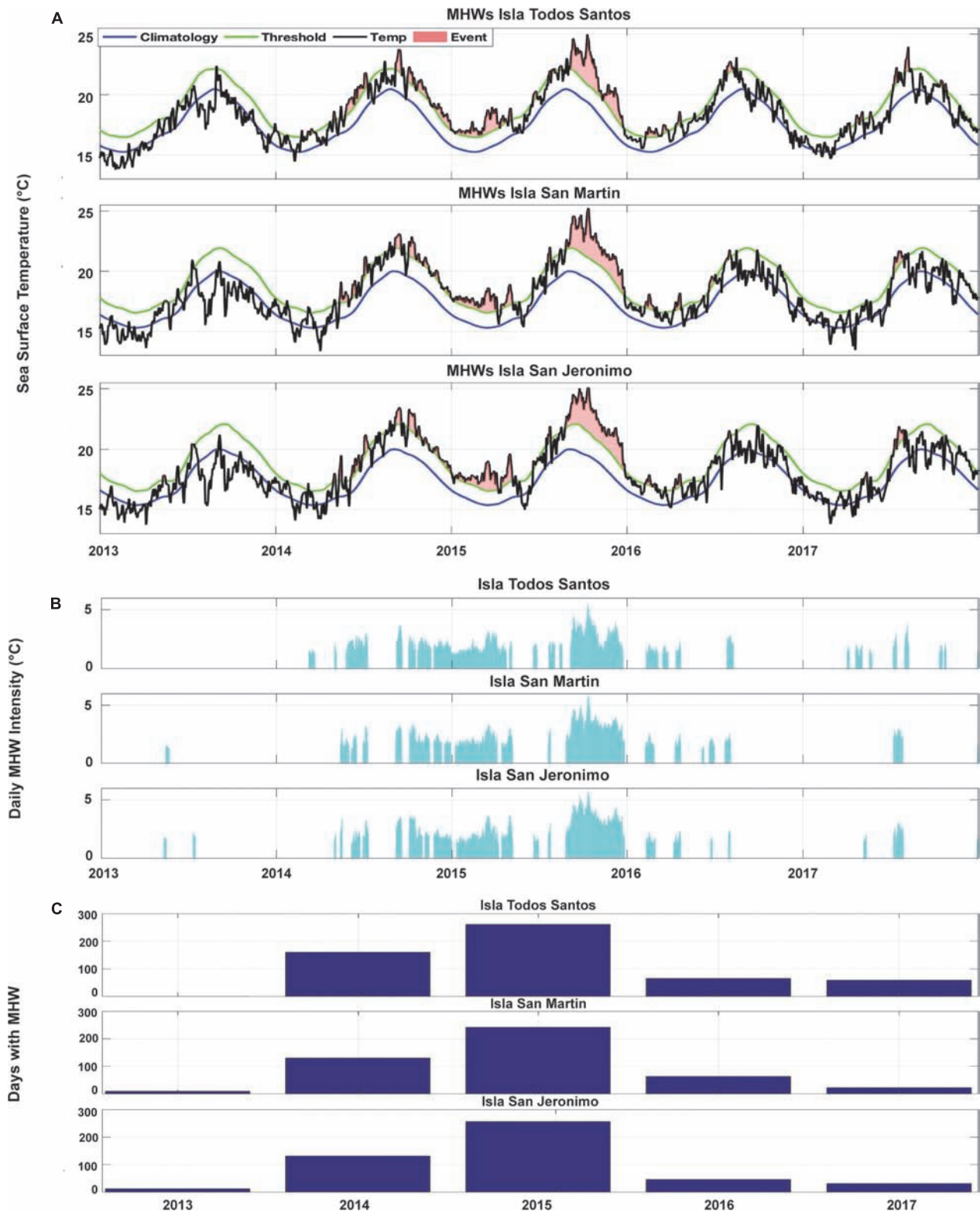


FIGURE 3 | (A) Blue lines indicate the sea surface temperature (SST) climatology, green lines represent the 90th percentile that defines a marine heatwave (MHW), black lines are the SST time series, and the orange shaded region indicates all MHWs identified. **(B)** The daily MHW intensity, **(C)** the number of MHW days registered during 2013–2017 for Isla Todos Santos, Isla San Martin, and Isla San Jeronimo.

1982–1984 (4.1, 3.3, and 3.3°C) and 1997–1998 El Niños (3, 3.4, and 3.7°C) (Supplementary Figures S2, S3B).

Changes in *Macrocystis pyrifera*

We detected significant interactions between Island and Time in our Poisson GLMs models of the numbers of *M. pyrifera* individuals per transect as well as the numbers of fronds per individual before and after the MHWs (Table 1). For the northernmost island, ITS, the number of individuals increased significantly after the MHWs. In contrast, we found significant decreases at the southern islands, ISM and ISJ, with only a few individuals per transect observed after the MHWs (Figure 4A). For all the islands we found a strong, consistent and significant decline in the numbers of fronds per *M. pyrifera* individual (Figure 4B).

Remote-sensed kelp biomass estimates were highly variable, but we clearly detected the MHWs signal at both ISM and ISJ (Figure 4C). As was the case for number of *M. pyrifera* individuals (Figure 4A), kelp biomass at ITS contrasted from the pattern at ISM and ISJ, although in this case, the time series analysis suggested no long-term trend (Figure 4C). Irrespective, it was clear that kelp biomass during and after the MHWs at the southernmost islands, ISM and ISJ, was well beyond the bounds of natural variability observed prior to the MHWs. Qualitatively, satellite-derived kelp biomass estimates allowed us to document the loss of the kelp forests during the MHWs at all islands. Immediately after summer 2015, the satellite images did not detect kelp at the surface of the three islands, and the biomass remained negligible until the end of 2016 (Figure 4C). By winter and spring 2017, kelp biomass at ITS had recovered to previous seasonal values, but at ISM and ISJ there was no recovery, and values stayed very low until the end of the time series (end of 2018). Note that very low values of biomass do not necessarily mean that the kelp forest completely disappeared, since satellite images do not detect sub-surface smaller individuals.

TABLE 1 | Results from the analysis of deviance variance for Poisson generalized linear models (A) for the number of *M. pyrifera* individuals per 60-m² transect, (B) for the number of fronds per *M. pyrifera* individuals, and (C) for species richness of the fish and invertebrate assemblage.

Factors	DF	Deviance Resid	Df	Resid. Dev	Pr(> Chi)
(A) <i>M. pyrifera</i> individuals					
Island	2	238.13	32	911.38	2.20E-16
Time	1	70.09	31	841.28	2.20E-16
Island × Time	2	488.86	29	352.43	2.20E-16
(B) Number of fronds					
Island	2	37.85	312	2834.2	6.03E-09
Time	1	1093.59	311	1740.5	<2.2E-16
Island × Time	2	19.51	309	1721.0	5.79E-05
(C) Species richness					
Island	2	11.13	32	67.168	3.83E-03
Time	1	40.737	31	26.432	1.74E-10
Island × Time	2	2.391	29	24.040	3.03E-01

Community Changes

Fish and Invertebrates

For the combined fish and invertebrate assemblages, our Poisson GLM of species richness (Figure 5A and Table 1) found significant and consistent declines from before to after the MHWs at all islands (significant main effect for Time). Species richness was significantly higher at ITS than the more-southerly islands (significant main effect for Island), but the analysis revealed no evidence that this decline differed by Island (no significant Time × Island interaction). Proportionally, we observed similar reductions for fish and invertebrate species richness at ITS (57 and 54%, respectively), but the decline in invertebrate species richness was greater at ISM (39 and 53%) and it was dramatic at ISJ (41 and 81%) (Figures 6, 7).

Corresponding multivariate analysis of assemblage structure for fish and invertebrates (PERMANOVA) (Table 2) and associated *post hoc* tests (Supplementary Table S4A) revealed not only differences among islands and among times, but that the magnitude of the multivariate difference from before to after the MHWs differed by island (significant Time × Island interaction). The nMDS biplot shows clear differences in assemblage structure from before the MHWs to after (Figure 5B). *Post hoc* tests confirmed that significant changes in assemblage structure occurred from before the MHWs to afterward at each island ($p < 0.043$). Because we are most interested in species characterizing the periods before and after the MHWs (rather than differences among islands), we identified species with significant indicator-species values characteristic of these periods (Supplementary Table S6). Before the MHWs, assemblages were characterized by four fish species and fourteen invertebrate species (with the first five most important invertebrate species being more important indicator species than any of the fish). In accordance with the declining species richness in surveys after the MHWs, this period was characterized by four fish species and only one invertebrate species (Supplementary Table S6).

The loss or decrease of many species with cool-water affinities and the increase or appearance of some warm-affinity species (two species appeared after the MHWs) (Figure 6) drove the fish assemblage changes. The ten species exhibiting the northernmost distributions (based on their latitudinal centroid) (Supplementary Table S5) were absent at the three islands after the MHWs. All *Sebastes* species, except *S. atrovirens* and *S. serripes* (which registered only one individual of each species at ITS in 2016), disappeared from the islands. *S. atrovirens* and *S. serripes* are the most southerly of the *Sebastes* species recorded here, with distribution centroids in central California to central Baja California, compared to other *Sebastes* spp., which have centroids from northern California up to Alaska (FishBase). The three-characteristic fish species before the MHWs, *Oxylebius pictus*, *Rhinogobiops nicholsii* and *Rhacochilus toxotes* (Supplementary Table S6), have a centroid distribution from Oregon, north California and south California, respectively. Of the four-characteristic species after the MHWs, *Halichoeres semicinctus*, *Hypsypops rubicundus*, *Paralabrax clathratus* and *Semicossyphus*

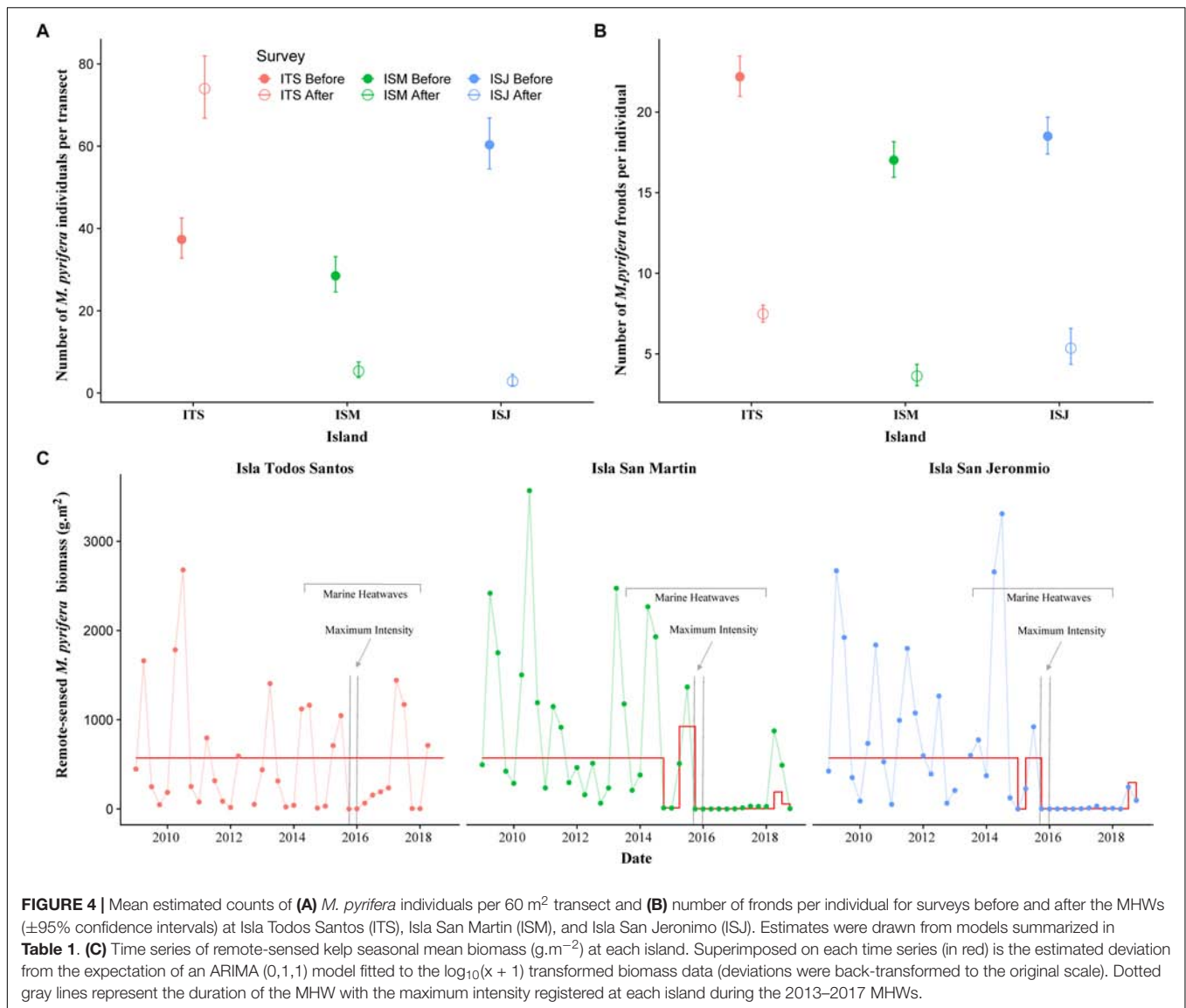


FIGURE 4 | Mean estimated counts of **(A)** *M. pyrifera* individuals per 60 m² transect and **(B)** number of fronds per individual for surveys before and after the MHWs ($\pm 95\%$ confidence intervals) at Isla Todos Santos (ITS), Isla San Martin (ISM), and Isla San Jeronimo (ISJ). Estimates were drawn from models summarized in **Table 1**. **(C)** Time series of remote-sensed kelp seasonal mean biomass (g.m⁻²) at each island. Superimposed on each time series (in red) is the estimated deviation from the expectation of an ARIMA (0,1,1) model fitted to the log₁₀(x + 1) transformed biomass data (deviations were back-transformed to the original scale). Dotted gray lines represent the duration of the MHW with the maximum intensity registered at each island during the 2013–2017 MHWs.

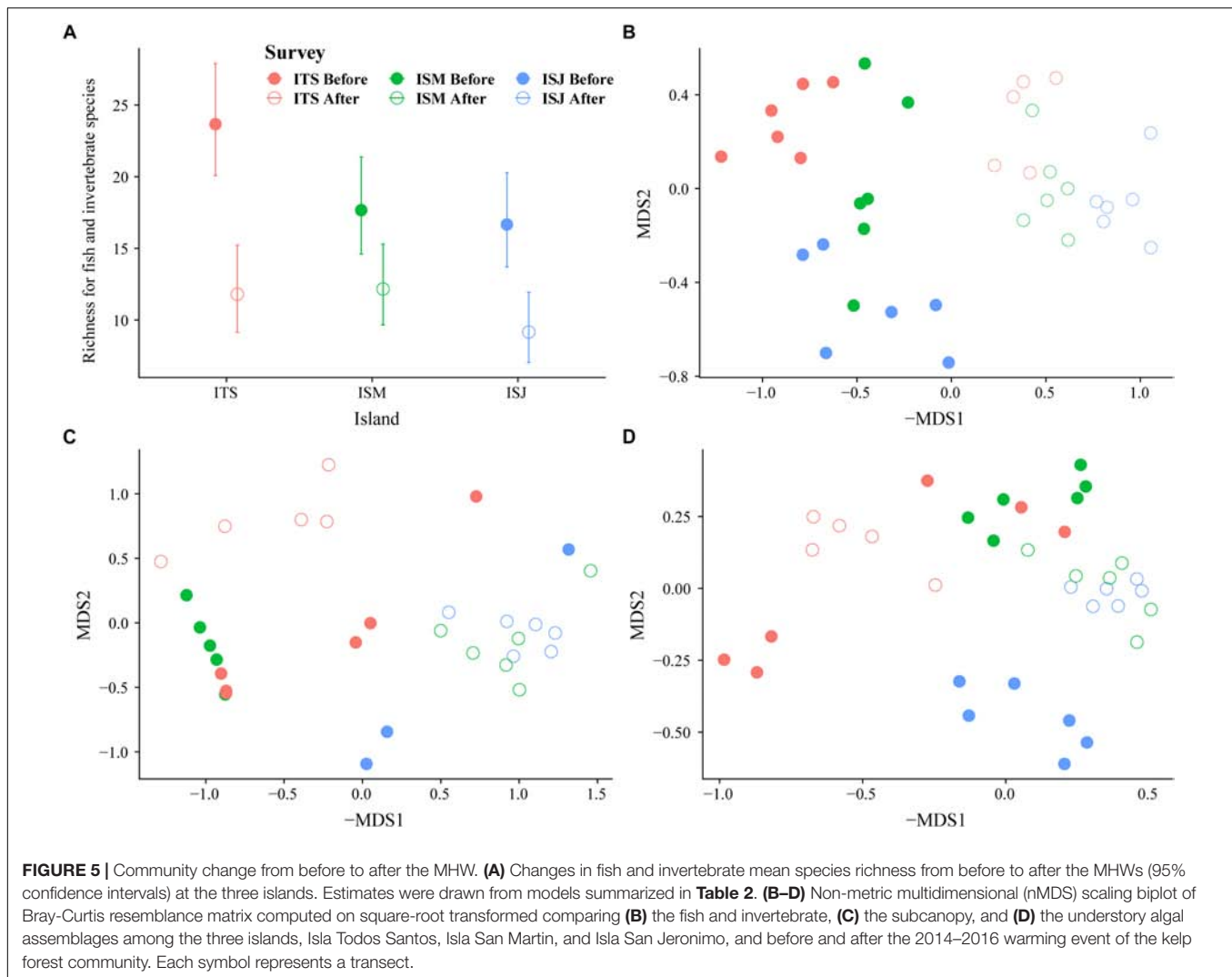
pulcher, all except *P. clathratus* have a southerly distribution, with centroids from northern to central Baja California (**Supplementary Tables S5, S6**).

A generalized decrease in species richness drove invertebrate assemblage changes (**Figure 7**). The number of species in all studied taxonomic groups declined from before to after the MHWs, with the loss of almost all sessile invertebrate species, especially cnidarians. Non-sessile species were also negatively affected. The number of echinoderm species decreased at ITS and ISM, with a notable decline at ISJ, where no echinoderms were present after the MHWs (**Figure 7**). Both red (*Mesocentrotus franciscanus*) and purple urchin (*Strongylocentrotus purpuratus*) densities decreased at ITS and ISM, while *Centrostephanus coronatus*, absent before the MHWs, appeared after at both islands (**Figure 7**). The starfish *Henricia leviuscula* and *Patiria miniata* were common before the MHWs, and almost disappeared afterward; furthermore, *Pisaster*

giganteus disappeared from all islands (**Figure 7**). The only invertebrate species that was characteristic after the MHWs is *C. coronatus* (**Supplementary Table S6**), which has a southern distribution from southern California, United States, to the Galapagos Islands, Ecuador.

Subcanopy and Understory Algae

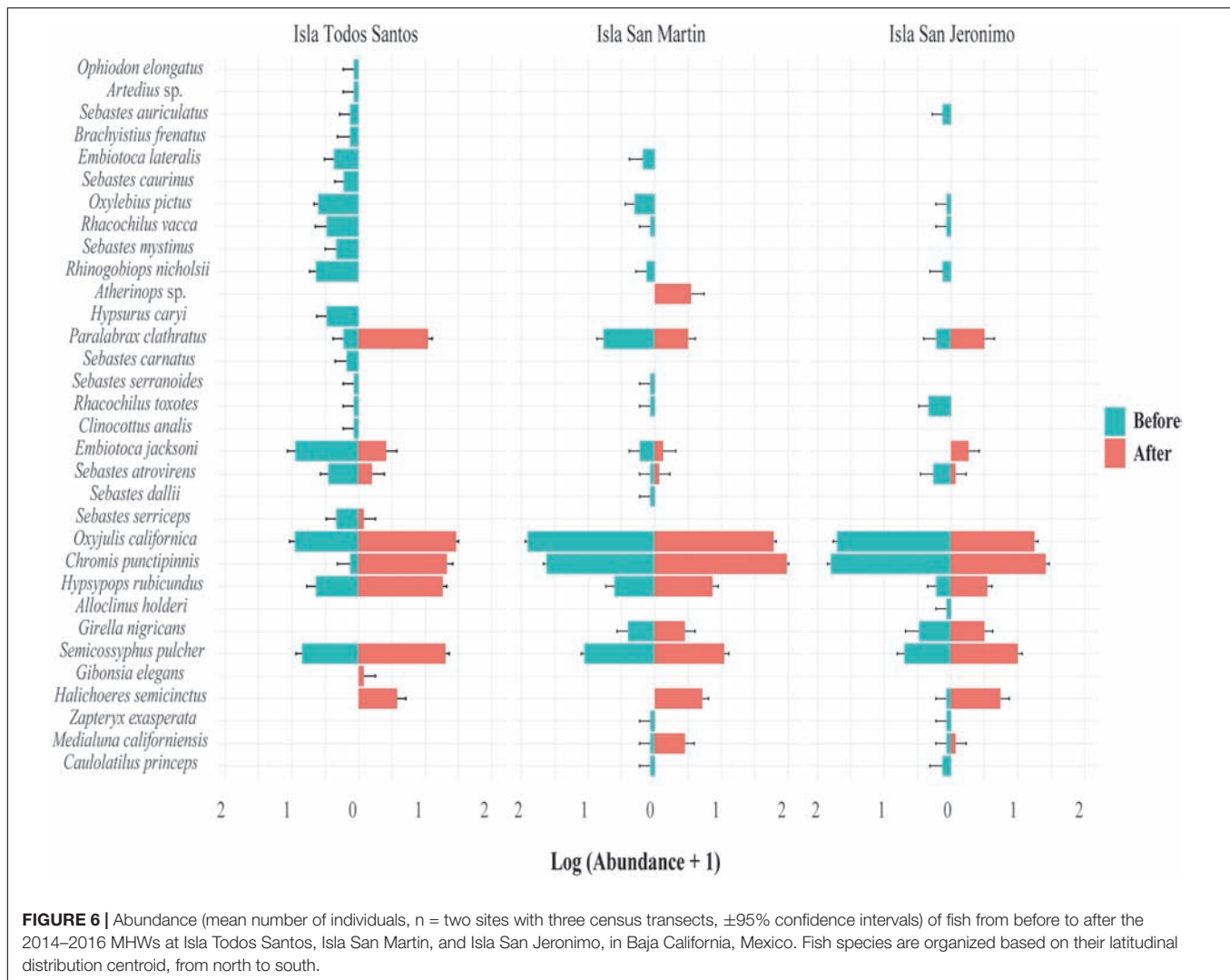
For both subcanopy and understory algae, PERMANOVA revealed not only that the assemblage structures differed significantly from before to after the MHWs ($p < 0.0135$ and 0.0063 for subcanopy and understory species, respectively), but also that the magnitude differed by island (**Table 2**). This pattern was reflected in corresponding nMDS biplots (**Figures 5C,D**) and associated *post hoc* tests (**Supplementary Tables S4B,C**). For subcanopy assemblage structure, only ISM and ITS differed significantly ($p = 0.0086$) before the MHWs (largely due to the substantial variability in assemblage structure within



islands – **Figure 5C**). After the MHWs, assemblage structure differed significantly among ITS and the southernmost islands ($p = 0.0086$), but not between ISM and ISJ. For understory species, assemblage structure differed significantly among islands before the MHWs ($p < 0.0298$) and afterward ($p < 0.0063$), except between the southernmost islands. The limited number of species in each of these analyses meant that there were few significant indicator species in each instance. Previously absent introduced algae species, *Undaria pinnatifida*, appeared after the warming event at ITS, and *Sargassum hornerii* at ISM and ISJ (**Figure 8A**). For subcanopy species, *Laminaria farlowii* was characteristic of assemblages before the MHWs, while *Ecklonia arborea*, *Cystocira* sp., and the introduced *S. hornerii* were characteristic afterward (**Figure 8A** and **Supplementary Table S6**). For the understory algal assemblages, red crustose algae were characteristic before the MHWs, with brown algae and articulated coralline species characteristic afterward (**Figure 8B** and **Supplementary Table S6**). In the three islands, the percent cover of non-coralline crustose algae increased after the warming event (**Figure 8B**).

DISCUSSION

Anthropogenic climate change is expected to remain one of the main threats to biological systems throughout the 21st century (Thomas et al., 2004; Pereira et al., 2010; Pecl et al., 2017), making it a central theme in ecology, and challenging science to understand and predict ecosystems' responses to these changing conditions. Among the manifestations of climate change is the intensification of MHWs (Oliver et al., 2018), with corresponding impacts reported globally in different taxonomic groups and geographic areas (Garrahou et al., 2009; Marba and Duarte, 2010; Smale and Wernberg, 2013; Voerman et al., 2013; Short et al., 2015; Cavole et al., 2016; Oliver et al., 2017; Tuckett et al., 2017; Ruthrof et al., 2018; Smale et al., 2019). In this context, it is relevant to identify and monitor those areas where sentinel species for climate change are more responsive to warming and to MHWs in particular, such as near warm edge distribution limit. We evaluated changes in the kelp forest community structure after the extreme 2014–2016 warming event, near the southern distribution limit of *M. pyrifera* in the CCS. The timing of this



study revealed the sensitivity of our study sites to the MHWs, with loss of *M. pyrifera* forests and significant assemblage changes for fish, invertebrates and algae.

MHWs and the Loss of *M. pyrifera*

The 2014–2016 warming was the most intense and sustained event, with the highest percentage of MHW days registered, in the 37-year historical series for the CCS. Contrary to past El Niños, which appeared after negative temperature anomalies, the strong 2015–2016 El Niño began with an already warmer ocean (“Blob”) (Jacox et al., 2016). The unprecedented combination of these two events preceded the loss of *M. pyrifera* after summer of 2015, corresponding with the maximum temperature anomalies, which peaked at 5.9°C warmer than the climatology (this heatwave lasted for around 4 months). These anomalies were ~2°C warmer than any previous registered (El Niños), most likely with temperatures exceeding physiological thresholds for growth, survival, and reproduction of *M. pyrifera* (Zimmerman and Robertson, 1985; Hernández Carmona, 1988; Tegner et al., 1997; Hernandez-Carmona et al., 2001). The absence of significant

wave disturbance during this event (Reed et al., 2016) suggests a combination of thermal stress and nutrient-poor waters (Whitney, 2015) as the primary drivers behind kelp canopy disappearance in Baja California. Our results are consistent with previous work that reports the sensitivity of *M. pyrifera* in southern California and Baja California to warm, nutrient-poor waters (Zimmerman and Kremer, 1984; Hernandez-Carmona et al., 2001) during El Niño events (Dayton and Tegner, 1984; Dayton, 1985; Zimmerman and Robertson, 1985; Tegner and Dayton, 1987, 1991; Hernández Carmona, 1988; Tegner et al., 1996; Ladah et al., 1999; Hernandez-Carmona et al., 2001; Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006).

Reed et al. (2016) found no ecosystem effects in *M. pyrifera* kelp forests at Santa Barbara, California, to the same extreme warming event. They argued that the variability of giant kelp biomass was high during the 15 studied years and that the observed decline was within normal variability. However, fewer impacts to kelp forests located at Santa Barbara are expected since they are located ~1000 km north of the southern

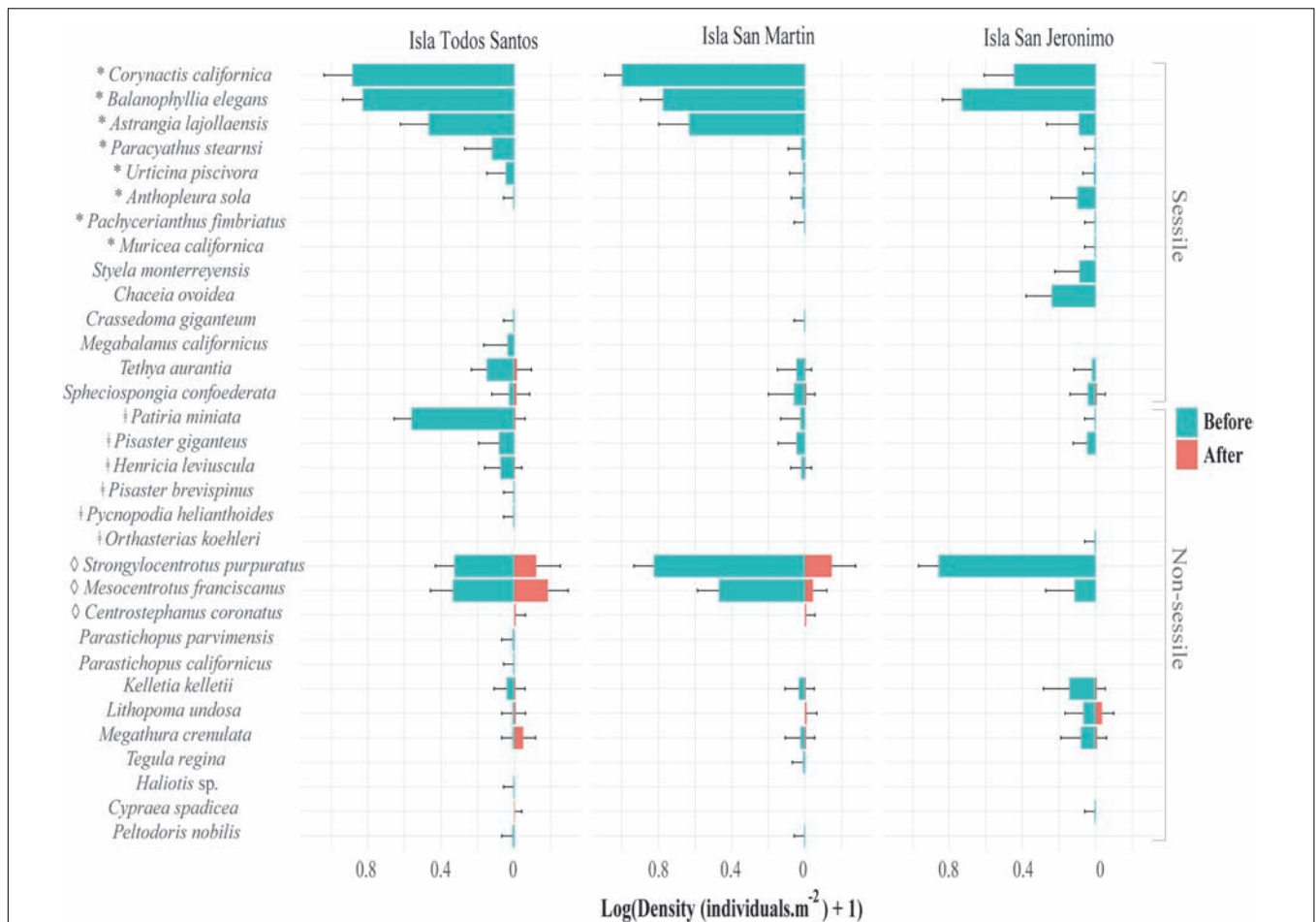


FIGURE 7 | Density of invertebrate species (mean number of individuals.m⁻², n = two sites with three video transects, ±95% confidence intervals) from before to after the 2014–2016 MHWs at Isla Todos Santos, Isla San Martin, and Isla San Jeronimo, in Baja California, Mexico. *Represents cnidaria species, ‡ sea star species, and ◇ sea urchin species.

distribution limit (i.e., the upper limit of thermal tolerance of *M. pyrifera*). There, average SSTs are ~3.3°C cooler than at our study sites, providing a greater population-level thermal safety margin (Pinsky et al., 2019). We found similar results in our northernmost site, ITS, located ~400 km south of Santa Barbara (nevertheless satellite derived biomass estimates remained very low during autumn 2015 and all 2016). However, in the southernmost sites, ISM and ISJ, located 550 and ~650 km south of Santa Barbara, respectively, we clearly detected the MHWs signal on *M. pyrifera* forests. Thus our results support previous studies in the CCS and other regions (Edwards, 2004; Edwards and Estes, 2006; Johnson et al., 2011; Wernberg et al., 2013, 2016; Horta e Costa et al., 2014), which reported kelp forest located near temperate-subtropical transition zones to be more vulnerable to historical warming events than those at higher latitudes. For example, following the MHWs of 2011 in Western Australia, Wernberg et al. (2016) reported a regime shift from a kelp to a seaweed turf dominated ecosystem in sites located near temperate-subtropical transition zones, but little or no change in communities at higher latitudes. Similarly, after 2017/2018

MHWs in New Zealand, Thomsen et al. (2019), found that *Durvillaea* spp. species located at warmer sites were more affected than those found in cooler ones. Although Reed et al. (2016), challenged the status of *M. pyrifera* as a sentinel species for climate change, our work suggests that sentinel status should be evaluated in a site-by-site or regional basis, and reinforces the status of Baja California as a sentinel area for climate change (Hobday and Pecl, 2014).

Macrocystis pyrifera forests in the CCS have proven to be dynamic and resilient ecosystems (Dayton et al., 1992; Filbee-Dexter and Scheibling, 2014), recovering quickly after previous El Niño events. La Niña conditions that usually follow El Niño events bring cold, nutrient-rich waters, representing favorable conditions for *M. pyrifera* (Dayton et al., 1992; Tegner et al., 1997; Edwards and Estes, 2006). The lack of La Niña conditions after the 2014–2016 warming event and the persistence of anomalously high SST during 2017 (around 50 days registered as MHWs) is probably challenging the capacity of *M. pyrifera* to recover.

Nevertheless, after the warming event *M. pyrifera* recovered at ITS, the northernmost site. We found higher densities of

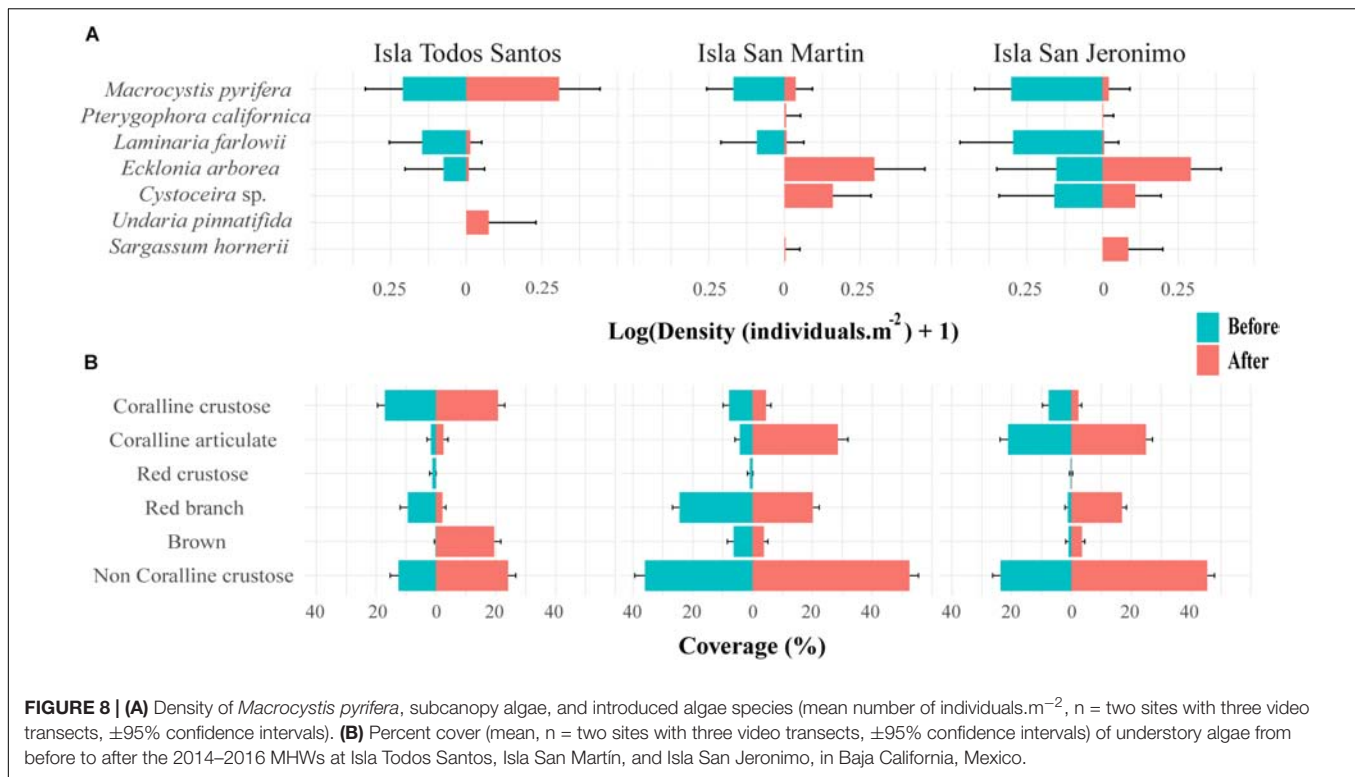


TABLE 2 | Results from the analysis of multivariate variance for PERMANOVAs of response variables as a function of the crossed factors Island and Time based on Bray-Curtis distance matrices derived from square-root transformed data, for (A) density of fish and invertebrate, (B) relative abundance of subcanopy algae, and (C) percent cover of understory algae species per survey.

Factors	Df	Sums of Sqs	Mean Sqs	F. Model	R ²	Pr(>F)
(A) Fish and invertebrates						
Island	2	1.2449	0.62243	7.300	0.17383	0.001
Time	1	2.8081	2.80806	32.934	0.39212	0.001
Island × Time	2	0.6357	0.31786	3.728	0.08877	0.005
Residuals	29	2.4726	0.08526		0.34528	
Total	34	7.1612			1	
(B) Subcanopy algae						
Island	2	1.1518	0.57591	5.0149	0.13323	0.002
Time	1	2.4372	2.43724	21.2231	0.28191	0.001
Island × Time	2	1.8408	0.92040	8.0147	0.21292	0.001
Residuals	28	3.2155	0.11484		0.37193	
Total	33	8.6454			1	
(C) Understory algae						
Island	2	1.22335	0.61168	20.6507	0.43458	0.001
Time	1	0.34778	0.34778	11.7413	0.12354	0.001
Island × Time	2	0.38492	0.19246	6.4975	0.13674	0.001
Residuals	29	0.85899	0.02962		0.30514	
Total	34	2.81504			1	

individuals than before the MHWs, but with significantly lower number of fronds per individual, indicating the dominance of young *M. pyrifera* individuals. The presence of some productive individuals (≥ 16 fronds/individual) implies that *M. pyrifera* did not lose its reproductive capacity, since sporophylls begin

to differentiate and have fertile sori when they have around 16 fronds/individual (Dayton et al., 1992). We found a strong effect of the MHWs on *M. pyrifera* densities and number of fronds per individual at the southernmost sites, ISM and ISJ, suggesting a very low density of fertile individuals. Biomass satellite time-series corroborate that kelp forest at ITS recovered after the MHWs, while at ISM and ISJ biomass values remained below average seasonal values throughout 2018. The three islands have similar mean SSTs, suggesting similar thermal safety margins, however, SSTAs and the maximum intensities registered during the MHWs were slightly higher at the southernmost sites than at ITS, which could explain the different latitudinal responses of the kelp forest to the extreme warming. However, it is also true that the differences in the anomalies were very small ($\sim 0.2^\circ\text{C}$) between islands and other factors such as local seascape complexity, which might create “microclimates” (Woodson et al., 2018; Pinsky et al., 2019), could also contribute to the observed differences. Previous studies found that deeper sites represented local refugia and individuals living there could find and survive strong warming events such as El Niño, possibly serving as a source of spores and recruits to colonized shallower rocky areas (Ladah et al., 1999). Further research could test whether the observed differences are a result of local seascape variability, latitudinal gradients in SSTAs, or perhaps a combination of both.

Community-Level Impacts

The extreme conditions resulted in dramatic changes in the invertebrate, fish, and algal assemblages, with the loss of over half of invertebrate species. The significant reduction or disappearance of *M. pyrifera* can have profound effects on other

members of the community (Graham, 2004) due to a release of resources (space and light) (Reed and Foster, 1984; Dayton, 1985) and a decrease in food availability (Ebeling et al., 1985; Harrold and Reed, 1985). Although we found evident changes, we cannot separate between the effects of high SSTs and loss of canopy on the community, since both are synergistically affecting all food web levels. Importantly, we found that *M. pyrifera* dynamics at the two southernmost islands in our study immediately after the MHWs were beyond the limits of natural variation in the previous 5 years, and remained that way until the end of our study in 2018. Although all other metrics we analyzed represented only two periods, a year before and a year after the MHW, this finding that kelp biomass was significantly and persistently impacted by the MHW gives us some confidence in attributing community-wide impacts to the effects of the MHWs.

Loss of Sessile Invertebrates and Sea Stars

After the warming event, almost all sessile invertebrates disappeared, and all cnidarians were absent. Sessile invertebrates are highly sensitive to extreme temperature conditions due to their inability to escape from unfavorable conditions (Przeslawski et al., 2008) and their dependence on phytoplankton and suspended organic matter as food sources that might decrease during warming events (e.g., during El Niño events, when upwelling is suppressed). Reports of mass mortality of sessile species and bleaching of corals in temperate and tropical ecosystems (Berkelmans and Willis, 1999; Hoegh-Guldberg, 1999; Cerrano et al., 2000; Marshall and Baird, 2000; Perez et al., 2000; Garrabou et al., 2001, 2009; Caputi et al., 2014; Couch et al., 2017; Hughes T. P. et al., 2017) suggest that SSTs at our sites probably peaked at values in excess of their physiological tolerances (Lejeune et al., 2010). Moreover, almost all sea star species disappeared or dramatically decreased their abundance. In 2014, an epidemic outbreak of wasting disease from Alaska to Mexico led to mass mortalities of many sea star species (Hewson et al., 2014). Anomalously warm water conditions in the CCS have been suggested to favor the spread of the densovirus linked to this disease and thus increase the mortality rate in sea stars (Eckert et al., 2000; Hewson et al., 2014).

Loss of Cold-Water Species and Increase in Some Warm Affinity Ones

For the entire community, we report the loss or decrease in abundance of many species with cold-water affinities and the appearance or increase in abundance of some species with warm-water affinities. The tropicalization of fish species near temperate transition zones has already been attributed as the primary driver of composition change in the fish assemblage (Wernberg et al., 2013, 2016; Caputi et al., 2014; Horta e Costa et al., 2014; Vergés et al., 2014; Smale et al., 2019). The loss of the ten fish species having the most northerly distribution centroids suggests SSTs peaked above their thermal tolerances and favored species with stronger affinity to warmer waters, such as *H. semicinctus* (Fishbase). We also reported the presence of the sea-urchin *C. coronatus* at ITS and ISM, which has the southernmost

distribution range of invertebrate species described in this study. Similar patterns favoring *C. coronatus* have been reported during El Niño 2009–2010, where populations in one site at Oaxaca (Pacific southern Mexico) increased (López-Pérez et al., 2016), and during El Niño 2015 in southern California, with reports of poleward range expansion (Freiwald et al., 2016). Another example is a species from the same genus, *Centrostephanus tenuispinus*, which was the main winner after an extreme MHW in 2011 on the west coast of Australia (Smale et al., 2017).

The effect of warm water temperatures was also evident in kelp forest subcanopy species *L. farlowii* and *E. arborea*. *L. farlowii* was the characteristic subcanopy species before the MHWs, probably due to the absence (or very low densities) of the competitively superior *Pterygophora californica* (Tegner et al., 1997). In 2016, abundance of *L. farlowii* dramatically decreased, despite favorable niche conditions (light and space) after the loss of *M. pyrifera* forest. The sensitivity of *Laminaria* species to warm water conditions (Schiel et al., 2004) might explain its decrease after the extreme warming. On the contrary, abundances of *E. arborea*, known to be favored during El Niño conditions due to its tolerance to warm, nutrient-poor conditions (Dayton et al., 1984; Hernandez-Carmona et al., 2000; Matson and Edwards, 2007), increased at the two southernmost islands.

The influence of the warming event on the understory algae was less evident and more variable than for the rest of the community. For the southernmost islands (ISM and ISJ), we found a decrease in cover of coralline crustose algae, which have been reported to be sensitive to MHWs (Martin and Gattuso, 2009; Smale and Wernberg, 2013; Voerman et al., 2013; Wernberg et al., 2013, 2016; Short et al., 2015; Thomsen and South, 2019). However, the role of heatwaves in regulating abundance of coralline algae is still not clearly understood, since other factors, such as the loss of canopy cover (Irving et al., 2004, 2005; Flukes et al., 2014) or ocean acidification (McCoy and Kamenos, 2015), might also be influential for this group. The presence of coralline crustose algae can be facilitated by canopy-forming kelp species as they exclude other macroalgal competitors (Thomsen and South, 2019). This could explain the decrease of this taxon at the southernmost islands after the MHWs, while at the northernmost site, their cover and the abundance of *M. pyrifera* remained high. Little attention has been paid to coralline crustose algae, despite representing important habitats, and food sources for diverse epifaunal invertebrates (Graham et al., 2007; Thomsen and South, 2019), as well as providing chemical cues for abalone settlement (Morse et al., 1979; Miner et al., 2006). A generalized increase in the coverage of non-crustose coralline understory algae at all sites suggests that the combined loss of canopy kelp, sessile invertebrates, and coralline crustose algae might have modified light conditions and liberated free space for recruits (Reed and Foster, 1984), which probably favored the rest of the understory assemblage (Reed and Foster, 1984; Dayton et al., 1992; Tegner et al., 1997; Clark et al., 2004).

The Appearance of Invasive Species

Finally, we report the appearance of two invasive macroalgal species, *U. pinnatifida* at ITS and *S. hornerii* at ISM and

ISJ. In Baja California, *U. pinnatifida* was first detected in 2003 (Aguilar-Rosas et al., 2004) and *S. hornerii* in 2005 (Aguilar-Rosas et al., 2007). In 2013, both species appeared during monitoring surveys at the protected side of the three islands, but were absent from the exposed sides (our study sites) (Montaño-Moctezuma et al., 2014). *U. pinnatifida* is an opportunistic cosmopolitan invasive species (Lowe et al., 2000) able to tolerate a wide range of temperatures (Morita et al., 2003), allowing this species to colonize empty spaces left by canopy-forming kelps. Nevertheless, without disturbance, *U. pinnatifida* rarely establishes under a dense canopy (Valentine and Johnson, 2003; Thomsen and South, 2019; Thomsen et al., 2019). Similar findings have been reported in other parts of the world as a result of both MHWs (Thomsen et al., 2019) and manipulated removal experiments (Thomsen and South, 2019). For example, in summer 2017–2018, strong MHWs in New Zealand caused the decline of the canopy-forming kelp species *Durvillaea* spp., and a successive subsequent invasion by *U. pinnatifida* (Thomsen and South, 2019; Thomsen et al., 2019). Our study supports previous research that opportunistic and invasive species are usually outcompeted by native species, but adverse conditions can leave empty niche space and trigger their expansion (Valentine and Johnson, 2003, 2004; Occhipinti-Ambrogi, 2007; Epstein and Smale, 2017; South et al., 2017). Although it is difficult to predict the long-term effect of invasive species, more frequent MHWs might increase the probability that invasive species colonize and perhaps displace native species.

General Implications

With one-time observation before and after, the ecological changes we describe cannot be confidently attributed to the MHWs. However, we chose our study sites on inhabited islands, since they are less impacted by cumulative human activities (Arafeh-Dalmau et al., 2017) than coastal areas, but are vulnerable ecosystems due to their isolation (Johnson and Black, 2006; Bell, 2008) making them ideal sites to understand kelp forests response to MHWs. Our study sites span a 250-km latitudinal gradient (almost half of the distribution of kelp in Baja California), allowing us to capture a good portion of the biogeographic variability of the region. There is also strong circumstantial evidence that the MHWs were, indeed, the driver of the observed changes: not only was there a corroborating signal in remote-sensed time series of kelp biomass, but we are unaware of any other plausible human-induced changes during the 2013–2018 period that could have altered the community structure in this way. Nevertheless, considering that the response of communities to the same disturbance might vary within the same region (Wernberg et al., 2013, 2016; Thomsen et al., 2019) and even within sites (Woodson et al., 2018), we acknowledge the need to understand the dynamics of these ecosystems at broader spatial and temporal scales and emphasize that our results should not be extrapolated without due care.

Kelp forest coverage has been reduced worldwide (Krumhansl et al., 2016; Wernberg et al., 2019), in part, due to climate change. Moreover, in some areas, their historical distribution limit has contracted poleward (Johnson et al., 2011; Wernberg et al., 2013, 2016), with clear signs of tropicalization of temperate ecosystems

(Vergés et al., 2014). If positive temperature anomalies persist (2018 was still an anomalously warm year), the chronic effects of these warming events might shift Baja California's ecosystems to a new alternative state, potentially precipitating range contractions for *M. pyrifera* and other species. Although future ecological states are difficult to predict in such dynamic ecosystems, our findings might be an early indication of a possible tropicalization of Baja California's kelp forest (Cheung et al., 2013) under climate change, emphasizing the need to monitor and manage these ecosystems.

Southern kelp forests of the CCS are a shared marine resource between the south of California and the north of Baja California (Ramírez-Valdez et al., 2017). Advancing the understanding of the ecological impacts of MHWs (Hobday and Pecl, 2014) in this transboundary region to promote adequate management strategies will require a binational effort (Aburto-Oropeza et al., 2018). Thus, the protection of these valuable ecosystems needs immediate actions and close collaboration between southern California and Baja California (Arafeh-Dalmau et al., 2017). If we fail to act, once-abundant, extensive *M. pyrifera* forests could experience important local declines, as they have in other regions (Johnson et al., 2011), leading to detrimental ecological and socio-political outcomes (Frölicher and Laufkötter, 2018).

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

GM-M, GT-M, and NA-D designed the initial project with the final review of RB-L, JM, and DS. NA-D, GT-M, RB-L, and JM collected the data. NA-D, GM-M, and DS conducted the data analysis and interpretation and were discussed by all other authors. NA-D and GM-M drafted the work and was revised by all other authors. All authors approved the version to be published and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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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.2019.00499/full#supplementary-material>

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Photophysiological Responses of Canopy-Forming Kelp Species to Short-Term Acute Warming

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The frequency of short-term oceanic warming events [“marine heatwaves” (MHWs) or heat spikes] has increased over the past century and is projected to further increase because of anthropogenic climate change. Given that marine organisms are strongly influenced by temperature, an increased occurrence of warming events could alter the structure of populations, communities, and ecosystems. The distribution and ecophysiological performance of kelp species – globally important foundation species that play significant roles in nutrient cycling and habitat creation in temperate coastal systems – is particularly constrained by temperature. However, their photophysiological responses to warming events remains unclear, which hinders attempts to understand, and predict the effects of ocean warming on kelp populations and the ecosystems they underpin. Here, we experimentally simulated a heat spike (+2°C and +4°C in magnitude, 3 days in duration, and compared with ambient controls) and examined the photophysiological responses of two canopy-forming kelp species widely distributed across the northeast Atlantic – *Laminaria digitata* and *Laminaria hyperborea*. Both species were resilient to the realistic warming treatments in terms of their photosynthetic characteristics. However, we found that *L. digitata* individuals, which were collected from populations found toward the upper limit of this species’ thermal range, exhibited increased oxygen production at higher temperatures, particularly after multiple days of exposure to the warming event. *L. digitata* also exhibited a greater poise for dissipating excess energy through non-photochemical pathways. In contrast, *L. hyperborea*, which extends further south into warmer waters and tends to occupy deeper reefs that are almost constantly submerged, appeared to be photo-physiologically insensitive to the heat spike. This study enhances our mechanistic understanding of the photophysiological and photoprotective responses of kelps to short-term acute warming events – features which are likely to emerge as important drivers of ecological change in coming decades.

Keywords: kelp, photophysiology, PAM fluorescence, marine heatwave, *Laminaria digitata*, *Laminaria hyperborea*, macroalgae

INTRODUCTION

The upper layers of the global ocean have warmed at a rate of $\sim 0.1^{\circ}\text{C}$ per decade since the mid-20th century, albeit with pronounced regional, and seasonal variability (IPCC, 2013). Recent climatic changes have caused changes in the distribution of species (Pinsky et al., 2013; Poloczanska et al., 2013), the structure of communities and ecosystems (Vergés et al., 2014; Wernberg et al., 2016), and the provision of ecosystem services (Pecl et al., 2017). Superimposed onto gradual warming trends are discrete extreme warming events – “marine heatwaves” [MHWs] or “heat spikes” – during which sea temperatures are anomalously high for periods of days to months or even years (Hobday et al., 2016, 2018). Recent research has shown that over the past century MHW frequency and duration increased by 34 and 17%, respectively, and that many regions have experienced rapid intensification of MHWs (Oliver et al., 2018). Moreover, it is likely that MHWs will intensify in coming decades, as a result of anthropogenic climate change (Frölicher et al., 2018). As the distribution of marine species is highly constrained by temperature, with many populations persisting toward the upper limits of species’ thermal niches (Sunday et al., 2012), continuation of both long- and short-term warming will drive redistribution of species, and reconfiguration of communities and ecosystems at the global scale (García Molinos et al., 2016; Hughes et al., 2017).

Kelps (macroalgae of the Order Laminariales) are distributed along approximately one-quarter of the world’s coastlines, across temperate and subpolar latitudes in both hemispheres, where they function as foundation species in nearshore marine ecosystems (Steneck and Johnson, 2013; Teagle et al., 2017). By providing complex biogenic habitat and exhibiting high rates of primary productivity, kelps enhance local biodiversity, fuel inshore food webs, and elevate secondary productivity (Steneck et al., 2002; Teagle et al., 2017, 2018). With regards to inshore carbon cycling, kelps fix and transfer globally significant amounts of carbon (Krause-Jensen and Duarte, 2016) that may eventually become trapped and stored in sediments, and thus contribute toward natural carbon sequestration (Krause-Jensen and Duarte, 2016; Smale et al., 2018). However, the ecophysiology and spatial distribution of kelp species is strongly influenced by temperature (Eggert, 2012); recent ocean warming trends have been linked with major shifts in the structure and functioning of some kelp populations and their associated communities (Wernberg et al., 2016). Increased temperature may also impact rates of primary productivity and carbon assimilation and transfer, with knock-on effects for interconnected habitats (Pessarrodona et al., 2019). That said, a recent global analysis (Krumhansl et al., 2016) showed that temporal trends in kelp populations are highly variable between different species and biogeographical regions. Whilst there is a general consensus that continued ocean warming will drive shifts in the geographical ranges of kelp species and changes in kelp-dominated communities (Harley et al., 2012; Brodie et al., 2014), the underlying physiological mechanisms and the

drivers of observed variability in contemporary responses are poorly understood.

Kelps are distributed along rocky coastlines throughout the NE Atlantic from Portugal and Morocco to northern Norway and Iceland (Bolton, 2010). Multiple kelp species are found within this region, each with varying environmental requirements, so that different species persist and dominate under different environmental conditions (Smale et al., 2013). Recent warming trends have driven some shifts in kelp distributions, with cool-affinity species declining at their warm trailing range edge (Raybaud et al., 2013; Tuya et al., 2014) and warm-affinity species expanding at their cool leading range edge (Smale et al., 2015), resulting in changes in local diversity (Teagle and Smale, 2018), and ecosystem functioning (Pessarrodona et al., 2019). Conversely, some kelp populations have remained relatively constant and stable over time (Krumhansl et al., 2016). At the physiological level, the temperature range within which kelps can carry out critical processes such as photosynthesis varies between species, life stages and the processes themselves (Delebecq et al., 2016), so that determining the thermal niche is complex. Even so, the extreme temperatures that macroalgal populations are exposed to during MHWs can exceed thermal thresholds, inducing protective responses (e.g., heat shock proteins, see King et al., 2019) and leading to impaired performance (Hargrave et al., 2017), altered physiology (Gouvêa et al., 2017), and ultimate mortality (Wernberg et al., 2013). Inter-specific variability in photophysiological mechanistic responses to short-term acute warming events remains unclear, but would allow for improved predictions of the future effects of ocean warming on kelp populations and the communities they underpin.

Here, we examined photosynthetic characteristics (as net oxygen flux in the light and chlorophyll-a fluorescence) of two critical habitat-forming kelp species – *Laminaria digitata* and *Laminaria hyperborea* – during a short-term acute warming event. These kelp species dominate wave exposed rocky reef habitats along much of the NE Atlantic coastline. Both species have a northern Boreal distribution: *L. hyperborea* is distributed from the Arctic to northern Portugal while *L. digitata* is distributed from the Arctic to a southerly range limit in northern France in the NE Atlantic. The current warm water limit of *L. digitata* is ~ 100 nautical miles south of the location of the current study; range edge populations are subjected to a similar climatic environment as those examined here. As well as differences in latitudinal ranges, these species differ in their vertical distributions as *L. digitata* is primarily found in the low intertidal zone whereas *L. hyperborea* tends to dominate deeper reefs, extending from the extreme low intertidal to subtidal reefs. Differences in latitudinal extensions and vertical distributions may manifest in differing responses to contemporary and predicted future ocean warming, although previous experimental work suggests they have similar upper thermal tolerances (Bolton and Lüning, 1982; tom Dieck, 1993). The aim of this study was to determine photophysiological responses of populations of these ecologically important species to short-term warming events.

MATERIALS AND METHODS

Experimental Set-Up

Both *Laminaria digitata* and *L. hyperborea* were collected by removing whole plants from their *in situ* environment; individuals were carefully removed by prising the holdfast from the rocky substratum. Both species were collected from within Plymouth Sound – *L. digitata* was collected from the shore during a low spring tide and *L. hyperborea* was collected by SCUBA divers at ~1 m depth (BCD). In total, 24 mature, medium sized (stipe length 30–50 cm) individuals of each species were collected, stored in seawater containers and immediately returned to the laboratory. The experiment described below was first conducted with *L. digitata* and subsequently with *L. hyperborea* using exactly the same approach. Kelp specimens were collected immediately prior to their respective experiment so the length of time between field collection and the start of the experiment was the same for both species. All experimentation was completed during a 16-day period in July 2017.

During each experiment, two plants were placed into each of 12 individual 130 L tanks filled with local filtered seawater within a recirculating system. Plants were orientated in an upright position by securing holdfasts to rocks using cable ties; duplicate plants were placed at opposite ends of the tanks, ~50 cm apart, to simulate actual densities recorded in the field (e.g., Smale et al., 2016; Hereward et al., 2018). Two plants were placed in each tank to reflect natural populations (i.e., plants are generally found in stands rather than individually) and to capture between-plant variability. Seawater was maintained at the desired temperature (see below) with aquarium chillers (DC-750, Deltec, Delmenhorst) or heaters (300W DR-9300, Boyu, Guangdong) as necessary. Turbulent water flow was generated with a wave maker in each tank (WM-6000, All Pond Solutions, Uxbridge). Salinity was maintained at 35 with the addition of fresh water as necessary. Lamps specifically designed for aquatic plants (Reef Daylight T8 36 W, Interpret, Dorking) were used to generate a 14:10 h light–dark regime with PAR irradiance levels of ~100 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (recorded with an Odyssey PAR meter). Average daily light intensity (measured with a Hobo pendant logger, 15 min intervals, daytime only) during the experiment was 1970 ± 163 Lux. As such, levels of PAR and light intensity, as well as the daylight regime used in the study were comparable to those experienced by natural populations *in situ* during typical summer months (Pedersen et al., 2014; Smale et al., 2016).

Plants were held at ambient water temperature for 60 h to acclimate to tank conditions. Ambient temperature was set at ~16°C, which is typical of local summer sea temperatures from the surface to >20 m depth – well within the depth ranges inhabited by the study species (Smyth et al., 2009; Brewin et al., 2017). Following this, the water temperature of four replicate tanks was gradually increased by ~2°C over a 48-h period. The water temperature of four other replicate tanks was increased over the same 48-h period by ~4°C. The water temperature of the remaining four tanks was maintained at ambient temperature. These temperature treatments were selected as they are representative of the magnitude of actual

warming events, both generally (Hobday et al., 2016) and specifically within the study location (Joint and Smale, 2017). Each set of four tanks were fed by a larger header reservoir, so that water temperature in each tank within each treatment was consistent. Water changes were conducted daily (~10% of total volume) using local filtered seawater. Experimental temperatures were maintained for a further 3 days to simulate short-term acute warming events of differing magnitude (i.e., ~+2°C and ~+4°C); the temperature treatments of ambient conditions, low magnitude and high magnitude warming are hereafter referred to as T_0 , T_1 , and T_2 , respectively (**Supplementary Figure S1**). Temperature was monitored in each set of tanks using Hobo pendant loggers, which recorded temperature every 15 min throughout the experiment. Net daytime oxygen flux was measured on days 1–3 of the heat spike period, whilst photosynthetic characteristics were measured on days one and two only (analytical details below).

Net Oxygen Flux

Net O₂ flux from kelp individuals was measured using unstirred benthic chambers placed over the basal meristematic area of the blade, which were weighed down to avoid movement during the incubation (270 ml volume, 95 cm² surface area, and transparent to incoming PAR). At the start of the incubation, the oxygen concentration of the water inside the chamber was measured using an oxygen optode system (PreSens Fibox 3), with optode sensor spots fixed to the inside chamber wall. Incubations lasted for ~2 h (exact time noted for each incubation), following which a second O₂ concentration measurement was made. Net change in O₂ concentration from the start to the end of the incubation was used to determine the net O₂ flux between the kelp frond and the overlying water column (i.e., net increase in O₂ concentration over time = net O₂ production by the kelp). Net O₂ flux of each plant within each tank was measured on days 1, 2, and 3 of the warming treatments at the same time of day for each sample.

Photophysiological Responses

Chlorophyll-a fluorescence measurements were conducted using Pulse Amplitude Modulation fluorometry, with a Diving-PAM instrument (Walz GmbH) and used to calculate photosynthetic characteristics of the kelp plants. Measurements were taken following previous methodologies and notations (Burdett et al., 2012, 2014). Notation and parameter calculations are provided in **Supplementary Table S1**. A 5-mm-diameter fiber optic probe was used for all measurements, positioned 10 mm from the surface of the kelp plant. Quasi-dark acclimation (Hennige et al., 2008) was achieved by using the “Surface holder” Walz accessory and placing this over the kelp plant for 10 s prior to taking rapid light curve (RLC) measurements – this is known to be sufficient time to achieve results statistically similar to full dark acclimation in a range of marine photosynthetic organisms (Hennige et al., 2008; Burdett et al., 2012). PAM settings were: measuring light intensity = 3, damping = 3, gain = 8, saturation pulse intensity = 2, saturation pulse width = 1.0, and actinic light intensity = 1.

Rapid light curves, where organisms are exposed to pulses of saturating actinic light interspersed with short periods of

increasing levels of irradiance, were conducted on both the basal (meristematic) area and distal ("old" growth) area of the blade. Measurements were obtained (at approximately the same time of day) from each plant on days 1 and 2 of the warming. RLCs have become well established within PAM fluorometry and provide information on energy dissipation from light-limiting through to light-saturating conditions (Ralph and Gademann, 2005). However, due to the short exposure time at each irradiance step, steady-state conditions are not achieved (Ralph and Gademann, 2005). Thus, in contrast to traditional light curves, results from RLCs reflect actual, rather than optimal, photosynthetic state (Ralph and Gademann, 2005), yielding data on dark/light-acclimated minimum fluorescence (F_o and F_o' , respectively), dark/light acclimated maximum fluorescence (F_m and F_m' , respectively), fluorescence under actinic light (F'), and quenched fluorescence [F_q' , defined as $(F_m - F')$]. In this experiment, the RLCs used eight irradiance steps each of 10 s duration ranging from 1 to 569 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$.

Maximum photosynthetic efficiency, F_v/F_m , was defined as $(F_m - F_o)/F_m$. The minimum saturating intensity (E_k – the irradiance level at which light shifts from being photosynthetically limiting to photosynthetically saturating; units = $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) and initial photosynthetic rate [α (no units)] were calculated by fitting RLC data to the irradiance-normalized non-linear least squares regression model of Jassby and Platt (1976) in the R package Phytotools (Silsbe and Malkin, 2015) to describe the light response of quantum efficiency using the following equation:

$$y = (1/x) * \alpha * E_k * \tanh(x/E_k)$$

Where x = PAR levels of each RLC step and $y = F_q'/F_m'$ at each RLC step. All model fits were statistically significant (model p -value < 0.0001 for all). Maximum relative electron transport rate ($rETR_{\text{max}}$) was calculated as $E_k * \alpha$. Effective photochemical efficiency under actinic light (F_q'/F_m') was defined as $F_q'/F_m' = (F_m - F')/F_m'$. Quasi-non-photochemical quenching (NPQ) was defined as $NPQ = F_m - F_m'/F_m'$ (Bilger and Björkman, 1990) under peak RLC irradiance. A second non-photochemical quenching parameter (qN) is defined as $qN = F_v'/F_m'$ at each RLC step. Photochemical quenching (qP) is defined as $qP = F_q'/F_v'$ at each RLC step. F_q'/F_m' , NPQ, qN, and qP were expressed against E/E_k (where E = RLC light level) to assess sample response relative to limiting/optimal/saturating irradiance for photosynthesis when $E/E_k < 1$ / $E/E_k = 1$ / $E/E_k > 1$, respectively.

Statistical Analysis

Duplicate plants within each tank were treated as subsamples and response variable measurements were averaged across plants to yield a single value per tank; all analyses were conducted with tanks as true replicates. Repeated measure analysis of variance was conducted to examine the effects of temperature treatment (3 levels, fixed), tank (repeated, nested within temperature), and experimental day (3 levels, fixed) on net oxygen production. As each species was experimented on separately in serial manipulations, data on each was analyzed

separately and informal comparisons across species were made. Data were first tested for normality and homogeneity of variance and transformed were necessary. Where significant main effects or interactions were detected (at $p < 0.05$), further pairwise tests (SNK) were conducted to explore further. A similar approach was adopted to examine variability in photophysiological response variables. Data from the basal and distal sections of the blade were analyzed separately using a model similar to that described above: temperature treatment (3 levels, fixed), tank (repeated, nested within temperature), and experimental day (2 levels, fixed).

RESULTS

Experimental Conditions of the Simulated Heat Spike

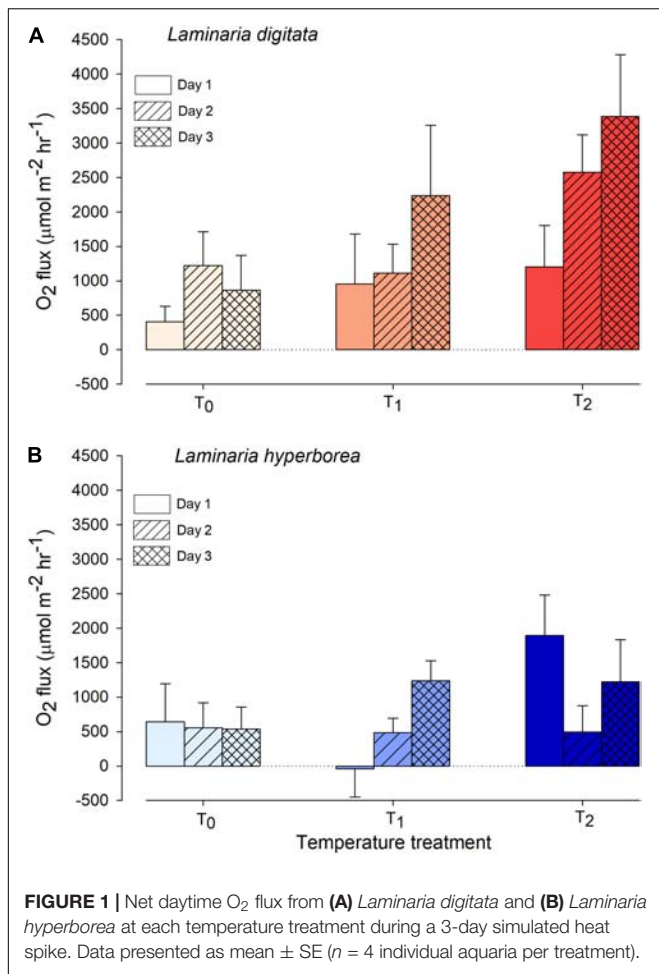
During the first experiment, on *L. digitata*, daily mean temperatures in the treatments during the 3-day warming event were: $T_0 = 15.7 \pm 0.1^\circ\text{C}$, $T_1 = 18.4 \pm 0.0^\circ\text{C}$, and $T_2 = 19.9 \pm 0.0^\circ\text{C}$, which corresponded to ambient conditions, +2.7°C and +4.2°C treatments, respectively. In the second experiment, on *L. hyperborea*, daily mean temperatures in the three treatments were: $T_0 = 15.6 \pm 0.1^\circ\text{C}$, $T_1 = 18.3 \pm 0.1^\circ\text{C}$, and $T_2 = 20.1 \pm 0.1^\circ\text{C}$, corresponding to ambient conditions, +2.7°C and 4.5°C, respectively (Supplementary Figure S1).

Net Oxygen Flux

For *Laminaria digitata*, O_2 production tended to increase with increased temperature and with experimental day (Figure 1). By the third day, net O_2 flux was more than four times greater in the T_2 treatments compared with T_0 (Figure 1). The effect of temperature was statistically significant: pairwise tests showed that O_2 production was greater at T_2 compared with T_0 and T_1 (Table 1). Duration of exposure was also important, as O_2 production was greater on experimental Day 3 compared with Day 1 (Table 1). For *L. hyperborea*, the effect of warming on O_2 production was less evident, with no consistent responses to either temperature treatment or experimental day (Figure 1). Statistically, the interaction term between the main factors was significant (Table 1), with pairwise tests indicating that the effect of temperature treatment was significant on Day 1, but not on Day 2 and 3. By Day 3 of the warming, no differences in net O_2 production between treatments were recorded (Table 1). Informal comparison between the species indicated that O_2 production rates for *L. digitata* were generally greater than *L. hyperborea*, particularly under the higher warming treatments (Figure 1).

Photophysiological Responses

For *Laminaria digitata*, photosynthetic efficiency (F_v/F_m) values were relatively consistent between factors, with mean values ranging from ~0.72 to ~0.74 (Figure 2). For basal blade tissue, we recorded a significant effect of experimental day as F_v/F_m values were lower, overall, on Day 2 (Table 2). For distal blade tissue, no significant variability was detected (Table 2). For *L. hyperborea*, mean F_v/F_m was higher, ranging from ~0.74



to 0.76 (Figure 2). For both basal and distal blade tissue, no significant effects of time or temperature were recorded (Table 2). Overall, F_v/F_m values were slightly lower for *L. digitata* compared with *L. hyperborea* (Figure 2). A similar pattern was observed for alpha (α), a measure of initial photosynthetic rate, in that the basal blade tissue of *L. digitata* exhibited the greatest response, with a general decline in α with increasing temperature and significantly lower values on Day 2 of experimentation (Supplementary Table S2 and Supplementary Figure S2).

For *Laminaria digitata*, saturation intensity (E_k) measured on basal blade tissue varied markedly between experimental days, with overall values on Day 2 being significantly higher than on Day 1 (Figure 3 and Table 2). There was a general increase in E_k with increasing temperature treatment, although between-sample variability meant that this trend was not significant. For distal blade tissue, E_k values were relatively consistent between temperature treatments and days (Figure 3). For *L. hyperborea*, E_k values measured in basal blade tissue were relatively consistent across treatments and days, and no significant effects were detected (Figure 3 and Table 2). In contrast, E_k values measured in distal blade tissue varied markedly between days, with overall values on Day 2 being significantly lower than on Day 1 (Figure 3 and Table 2). A similar pattern was observed for maximum relative electron transport rate ($rETR_{max}$; Supplementary Table S2 and Supplementary Figure S3).

When $E/E_k = 1$, the RLC light level is “optimal” and neither saturating nor limiting. Under limiting light levels (and up to $E/E_k \sim 0.5$), effective photochemical efficiency under actinic light (F_q'/F_m') was between 0.7 and 0.8, suggesting a 70–80% photosynthetic efficiency. When $E/E_k = 1$, despite being theoretically optimal, F_q'/F_m' and photochemical quenching (qP) had decreased from initial values by ~ 20 –30% reaching a minimum when RLC light levels were $\sim 10 \times E_k$ (Figure 4). For non-photochemical quenching (qN and NPQ), a slight increase began at $E/E_k = 0.1$, rising rapidly at $E/E_k > 1$ and reaching a maximum at $E/E_k \sim 10$, although this was characterized by a wide variability (Figure 4). *L. digitata* tended to have higher qN and NPQ values across a wider range of E/E_k (Figure 4).

DISCUSSION

We examined sub-lethal photophysiological responses of two canopy-forming kelp species to a short-term acute warming event. In terms of net oxygen flux in the light (i.e., net photosynthesis), *L. digitata* exhibited a significant ecophysiological response, whilst *L. hyperborea* appeared less sensitive with no apparent effect on net photosynthesis. Investigation of the associated photosynthetic characteristics revealed no significant trends in either species as a result of warming, despite the significant increase in net oxygen release in *L. digitata*. This suggests these kelp species exhibit a degree of photophysiological resilience to short-term acute warming.

TABLE 1 | The effect of temperature treatment, tank and experimental day on net oxygen flux as determined by RM ANOVA for both *Laminaria digitata* and *Laminaria hyperborea*.

Spp	Temp [2]			Tank (Temp) [9]	Day [2]			Temp x Day [4]			Res [18]
	MS	F	P	MS	MS	F	P	MS	F	P	MS
LD	7.3×10^6	9.73	0.006	7.6×10^5	5.1×10^6	4.39	0.028	1.1×10^6	0.97	0.446	1.2×10^6
	Pairwise tests; temp: $T_0 = T_1 < T_2$. Day: $3 > 1, 3 = 2, 2 = 1$										
LH	1.6×10^6	2.76	0.116	5.7×10^5	7.3×10^5	1.89	0.109	1.4×10^6	3.72	0.007	2.9×10^5
	Pairwise tests; interaction: Day 1: $T_0 = T_1 < T_2$. Day 2: $T_0 = T_1 = T_2$. Day 3: $T_0 = T_1 = T_2$										

P-values shown in bold are significant (at $P < 0.05$); pairwise tests (SNK) were conducted as necessary. “Spp,” species (LD, *Laminaria digitata*; LH, *Laminaria hyperborea*); “Res,” residual. Degrees of freedom (df) associated with each factor are shown in squared brackets.

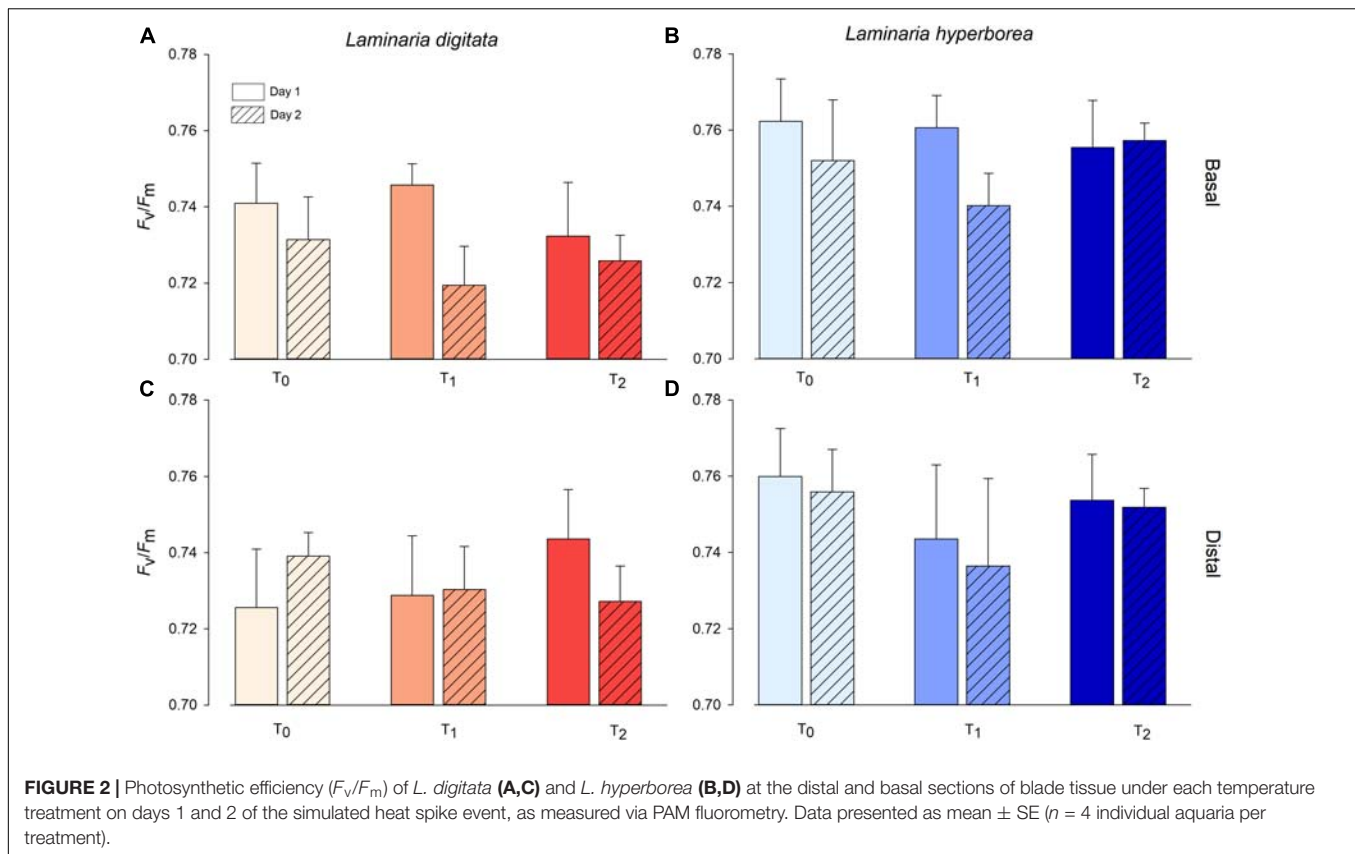


TABLE 2 | The effect of temperature treatment, tank and experimental day on F_v/F_m and E_k , as determined by RM ANOVA for *Laminaria digitata* and *Laminaria hyperborea* for both basal and distal blade tissue.

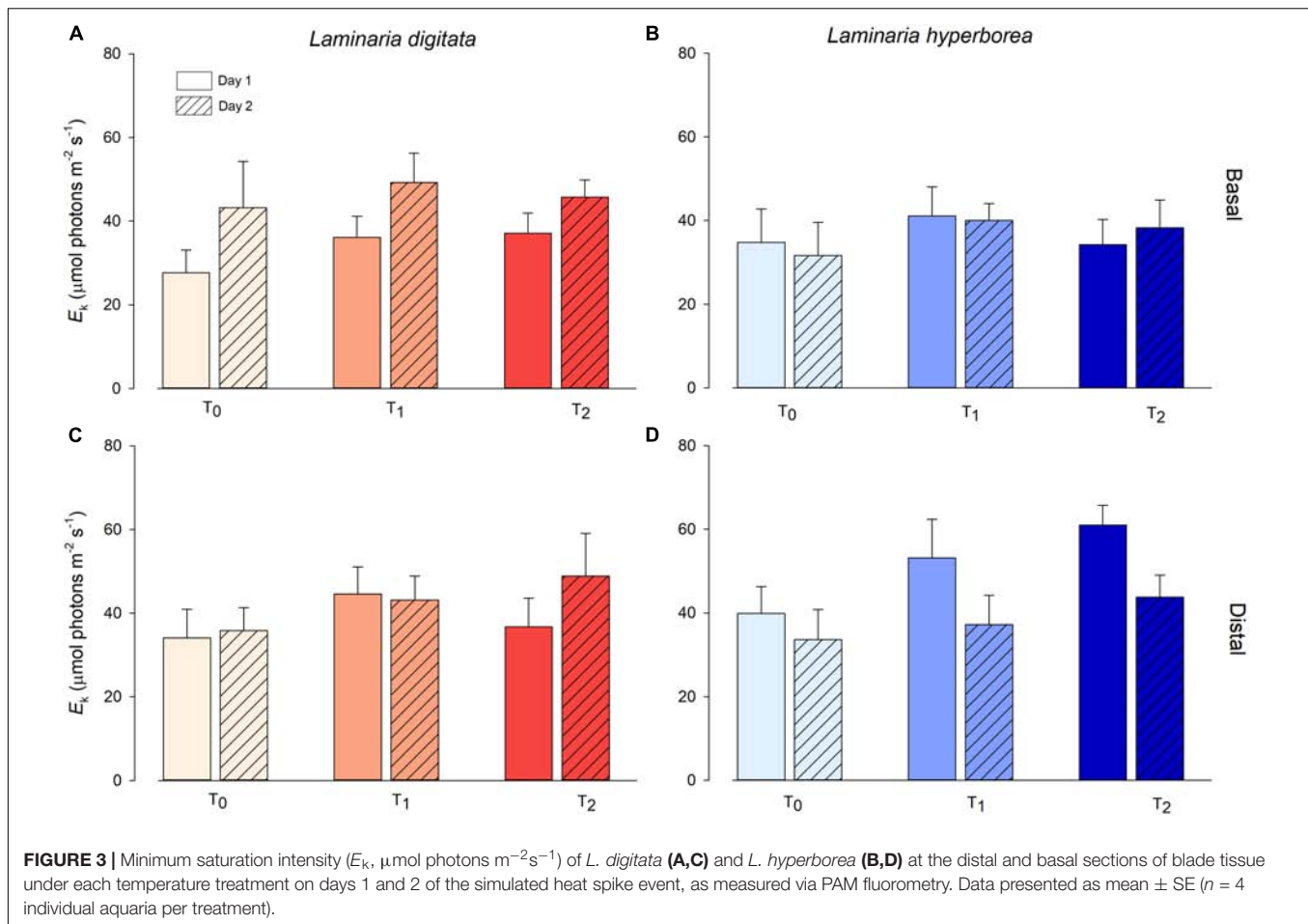
Spp	Var	Sect	Temp [2]			Tank (Temp) [9]		Day [1]			Temp x Day [2]			Res [9]	
			MS	F	P	MS		MS	F	P	MS	F	P	MS	
LD	F _v /F _m	Basal	9.0 × 1 ⁻⁵	0.54	0.599	1.7 × 10 ⁻⁴		1.2 × 10 ⁻³	15.07	0.004	2.2 × 10 ⁻⁴	2.79	0.114	8.0 × 10 ⁻⁵	
		Distal	5.0 × 10 ⁻⁵	0.19	0.834	2.8 × 10 ⁻⁴		3.7 × 10 ⁻⁷	0.01	0.969	3.0 × 10 ⁻⁴	1.28	0.323	2.3 × 10 ⁻⁴	
	E _k	Basal	118.3	1.26	0.327	93.2		954.7	17.61	0.002	21.0	0.38	0.689	54.2	
		Distal	199.1	1.63	0.248	121.9		104.6	2.63	0.139	118.8	2.99	0.101	39.6	
	Pairwise tests: F _v /F _m basal; Day: 1 > 2														
	E _k basal; Day: 1 < 2														
LH	F _v /F _m	Basal	1.1 × 10 ⁻⁴	0.31	0.741	3.7 × 10 ⁻⁴		4.2 × 10 ⁻⁴	3.00	0.117	3.4 × 10 ⁻⁴	2.38	0.147	4.2 × 10 ⁻⁴	
		Distal	6.8 × 10 ⁻⁴	2.46	0.140	2.7 × 10 ⁻⁴		1.1 × 10 ⁻⁴	0.23	0.644	1.3 × 10 ⁻⁵	0.02	0.973	4.9 × 10 ⁻⁴	
	E _k	Basal	108.5	0.87	0.452	124.7		18.9	0.51	0.492	2.7	0.07	0.929	36.9	
		Distal	490.0	3.42	0.078	143.2		1036.7	39.48	0.001	72.3	2.75	0.117	160.2	
	Pairwise tests: E _k distal; Day: 1 > 2														

P-values shown in bold are significant (at $P < 0.05$); pairwise tests (SNK) were conducted as necessary. "Spp," species (LD, *Laminaria digitata*; LH, *Laminaria hyperborea*); "Var," response variable; "Sect," section; "Res," residual. Degrees of freedom (df) associated with each factor are shown in squared brackets.

Temperature Responses

Up to a certain threshold, increasing temperature is expected to increase macroalgal oxygen production, due to higher electron transport rate through the photosystems (Delebecq et al., 2016). This trend was clearly observed for *L. digitata*, even after just 3 days of acute exposure to the high-magnitude T_2 warming treatment. Chronic, longer-term exposure to the absolute temperatures used here for the warming treatments

(i.e., ~ 18 – 20°C) is known to result in reduced ecophysiological performance (Simonson et al., 2015; Hargrave et al., 2017), increased mortality (Bartsch et al., 2013; Wilson et al., 2015), and consequent population-level impacts (Raybaud et al., 2013) for *L. digitata*, reinforcing the sensitivity of this species to elevated temperature. In contrast to *L. digitata*, a consistent oxygen production response was not observed in *L. hyperborea*, suggesting a degree of variability and/or insensitivity to



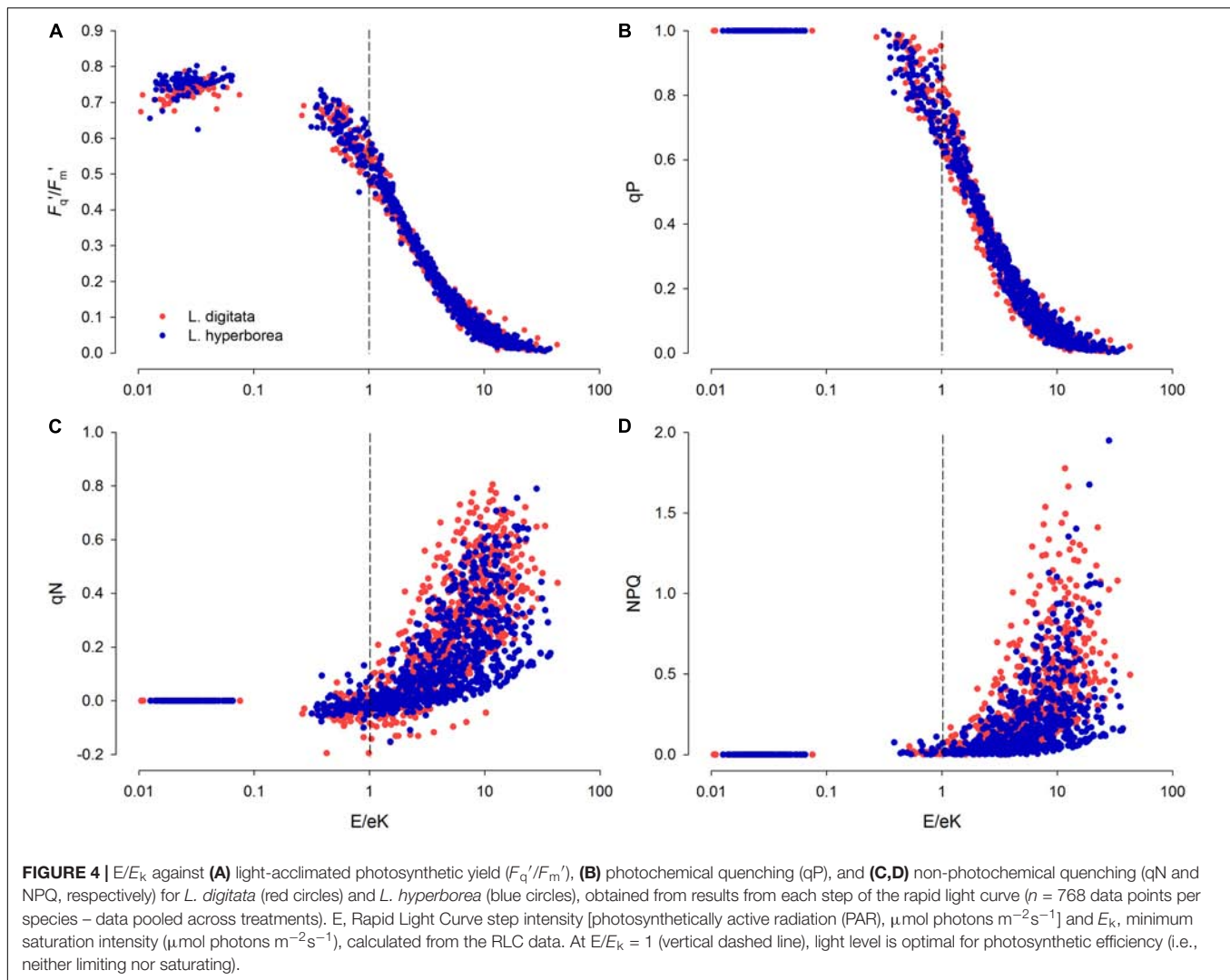
the temperature increases tested in this study. Oxygen flux measurements are only available in the light, preventing an assessment of net respiration rates. While this limits the extent of physiological insight, it does not diminish the significant trends in daytime net oxygen flux under simulated warming event. In the field, this physiological response could have significant biogeochemical implications since macrophytic photosynthesis is also major driver of daytime oxygen elevation in coastal systems (Burdett et al., 2013; Attard et al., 2015). In the absence of dark net respiration rates it is not yet possible to determine the full effect a warming event might have on the magnitude of diel oxygen variation. Interestingly, despite a significant response in net daytime oxygen production, no significant response in photosynthetic characteristics were observed in either species, suggesting that during acute, short-term warming events core photophysiological processes can be maintained with only a physiological response. Trends in F_v/F_m , E_k and rETR_{max} suggest that increased temperature may have increased the electron transport rate through photosystem II and reduced photosynthetic, but not to such an extent as to be beyond the natural between-plant variability and temperature-driven increase in oxygen-flux kinetics.

The insensitivity of photosynthetic characteristics to elevated temperature allows us to compare the two species responses.

Via an elevated and more light-responsive non-photochemical quenching response (an effective method for dissipating excess absorbed energy), *L. digitata* may have a greater potential capacity for photo-protection. This was driven by an elevated maximal fluorescence (F_m') – which can also correspond to an up-regulation of photo-protective xanthophyll cycling (Lavaud et al., 2002). Further pigment-level analyses would be required to confirm this mechanism. For *L. digitata*, experimental day also had an effect on the photosynthetic characteristics of the basal tissue. The meristoderm of kelps (the peripheral layer of photosynthetically active cells of the basal tissue) is known to be highly biogeochemically active and capable of accumulating significant iodine concentrations (Küpper and Carrano, 2019). Such biogeochemical activity may increase the sensitivity of this tissue to altered environmental conditions (whether via experimental treatment or laboratory conditions) leading to the integrated observational response seen in this study.

Ecological Implications

Laminaria digitata and *Laminaria hyperborea* are critical components of coastal marine ecosystems in the NE Atlantic, as they provide complex habitat for a wide range of associated flora and fauna (Blight and Thompson, 2008; Schaal et al., 2016; Teagle et al., 2018) and exhibit high rates of carbon



capture and release (Schaal et al., 2009; Hereward et al., 2018; Pessarrodona et al., 2018). Recent and projected warming trends have been linked with population losses and range contractions at the equatorward limit of the distributions of both *L. digitata* (Raybaud et al., 2013) and *L. hyperborea* (Voerman et al., 2013; Casado-Amezúa et al., 2019) in France and Spain/Portugal, respectively. Prolonged exposure to warmer-than-average sea temperatures can manifest in responses at the organism level, such as decreased growth (Hargrave et al., 2017), and at the population level, such as reproductive failure (Bartsch et al., 2013). Similarly, exposure to acute air temperature stress during periods of low-tide emersion can have impacts at the physiological and individual level (King et al., 2018b). Ultimately, warming can lead to the loss of kelp populations at the range edge, with subsequent shifts in the structure of communities (Voerman et al., 2013) and even ecosystems (Wernberg et al., 2016).

The scale of the heating spike simulated in this study (in terms of duration and magnitude) is frequently observed in the study region, which experiences short-term temperature variability as

well as longer-lasting MHW events (Joint and Smale, 2017; Brewin et al., 2018). Both species exhibited photophysiological resilience to an acute period of high temperature; short-lived warming events may therefore not physiologically impact these kelp species. The significant increase in net daytime oxygen flux by *L. digitata* suggests that this species has a lower sensitivity threshold, perhaps because it is near the southerly range edge of its distribution, and already under physiological pressure. It is likely that increased exposure to acute warming events (whether seawater or air temperatures) combined with longer-term exposure to gradual increases in mean sea temperature, will negatively impact range edge populations, leading to shifts in the species distribution and altered community structure (Raybaud et al., 2013; Filbee-Dexter et al., 2016). However, it should be noted that this study was conducted on single populations over a single event and did not account for any local adaptation that could lead to between-population variability in thermal tolerance. Indeed, thermal divergence between populations has been shown for several kelp species (Gerard and Du Bois, 1988; King et al., 2019) and may be commonplace in marine macrophyte

species more generally (King et al., 2018a). Clearly, further work comparing photophysiological responses to temperature across multiple populations within these species' ranges and in response to varied temperature regimes is needed to confirm the photophysiological resilience of these species to the chronic and acute ocean warming projected for the coming decades. Recent advances *in situ* experimentation via manipulation of environmental conditions within an incubation chamber (e.g., Gattuso et al., 2014; Burdett et al., 2018) provide the opportunity to conduct comparable experiments with reduced laboratory artifacts and the capacity to investigate these questions at the organism to community scale.

Canopy-forming kelp species are vital components of mid and high-latitude coastal ecosystems, underpinning core ecological processes such as primary productivity, trophic connectivity and habitat provision (Blight and Thompson, 2008; Smale et al., 2013). As macroalgal species' distributions are strongly constrained by temperature, recent warming trends have driven shifts in their geographical ranges (e.g., Raybaud et al., 2013; Schaal et al., 2016; Pessarrodona et al., 2018) and projected warming will continue drive changes in the coming decades (Müller et al., 2009; Hereward et al., 2018). MHW events further compound decadal-scale ocean warming by exerting acute and intense stress onto organisms, populations, communities, and ecosystems. Projected increases in MHW activity in coming decades (Frölicher et al., 2018) will likely coincide with current kelp population distributions. This study suggests that those populations near their upper thermal limit may be most affected (i.e., equator range edge – *L. digitata* in this study) because of a slight increase in photophysiological sensitivity. Prolonged or repeated responses in terms of net oxygen production may provide short-term metabolic benefits in some species (via increased oxygen production), but also increased energy use and

demand in the longer term. A deeper mechanistic understanding of ecophysiological responses to increased temperature is needed to better predict near-future impacts of ocean warming on kelp populations and communities.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

HB and DS co-designed the experiment and analyzed the data. All authors performed the experiment, took the samples, made measurements, and wrote 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.2019.00516/full#supplementary-material>

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Regional Structure in the Marine Heat Wave of Summer 2015 Off the Western United States

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One of the largest warm water anomalies (marine heat waves [MHWs]) ever recorded occurred in the northeast Pacific during 2014–2016. This MHW was caused by large-scale atmospheric ridging and affected fisheries and ecosystems from Alaska through California, including a bloom of toxic algae spanning the entire coastline. Regional variations in MHW severity are common along coastlines worldwide but are generally unexplained. During the 2014–16 MHW, the summertime sea-surface temperature (SST) anomalies were often stronger along the southern half of the coastline off the western continental United States. The reason for this north-south difference in severity of the MHW within the California Current System (CCS) has remained unclear. The scientific community's lack of understanding of regional variations within MHWs prevents accurate prediction of SST anomalies and resulting ecological and economic impacts. We show the north-south difference in SST anomalies was due to a known wind pattern determined by the coastline shape. The wind anomalies in summer have a quasi-dipole structure: the northern lobe extends southwest from Washington/Oregon, and the southern lobe has opposite sign and extends south from Cape Mendocino in a triangle due to a hydraulic expansion fan in the marine boundary layer. The alternating wind intensifications and relaxations typically last several days. However, the large-scale ridging during the MHW was associated with unusual persistence in this pattern: in summer 2015 a single wind relaxation in the southern lobe lasted 2 weeks. These wind anomalies induce changes in SST, likely via changes in wind-driven vertical entrainment of cold water from below the mixed layer, and mixed-layer shoaling; the net air-sea heat flux anomaly is small. The July 2015 wind relaxation persisted so long that the changes in SST exceeded pre-existing SST variations. The resulting SST anomalies have a dipole pattern similar to the wind anomalies. These dipole SST anomalies explain the north-south asymmetry in the CCS MHW. We suggest that during future persistent ridging events, the SST anomalies off the western continental U.S. will develop a north-south split structure similar to July 2015.

Keywords: marine heat wave, heat budget, mixed layer, air-sea flux, California Current, 2015, coastal wind patterns, upwelling system

1. INTRODUCTION

1.1. The Marine Heat Wave Off Western North America in 2014–2016

One of the largest warm water anomalies (marine heat waves [MHWs]) ever recorded in the northeast Pacific occurred during 2014–2016. During this MHW, sea-surface temperatures (SSTs) in the Gulf of Alaska (GoA) were $\sim 3^{\circ}\text{C}$ higher than normal (e.g., **Figure 1A**) for prolonged periods. This MHW in the GoA was caused by large-scale atmospheric high pressure ridging over the eastern North Pacific and western North America (Bond et al., 2015; Hartmann, 2015) and associated with record-low sea level along the coast of Alaska during winter 2013–2014 (Wang et al., 2019). The GoA MHW became known in the popular press as “the Blob” (Bond et al., 2015). By 2015, the MHW extended along the coast of the western continental United States (U.S.) (Gentemann et al., 2016; Zaba and Rudnick, 2016; Myers et al., 2018). The MHW persisted over multiple years due to atmospheric teleconnections from the tropics (Di Lorenzo and Mantua, 2016; Liang et al., 2017; Tseng et al., 2017). This prolonged MHW in the northeast Pacific eventually overlapped with the 2015–16 El Niño (Jacox et al., 2016; Zaba and Rudnick, 2016; Chao et al., 2017; Zaba et al., 2018), though the impacts of the El Niño were weaker than usual along western North America (Barnard et al., 2017; Frischknecht et al., 2017; Paek et al., 2017). This MHW caused major damage to economically important fisheries and other ecosystems from Alaska through California associated with species shifts (Whitney, 2015; Cavole et al., 2016; Auth et al., 2017; Daly et al., 2017; Peterson et al., 2017; Du and Peterson, 2018; Gomez-Ocampo et al., 2018; Kahru et al., 2018) and an unprecedentedly large bloom of toxic algae that spanned the entire coastline (McCabe et al., 2016).

Along the coast of the western continental U.S., the MHW developed an unexplained “split” structure in summer 2015. The monthly sea-surface temperature (SST) anomalies were generally much stronger along the southern half of the continental U.S.

coastline, i.e., California, than the northern half, Washington and Oregon (Gentemann et al., 2016). When and where upwelling-favorable winds were present along the coast, those winds mitigated the SST anomalies, particularly in the spring upwelling season; in summer and early fall the winds were more variable and the warm SST anomalies frequently returned, particularly along the southern part of the coast. This north-south difference was so strong by July 2015 that the MHW split into two parts, one in the GoA and one extending from central California to Baja California (**Figure 1B**). The two warm anomalies were separated by a “cool corridor” (Gentemann et al., 2016). This split structure was described as Phase III of the development of the MHW (Peterson et al., 2016) and the split was reported in the journal *Science* as “flummoxing” climate experts (Kintisch, 2015).

The reason for this split in the MHW has to date remained unclear. The strong regional variation in SST anomalies within the 2014–2016 northeast Pacific MHW is consistent with region-specific variations worldwide in (i) the frequency of MHWs (Scannell et al., 2016), (ii) the intensity and duration of MHWs (Oliver et al., 2018), (iii) the rate of change of the number of days with extremely cold or warm SST along the coast (Lima and Wethey, 2012), and (iv) the physical forcing of MHWs (Holbrook et al., 2019). The scientific community’s lack of understanding of the causes of these regional variations within MHWs, especially events not associated with El Niño, prevents accurate prediction of MHWs and the resulting economic and ecological impacts (Jacox et al., 2019). Here, we link the regional variations in the northeast Pacific MHW to a characteristic regional wind pattern that also occurs during “normal” years but was unusually persistent during the 2015 MHW.

1.2. Typical Regional Wind Patterns Over the California Current System in Summer

The mean wind pattern over the California Current System (CCS) in summer consists of equatorward wind everywhere along the coast of the western continental U.S. (e.g., **Figure 2A**). This prevailing wind is driven by the pressure gradient between

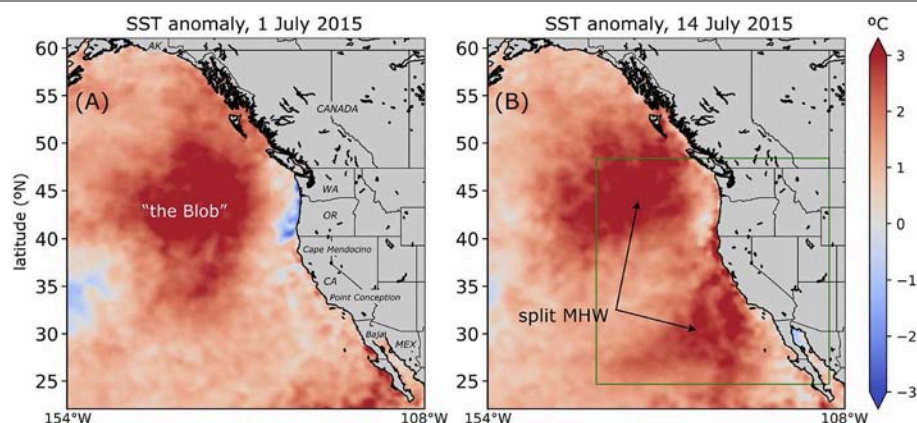
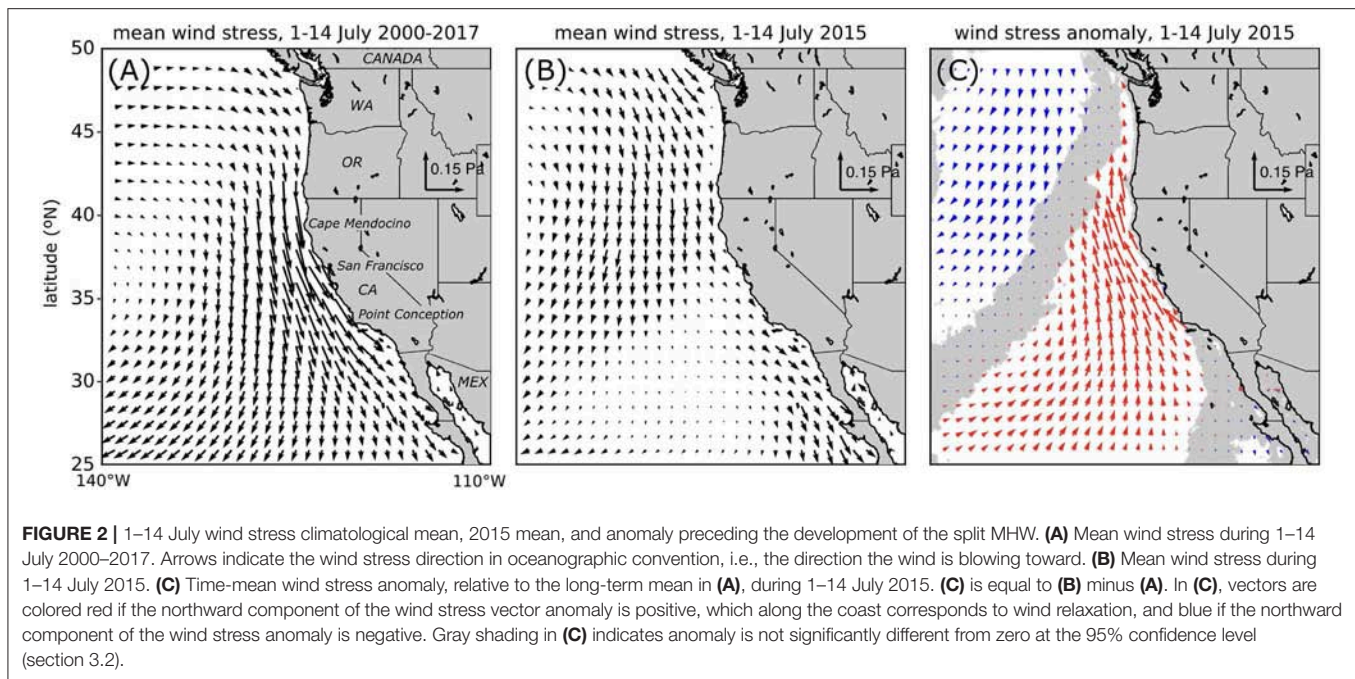


FIGURE 1 | SST anomalies before and after the formation of the July 2015 split MHW: **(A)** 1 July 2015 and **(B)** 14 July. The SST anomaly at each location is calculated relative to a daily long-term climatology using the CMC SST product (section 2.2). The vertical axis limits are 22 and 61°N. Green rectangle in **(B)** shows area covered by **Figures 2, 4**.



the offshore subtropical North Pacific High atmospheric pressure system and the desert heat low pressure area over the southwest U.S. (e.g., Neiburger et al., 1961; Halliwell and Allen, 1987); see the introduction of Fewings et al. (2016) for a brief review of the related literature. The wind direction is polarized along the coast due to the influence of the coastal mountains, except near gaps, such as San Francisco Bay. Off California, the strength of the wind is intensified for several hundred km offshore by hydraulic effects of the large-scale bend in the coastline at Cape Mendocino (**Figure 2A**) (Edwards et al., 2002).

Superimposed on this mean wind pattern are strong wind fluctuations on time scales of days. The synoptic, or weather-band, fluctuations in the along-coast wind velocity have amplitudes comparable to the mean in the northern half of the system and greater than the mean in the southern half of the system (Halliwell and Allen, 1987). As a result, at any location along the coast, the along-coast wind velocity frequently weakens to near zero (“relaxes”) or even reverses direction for several days (Bond et al., 1996; Mass and Bond, 1996; Nuss et al., 2000). Interspersed with these wind relaxations and reversals are wind intensification events where the wind is upwelling-favorable and stronger than the mean (Halliwell and Allen, 1987; Taylor et al., 2008). The wind relaxations or reversals, and the intervening intensifications, are forced by groups of three related air pressure anomalies: (1) mid-level troughing over Washington and Oregon is followed by (2) mid-level ridging as Rossby waves or extra-tropical cyclones are advected eastward on the jet stream (Halliwell and Allen, 1987; Bond et al., 1996; Mass and Bond, 1996; Bane et al., 2005, 2007). This ridging causes an anticyclonic circulation that advects low-pressure air offshore from over the desert in the southwestern U.S., causing (3) low pressure at sea level off California (Nuss, 2007). The resulting

fluctuations in the along-coast pressure gradient along the coast at sea level drive a coherent pattern of wind intensifications and relaxations that accompanies the three air pressure anomalies: (1) wind relaxation or reversal off Oregon/Northern California (Halliwell and Allen, 1987; Bane et al., 2005, 2007) accompanied by intense upwelling-favorable winds off central California, then (2) intensified upwelling-favorable winds off central California (Taylor et al., 2008), then (3) wind relaxation (Melton et al., 2009) or rarer reversal (Nuss, 2007) off central California accompanied by intensified winds off Oregon/Northern California (Fewings et al., 2016). This coherent cycle of wind relaxations and intensifications tends to repeat every ~10–20 days throughout the summer, with individual wind relaxation or intensification stages (1)–(3) each lasting 2–5 days (Fewings et al., 2016).

These wind fluctuations can be understood as part of a regional quasi-dipole wind pattern. The pattern extends 1600 km along the coast, from Washington past California, and ~600 km offshore: when upwelling-favorable winds are enhanced over the north part of the CCS, the winds tend to be reduced (relaxed) over the south part of the CCS, and vice versa (Fewings et al., 2016). We refer to stages (1) and (3) described above as the “northern relaxation” and “southern relaxation” phases, respectively, of the wind quasi-dipole pattern. One way to quantify the quasi-dipole wind pattern is with Hilbert Empirical Orthogonal Function (HEOF) analysis (section 3.3). There is some poleward propagation in the wind fluctuations, which leads to the need for HEOF analysis instead of standard EOF analysis (Fewings, 2017). The propagation is partly due to east-west propagating pressure anomalies crossing an angled coastline, resulting in apparent along-coast propagation [there is also propagation of coastal-trapped wind reversals due to smaller-scale dynamics within ~10s of km of the coast (Nuss et al., 2000), but trapped

reversals are not the focus of this study]. The leading HEOF of along-coast wind velocity (HEOF 1) along the U.S. West Coast for May–August 1981–2009 captures 60% of the variance on time scales of days to months (Fewings, 2017). The spatial phase of HEOF 1 captures the quasi-dipole wind pattern, with wind fluctuations off Washington and Oregon $\sim 140^\circ$ out of phase with wind fluctuations at Point Conception on average. The “southern relaxation” wind anomaly stage described above is well represented by the positive phase of HEOF 1: when HEOF 1 is composited over an index of known wind relaxations from NOAA buoys (Melton et al., 2009), the southern relaxations and opposite northern relaxation phase both appear in the composites (Fewings, 2017). Therefore, zero crossings of the HEOF are associated with the onset of local wind relaxation off central California (Fewings, 2017). In a typical summer, the wind quasi-dipole oscillation cycles every ~ 10 – 12 days, with the southern and northern relaxation states each lasting ~ 2 – 5 days (Fewings et al., 2016; Fewings, 2017).

The offshore extent and spatial shape of the quasi-dipole wind structure is determined by both the atmospheric pressure patterns and the shape of the coastline. The prevailing wind in the marine boundary layer off California in summer has transcritical Froude number (Rogerson, 1999) and becomes intensified downstream of the large-scale bend in California at Cape Mendocino due to a hydraulic expansion fan extending hundreds of km to the southwest (Edwards et al., 2002). This gives a triangular shape to the region of enhanced winds off California during stage (1) above, with the apex near Cape Mendocino. The wind in this triangular area weakens during stage (3). This creates a negative wind velocity anomaly, relative to the summer mean, with the same triangle shape as the “missing” expansion fan (Fewings et al., 2016). Therefore, the wind quasi-dipole is not only a “coastal” mode, but also has regional-scale impacts hundreds of km offshore. This wind quasi-dipole pattern is endemic to the CCS eastern boundary upwelling system. The wind dipole and its triangular southern lobe of coherent wind fluctuations off California results from the particular shape of the coastline of western North America: a large bend in the coastline is located near the central latitude of the dominant atmospheric pressure gradient forcing pattern. A key point for this study is that stage (3), wind relaxation off California, occurs during atmospheric ridging (Nuss, 2007; Fewings et al., 2016).

1.3. SST and Air-Sea Heat Flux Anomalies Associated With Typical CCS Wind Patterns

The regional wind relaxations and intensifications described above are accompanied by changes in SST. In particular, the wind quasi-dipole pattern is associated with dipole anomalies in SST trends (Flynn et al., 2017). During a typical “southern relaxation,” the SST anomaly off central California increases by ~ 0.25 – 0.5°C for several days, with a lag of ~ 2 days following the onset of the wind relaxation. However, the actual SST anomaly usually remains negative or near zero because southern wind relaxations are typically preceded by wind intensifications, i.e., the opposite

phase of the quasi-dipole, and those wind intensifications create negative SST anomalies (Flynn et al., 2017). The increase in SST anomaly during the following wind relaxation then restores the SST from a negative anomaly to near the climatological value (zero anomaly). During the subset of southern wind relaxations driven by stronger pressure anomalies, which involve coastal wind reversal rather than just weak wind, warm SST anomalies $\sim 1^\circ\text{C}$ develop off central California (Juliano et al., 2019).

During the typical regional wind relaxations, the net air-sea heat flux anomalies are too small to explain the SST warming trend off California (Flynn et al., 2017). There is not a strong positive air-sea heat flux anomaly during the southern relaxation events because the events are accompanied by reduced shortwave radiation, due to increased cloudiness. A scaling analysis of other terms in the 3-D heat budget indicates that offshore of the ~ 200 -km wide coastal upwelling region, the warming in SST during the wind relaxations off California is likely from shoaling of the ocean surface mixed layer (ML) due to reduced wind-driven vertical mixing and Ekman pumping (Flynn et al., 2017). The ML can then warm because the (climatological) air-sea heat flux heats a shallower ML, and because entrainment at the base of the ML is presumably reduced during wind relaxations.

1.4. This Study

The characteristic quasi-dipole wind pattern recently described off the western U.S. (Fewings et al., 2016; Fewings, 2017), and the changes in SST typically associated with that wind pattern (Flynn et al., 2017; Juliano et al., 2019), discussed above, have not been considered as a possible cause of regional variation in SST anomalies during MHWs. Here, we show that the splitting of the MHW in summer 2015 (**Figure 1B**) can be explained by the existence of this wind dipole pattern. We suggest that regional variations within the MHW occurred because the unusual atmospheric ridging that caused the northeast Pacific MHW also triggered the wind dipole pattern characteristic of the CCS to persist for an unusually long time in its southern relaxation state. Together with the preexisting “background” warm SST anomaly in the GoA, a wind-forced dipole-like SST anomaly along the western continental U.S. explains the split MHW pattern described in section 1.1.

We focus on 1–14 July 2015 as a clear case of the MHW developing a split structure. We analyze a heat budget for the ocean surface mixed layer to understand the cause of SST changes during the development of the split MHW. Many studies of the causes, spatial pattern, and timing of the northeast Pacific MHW of 2014–2016 focus on monthly anomalies (e.g., Bond et al., 2015; Di Lorenzo and Mantua, 2016; Gentemann et al., 2016; Chao et al., 2017), but those anomalies can be due to the presence of a few strong anomalies, or even a single anomaly, on synoptic time scales. Our study relates the SST variability to a wind forcing pattern that normally has a time scale of days, but during summer 2015 lasted for 2 weeks. This anomaly would be blurred in an analysis based on monthly averages. We use HEOF analysis (Fewings, 2017) to analyze scatterometer winds from RapidSCAT on the International Space Station and other satellites during summer 2000–2017, placing the 2014–2016 wind

anomalies in the context of the typical wind patterns previously described for the region.

2. DATA

2.1. Satellite Ocean Vector Wind Data

We use L2 ocean vector wind swath data to analyze wind stress and wind velocity along the coast. Reanalysis wind fields are inaccurate within ~ 2 grid cells of the coast (Wallcraft et al., 2009), especially in regions with hydraulic expansion fans, such as our study area (Perlin et al., 2004). In particular, reanalysis winds poorly represent the wind intensifications and relaxations in this region (Fewings et al., 2016). Another advantage of scatterometer-only winds over reanalysis winds for this study is that effects of SST-stress interaction (e.g., Small et al., 2008) are intrinsically included in scatterometer wind data, whereas reanalyses enforce prescribed planetary boundary layer physics parameterizations.

The satellite ocean vector wind data used in this work are from three satellite microwave scatterometer missions: QuikSCAT on SeaWinds during 2001–2009 (Fore et al., 2014), RapidSCAT on the International Space Station (ISS) during 2014–2016 (RapidScat Project, 2016), and ASCAT on Metop-A during 2010–2019 (Verhoef et al., 2012; Verhoef and Stoffelen, 2013). QuikSCAT was, and ASCAT is, flown on a sun-synchronous, polar-orbiting satellite, providing nearly global coverage approximately twice daily. The QuikSCAT overpasses are at $\sim 6:00$ am and 6:00 pm local time. The ASCAT overpasses are at $\sim 10:00$ a.m. and 10:00 p.m. local time. In contrast, the ISS is not in a polar orbit, so the data coverage from RapidSCAT is restricted to $\sim 61^\circ\text{N}$ to 61°S , and the timing of swath overpasses is distributed more widely throughout the day than for the polar orbiting satellites. All three data sets are in the form of swaths, which are 1,800 km wide for QuikSCAT, 1100 km wide for RapidSCAT, and 2 parallel 512-km wide swaths with a 737-km wide “nadir gap” in between for ASCAT. The data are available as individual swath orbit files: QuikSCAT L2B v3.1 at https://podaac.jpl.nasa.gov/dataset/QSCAT_LEVEL_2B_OWV_COMP_12_LCR_3.1; RapidSCAT L2B Climate v1.0 at https://podaac.jpl.nasa.gov/dataset/RSCAT_LEVEL_2B_OWV_CLIM_12_V1; and ASCATA L2 Coastal PODAAC-ASOP2-12C01 at <https://podaac.jpl.nasa.gov/dataset/ASCATA-L2-Coastal>. The effective spatial resolution is ~ 40 km for QuikSCAT (SeaPAC, 2016) and RapidSCAT (RapidScat Project, 2016), and ~ 25 km for ASCAT (KNMI, 2010; Verhoef and Stoffelen, 2013).

The L2 scatterometer data are provided as equivalent neutral 10-m wind velocity estimates on an irregular but ~ 12.5 -km spaced “swath grid.” High-quality data are available during both clear and cloudy conditions, and even during moderate rain, although rain is rare in our study area in summer.

2.2. SST and Air-Sea Heat Fluxes

We use the Canada Meteorological Center (CMC) 0.2° SST product available at <https://podaac.jpl.nasa.gov/dataset/CMC0.2deg-CMC-L4-GLOB-v2.0> from the Group for High Resolution Sea Surface Temperature. The SST is available with daily temporal resolution and 0.2°C spatial resolution from 1991–2017. The product merges infrared and microwave data from

multiple satellites and buoy and ship data to form a “Level 4” gap-free SST analysis (Brasnett, 2008; Canada Meteorological Center, 2012).

For latent and sensible air-sea heat fluxes, we use the OAFlux products (oafux.whoi.edu). OAFlux provides objectively analyzed estimates of latent and sensible turbulent air-sea fluxes daily from 1958–present with global coverage on a 1° grid (Yu and Weller, 2007; Yu et al., 2008). The SST used to estimate those fluxes is available on the same grid. The results presented below are similar if we instead use the SeaFlux product (Clayson et al., 2016) for latent and sensible air-sea heat fluxes (see Appendix in **Supplementary Material**). For radiative fluxes, we use the downwelling and upwelling shortwave and longwave radiative fluxes from CERES (Clouds and the Earth’s Radiant Energy System, <http://ceres.larc.nasa.gov>).

3. METHODS

3.1. Wind Stress: Calculating, Gridding, and Averaging

We calculated vector wind stress $\vec{\tau}$ using the COARE v3.5 neutral-stability bulk algorithm (Edson et al., 2013) for each L2 swath in swath coordinates, as in Fewings et al. (2016). The wind velocity and vector wind stress were then gridded onto a $0.1 \times 0.1^\circ$ latitude-longitude grid using linear interpolation. The various angles at which individual satellite swaths cross the coast result in some locations very near the coast having more data from morning than evening satellite passes or vice versa. To avoid biases from the diurnal cycle when calculating means over several days or weeks (section 3.2), we processed the L2 swath data for morning and evening passes separately, as in Fewings et al. (2016): taking the mean of morning passes and separately taking the mean of evening passes, then calculating the mean of the morning and evening results.

3.2. Calculating Climatologies, Means, and Anomalies

For SST, we calculated a climatology using daily means for 1 July or 14 July 2000–2017. For vector wind stress and for air-sea heat flux components, we calculated climatologies as the mean over the 2-week period 1–14 July 2000–2017. We then calculated anomalies relative to those climatologies. For the wind stress climatology, we used QuikSCAT and ASCAT, but not RapidSCAT, to avoid double-weighting the 2014–2016 time period. For the wind stress anomaly in 2015, we used both ASCAT and RapidSCAT to increase the number of overpasses available for calculating the anomaly.

To determine statistical significance of the anomalies, at each location we tested the anomaly (e.g., mean northward component of wind stress vector anomaly during 1–14 July 2015) against a mean anomaly of zero using a one-sample *t*-test, separately for ascending and descending passes. We combined the ascending and descending *p*-values at each location following Fisher (1992) and corrected for multiple hypothesis testing following Benjamini and Hochberg (1995). This combined, corrected *p*-value was then compared to 0.05 to determine where

the anomaly value was significantly different from zero at the 95% confidence level.

3.3. Hilbert EOFs

As a tool for capturing the synoptic-scale wind velocity anomalies, we used the Hilbert Empirical Orthogonal Function (HEOF) analysis method (e.g., Hannachi et al., 2007). This modification of standard EOF analysis is necessary to study the wind relaxations because standard EOF analysis is only designed to handle stationary patterns, but the wind relaxations propagate in space and time (Fewings, 2017). In standard EOF analysis, any propagating fluctuations are split between two EOFs that are not statistically separate and should not be considered independently. In contrast, the same propagating fluctuations can be captured by a single HEOF. The HEOF calculation involves adding an existing time series to i times a new time series based on the Fourier coefficients of the original, but constructed so that each frequency component is phase-shifted by 90° , where $i = \sqrt{-1}$. Time-domain EOFs are then calculated from the resulting complex time series following the usual EOF method but allowing for complex values. A more detailed review of the steps, including scaling and tapering, based on previous literature is available in Fewings (2017). The resulting HEOFs are complex, so each mode has both a spatial and temporal amplitude and, unlike in regular EOF analysis, a spatial and temporal phase. A modification of the above methods to calculate HEOFs from time series with gaps (in this case, the “gaps” between individual summers) is described in Fewings (2017); the method involves taking the Hilbert transform of the summer time series for each year separately, then joining the transformed time series together to form a single time series for all years, then proceeding with the typical steps of a complex EOF analysis in the time domain. Here, we use HEOF 1 as an index of the wind forcing state over the CCS to identify relaxations.

3.4. Ocean Surface Mixed Layer Heat Budget

We calculate a 1-dimensional (1-D, vertical) heat anomaly budget for the mixed layer using the same method as Flynn et al. (2017). The time-integrated heat budget anomaly equation can be written

$$SST'(t) - SST'(t_0) - \int_{t_0}^t \frac{Q'_{net}}{\rho_0 c_p h} dt = \int_{t_0}^t R dt \quad (1)$$

where SST' is the SST anomaly relative to climatology; t is time and t_0 is the initial time (here, $t_0 = 1$ July 2015); Q'_{net} is the anomaly in net air-sea heat flux, relative to climatology, with positive indicating anomalous ocean warming (or less cooling than in the climatology); ρ_0 is a reference density of seawater; c_p is the specific heat capacity of seawater; and h is the depth of the ocean surface mixed layer. Because estimates of mixed-layer depth are not available for the entire region with the required time resolution of ~ 1 day, for the heat budget analysis we proceed similarly to Flynn et al. (2017) and use a constant mixed-layer depth of $h = 20$ m based on the climatological mean summer mixed layer depths in the region (Holte et al., 2010). The

residual R includes terms due to penetrating radiation that passes below the mixed layer, horizontal advection and horizontal eddy dispersion of climatological and anomalous SST gradients by the climatological and anomalous velocity fields, changes in mixed-layer depth with time, and vertical variations in velocity and temperature within the mixed layer (see e.g., Flynn et al., 2017, for details). The penetrating radiation term is typically negligible in this region (Flynn et al., 2017), as is the effect of vertical variations within the mixed layer if the layer is relatively well-mixed. Away from the ~ 200 -km wide upwelling zone near the coast, the horizontal advection and dispersion terms are typically also negligible on time scales of a few days (Swenson and Niiler, 1996; Flynn et al., 2017). Therefore, on time scales of a few days, the most important terms in the residual are likely associated with vertical processes, such as changes in entrainment at the base of the mixed layer. For the heat budget, instead of the CMC SST we use the SST from OAFlux (section 2.2) for consistency with the air-sea flux estimates.

4. RESULTS

4.1. Similarity of the SST Anomaly Pattern in July 2015 to a Known Regional Wind Pattern

There is a striking similarity between the spatial structure of the regional SST anomaly off central California during mid-July 2015 (**Figure 1B**) and the typical spatial structure of wind relaxation events off central California [section 1.2 and Fewings et al. (2016), their Figure 6, day 2]. The warm SST anomaly that forms the southern part of the split MHW in **Figure 1B** is roughly triangular, with the apex near Cape Mendocino and the region of unusually warm SST widening toward the equator and extending hundreds of kilometers offshore and southward. The warm SST anomaly is connected to the coast from Cape Mendocino to Point Conception. From Point Conception southward, however, the warm SST anomaly is separated from the coast; the Southern California Bight and the coastal waters along Baja California do not have strong SST anomalies in mid-July 2015. The region of warming SST and weak wind during typical “southern relaxation” events has the same triangular structure (sections 1.2, 1.3). Motivated by this similarity, we examine whether the wind anomalies exhibit a southern relaxation during the days or weeks preceding the 15 July 2015 split MHW SST pattern in **Figure 1B**.

4.2. Unusual Persistence of “Southern Relaxation” Wind Pattern Before the Split MHW

During the MHW in summer 2015, the regional wind relaxations persisted longer than in a typical summer. In a more typical year, the relaxation events tend to last 2–5 days (Melton et al., 2009; Fewings et al., 2016). An example of a typical summer, 2009, is shown in **Figure 3A**. In contrast, in summer 2015 the relaxations typically lasted 1–2 weeks (red in **Figure 3C**). These unusually long relaxations are consistent with the persistent mid-level ridging that led to the large-scale MHW in the GoA (section 1.1): because mid-level ridging on synoptic

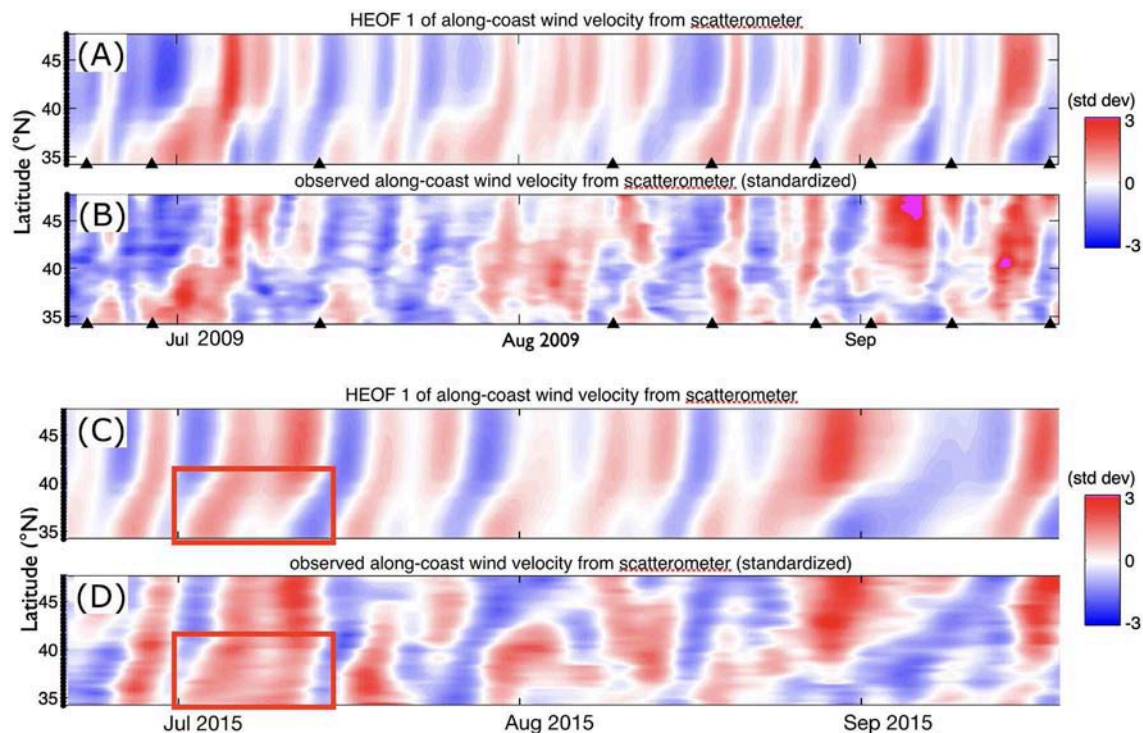


FIGURE 3 | Hovmöller diagrams of along-coast wind velocity and HEOF 1 of wind velocity along the west coast of the United States during summer: **(A,B)** 2009 from QuikSCAT and **(C,D)** 2015 from ASCAT. In **(B,D)** the mean wind velocity was removed and the data scaled by the standard deviation of wind velocity at each site. For **(C)**, the wind velocities from ASCAT in 2015 were projected onto the HEOF 1 spatial pattern calculated in Fewings (2017). Red boxes indicate 1–14 July 2015, the period preceding the appearance of the split MHW. Red indicates the along-coast wind velocity is below the mean value at that location (i.e., a wind relaxation is occurring). Panels **(A,B)** are reused from Fewings (2017) with permission; black triangles indicate the onset of wind relaxations at Point Conception, California discussed in that study.

time scales causes the southern relaxation state of the wind dipole off the western continental U.S. (section 1.2), it is not surprising that the more persistent mid-level ridging during 2014–2016 (Bond et al., 2015; Hartmann, 2015) was associated with more persistent southern relaxations. A particularly prolonged wind relaxation occurred during 1–14 July 2015 (red boxes in **Figures 3C,D**). This 2-week period encompassed the transition of the MHW from a single “Blob” in the GoA (**Figure 1A**) to a split MHW structure with two warm anomalies, one in the GoA and one off California (**Figure 1B**). Therefore, we focus on the 1–14 July 2015 period as a case study for the development of a split MHW structure during regional wind relaxation.

The spatial structure of the wind anomalies during the extended “southern relaxation” of 1–14 July 2015 is qualitatively consistent with the more typical synoptic wind relaxations described in section 1.2. The average wind stress anomalies during that 2-week period did have a dipole structure, with stronger than typical winds in the north part of the study region (blue in **Figure 2C**) and weakened winds (red in **Figure 2C**) south and west of Cape Mendocino in a roughly triangular shape with the apex near the Cape. Consistent with the more typical synoptic relaxation events discussed in sections 1.2, 1.3, the region with weakened winds in 1–14 July 2015 is similar in shape to the region of warm SST anomaly that developed off California

during the same period (**Figure 1B**). Note that this 2-week wind forcing anomaly is likely to dominate a monthly average wind forcing anomaly, but may simultaneously not be well-represented by a monthly average. To understand how this wind relaxation was related to the SST anomaly in **Figure 1B**, below we consider a heat budget for the ocean surface mixed layer.

4.3. Small Air-Sea Heat Flux Anomalies in the Warm SST Anomaly Region

To determine whether air-sea heat flux anomalies associated with the wind relaxation of 1–14 July 2015 could explain the warm SST anomaly that developed off California, we examine the ocean surface mixed layer heat budget during that period. First, we consider the trend in SST anomaly during 1–14 July 2015. The SST anomalies relative to climatology increased by $\geq 1^\circ\text{C}$ over most of the region in and offshore of the CCS (red in **Figure 4A** extending from marked area 1 to area 3). The anomalous warming was strongest offshore of central and southern California, where the SST anomaly increased by $\sim 3.5^\circ\text{C}$ (**Figure 4A**). The SST anomaly decreased during this period in the open ocean ~ 1000 km offshore of California (region 3 in **Figure 4A**). To determine whether anomalies in atmosphere-ocean heat flux can explain these areas of anomalous warming and cooling, we used the

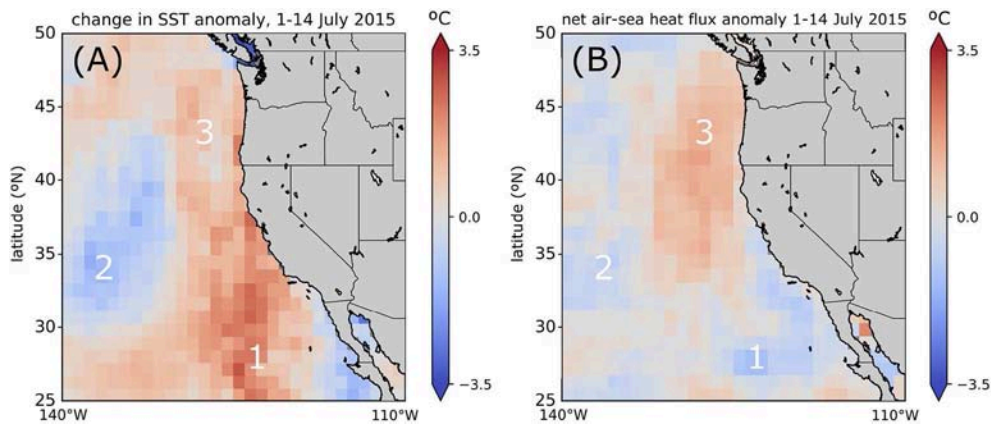


FIGURE 4 | Terms in a time-integrated 1-D heat anomaly budget for the ocean surface mixed layer (section 3.4) during 1–14 July 2015. **(A)** Change in SST anomaly from 1 July to 14 July at each location, relative to a daily climatology. **(B)** Accumulated anomaly in the net air-sea heat flux during 1–14 July. Positive indicates anomalous ocean warming (or equivalently, weaker cooling than in the climatology). If the 1-D heat budget closed exactly, the two panels would look the same. For consistency, **(A)** is based on the SST product distributed with OAFlux, not the CMC SST used elsewhere in this study, but the CMC product gives a very similar result (not shown). To facilitate comparison with **(A)**, the heat flux anomalies in **(B)** are converted to the change in SST that would be generated for a climatological mixed layer depth of ~20 m, following Flynn et al. (2017) (i.e., each heat flux is scaled by $\rho_0 c_p h$ with $h = 20$ m). White numbers mark regions referred to in section 4.3.

OAFlux and CERES products to estimate terms in the mixed layer heat budget as described in section 3.4. The main features are described below for the regions marked 1–3 in **Figures 4, 5**.

- Region 1: The net air-sea heat flux anomaly was negative south of Point Conception and offshore of Baja California (region 1, **Figure 4B**). The CERES product indicates this negative air-sea heat flux anomaly was mostly due to reduced net shortwave radiation (“more cloudy” in **Figure 5A**) that overcame a small increase in net longwave radiation (light red in **Figure 5B**). These radiative flux anomalies are attributable to unusually cloudy conditions. The clouds typically observed in the region in this season are low marine stratus (Iacobellis and Cayan, 2013). For an increase in this type of cloud, the resulting decrease in downwelling shortwave radiation tends to outweigh the increase in downwelling longwave radiation, leading to a net reduction in radiative ocean warming (Hartmann et al., 1992; Klein and Hartmann, 1993). There was also some contribution from a negative anomaly in latent heat flux, i.e., there was increased evaporation (light blue along southern California and Baja in region 1 of **Figure 5C**).

The negative air-sea heat flux anomaly in region 1 (blue, **Figure 4B**) is the wrong sign to explain the warming in SST observed in the same region (red in **Figure 4A**), so the residual in the 1-D heat budget is large (red in region 1 in **Figure 6A**).

- Region 2: In part of the offshore region where SST cooled (region 2 in **Figure 4A**), the net air-sea heat flux anomaly was negative (blue in region 2 in **Figure 4B**). The negative heat flux anomaly is again attributable to an increase in cloudiness (blue in region 2 in **Figure 5A**). In this relatively small region, the air-sea heat flux anomaly does explain

part of the observed change in SST anomaly, and the residual in the 1-D heat budget is smaller in region 2 than in region 1 (**Figure 6A**). However, air-sea flux does not explain all the cooling in SST offshore in **Figure 4A**; there is residual, unexplained cooling in the northern part of the region where SST cooled (blue between 2 and 3 in **Figure 6A**).

- Region 3: The net air-sea flux anomaly was positive in the region along Washington and Oregon (red in region 3 in **Figure 4B**). The anomalous warming was mainly due to increased shortwave radiation, i.e., reduced cloudiness (red in region 3 in **Figure 5A**). In this region, the air-sea heat flux anomaly accounts for enough heating to explain the observed change in SST anomaly, and the residual has a smaller magnitude than in region 1 (light blue in region 3 in **Figure 6A**).

In general, the net air-sea heat flux anomalies during 1–14 July 2015 cannot explain the strong warming in SST to the west and south of California during that period (region 1 in **Figure 4A**). If the heat budget for the mixed layer were a 1-D (vertical) balance between air-sea heat flux and change in SST, **Figures 4A,B** would look the same. Instead, those panels look very different except off Washington/Oregon (region 3) and in one part of the region where SST cooled anomalously (region 2). Strikingly, in the region of greatest SST increase (region 1), the anomaly in net air-sea heat flux was near zero or the wrong sign to explain the increase in SST.

The failure of air-sea heat flux anomalies to account for the observed ocean warming off California is consistent with the heat budget in the shorter-lived “southern wind relaxation” events in Flynn et al. (2017). During typical synoptic southern relaxations, (i) the net air-sea heat flux anomalies are small in

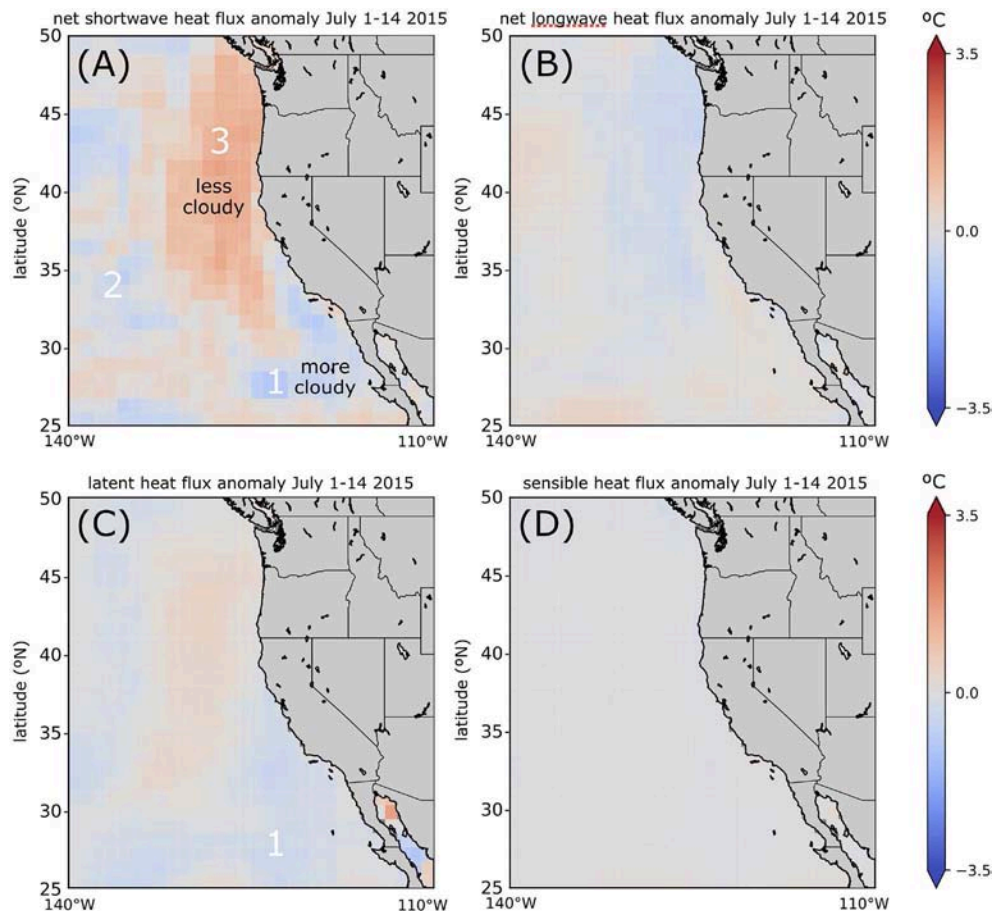


FIGURE 5 | Components of the net air-sea heat flux anomaly in the time-integrated 1-D budget during 1–14 July 2015 (**Figure 4B**). Positive indicates anomalous ocean warming (or equivalently, weaker cooling than in the climatology). The panels show accumulated anomalies in **(A)** net shortwave radiation, **(B)** net longwave radiation, **(C)** latent heat flux, and **(D)** sensible (conductive) heat flux. To facilitate comparison with **Figure 4**, the heat flux anomalies have again been converted to the change in SST that would be generated for a climatological mixed layer depth of ~ 20 m, following Flynn et al. (2017) (i.e., each heat flux is scaled by $\rho_0 c_p h$ with $h = 20$ m). The color scale is the same for all panels. White numbers mark regions referred to in section 4.3.

the region of weak winds, and (ii) the region of weak winds is where the greatest warming occurs (section 1.3). During the more persistent relaxation in July 2015, the same general pattern holds: (i) the air-sea heat flux anomalies during 1–14 July 2015 are small or negative (region 1, **Figure 4B**) in the region of weak winds (red in **Figure 6B**), which (ii) coincides with the region of strongest warming (region 1, **Figure 4A**). The partial success of air-sea heat flux anomaly in accounting for SST changes in the northern region of intensified winds during 1–14 July 2015 (region 2) is also consistent with the heat budget in the more typical synoptic events described in Flynn et al. (2017). The magnitude of SST warming off California during the July 2015 event, $\sim 3^\circ\text{C}$, is much larger than for typical events, $O(0.25\text{--}0.5^\circ\text{C})$ (Flynn et al., 2017). Nevertheless, because the air-sea heat flux anomalies are too small to explain much of the SST anomaly pattern (as discussed above), the most likely explanation for the SST changes in early July 2015 is changes in wind-driven mixing and entrainment, as in the more typical synoptic events (the anomaly in wind stress curl is negligible

offshore; not shown). Supporting this interpretation that changes in wind-driven mixing or entrainment are important in driving the SST anomalies, the spatial pattern of the residual heating and cooling “missing” from the heat budget (**Figure 6A**) is strikingly similar to the spatial pattern of the change in mean wind stress magnitude during the same period (**Figure 6B**).

4.4. Forming SST and Wind Stress Anomalies With the Same Shape: Persistence Is Key

The SST tendency during 1–14 July 2015 (**Figure 4A**; also see Appendix in **Supplementary Material** for daily SST anomaly plots) off California has a spatial pattern similar to the wind stress anomalies during the same period (**Figures 2B, 6B**), with the SST and wind stress anomalies having opposite signs. The unusual persistence of this southern wind relaxation was key to the development of an SST anomaly, rather than only an SST trend, in the shape of the wind anomaly. During more typical

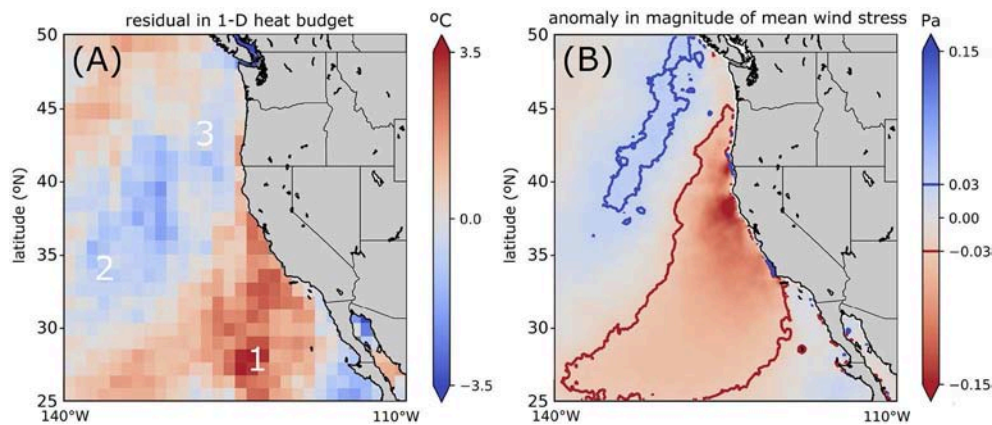


FIGURE 6 | (A) Residual in the 1-D budget for the ocean surface mixed layer heat anomaly during 1–14 July 2015, equal to **Figure 4A** minus **Figure 4B**. Red indicates unexplained ocean warming. **(B)** Anomaly in the magnitude of the mean wind stress during 1–14 July 2015, equal to the magnitude of the arrows in **Figure 2B** minus the magnitude of the arrows in **Figure 2A**. Note that in **(B)**, red indicates weaker mean wind stress, and blue indicates stronger mean wind stress, in 2015 as compared to 2000–2017. This reversed color convention for the wind stress anomaly is to facilitate comparison of the two panels. The ± 0.03 Pa contours are shown as a threshold for a non-negligible wind stress anomaly, following previous studies (e.g., Fewings et al., 2008). White numbers mark regions referred to in section 4.3.

shorter wind relaxation events off California, the warming in SST is not strong enough to dominate over preexisting SST anomalies (section 1.3). During 1–14 July 2015, however, the warming trend in SST in the region of relaxed winds lasted so long that it overcame preexisting SST anomalies, resulting in an SST anomaly with the triangular shape of the California-scale region of high winds (Edwards et al., 2002) that is “turned off” during southern wind relaxations (section 1.2).

5. DISCUSSION

5.1. Development of a Split MHW

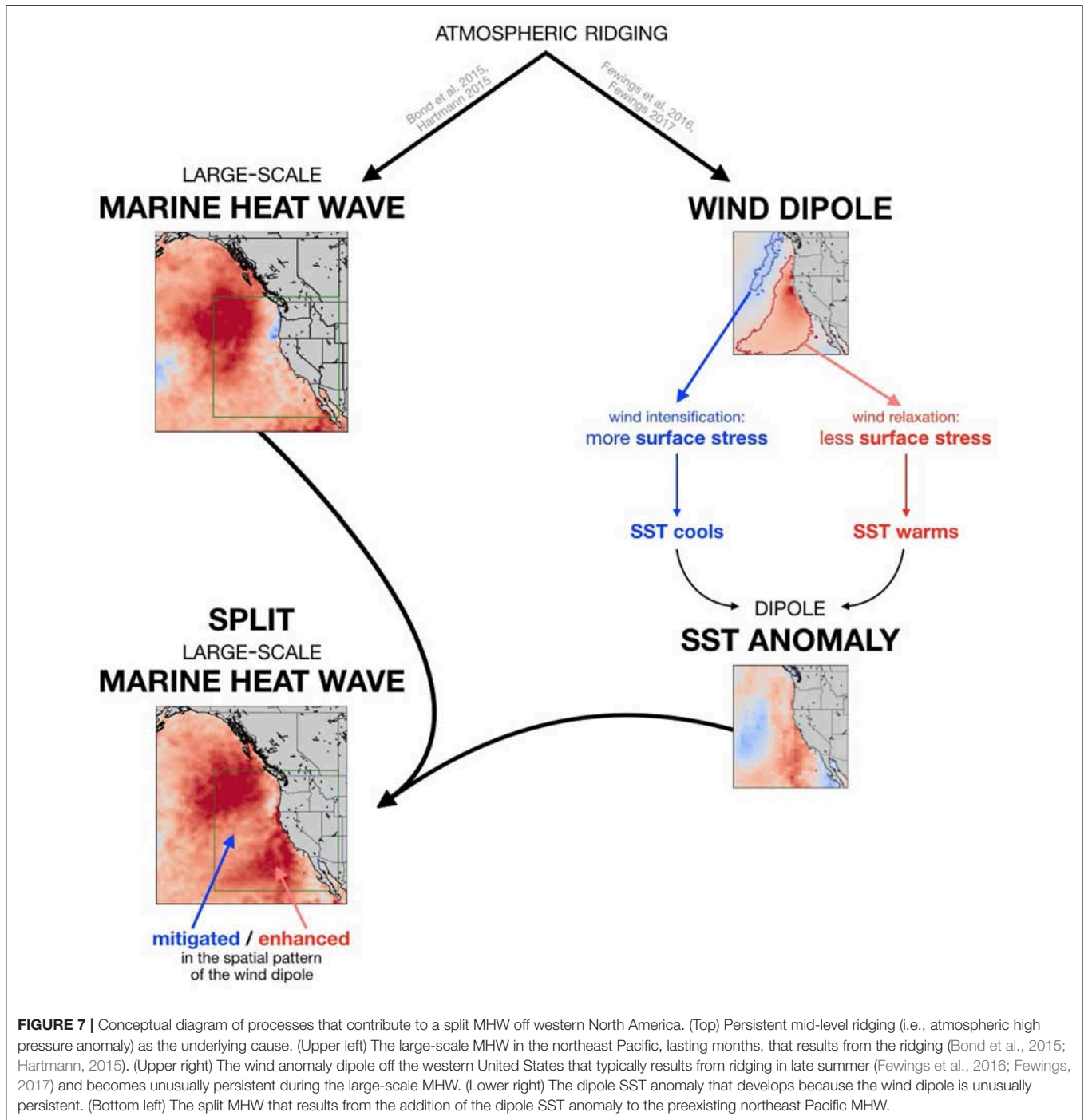
When superimposed on the preexisting northeast Pacific MHW, the changes in SST during 1–14 July 2015 (**Figure 4A**) can explain the split MHW structure previously described as part of Phase III of the MHW (Peterson et al., 2016), as well as the “cool corridor” described in Gentemann et al. (2016). We propose the following scenario for the development of a split MHW. First, persistent mid-level ridging leads to the formation of a MHW in the GoA (e.g., Bond et al., 2015; Hartmann, 2015) (**Figure 7**, top left). Second, during summer the persistent ridging prolongs a typical synoptic wind relaxation off California, causing the “southern relaxation” wind pattern to last for weeks instead of the usual few days (e.g., **Figures 3C,D**, **7**, top right). Third, this prolonged weak wind anomaly off California causes a warming trend in SST; conversely, the strong wind anomaly off the northern half of the CCS causes a cooling trend in SST (**Figure 4A**, regions 1 and 2). This dipole in SST trends lasts long enough to create a dipole SST anomaly pattern with the same spatial pattern but opposite sign from the wind anomalies: colder SST off Washington/Oregon and warmer SST off California (**Figure 7**, lower right). When superimposed on the preexisting MHW in the GoA, this CCS SST dipole creates a split MHW SST pattern, with warm SSTs in the GoA, a “cool corridor” (Gentemann et al., 2016) extending

offshore from the northern CCS, and warm SSTs off California (**Figures 1B**, **7**, bottom left).

Key aspects of the formation of the split MHW are (a) atmospheric ridging leads to both a MHW in the GoA and unusual persistence of the southern wind relaxation pattern off the western continental U.S., (b) the southern wind relaxation persists long enough for the resulting trends in SST to overcome any preexisting SST anomalies offshore of the CCS, (c) the resulting dipole SST anomaly is dominated by anomalies in wind-driven mixing, not air-sea flux anomalies, so (d) the spatial structure of the new SST anomaly is similar to the spatial structure of the wind anomaly, and (e) the spatial structure of the wind anomaly is set by the shape of the coastline and resulting expansion fan (Edwards et al., 2002). The end result is that persistent atmospheric ridging creates not only a warm SST anomaly in the GoA but also a warm SST anomaly shaped like a triangle extending southward from Cape Mendocino. Together, these two warm anomalies form the split MHW. The split MHW structure is further enhanced by the cold SST anomaly in between the two warm anomalies, which is associated with the wind intensification offshore of Washington/Oregon that accompanies southern wind relaxation and forms the other half of the wind dipole (**Figures 2C**, **6B**, blue). Overall, we propose that the split MHW of July 2015 occurred when the wind dipole mode endemic to the CCS (Fewings, 2017), during a particularly persistent southern relaxation, imprinted a dipole SST anomaly on top of the pre-existing northeast Pacific warm SST anomaly.

5.2. Similarities and Differences Between Typical and Prolonged Wind Relaxations

To first order, the dynamics of the “extreme” or prolonged southern relaxation event during 1–14 July 2015 are the same as more typical synoptic wind quasi-dipole events described



in Fewings et al. (2016) and Flynn et al. (2017). The net air-sea heat flux anomaly is too small to explain the SST anomaly (section 4.3, region 1), so we infer the SST signal is due to reduced wind-driven mixing and mixed-layer shoaling, as in more typical shorter events Flynn et al. (2017).

There are some details that differ between the prolonged relaxation event of July 2015 and the typical synoptic relaxation events. (a) The node of the dipole wind anomaly along the

coast was farther poleward during 1–14 July 2015 (**Figure 2B**) than during typical events, in which the node is near Cape Mendocino (Fewings et al., 2016). (b) It is possible that during very prolonged wind relaxations, changes in horizontal advection of temperature gradients could become important even in the region offshore of the upwelling zone, as the scaling analysis for that term assumes synoptic time scales of days (Flynn et al., 2017).

5.3. Implications for the Spatial Structure of Future MHW in the CCS

The association of persistent ridging, persistent southern wind relaxation, and development of a split MHW with a particular shape determined by a coastline bend lends insight into which areas along the western continental U.S. are likely to have enhanced or mitigated SST anomalies during future MHWs. We expect that future large-scale MHWs similar to the 2014–2016 event will also split into two parts along the western continental U.S. during the summer. This region includes the California Current eastern boundary upwelling system, which supports substantial export production and fisheries (e.g., Falkowski et al., 1998). Species shifts and fisheries and ecosystem disruptions may still occur across the entire system due to the effects of the MHW in fall and winter before the MHW is mitigated along the coast at the beginning of upwelling season and then splits in two during the upwelling season, as observed during 2014–2016 (Gentemann et al., 2016). However, our expectation is that warm SST anomalies and associated ecosystem disruptions during the summer will be stronger in the southern than the northern half of the upwelling system. Based on the particular relation of SST anomalies to wind stress anomalies offshore of the CCS region, the spatial structure of future MHWs off western North America in summer may be foreseeable, even if the timing of the MHWs is not.

5.4. A Corollary for Future Climate?

It has been suggested that the prevailing summertime equatorward wind forcing along eastern ocean boundaries in midlatitudes, i.e., over the CCS and other eastern boundary upwelling systems (EBUS), will strengthen in a warming global climate due to enhanced temperature contrast between ocean and land (Bakun and Nelson, 1991). In contrast, simulations with the Community Earth System Model suggest that summer mean wind forcing patterns over EBUS will not strengthen, but will shift poleward (Rykaczewski et al., 2015). In the case of the CCS, this would result in stronger upwelling-favorable wind forcing on average over the poleward half of the system, off Oregon, and weaker wind forcing on average off California. Because the wind fluctuations over the CCS are comparable to or stronger than the mean (Halliwell and Allen, 1987), a change in the mean wind forcing requires a change in the statistics of the fluctuations. Therefore, the suggested changes in the mean wind forcing in a warmer climate imply the system would spend more time in the southern wind relaxation state described in Bond et al. (1996) and Fewings et al. (2016). If the MHW of 2014–16, and in particular the 1–14 July 2015 pattern discussed in this study, can be viewed as an example of the future climate “normal” for EBUS, then this study supports the suggestion in Rykaczewski et al. (2015) of strengthened wind forcing over the poleward half of the California Current system and weakened wind forcing in the equatorward half. Based on the relation of warm SSTs to the region of relaxed winds described here, if the relation of wind relaxations to increased cloudiness off California also persists in a warmer climate, then the future climate “normal” for the CCS will have warmer SSTs compared to today from Cape Mendocino southward, and cooler SSTs from Cape Mendocino northward.

5.5. Summary

This analysis was driven by the striking similarity between recent MHWs off the western continental U.S. and a previously described regional wind relaxation dipole. This case study suggests that a characteristic regional wind dipole pattern off Washington, Oregon, and California in summer (Fewings, 2017), which has a spatial structure determined by the coastline shape (Edwards et al., 2002) and is triggered by atmospheric ridging (Nuss, 2007), played a crucial role in determining the regional spatial structure of the MHW of 2015. We suggest that during the extended midlatitude MHWs off western North America during 2014–2016, and due to the accompanying persistent ridging, the wind dipole mode persisted unusually long in the “southern relaxation” state described by Fewings et al. (2016) and Fewings (2017). This reduced and increased SST in the poleward and equatorward parts of the domain, respectively, thus “splitting” the MHW. If the air-sea flux anomalies during wind relaxations over other eastern boundary upwelling regions are small as in the CCS, the summer wind patterns set by the coastlines of the Chile-Peru, Benguela, and Canary Current Systems may also provide projections for the spatial structure of MHW in those systems.

DATA AVAILABILITY

All data sets analyzed in this work are publicly available through the repositories indicated in Data.

AUTHOR CONTRIBUTIONS

MF carried out the calculations for **Figure 3** and guided the remaining calculations, made **Figures 3, 7** and assembled the other figures, and contributed the bulk of the text. KB wrote the python code to carry out the remaining calculations, produced the panels for all figures except **Figures 3, 7**, and assisted in the writing of 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.2019.00564/full#supplementary-material>

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Characteristics of an Advective Marine Heatwave in the Middle Atlantic Bight in Early 2017

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There has been wide interest in Marine Heatwaves and their ecological consequences in recent years. Most analyses have focused on remotely sensed sea surface temperature data due to the temporal and spatial coverage it provides in order to establish the presence and duration of Heatwaves. Using hydrographic data from a variety of sources, we show that an advective Marine Heatwave was initiated by an event in late December of 2016 south of New England, with temperature anomalies measuring up to 6°C and salinity anomalies exceeding 1 PSU. Similar features were observed off of New Jersey in February 2017, and are associated with the Shelfbreak Front migrating from its normal position to mid-shelf or further onshore. Shelf water of 34 PSU was observed just north of Cape Hatteras at the 30 m isobath and across the continental shelf in late April 2017. These observations reveal that the 2017 Marine Heatwave was associated with a strong positive salinity anomaly, that its total duration was approximately 4 months, and its advective path extended roughly 850 km along the length of the continental shelf in the Middle Atlantic Bight. The southward advective velocity implied by the arrival north of Cape Hatteras is consistent with previous estimates of alongshelf velocity for the region. The origin of this Marine Heatwave is likely related to cross-shelf advection driven by the presence of a Warm Core Ring adjacent to the shelfbreak south of New England.

Keywords: Heatwave, Middle Atlantic Bight, shelfbreak front, warm core ring, coastal ocean circulation

INTRODUCTION

There has been considerable attention focused recently on Marine Heatwaves, which are warm anomalies persisting for days to months and on spatial scales from one to a thousand kilometers or more (Hobday et al., 2016). Further studies have examined the frequency of Marine Heatwaves in the North Pacific and North Atlantic (Scannell et al., 2016), the influence of global warming on the frequency of Marine Heatwaves under various carbon emission scenarios (Frohlicher et al., 2018), significant historical changes globally based on historical data (Oliver et al., 2018), and the contributions of various ocean-atmosphere modes on the global distribution of heatwaves (Holbrook et al., 2019).

While Marine Heatwaves lasting over days may disturb the marine environment, it is the long lasting events that have the most significant impact. The most dramatic recent example in the Northwest Atlantic coastal ocean was the warming of 2012 (Mills et al., 2013; Chen et al., 2014). This event, which lasted over 6 months with ocean temperature anomalies exceeding 2°C, was caused by a northward shift in the atmospheric Jet Stream during winter that resulted in a 50% reduction of heat loss from the ocean to the atmosphere compared to a normal winter (Chen et al., 2014).

As recent technological improvements and deployment of ocean observatories have allowed further examination of shelf and slope processes, it has become apparent that offshore forcing of the continental shelf and slope is becoming more prevalent and that processes driving shelfbreak exchange may be significant contributors to Marine Heatwaves in the Middle Atlantic Bight. Two observational programs that have been particularly important in recent years are the Ocean Observatories Initiative (OOI) Pioneer Array (Gawarkiewicz and Plueddemann, 2019) and the Commercial Fisheries Research Foundation/Woods Hole Oceanographic Institution Shelf Research Fleet (Gawarkiewicz and Malek Mercer, 2019). The Pioneer Array is a multi-scale shelfbreak observatory designed to study shelfbreak exchange processes, while the Shelf Research Fleet utilizes the commercial fishing fleet in Rhode Island to regularly sample the continental shelf using CTDs provided by Woods Hole Oceanographic Institution (WHOI). Data from these two programs have revealed a dramatic warming event in January 2017 south of New England in which warm water fish typically found in the Gulf Stream were caught at the 30 m isobath off Block Island, RI (Gawarkiewicz et al., 2018). The magnitude of the temperature anomaly reached 6°C relative to a monthly climatology of shelf temperature in the region (Fleming, 2016). However, this event was not examined closely in context with historical data from the region, nor was the fate of the warm water flooding the continental shelf established in Gawarkiewicz et al. (2018).

In this study, we examine a broad suite of observations to characterize the origin of the event, compare its statistical properties with a Marine Heatwave definition, and track the fate of the anomalous water mass on the northeast US Shelf. The outline of the paper is as follows. Section “Data Sources and Methods,” describes the data sources used to examine the 2017 event as well as the criteria used to qualify as a Marine Heatwave using limited sub-surface data. The characteristics of the warm and salty anomalies and their duration south of New England are described in section “Shelfbreak Exchange–Initiation of the Marine Heatwave South of New England.” Anomalous conditions subsequently observed over the New Jersey shelf are described in section “The Marine Heatwave Over the New Jersey Continental Shelf.” The fate of the Heatwave is presented in section “The Fate of the Marine Heatwave” using data showing the anomalous water mass over the continental shelf north of Cape Hatteras. A discussion follows, which includes ecosystem effects and directions for future research. The results are briefly summarized in the final section.

DATA SOURCES AND METHODS

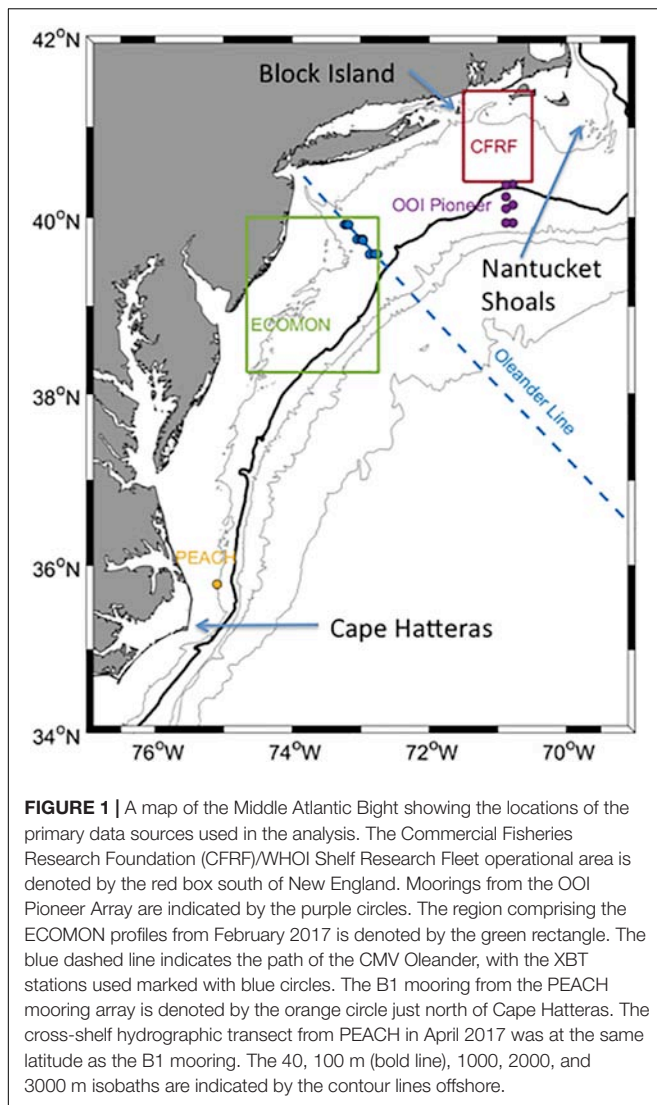
Because of the spatial and temporal extent of this Extreme Shelfbreak Exchange Event, a number of different data sources were used to track the thermohaline anomalies along the length of the Middle Atlantic Bight. These include the Commercial Fisheries Research Foundation/Woods Hole Oceanographic Institution (CFRF/WHOI) Shelf Research Fleet, the Ocean Observatories Initiative Pioneer Array, the CMV Oleander ship of opportunity temperature data set, the National Marine Fisheries Service (NMFS) Ecosystem Monitoring (ECOMON) program, and the National Science Foundation Processes driving Exchange At Cape Hatteras (PEACH) experiment. It is interesting to note that the first identification of this Marine Heatwave event was from Captain Michael Marchetti of the F/V Mister G based in Point Judith, Rhode Island, who emailed photographs and descriptions of unusual conditions and catch to Anna Malek Mercer at CFRF and Glen Gawarkiewicz at WHOI. As reported in Gawarkiewicz et al. (2018), Marchetti noted several unusual species in his catch in January 2017, including Gulf Stream flounder and juvenile black sea bass. Marchetti is a participant in the CFRF/WHOI Shelf Research Fleet, and thus has frequent communications with both CFRF and WHOI.

CFRF/WHOI Shelf Research Fleet

The CFRF/WHOI Shelf Research Fleet was initiated in November, 2014 to enhance interactions between scientists and local communities to discuss adaptation to climate change impacts from the ocean in southern New England. Since then, a fleet of commercial fishing vessels, all based out of Rhode Island, have collected biweekly water column profiles within a region ranging from 40°00' North to 41°18' North and 70°30' West to 71°30' West. The depth range of the profiles used in the analysis in section “Shelfbreak Exchange–Initiation of the Marine Heatwave South of New England” extended from the 37 to 88 m isobaths. A description of the Shelf Research Fleet activities appears in Gawarkiewicz and Malek Mercer (2019). The domain of Shelf Research Fleet sampling appears in **Figure 1**.

Participant fishing vessels are trained to use the RBR Concerto CTD to collect water column profiles. The CTDs are routinely rotated and calibrated at RBR facilities in Ontario, Canada. Typical accuracy of the data for this particular CTD is ± 0.03 mS/cm and $\pm 0.002^\circ\text{C}$. The two primary considerations driving this choice of instrument were the high degree of accuracy as well as the wireless data communications that enable real-time plotting and viewing of profiles on an iPad without connecting cables to the CTD. Further details on the use of CTDs by the Shelf Research Fleet appear in Gawarkiewicz and Malek Mercer (2019).

Profiles of temperature and salinity sampled by commercial fishers as part of Shelf Research Fleet sampling were examined for December 2016 and January/February 2017. Ten profiles were collected in December 2016, 11 in January 2017, and 24 profiles were collected in February 2017.



Historical Hydrographic Data Archive and Sea Surface Temperature

In order to produce statistics on historical temperature and salinity distributions south of New England, we used the World Ocean Database (WOD) 2018 from the National Center for Environmental Information. For southern New England, profiles from January were used to calculate the distribution of depth-averaged temperature and salinity to compare to data collected by the Shelf Research Fleet during January 2017. Historical profiles from 40°24' North to 41°18' North and 71°30' West to 70°30' West were included, spanning the northern edge of the Shelf Research Fleet operational area south to the latitude at which frequent excursions of the Shelfbreak Front were no longer evident in the historical data (40°24' North). Forsyth et al. (2015) have shown that enhanced warming in the Middle Atlantic Bight (over the New Jersey shelf) has occurred since 2004. We wished to explicitly compare the 2017 warm event to conditions that occurred before the recent decadal warming.

Thus we use all the historical profiles in WOD 2018 before 2004 for comparisons.

The profiles within the historical archive for the months of January through March extend from 1940 to 1996 within the region defined by the sampling domain of the Shelf Research Fleet north of the typical range of variability of the Shelfbreak Front. For the purposes of comparison, the historical data was limited to 40°24' North to 41°18' North and 70°30' West to 71°30' West.

For the purposes of calculating anomalies for temperature and salinity, the four-dimensional climatology compiled by Fleming (2016) is used. The climatological fields are monthly and are gridded onto a three dimensional field using a weighted least squares regression technique. The climatological fields, named MOCHA (Middle Atlantic Climatological and Hydrographic Atlas) are also described in Levin et al. (2018).

The cross-shelf temperature and salinity fields from MOCHA along 71°00' West in January appear in **Figure 2**. The Shelfbreak Front is the area of pronounced gradients extending offshore from the 100 m isobath. Typical shelf temperature values in January range from 4 to 7°C and typical shelf salinities are in the range of 32–34 PSU. For the purposes of interpretation, we take the inshore boundary of the Shelfbreak Front to be the 10°C isotherm and the 34.0 PSU isohaline. Slope Water is present offshore of the Shelfbreak Front with typical temperatures of 12–14°C and salinities greater than 35.0 PSU.

A common feature in recent years south of New England are Warm Core Rings abutting the continental shelf. These have substantially increased in numbers since 2000 (Gangopadhyay et al., 2019). The rings are anti-cyclonic with typical diameters of 50–100 km and lifetimes on the order of months. Water mass properties include temperatures near 18°C and salinities greater than 35.5 PSU for rings nearing the edge of the continental shelf.

The SST images are based on the Advanced Very High Resolution Radiometer (AVHRR) unmasked data provided by the Mid-Atlantic Regional Association Coastal Ocean Observing System (Dr. Matthew Oliver, University of Delaware)¹.

Long-Term Ship of Opportunity Temperature Measurements Off New Jersey

To trace the Marine Heatwave through the New Jersey shelf, we utilize the CMV Oleander datasets. The CMV Oleander is a container ship that traverses a round trip from New Jersey to Bermuda every week (**Figure 1**). Since 1977, expendable bathythermographs (XBTs) have been deployed from the Oleander creating a consistent and continuous record of temperature across the shelf and to the Gulf Stream. XBTs are deployed along the line approximately 14 times a year, generally once a month during January for the time period of analysis. Here we restrict the XBT data set to the shelf region, only using data collected between the 40 m isobath and the 80 m isobath, the latter corresponding with the climatological position of the foot of the shelfbreak front (Linder and Gawarkiewicz, 1998). For comparison with the New England shelf data we consider

¹<http://tds.maracoos.org/thredds/dodsC/AVHRR/>

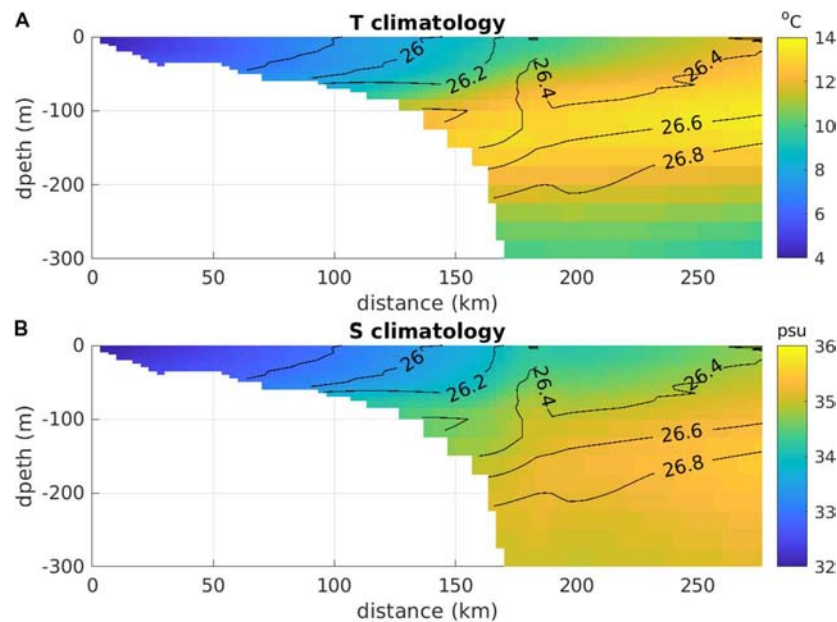


FIGURE 2 | Cross-shelf sections of Climatological mean temperature (A) and salinity (B) in January across the continental shelf and slope south of New England along 71°00' West. The black contour lines indicate isopycnals. Units are Degrees Centigrade for temperature, Practical Salinity Units for salinity, and kg/m³ for density.

data from the months of January to March from 1977 to 2017 as our baseline to calculate Heatwave statistics. This baseline includes 24 cross-shelf transects of XBT data. Four transects were occupied during the period of the event, including January 14th, January 21st, February 18th, and March 18th in 2017. We also use thermosalinograph (TSG) data from January to March to track surface salinity and temperature changes through the New Jersey Bight. Data from the CMV Oleander have been previously used to describe the variability of the shelf and slope velocity structure (Flagg et al., 2006) as well as recent accelerated warming over the New Jersey shelf (Forsyth et al., 2015).

The Ecosystem Monitoring Program in the Middle Atlantic Bight

The Ecosystem Monitoring program (ECOMON) is a long term hydrographic and ecosystem monitoring program that has been in operation since 1992. Earlier efforts with joint hydrographic and plankton sampling in this region extend back to the 1970s. It is conducted under the auspices of the Oceans and Climate Branch of NOAA's Northeast Fisheries Science Center in Woods Hole, MA. Typically two of the ECOMON cruises in a given year are conducted jointly with bottom trawl surveys and four of the surveys involve both hydrographic and plankton sampling.

Cruises normally involve stratified sampling with CTD profiles at 120 randomly selected stations and 35 stations at fixed locations in the northeast. The geographical coverage extends from Cape Hatteras in the south through the Gulf of Maine and Georges Bank.

In February 2017, an ECOMON cruise on the R/V Henry Bigelow collected 23 CTD profiles over the New Jersey

continental shelf in water depths ranging from 13 to 196 m. The profiles were collected between February 12 and 16, 2017.

The Processes Driving Exchange at Cape Hatteras (PEACH) Experiment

In addition to the long-term observational programs described above, a National Science Foundation sponsored experiment, the Processes driving Exchange at Cape Hatteras (PEACH) experiment was initiated in April 2017 with hydrographic sampling and mooring deployments from the R/V Neil Armstrong. The cruise occurred from April 15 to 29. Two cross-shelf CTD transects were sampled along 35°45' North on April 18 and 25, 2017. Sampling was conducted with a SeaBird 911 + CTD.

A surface meteorological buoy with CTDs at 3 and 15 m depths was deployed at 35°46.7' North and 75°05.7' West on April 17; a small bottom frame with CTD and ADCP was deployed on the 30 m isobath directly adjacent to the surface buoy. The time series from this mooring, designated B1 for this experiment, extended for 18 months until November 2018. Data from B1 is used to examine the progression of the anomalous water mass to the Cape Hatteras region, where it is evident as a salinity anomaly but only a mild temperature anomaly (section "The Fate of the Marine Heatwave").

Methodology for Identifying Marine Heatwave Status for the Sub-Surface

The methodology for identifying Marine Heatwaves, initially formulated by Hobday et al. (2016), is problematic for the analysis of sub-surface data. There is significantly less sub-surface data

than surface temperature data, so that the resolution in both time and space is orders of magnitude less than satellite-sensed surface temperature values. Two key criteria for the prior method are the use of a 30s year record and the use of a climatology with daily resolution. For sub-surface data, 30 years records are limited and daily resolution would likely be obtainable only from mooring records and not from hydrography.

We choose to present for our baseline the time period 1940 to 1996 because this is the time period for which there is January data south of New England in the WOD data archive (we note that there is no January data between 1997 and 2004, which was when the warming rate increased substantially). January is a particularly bad month in terms of the number of CTD profiles available in the WOD archive.

Fortunately, for the New Jersey shelf, we have data through the present and can use the data from the CMV Oleander for the time period from the start of the record (1977) through the present which extends through the significant warming period as described in Forsyth et al. (2015).

The WOD archive is used for calculating the percentile of the present observations compared to the statistics of the historical data. For calculating anomalies, we use the climatology compiled by N. Fleming (Fleming, 2016; Levin et al., 2018). This climatology calculates monthly averages for the entire Middle Atlantic Bight with a high resolution spatially enabling the detailed comparison for the locations of CTD profiles from 2017. There is a scale mis-match temporally, using monthly averages for the climatology, but this is the best climatological field at present.

We discuss the duration locally in terms of the 5 days duration criterion from Hobday et al. (2016). However, given the very intermittent nature of the hydrographic sampling, it is difficult to precisely define the duration at a specific location. A key point is that this thermohaline anomaly event occurred over a large alongshelf spatial scale, so time scales are both for the local passage as well as the eventual transport offshore north of Cape Hatteras. We also use the criterion of a temperature value above the 90th percentile, consistent with the definition of Hobday et al. (2016).

We explicitly compare the statistics of the 2017 event with the time period before 2004 because of the recent significant warming. As shown in Gawarkiewicz et al. (2018), shelfbreak exchange events with considerable onshore penetration across the continental shelf have occurred since 2014. We wish to understand the 2017 event within the context of a previous state of shelfbreak variability that has been described in the literature and covered by previous large field programs such as the Shelf Edge Exchange Processes program in the early 1980s south of New England. There have clearly been other unusual events in the past 5–10 years, but it is unclear if the sub-surface data have sufficient resolution to place recent individual events in a proper statistical context given the rapid rate of warming for the past decade. The availability of consistent data from the CMV Oleander allows us to use statistics up to the present for the New Jersey shelf as well as to the beginning of the enhanced warming in 2004.

SHELFBREAK EXCHANGE-INITIATION OF THE MARINE HEATWAVE SOUTH OF NEW ENGLAND

The Warm Core Ring intrusion that initiated this event was briefly described in Gawarkiewicz et al. (2018) and a review of the data presented there sets the stage for the current analysis. Glider data from the OOI Pioneer Array roughly along the 200 m isobath was used to show that Ring water with a temperature of 15°C was present on January 22–24, 2017. Sea Surface Temperature imagery showed the presence of a large Warm Core Ring abutting the continental shelf south of New England on January 25. The glider data from February 11–13 shows temperatures in the range of 9–13°C, and by March 13–16 the temperature in the top 100 m of the water column was approximately 7°C (see **Figure 5** in that paper). Two Shelf Research Fleet CTD profiles were presented to further detail the unusual conditions on the continental shelf south of New England. The first profile, from January 29, had a surface temperature of 10°C and a bottom temperature of 13.5°C, while the profile from February 14 had a well-mixed water column with a temperature of 7°C. The surface salinity value from January 29 was 33.9 PSU and the bottom value was 35 PSU. By February 14 the salinity was well mixed with a value of 33.2 PSU. These data all appear in Figure 5 of Gawarkiewicz et al. (2018). Climatological values of temperature and salinity from Fleming (2016) for January south of New England are 5°C and 33 PSU, so that the anomalies are over 5°C at the surface and 8.5°C at the bottom on January 29. Salinity anomalies were 0.9 PSU at the surface and 2.0 PSU at the bottom. Neither the temporal nor the spatial extent of the anomalies were addressed, nor the statistical properties relative to previous measurements.

Eleven profiles were collected by the Shelf Research Fleet in January 2017. The depth-averaged temperature from these 11 profiles relative to the historical distribution by latitude (north of 40°24' North) appears in **Figure 3A**. Seven of the 11 profiles from January 2017 exceed 10°C. The 11 profiles were collected between January 1 and January 31. The profile collected at 41°03' North is particularly striking with a value of 11.6°C while the historical range does not exceed 7.5°C.

The January 2017 values relative to the distribution of historical depth-averaged temperature data (January–March) appear in **Figure 3B**. The histogram is segmented into 1°C bins centered at integer values, with the most common value being centered at 6°C. The seven warmest profiles, that exceed 10°C, are above the 98th percentile of the historical values. Two of the coldest values of the month appear on January 29 and 30 (6.1°C) indicative of colder shelf water starting to sweep into the Shelf Research Fleet sampling area in 2017.

The distribution of depth-averaged salinity values for January 2017 versus the historical values appears in **Figure 4A**. Six of the 11 profiles show salinities exceeding 34.0 PSU, with one profile at 41°03' North with a value of 34.1 PSU. Only two of the historical profiles show values exceeding 34 PSU in this latitude range.

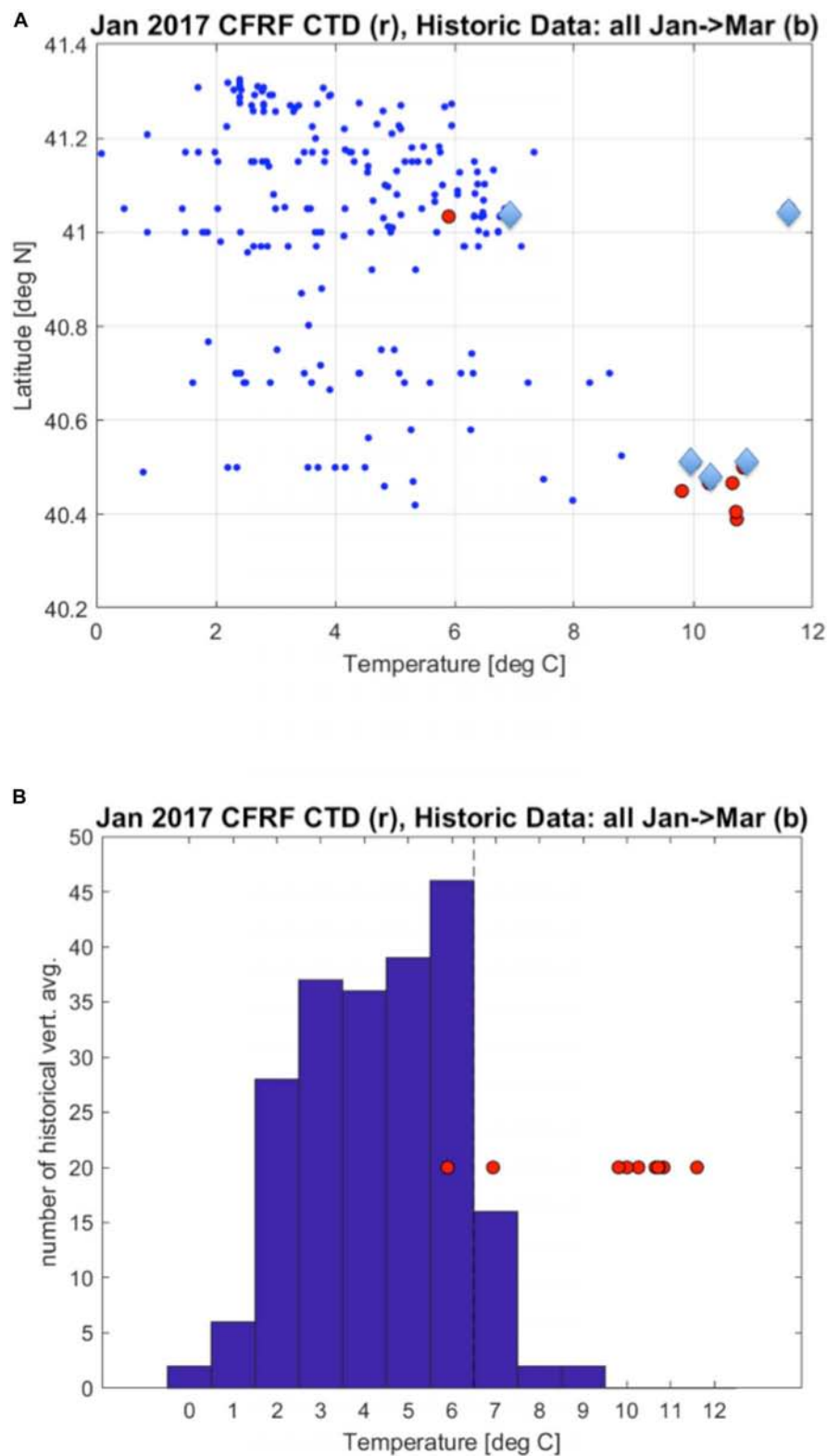


FIGURE 3 | (A) Latitudinal distribution of historical depth averaged temperature (blue circles) and January 2017 (red circles) from the Shelf Research Fleet. Values from January 2017 for which the positions are uncertain are denoted by the blue diamonds. **(B)** A histogram of historical depth-averaged temperatures compared to depth averaged values from January 2017 (red circles). The dashed line indicates the 90th percentile for the temperature in January–March for the historical data.

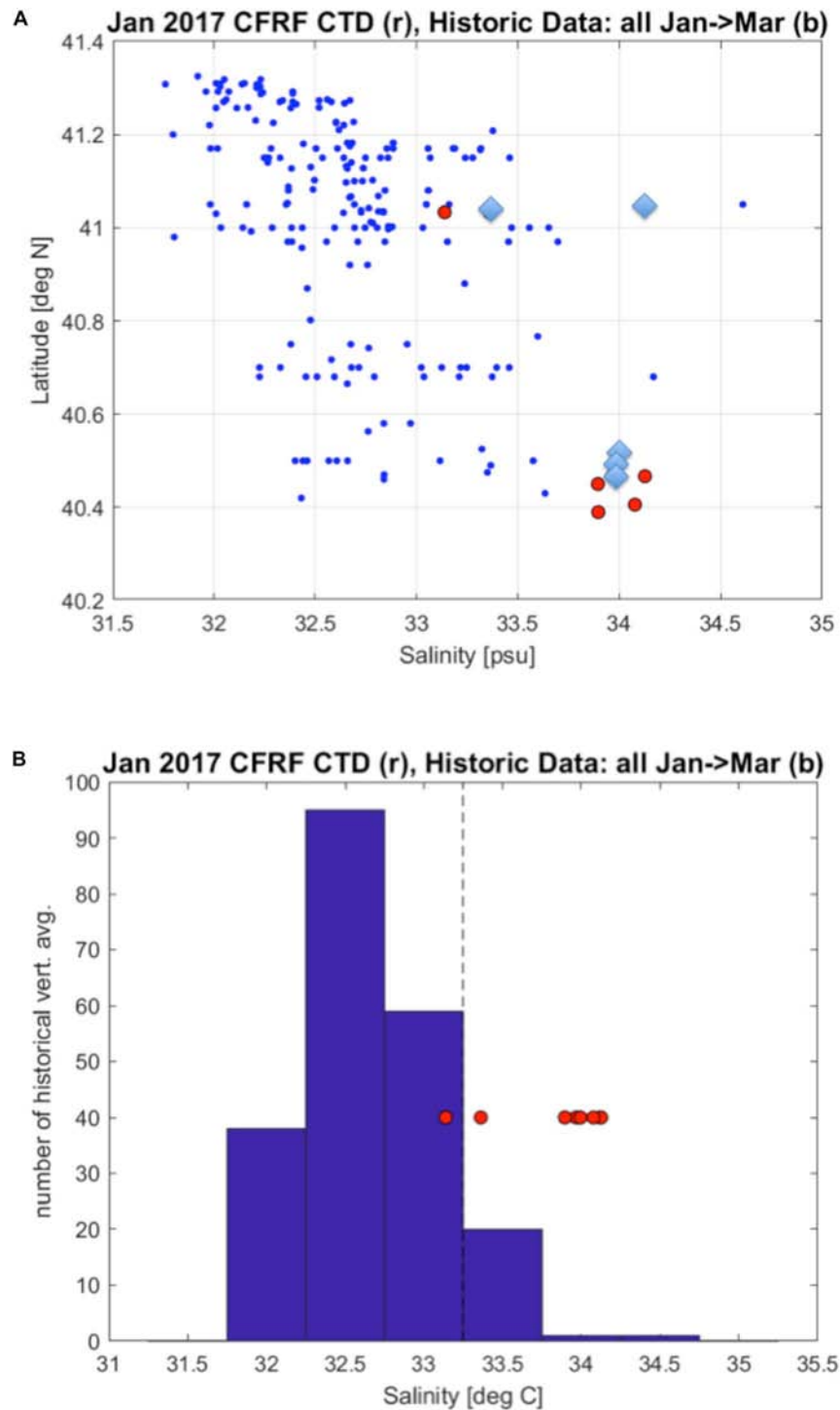


FIGURE 4 | Same as in **Figure 3** but with depth-averaged salinity.

There are a cluster of profiles with salinities above 33.8 PSU that occur above the 97th percentile of the historical values (**Figure 4B**). For both the temperature and salinity values, the January 2017 profiles exceed the 90th percentile, and the duration extends through all of January. Thus, the event in January

2017 exceeds the criteria established for a Marine Heatwave as defined in Hobday et al. (2016). The statistical thresholds are also exceeded for salinity. The high salinities combined with the warm temperatures strongly suggest that the origin of the anomalies was a Warm Core Ring abutting the continental shelf,

as suggested in Gawarkiewicz et al. (2018), with mixing processes reducing salinities to 34 PSU from typical ring values of 35.5 PSU. Temperatures in the intrusion moving across the continental shelf were 10–11°C, cooler than the 15°C temperatures recorded by the Pioneer Array glider on January 22–24. The cooling may have resulted from air-sea interaction or mixing with cooler shelf waters as Ring water moved onshore across the continental shelf.

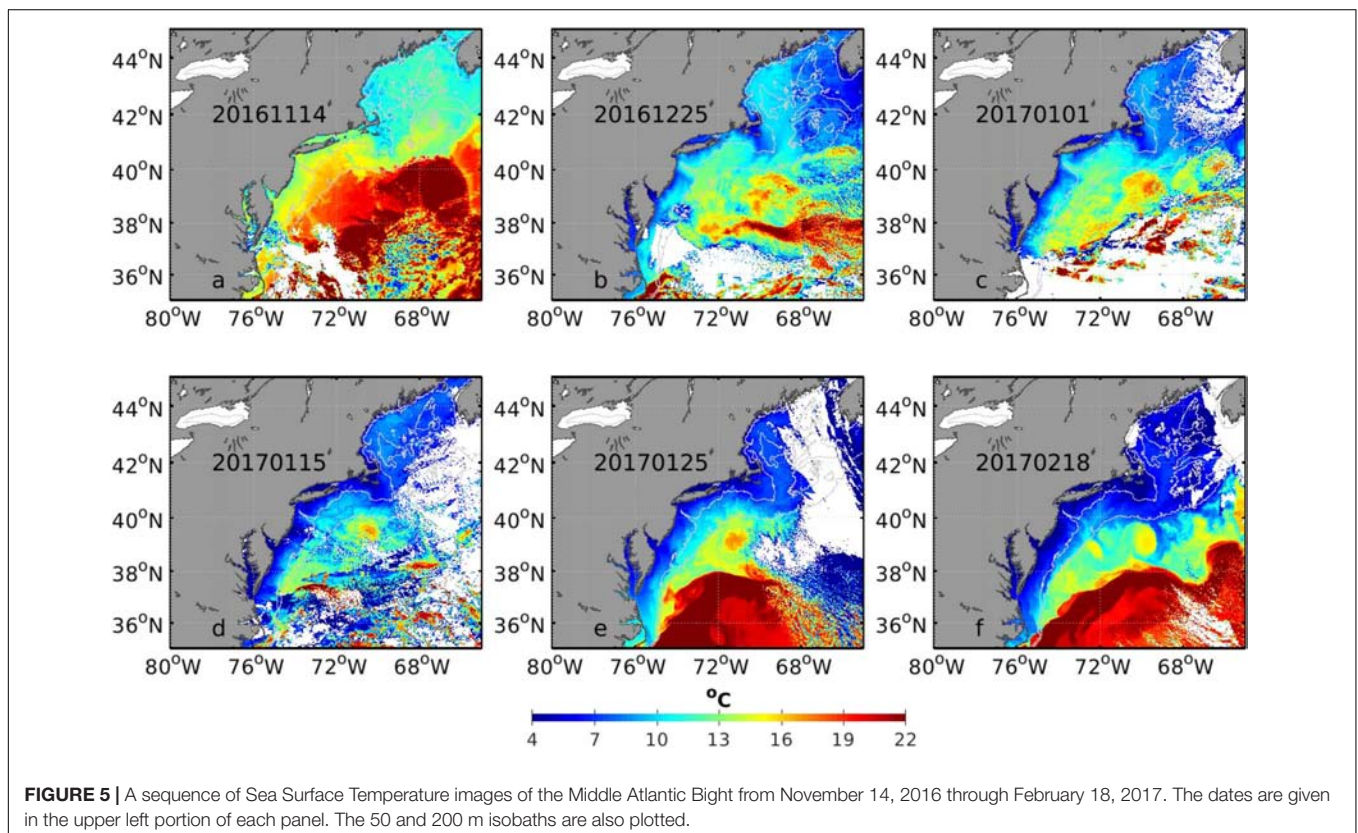
Two important sources of uncertainty exist relative to the criteria for choosing Marine Heatwave events presented in Hobday et al. (2016). The first is that we have chosen a non-standard time period for the historical archive instead of the 30 years reference period previously suggested. In the WOD archive January profiles prior to 2004 are available from 1940 to 1996 south of New England. The second limitation is the absence of position information for 5 of the 11 profiles collected by the Shelf Research Fleet. These were not recorded at the time of data collection. In order to include these points, we compared the depth of the collected profiles to the depth distribution of profiles collected in December 2016 and February 2017. We used the latitude of the December or February profile that was closest in depth. The points with uncertain positions are marked with blue diamonds in Figures 3A, 4A. This does introduce uncertainty in the exact latitude for the profiles. However, given the difficulty of collecting data in the middle of winter while active fishing activities are underway and rare nature of this event relative to historical data we feel

that it is important to include the 5 profiles even with the uncertainty in position.

In order to establish the spatial structure of the warm anomalies as well as establish the temporal evolution of the anomalously warm shelf water in winter ($>10^{\circ}\text{C}$), a sequence of Sea Surface Temperature images ranging from November 11, 2016 to February 18, 2017 appears in Figure 5. In mid-November 2016, an extremely large Warm Core Ring with surface temperatures of 20°C abutted the shelfbreak from approximately 66° – 68° West. Surface water warmer than 10°C extended from Nantucket Shoals to Delaware in the images at least from December 25, 2016 to January 1, 2017 across virtually the entire continental shelf (two upper right panels in Figure 5). Cooler water appears near the coast by January 25, and colder shelf water advects into the entire Shelf Research Fleet operational area by February 18, 2017. Because of long periods of cloud cover during the winter, these six images offer the best view of the spatial structure of the Sea Surface Temperature, but do not appear frequently enough to provide a detailed evolution of the spatial structure of the intrusion and surface temperature anomalies.

THE MARINE HEATWAVE OVER THE NEW JERSEY CONTINENTAL SHELF

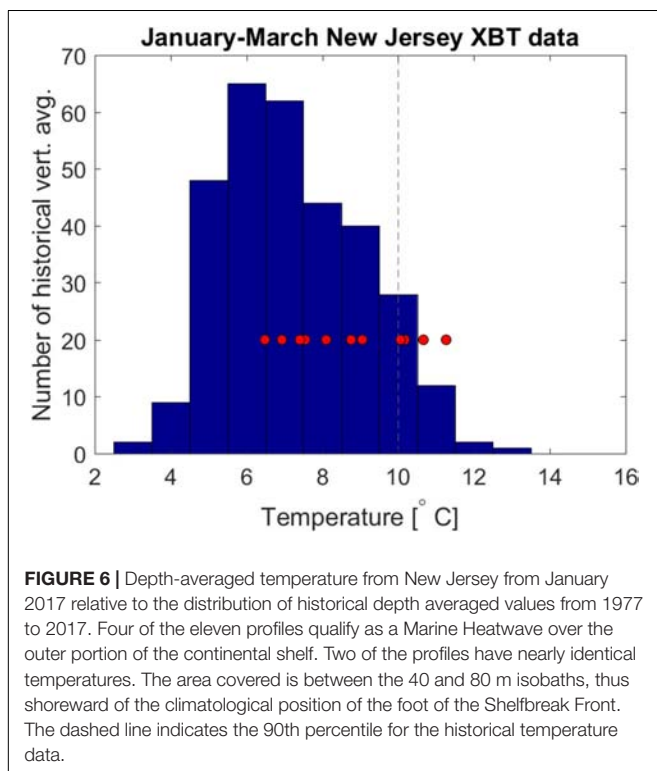
The normal continental shelf circulation in the Middle Atlantic Bight continues to the southwest from south of New England to



the Cape Hatteras region, where the shelf water deflects offshore under the influence of the Gulf Stream (e.g., Gawarkiewicz et al., 2008). As seen in the Sea Surface Temperature imagery, the warm water observed in January 2017 extended a substantial alongshelf distance to the southwest. Two sources of data can be used to examine the sub-surface thermohaline properties of this feature, the temperature data from the CMV Oleander XBT line and the temperature and salinity data from ECOMON surveys. We will use the CMV Oleander XBT data to examine the temperature fields to see if the anomalies reach the threshold of declaring a Marine Heatwave using data collected from the CMV Oleander from 1977 to 2017. We then use near surface data from the thermo-salinograph to further characterize the timing and cross-shelf extent of the anomalies.

The depth-averaged temperatures observed by CMV Oleander during January 2017 appear as filled red circles in **Figure 6**. These are superimposed on a histogram of temperature values from prior Oleander transects occupied between 1977 to 2017. Only temperature profiles from positions between the 40 and 80 m isobaths over the continental shelf are considered in order to minimize variability from the Shelfbreak Front and influence by the coastal current from the Hudson River. The dashed line in **Figure 6** indicates the 90th percentile for temperature for the historical depth-averaged data from January. Half of the XBT profiles in January 2017 exceed the criterion for designation as a Marine Heatwave.

The thermo-salinograph data confirms maximum cross-shelf penetration of warm saline water in late January (**Figure 7**).

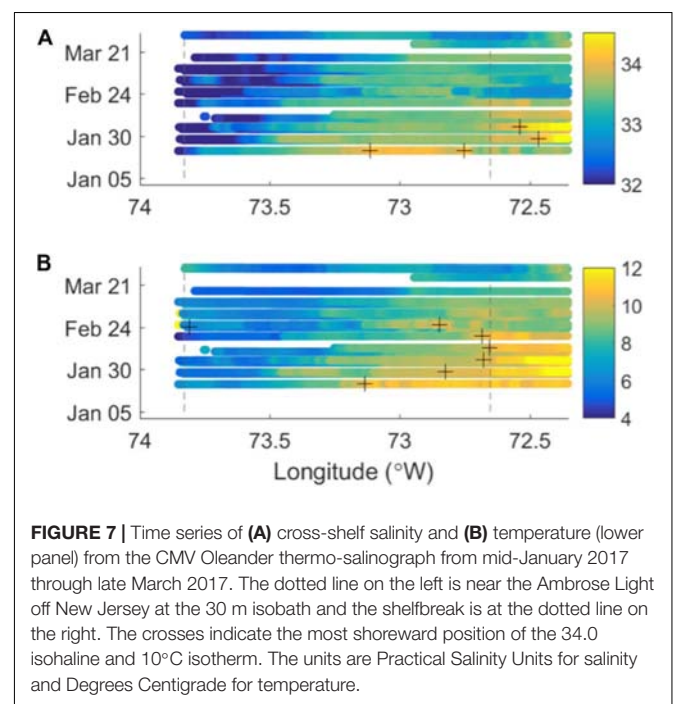


The temperature exceeded 10°C and 34.0 PSU as far west as 73°15' West on January 21, more than 50 km west of the shelfbreak (marked by the vertical dotted line in the figure). The Oleander data show that the Shelfbreak Front extended approximately halfway across the continental shelf in late January. The ECOMON data from February 2017 confirms this onshore displacement of the Shelfbreak Front and allows estimation of the duration of the Heatwave.

A map of the depth-averaged temperature from the ECOMON cruise in February 2017 appears in **Figure 8A**. The profiles with temperatures that exceed 10°C are generally seaward of the 80 m isobath, in contrast to both the Oleander data in January 2017 as well as observations from the shelf south of New England where 10°C water occurred well shoreward of the shelfbreak. Between the 40 and 80 m isobaths the temperature was generally in the range of 8–10°C (8 of 12 profiles) with the remaining values between 7 and 8°C.

The spatial pattern of the temperature anomalies in February 2017 relative to the climatology of Fleming (2016) appears in **Figure 8B**. The largest anomalies are located from mid-shelf to the coast, and range in value from 1.5 to 2.0°C.

The depth-averaged salinity distributions from the ECOMON cruise in February 2017 suggest that the Shelfbreak Front migrated well shoreward of its mean position. Typically, the foot of the front (bottom outcrop) is located at the 80 m isobath over the New Jersey shelf (Linder and Gawarkiewicz, 1998), but observations in 2017 show salinities exceeding 34.0 PSU as far inshore as the 40 m isobath with values over 34.5 PSU reaching the 60 m isobath. Lentz et al. (2003) have defined shelf water in the Middle Atlantic Bight as less than 34.0 PSU, with frontal water in the range of 34.0–35.0 PSU. By this definition the Shelfbreak Front did indeed translate onshore to the 40 m isobath, as shown



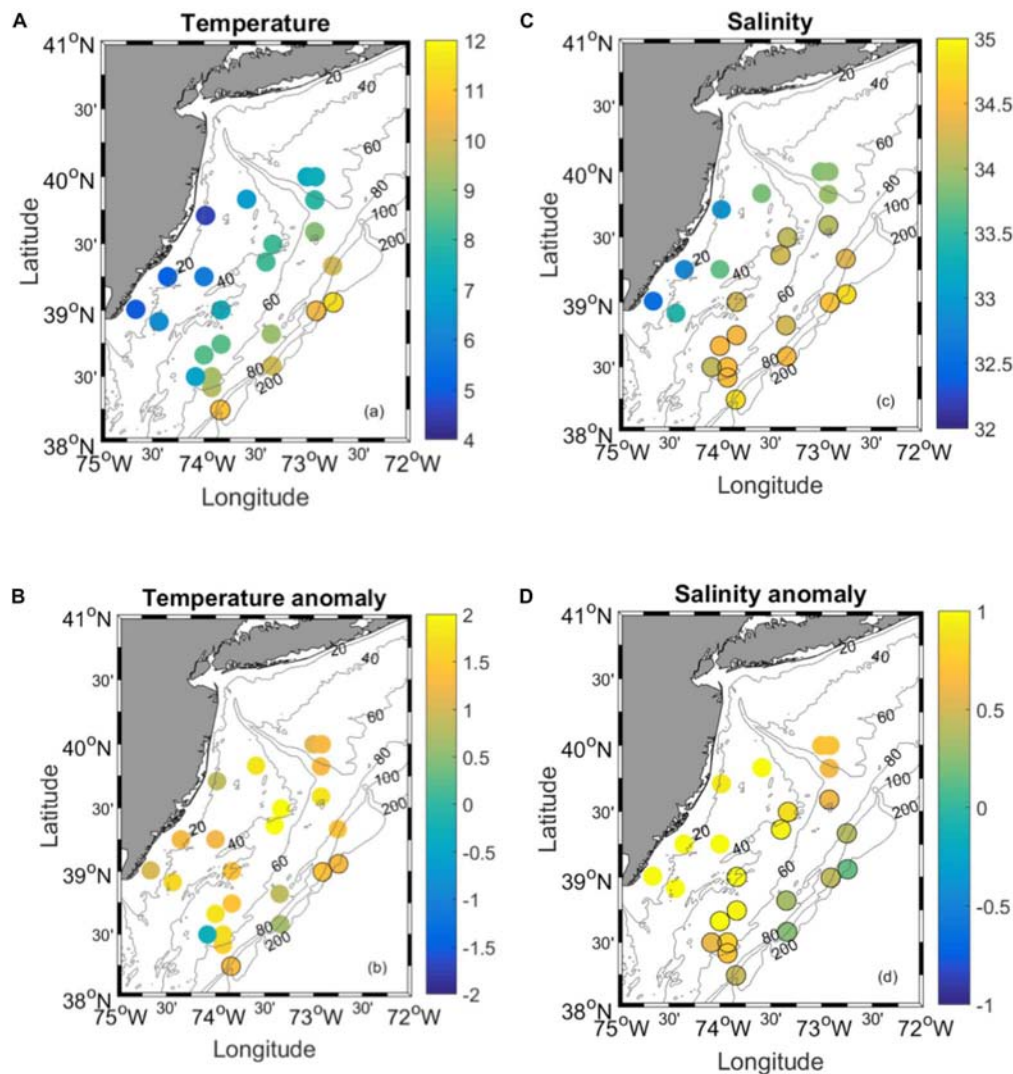


FIGURE 8 | (A) Depth averaged temperature from an ECOMON cruise of the R/V Bigelow in February 2017. Note the warm temperatures (8–9°C) extending to the 40 m isobath. **(B)** Temperature anomalies relative to the MOCHA climatology for January. **(C)** Depth-averaged salinity. Note that the 34.0 isohaline extends to the 40 m isobath, it is typically seaward of the 80 m isobath. **(D)** Salinity anomalies relative to the MOCHA climatology for January. The dark rings indicate stations in which either temperature is higher than 10°C or salinity is greater than 34.0 PSU.

in the map in **Figure 8C**. It is important to note that the foot of the front is likely further shoreward of the depth-averaged salinity value of 34.0 PSU for individual profiles.

The spatial pattern of the salinity anomalies appears in **Figure 8D**. The largest salinity anomalies, approaching 1 PSU, are adjacent to the coast extending offshore to the 50 m isobath. This is consistent with the pattern of the temperature anomalies. Combined, the patterns suggest that the thermohaline anomalies that originated up in New England are most unusual at their greatest cross-shelf extent, i.e., closer to the coast.

The ECOMON cruise on the R/V Henry Bigelow sampled the New Jersey continental shelf from February 12 to 16 and thus does not quite reach the 5 days duration used in the Hobday et al. (2016) criteria. The difficulty of collecting data during January and February in this region can be extreme as

this particular cruise was cut short due to stormy conditions. However, combined with the near-surface thermo-salinograph data from the CMV Oleander, the duration of the unusual conditions over the New Jersey shelf can be estimated. The time frame is roughly a month between the first CMV Oleander line in 2017 and the end of the ECOMON survey (January 14 to February 16).

THE FATE OF THE MARINE HEATWAVE

The mean flow over the continental shelf in the Middle Atlantic Bight progresses southward to the vicinity of Cape Hatteras where the flow is exported near the Gulf Stream (Savidge and Bane, 2001; Gawarkiewicz and Linder, 2006; Gawarkiewicz et al., 2008).

Fortunately, during 2017 a field program, the Processes driving Exchange at Cape Hatteras (PEACH), began on April 12–29 with a mooring deployment and hydrographic sampling cruise on the R/V Neil Armstrong.

The CTDs present near the surface (2 m depth) and bottom at the B1 mooring in the PEACH array (see **Figure 1** for location) indicate the arrival of a surge of near bottom Cold Pool water (Houghton et al., 1982) on April 23 2017 (**Figure 9**). During the initial deployment on April 18 there was a near bottom water mass present with a temperature of 14°C and salinity of 35.0 PSU, indicative of the presence of Slope water over the continental shelf. However, a strong southward flow appeared on April 23 with a velocity of over 0.4 m/s carrying near bottom temperature of 9.8°C and a salinity of 34.0 PSU. Relative to the climatology of Fleming (2016), the anomaly was approximately 1°C and 1 PSU along 35°45′ North.

While the evolution of temperature and salinity near Cape Hatteras (**Figure 9**) cannot conclusively establish that this is the same water mass initially transported onto the continental shelf in early January south of New England, a crude estimate of the advection rate offers a hint as to how plausible this scenario is. If we assume that the initial onshore transport of Warm Core Ring water occurred near 40°00′ North and 70°00′ West on January 1 2017, the estimated along-isobath distance to the PEACH array is approximately 850 km. The anomalous watermass was observed at the B1 mooring approximately 113 days after the Warm Core Ring intrusion on the New England Shelf, giving an estimated advection rate of 8.7 cm/s. This is in reasonable agreement with estimated flow rates of 5–10 cm/s over the outer continental shelf (e.g., Lentz, 2008). Thus we find it plausible for the pulse recorded at the B1 mooring of the PEACH array on April 23 to be a remnant of the upstream Marine Heatwave as it passed through

the Middle Atlantic Bight. Because of the extreme variability of the water mass properties over the continental shelf in the vicinity of Cape Hatteras, it is unlikely that the anomalies recorded in the hydrographic cross-shelf transect on April 25 (1°C and 1 PSU) exceeded the 90th percentile for temperature or salinity. Nevertheless, the similarity of the T/S properties (**Figure 10**) to those recorded south of New England and over the New Jersey shelf suggests that the ultimate fate of the water mass carried in the Marine Heatwave was to exit the shelf near Cape Hatteras. This is consistent with Lagrangian properties of the flow field near Cape Hatteras (e.g., Gawarkiewicz and Linder, 2006). While the temperature recorded in the hydrographic section and the B1 mooring does not meet the definition of a Marine Heatwave by Hobday et al. (2016), it is suggestive that the Warm Core Ring intrusion that initiated south of New England was carried the length of the Middle Atlantic Bight, influencing the continental shelf in this region over a 4 months period and an along-shelf span of 850 km. A schematic of the Ring Intrusion with the timing and temperature range at various locations is shown in **Figure 11**.

We suggest that the continental shelf south of Nantucket Shoals has in recent years become a hotspot for shelfbreak exchange, with Warm Core Ring water masses preferentially carried onshore in this region. Recent evidence has shown that the upper continental slope has become considerably more saline, from a 2.5 year record of glider transects from the OOI Pioneer Array (Gawarkiewicz et al., 2018). This is consistent with evidence from Sea Surface Height Anomalies that large amplitude meanders of the Gulf Stream have been more frequent and occur further to the west than in previous decades (Gawarkiewicz et al., 2012; Andres, 2016). There has been a recent regime shift occurring in the year 2000 with a substantial increase in the number of Warm Core Rings forming each year (33 per year from

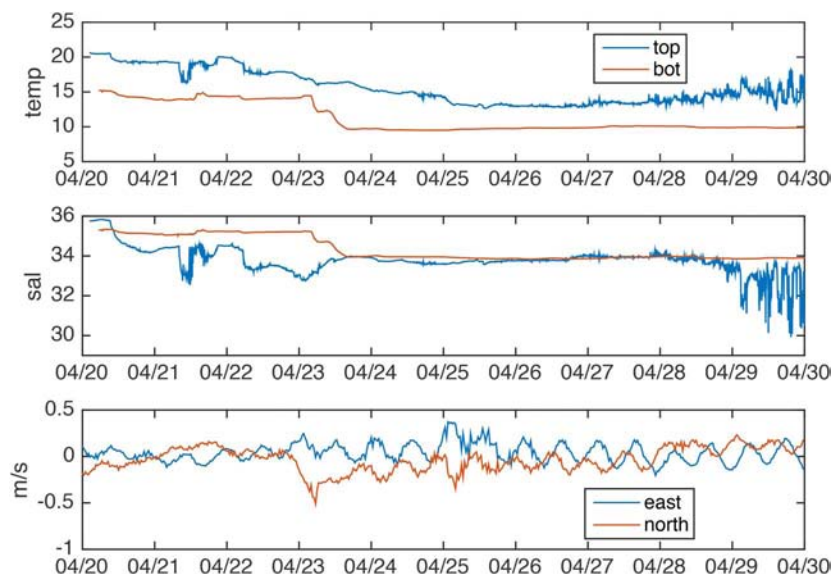
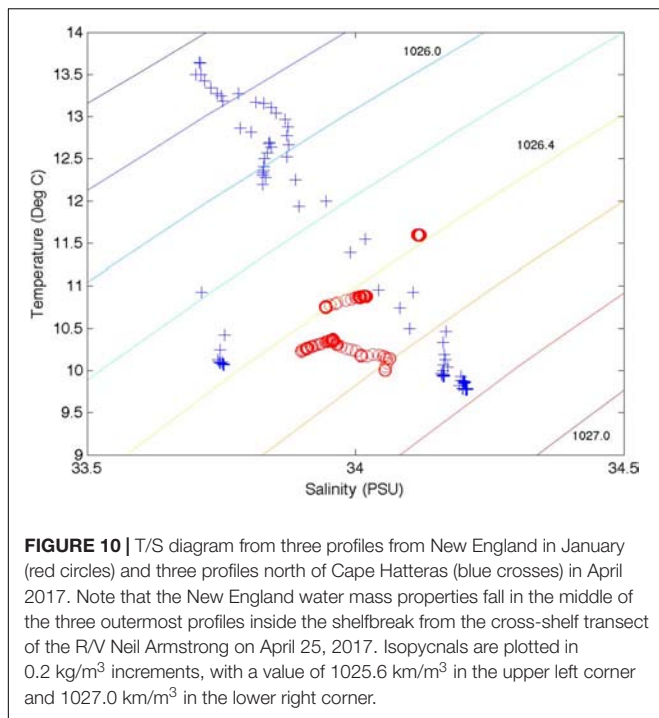


FIGURE 9 | Time series of temperature (**upper panel**) and salinity (**middle panel**) and depth-averaged velocity (**bottom panel**) from the B1 mooring in the PEACH array. Note the rapid drop in temperature and salinity near April 23, 2017, potentially indicative of the remnants of the Marine Heatwave reaching the continental shelf just north of Cape Hatteras.



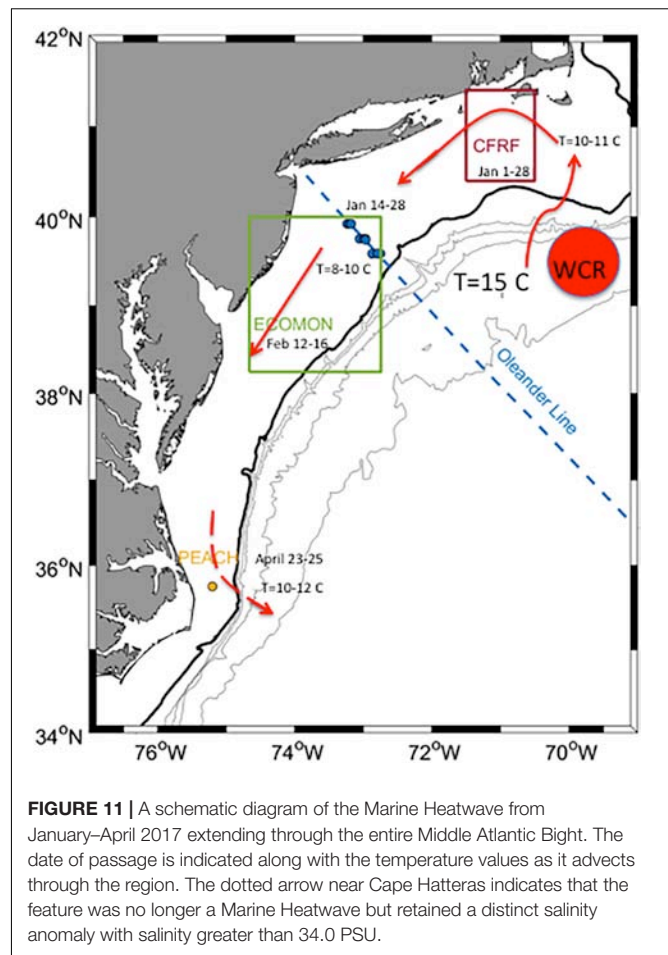
2000 to 2017 and 18 per year from 1980 to 1999; Gangopadhyay et al., 2019). We hypothesize that the continental shelf south of Nantucket Shoals traps Warm Core Rings. Because of the proximity of Nantucket Shoals, ring water masses that travel onshore here would flow along isobaths that curve well to the north toward Block Island, Rhode Island. Further investigation is warranted to see if other Marine Heatwaves that have occurred in recent years originate south of Nantucket Shoals to establish whether this area is indeed a new hot spot for shelfbreak exchange. We note that this area was not an area of enhanced onshore flow in the late 1990s, based on drifters released in the Gulf of Maine (Limeburner et al., 2000; Lozier and Gawarkiewicz, 2001). It is possible that the greater amplitude of Gulf Stream meanders combined with the more frequent appearance of Warm Core Rings may have resulted in the formation of a new hot spot for enhanced shelfbreak exchange.

DISCUSSION

Implications for the Marine Ecosystem

The Marine Heatwave in January 2017 was an unprecedented event that had significant impacts on the marine ecosystem, including unusual occurrences of warm water fish in Rhode Island coastal waters, as reported by commercial fishers.

According to the NOAA National Marine Fisheries Service ECOMON survey, the annual average sea surface temperature in 2017 was above 13°C, among the highest in the times series that stretches back to 1854. Conversely, the average chlorophyll *a* concentrations over the northeastern continental shelf in 2017 were the lowest since 1998 (approximately 1.06 mg/m³). In general, Chlorophyll *a* over the northeastern continental



shelf has been in decline since 2011, when the annual average value was approximately 1.49 mg/m³ (National Marine Fisheries Service [NOAA], 2018). While other factors, including mixing dynamics, impact chlorophyll production, the Marine Heatwave likely contributed to the low productivity on the northeastern continental shelf in 2017.

Another possible effect of the Marine Heatwave is the enhanced mortality of Humpback Whales. The National Marine Fisheries Service declared an unusual mortality event for Humpback Whales in 2017. Thirty-four strandings of Humpback whales were reported in 2017, with the majority occurring in the Middle Atlantic Bight. The strandings are broken down by state at <https://www.fisheries.noaa.gov/national/marine-life-distress/2016-2019-humpback-whale-unusual-mortality-event-along-atlantic-coast>.

We suggest that the onshore shift of the Shelfbreak Front in January/February south of New England and off New Jersey may have resulted in an onshore displacement of the Humpback Whales relative to their normal cross-shelf position. The Shelfbreak Front is known to have persistent upwelling (e.g., Linder et al., 2004; Zhang et al., 2013). It is quite possible that Humpback Whales may have tracked the frontal zone with associated upwelling cell and thus moved into areas with both higher concentrations of fishing gear as well as greater shipping

activity. NOAA reported that over 50% of humpback strandings had evidence of human activity in terms of either entanglement or ship strike. Further investigation is needed into the exact timing of the Humpback Whale mortality events relative to the passage of the Marine Heatwave in 2017.

Future Research Directions

There is a clear need to examine the dynamics of this Marine Heatwave using numerical hindcasts. The exact mechanisms and processes by which Warm Core Ring water is transported across the shelfbreak and eventually to the 30–40 m isobaths must be explored in detail to determine the triggering mechanism. Both vertical mixing processes as well as altered air-sea fluxes are likely to modify Warm Core Ring water as it passes onto the continental shelf. One possible mechanism for initiation of this event is the reversal of density gradients at the shelfbreak. We note that Zhang and Gawarkiewicz (2015) have previously shown that ring water may be less dense than shelf water during spring (April/May 2014) and this may even be more pronounced in winter. Further investigation is necessary to establish how density gradients across the shelfbreak may be varying in the presence of more frequent Warm Core Ring encounters with the outer continental shelf. The OOI Pioneer Array should be useful in providing systematic (seasonal and inter-annual) reversals of density gradients that might generate large temperature and salinity anomalies over the continental shelf.

Future research should also be directed to establish whether the shelfbreak south of Nantucket Shoals has become a recent Hot Spot for the onshore transport of Warm Core Ring water masses. The presence of the Great South Channel likely complicates the interaction of Warm Core Ring induced flows over the continental shelf due to bathymetric steering and the establishment of local along and cross-isobath pressure gradients. Further analysis of both sea surface temperature imagery and OOI Pioneer Array glider data is clearly warranted.

CONCLUSION

A suite of observations is used to establish the occurrence of a Marine Heatwave south of New England in January 2017 and over the New Jersey continental shelf in late January and February 2017. The warm anomalies reached 6°C relative to a long-term climatology and salinity anomalies as large as 1 PSU could be tracked downstream to the continental shelf north of Cape Hatteras in late April.

The Marine Heatwave and associated salinity anomalies traversed the entire Middle Atlantic Bight, moving from the

shelf south of Nantucket Shoals to a region just north of Cape Hatteras over a period of 4 months. Much more research is needed to investigate the dynamics of these ring intrusions and their frequency of occurrence as well as their possible effects on shelf and slope ecosystems.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

GG identified Heatwave event initially organized analysis, wrote first draft, directed figures and made some figures, identified possible link to Unusual Mortality Event for Humpback whales, oversaw edits, compiled references. KC analyzed SST data, discussed historical databases and obtained WOD data and analyzed this data, discussed interpretation and overall structure of manuscript at every stage, placed event into larger context of Heatwave literature. JF analyzed Oleander data from New Jersey, made figures, and wrote section. FB processed Shelf Fleet data, made preliminary figures, discussed choices of data presentation, extensively discussed comparisons between Shelf Fleet data and historical observations. AM and AE oversaw collection of Shelf Fleet data, added material on ecosystem impacts, and edited first draft of manuscript. PF provided ECOMON data and assisted in analysis and improvement of figures, provided important feedback and comments on first draft of manuscript. HS, SH, and LH deployed B1 mooring, made figures, commented on first draft, important edits, and feedback on first draft.

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Detecting Marine Heatwaves With Sub-Optimal Data

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Marine heatwaves (MHWs), or prolonged periods of anomalously warm sea water temperature, have been increasing in duration and intensity globally for decades. However, there are many coastal, oceanic, polar, and sub-surface regions where our ability to detect MHWs is uncertain due to limited high quality data. Here, we investigate the effect that short time series length, missing data, or linear long-term temperature trends may have on the detection of MHWs. We show that MHWs detected in time series as short as 10 years did not have durations or intensities appreciably different from events detected in a standard 30 year long time series. We also show that the output of our MHW algorithm for time series missing less than 25% data did not differ appreciably from a complete time series, and that the level of allowable missing data could cautiously be increased to 50% when gaps were filled by linear interpolation. Finally, linear long-term trends of 0.10°C/decade or greater added to a time series caused larger changes (increases) to the count and duration of detected MHWs than shortening a time series to 10 years or missing more than 25% of the data. The long-term trend in a time series has the largest effect on the detection of MHWs and has the largest range in added uncertainty in the results. Time series length has less of an effect on MHW detection than missing data, but adds a larger range of uncertainty to the results. We provide suggestions for best practices to improve the accuracy of MHW detection with sub-optimal time series and show how the accuracy of these corrections may change regionally.

Keywords: marine heatwaves, sea surface temperature, sub-optimal data, time series length, missing data, long-term trend

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INTRODUCTION

The idea of locally warm seawater disrupting species distributions or ecosystem functioning is not a novel concept. We have known for decades that transient warm water occurrences in the ocean could result in major impacts on marine ecosystems (e.g., Baumgartner, 1992; Salinger et al., 2016). The study of the effects of anomalously warm seawater temperatures began in earnest in the early 1980s when research into the ENSO phenomenon intensified (e.g., Philander, 1983). After the 1980s, researchers began noticing that warm water events were becoming more frequent and with large ecosystem impacts (e.g., Dayton et al., 1992), but it was not until 2018 that this was demonstrated with global observations (Oliver et al., 2018).

In order to quantify the increased occurrence and severity of these events it was necessary to develop a methodology that would be inter-comparable for any location on the globe. This was

accomplished in 2016 after the International Working Group on Marine Heatwaves (MHWs)¹ initiated a series of workshops to address this issue. This definition for anomalously warm seawater events, known as MHWs, has seen wide-spread and rapid adoption due to ease of use and global applicability (Hobday et al., 2016). One limitation with this definition that has not yet been addressed is the assumption that a researcher has access to the highest quality data available when detecting MHWs. In the context of MHW detection, a “high quality” time series is spatio/temporally consistent, quality controlled, and at least 30 years in length (Hobday et al., 2016, Table 3). While not stated explicitly in Hobday et al. (2016), a “high quality” time series should also not have any missing days of data. To avoid contention on the use of the word “quality,” time series that meet the aforementioned standards are referred to here as “optimal,” whereas those that do not meet one or more of the standards are referred to as “sub-optimal.” Another unresolved issue with the Hobday et al. (2016) algorithm, which does not fall within the requirements for optimal data, is how much of an effect the long-term (secular) trend in a time series may have on detection of MHWs compared to that same time series when the trend has been removed.

Most remotely sensed data, and more recently output from ocean models and reanalyses, consist of over 30 years of data and utilize *in situ* collected data or statistical techniques to fill gaps in their time series. This means that these “complete” data are considered optimal for MHW detection. A summary of remotely sensed products currently available, as well as their strengths and weaknesses, is provided by Harrison et al. (2019, Table 12.3). Even though remotely sensed data products are considered optimal, they still have other issues (e.g., land bleed, incorrect data flagging, spatial and temporal infilling) and so it may be necessary that for coastal MHW applications, researchers utilize sub-optimal data, such as sporadically collected *in situ* time series (Smit et al., 2013; Hobday et al., 2016).

This paper seeks to understand the limitations the use of sub-optimal data impose on the accurate detection of MHWs. Of primary interest are three key challenges:

1. The use of time series shorter than 30 years.
2. The use of temporally inconsistent (missing data) time series.
3. The use of time series in areas with large (steep) long-term sea surface temperature (SST) trends.

We use a combination of reference time series from specific locations and a global dataset to address these issues. The effects of the three sub-optimal data challenges on the detection of MHWs are quantified in order to provide researchers with the level of confidence they may express in their results. Where possible, best practices for the correction of these issues are detailed.

Defining Marine Heatwaves

The MHW definition used here is “a prolonged discrete anomalously warm water event that can be described by

its duration, intensity, rate of evolution, and spatial extent.” (Hobday et al., 2016). This qualitative definition is quantified with an algorithm that calculates a suite of metrics. These metrics may then be used to characterize MHWs and allow comparison with ecological observations. The calculation of these metrics first requires determining the mean and 90th percentile temperature for each calendar day-of-year (“doy”) in a time series. The mean “doy” temperatures, which also represent the seasonal signal in the time series, provide the expected baseline temperature whose daily exceedance is used to calculate the local intensity of MHWs. The 90th percentile “doy” temperatures serve as the threshold that must be exceeded for five or more consecutive days for the anomalously warm temperatures to be classified as a MHW and for the calculation of the additional MHW metrics.

In this paper we focus on the three metrics that succinctly summarize a MHW, from the set described in Table 2 of Hobday et al. (2016). The first metric, *duration*, is defined as the period of time that the temperature remains at or above the 90th percentile threshold without dipping below it for more than two consecutive days. The duration of an event may be used as a measurement of the chronic stress that a MHW may inflict upon a target species or ecosystem (e.g., Oliver et al., 2017; Smale et al., 2019). The second metric, *maximum intensity*, is the highest temperature anomaly during the event and is calculated by subtracting the climatological mean “doy” temperature from the recorded temperature on that day. This metric may be used as a measurement of acute stress (e.g., Oliver et al., 2017; Smale et al., 2019). A third metric, *cumulative intensity*, is used to determine the “largest” MHW in a time series (see section “Materials and Methods”). This metric is the integral of the temperature anomalies of a MHW, and so has units of °C-days, and represents the sum of temperature anomalies over the duration of the MHW. Cumulative intensity is comparable to the degree heating day metrics used in coral reef studies (Fordyce et al., 2019).

We used the R implementation of the Hobday et al. (2016) MHW definition (Schlegel and Smit, 2018), which is also available in python², and MATLAB (Zhao and Marin, 2019). We compared the R and python default outputs, assessed how changing the arguments affected the results, and compared the other functionality provided between the two languages. While some style differences exist as a result of the functionality of the languages, the climatology outputs are identical to within <0.001°C per “doy.” An independent analysis of the Python and MATLAB results also confirmed that they were functionally identical (pers. com. Zijie Zhao; MATLAB distribution author).

What Are Optimal Data for Detecting Marine Heatwaves?

When working with extreme values in a time series, such as MHWs, it is important that the quality of the data are high (Hobday et al., 2016). Hobday et al. (2016) stated that high quality data, referred to here as “optimal,” used for the detection of MHWs should meet the following criteria:

¹<http://www.marineheatwaves.org/>

²<https://github.com/ecjoliver/marineHeatWaves>

1. A time series length of at least 30 years.
2. Quality controlled.
3. Spatially and temporally consistent.
4. Be of the highest spatial and temporal resolution possible/available.
5. *In situ* data should be used to compliment remotely sensed data where possible.

Although the authors did not specifically state that time series must not contain large proportions of missing data, it can be inferred from the aforementioned requirements and the nature of the proposed algorithm. Another issue affecting the accurate detection of MHWs not discussed in Hobday et al. (2016) is the presence of long-term trends in a time series. Oliver et al. (2018) have shown how dominant the climate change signal can be in the detection of MHWs and we seek to quantify this effect here.

A time series with a sub-optimal length may impact the detection of MHWs by negatively affecting the creation of the daily climatology relative to which MHWs are detected in two primary ways. The first is that with fewer years of data, the presence of an anomalously warm or cold year will have a larger effect on the climatology than with a sample size of 30 years. The second cause is that because the world is generally warming (Pachauri et al., 2014), the use of a shorter time series will almost certainly introduce a warm bias into the results. This means, counterintuitively, that the MHWs detected in a shorter time series will appear to be cooler than the same MHWs detected in a longer time series. This is because the average temperature in a time series consisting of recent data will likely be warmer, which will raise the 90th percentile relative to the observed temperatures and the reported MHW metrics will appear to be less/lower than would be obtained with a longer time series.

The climatology derived from a time series serves two main roles (WMO, 2017); (1) it serves as a “benchmark” relative to which past and future measurements can be compared, and against which anomalies can be calculated, (2) it reflects the typical conditions likely to be experienced at a particular place at a particular time. The WMO Guide to Climatological Practices (WMO, 2011) stipulate that daily climatologies (which they call “climate normals”) must be based on the most recent 30-year period that ends on a complete decade (currently 1981–2010). The suggested length of a time series for MHW detection was based on this WMO guideline (Hobday et al., 2016), and a fixed reference period (e.g., 1983–2012) proposed (Hobday et al., 2018).

Some remotely sensed products suffer from “gappiness” that result in missing data. This may be due to cloud cover, the presence of sea ice, unsuitable sea states, etc., which become more prevalent at smaller scales, particularly nearer the coast. Some products interpolate to fill missing data gaps, but this results in smoothed SST fields that may mask small-scale spatial variations in surface temperatures. Remotely sensed products may also fill gaps by blending with data from other products, which may introduce other biases. It has been demonstrated that coastal SST pixels from remotely sensed products may have biases in excess of 5°C from *in situ* collected data (Smit et al., 2013), however; other research that has shown similarity between these different data

types (Smale and Wernberg, 2009; Stobart et al., 2016). These data are also prone to large gaps and so issues with regards to accurate MHW detection are also uncertain.

MATERIALS AND METHODS

To quantify the effects that time series length, missing data, and long-term trends have on MHW detection we compare the count, duration (days), and maximum intensity (°C) of MHWs from time series as they become increasingly sub-optimal. To ensure approximately equal sample sizes across all tests, only the results for MHWs in the final 10 years of data (2009–2018) are used for each test and are hereafter referred to as the “average MHWs.” The single largest MHW in each time series, as determined by cumulative intensity, is drawn from the same 10 year sample and is referred to hereafter as the “focal MHW.”

The amount of uncertainty that the sub-optimal tests (see sub-sections below) introduce into the results is calculated by measuring the percent of change in the results from the control (optimal) time series as the data become more sub-optimal. No significance test is used here, rather the increasing uncertainty range in the results is shown so as to provide a benchmark against which one may decide how much uncertainty is too much depending on the given application. Linear models are used to quantify the increasing rates of uncertainty that these sub-optimal tests introduce. These rates are analyzed at a global scale to investigate spatial patterns before being discussed in more depth in the Best Practices section.

We use the remotely sensed NOAA OISST dataset (Reynolds et al., 2007; Banzon et al., 2016) in this study. This daily remotely sensed global SST product has a 1/4 degree spatial resolution with 1982 the first full year of sampling. These data are interpolated and where possible verified against a database of *in situ* collected temperatures so that the final product does not have any spatial or temporal gaps. The NOAA OISST dataset was used during the creation of the MHW algorithm in Hobday et al. (2016) and is used here for consistency. A simple linear model is fit to the time series at each location (pixel) and the residuals are taken as the de-trended anomaly values on which the MHW algorithm is run. This must be performed to control for the effects of time series length and long-term trends separately. Once de-trended, each anomaly time series (hereafter referred to as “time series”) is treated to the suite of sub-optimal controls (see following sub-sections) and the results are extracted.

The percent change in the average and focal MHW results from sub-optimal data is highlighted with the three reference OISST time series from Hobday et al. (2016). These time series are taken from the coast of Western Australia (WA; **Figure 1A**), the Northwest Atlantic Ocean (NWA; **Figure 1B**), and the Mediterranean Sea (Med; **Figure 1C**). These time series are used here for ease of reproducibility and because they each contain a MHW that has been the focus of multiple publications (e.g., Garrabou et al., 2009; Wernberg et al., 2012; Mills et al., 2013). The effect of the sub-optimal tests on these three time series are overlaid on the effect of the same sub-optimal tests on 1000

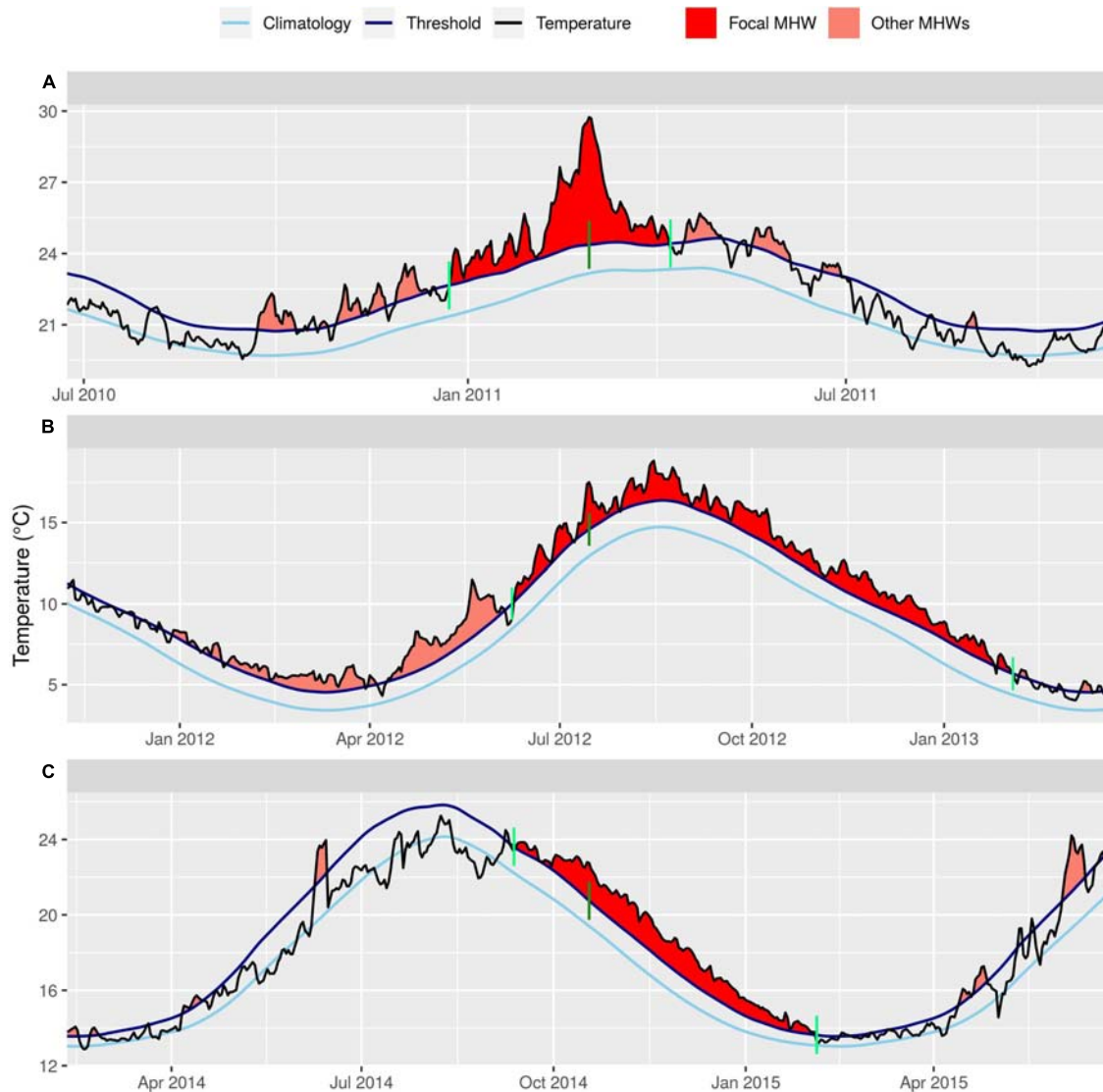


FIGURE 1 | The focal marine heatwaves (MHWs) shown in red for the three reference time series **(A)** Western Australia (WA), **(B)** Northwest Atlantic (NWA), and **(C)** Mediterranean (Med). Other MHWs shown in salmon. Each panel is centered around the peak date of the focal MHW, which is highlighted by a dark green vertical segment. The beginning and end of each MHW are demarcated with light green vertical segments. The seasonal mean climatology for each time series is shown as a light blue line, while the threshold climatology is shown with a dark blue line. The observed temperatures are shown as a black line. Note that only the WA focal MHW is the same as the event in the literature, the focal MHWs shown here for the NWA and Med time series are larger than the MHWs from the literature so are shown here in their stead.

randomly selected pixels from the global OISST dataset. The following three sub-sections describe how the three sub-optimal time series tests are implemented. While not a specific focus in this study, the effects that the sub-optimal tests have on the seasonal mean and threshold climatologies have been included in the **Supplementary Figure S1**.

Controlling for Time Series Length

There are currently 37 complete years of data available in the NOAA OISST dataset (1982–2018). In order to determine the effect that time series length has on the output we systematically shorten each time series 1 year at a time from 37 years down

to 10 years (2009–2018), before running the MHW detection algorithm. The MHW results for each 1 year step for each of the time series are then compared against the output from the 30 year (1989–2018) version of the same time series as the control.

In order to ensure equitable sample sizes we only compare the MHW metrics for events detected within the last 10 years of each test as this is the period of time during which all of the different tests overlap. This is also why we limited the shortening of the time series lengths to 10 years, so that we would still have a reasonable sample size for all of the other tests.

Because the lengths of the time series were being varied, and were usually less than 30 years in length, it was also necessary that

the climatology periods vary likewise. To maintain consistency across the results we use the full range of years within each shortened time series to determine the climatology. For example, if the time series had been shortened from 37 to 32 years (1987–2018), the 32 year period was used to create the climatology. If the shortened time series was 15 years long (2004–2018), this base period was used. The control time series were those with a 30 year length ending in the most recent full year of data available (1989–2018). Note that due to necessity this differs from the suggested climatology period of 1983–2012 that would more closely match the WMO standard (Hobday et al., 2018). The effect of shifting the 30 year climatology base is shown in the **Supplementary Figure S2**.

The *a priori* fix proposed to address the issue of short time series length is to use a different climatology estimation technique. The option currently available within the MHW detection algorithm is to expand the window half width used when smoothing the climatology. Other techniques, such as harmonic regression/Fourier analysis, would have a similar effect but are not used here in favor of the (Hobday et al., 2016) method. It is beyond the scope of this paper to compare every possible climatology calculation technique.

Controlling for Missing Data

In order to determine the effect of random missing data on the MHW results, each time series has 0–50% of its data removed in 1% steps before running the MHW algorithm. The control time series are the complete versions.

The *a priori* fix for missing data in the time series is to linearly interpolate over any gaps. There are many methods of interpolating (imputing) gaps in time series, such as spline interpolation, but we choose linear interpolation here due to its speed, simplicity, and it imposes fewer assumptions on the data. It is beyond the scope of this paper to account for every possible method of interpolation.

Controlling for Long-Term Trend

To quantify the effect of a long-term (secular) trend on the MHW results we add linear trends of 0.00–0.30°C/decade in 0.01°C/decade steps to each time series. The control time series are those with no added trend (e.g., 0.00°C/decade).

There is no proposed *a priori* method to correct for the added linear trend in these data as this would be simply not to add a trend. Rather it is proposed that the relationship between the slope of the added trend and the effect it has on the results be documented to determine if a predictable relationship may be used for any *post hoc* corrections.

RESULTS

Time Series Length

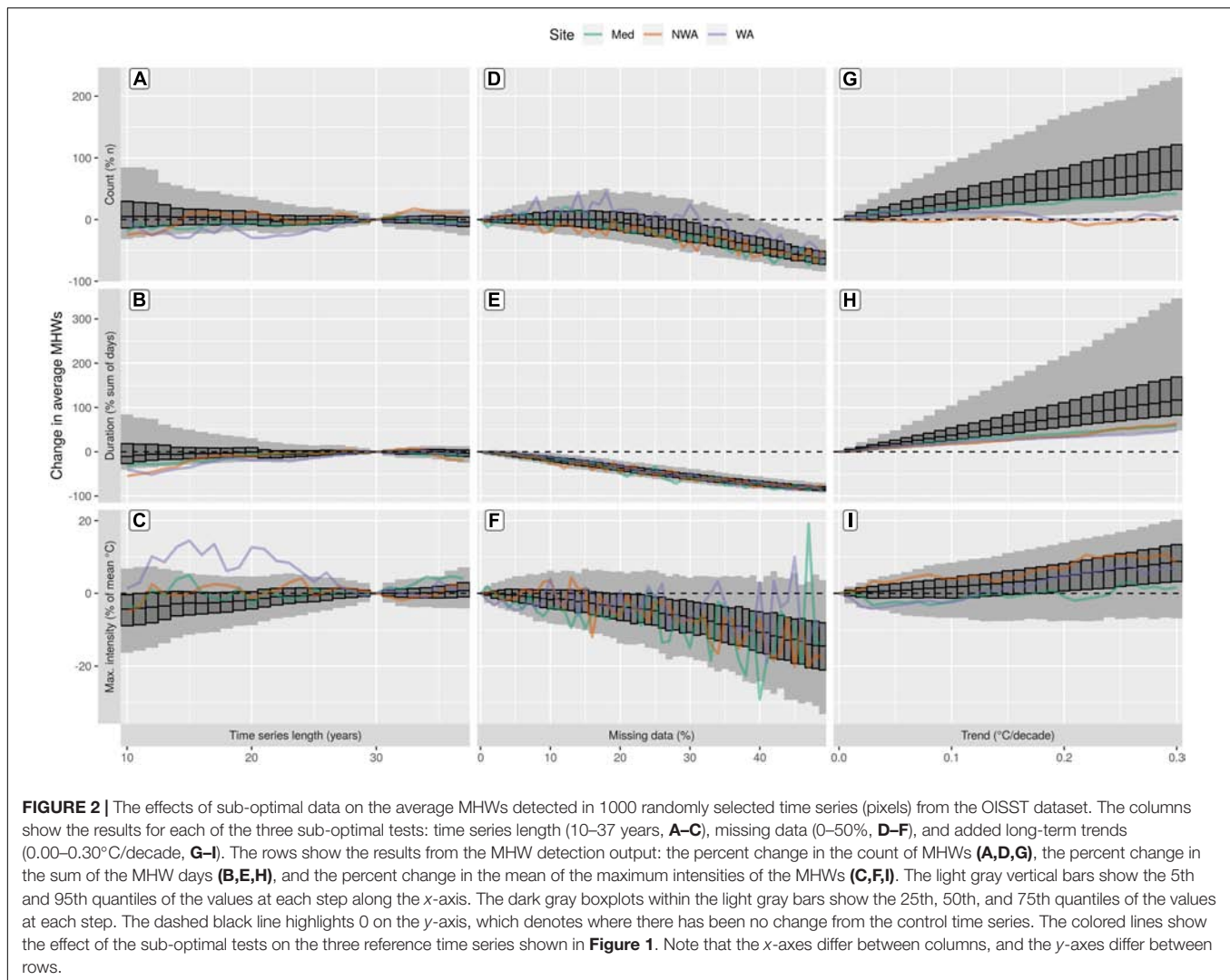
Shortening the length of a time series from 30 to 10 years had an unpredictable effect on the count of average MHWs (**Figure 2A**). At 10 years in length, 90% of the 1000 time series (pixels) tested had between 32% fewer to 85% more MHWs than the 30 year control. The overall increase or decrease in the count of average

MHWs was close to linear, meaning that one may be able to say what the change in the count of MHWs may be as a time series is shortened, but it does not allow us to say if this change is positive or negative. The change in the sum of days of the durations of the average MHWs from a 10 year time series ranged from 41% fewer to 84% more than the 30 year control (**Figure 2B**). This change is slightly more linear than for the count of MHWs, but again, the values may increase or decrease. The mean of the maximum intensities of the average MHWs also either increase or decrease, with 10 year time series having mean maximum intensities anywhere from 16% less to 7% more than the 30 year control.

Increasing the climatology period to more than 30 years had almost as rapid an effect on creating dissimilar results as using fewer years of data. This result stresses the importance of adhering to the WMO standard as closely as possible to ensure the comparability of results (Hobday et al., 2018). It also demonstrates the arbitrariness of the 30 year climatological base period.

Shortening time series length tended to decrease both the duration and maximum intensity of the focal MHW from each time series (**Figures 3B,C**), while the count of MHWs within the duration of the focal MHW increased (**Figure 3A**). This is because shortening a time series may increase the seasonal and threshold climatologies, so the shorter a time series becomes, the lower the maximum intensity and shorter the duration of the MHWs may become. MHWs with many spikes (**Figure 1A**), rather than a smooth hump (**Figure 1C**), will be particularly affected by this change in the climatology as it will more rapidly break the focal MHW into smaller events (**Figure 3A**).

There are clear global patterns in the changes in MHW results as time series are shortened from 30 to 10 years (**Figure 4**). The median change in the count of average MHWs due to changes in time series length is only 0.24%/year, but much of the western Pacific and northern Atlantic oceans show large rates of increasing MHW counts as time series are shortened (**Figure 4A**). The rates of change in the eastern Pacific, southern Atlantic, and the Indian Ocean show a mix of both increasing and decreasing counts of MHWs as time series become shorter. The patterns of change in the sum of MHW days closely resemble the change in the count of MHWs (**Figure 4B**). The median change in the maximum intensity of average MHWs throughout most of the oceans is –0.21%/year (**Figure 4C**). This means that, on average, a MHW detected in a 10 year time series will have a maximum intensity about 4.2% cooler than a MHW detected in a 30 year time series (0.21%/year times 20 year difference). This small difference shows the robustness of the MHW detection algorithm. There are areas where decreasing a time series increases the maximum intensities of the MHWs detected. These areas are roughly the same regions where the shortening of a time series causes a decrease in the count of MHW days detected. It is important to note that the long-term trends in these data were removed beforehand so the patterns observed in **Figure 4** are due to the properties of the time series themselves and not the climate change signal that would otherwise be dominant in the results.



The global patterns of the effect of shortened time series on the focal MHWs are similar to the average MHWs. Much of the ocean that shows a decrease in the count of MHWs as a time series is shortened (**Figure 4A**) also show an increase in the count of MHWs during the focal MHW at 10% more MHWs per year the time series is shortened (**Figure 4D**). This may seem contradictory, but this increase in the count of MHWs during the focal MHW in a time series is due to it being broken into smaller events. When this occurs on the smaller MHWs they may be broken up enough to no longer be counted, and therefore the count of average MHWs decreases. The decrease in the durations of the focal MHWs are greater than the decreases for the average MHWs and the spatial homogeneity of this pattern is more broken up (**Figures 4B,E**). The regions that show increasing durations in the focal MHW are spatially smaller than the average MHWs and the rates of increase are roughly one quarter of those for the average MHWs (**Figures 4B,E**). Finally, the rates of increase or decrease in maximum intensities were similar in scale between the average and focal MHWs, but differed in their spatial patterns. Whereas the average MHWs show clear

warming trends in the northeast and south Pacific (**Figure 4C**), these features are much reduced for the focal MHWs (**Figure 4F**). The strong cooling signal in the average MHWs north of Europe is replaced by a spatially broad warming trend in the focal MHWs in the area. The minor warming trend in the average MHWs around the Kuroshio Current is replaced by a spatially larger and more intense warming trend in the focal MHWs.

Missing Data

The effects of increasing missing data on MHW detection were more linear than the effects of time series length, with the exception of MHW count, which was the least linear effect of all tests (**Figure 2**). Up to 25% missing data, the count of average MHWs in a times series decreases by 45% or increases by 38% (**Figure 2D**). Past this point the count of MHWs falls at a roughly linear rate until there are 33–86% fewer MHWs when 50% data are missing. The effect of missing data on the sum of the average MHW days was linear at a rate of roughly 2% fewer MHW days in a time series for every 1% of missing data (**Figure 2E**). The effect of missing data on the maximum intensities of the average

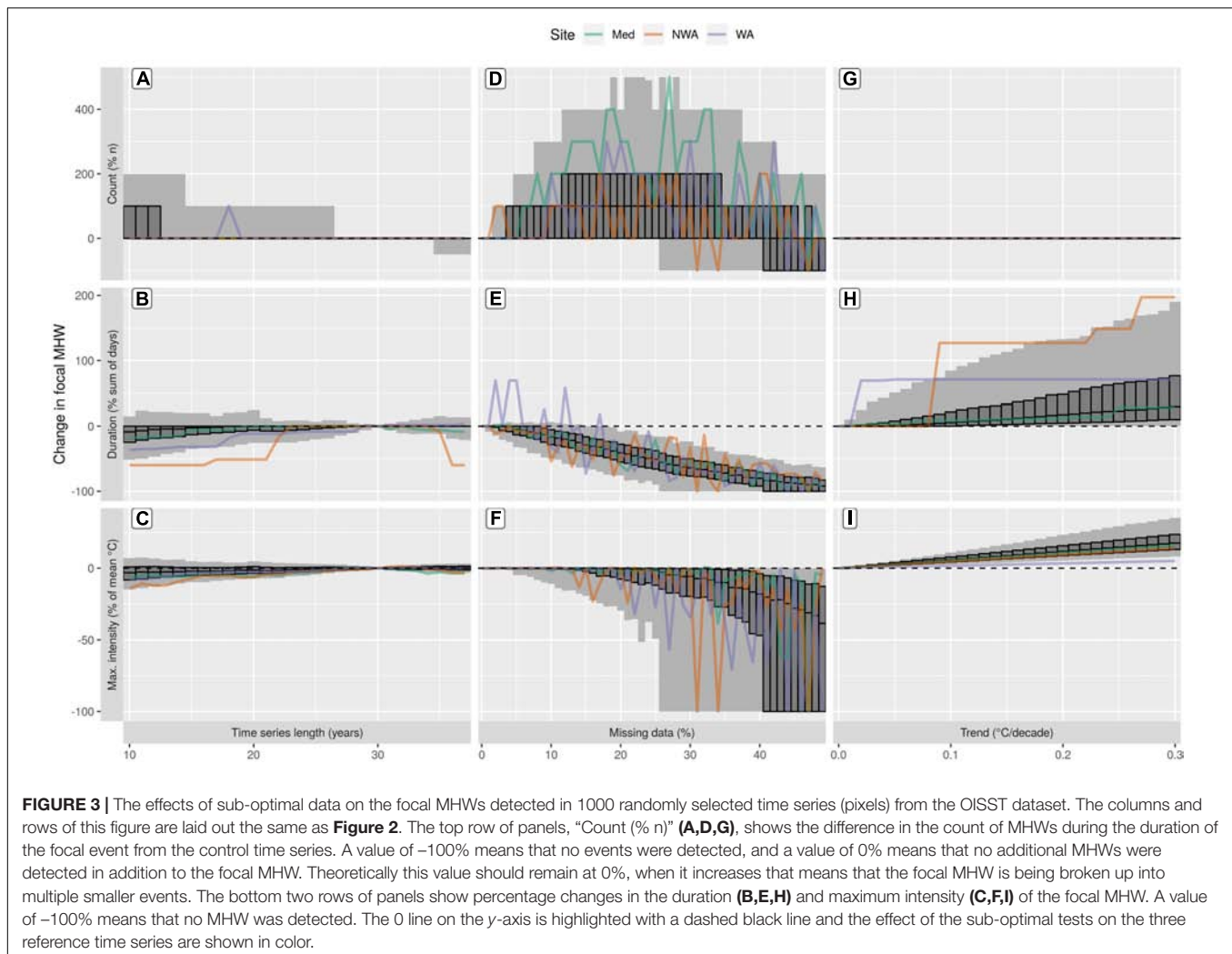


FIGURE 3 | The effects of sub-optimal data on the focal MHWs detected in 1000 randomly selected time series (pixels) from the OISST dataset. The columns and rows of this figure are laid out the same as **Figure 2**. The top row of panels, “Count (% n)” (**A,D,G**), shows the difference in the count of MHWs during the duration of the focal event from the control time series. A value of -100% means that no events were detected, and a value of 0% means that no additional MHWs were detected in addition to the focal MHW. Theoretically this value should remain at 0% , when it increases that means that the focal MHW is being broken up into multiple smaller events. The bottom two rows of panels show percentage changes in the duration (**B,E,H**) and maximum intensity (**C,F,I**) of the focal MHW. A value of -100% means that no MHW was detected. The 0 line on the y-axis is highlighted with a dashed black line and the effect of the sub-optimal tests on the three reference time series are shown in color.

MHWs was also linear, but very noisy. The maximum intensities of average MHWs detected in time series missing 50% of their data could decrease by 33% or increase by 3%.

The effect of random missing data on the focal MHW in each time series was dramatic. As missing data in a time series increased, it becomes increasingly likely that the focal MHW is broken into multiple smaller events. It is not uncommon for this to begin with as little as 1% missing data, and increases in severity up to 25–30% (**Figure 3D**). From this point the number of separate events the MHW is broken into decreases as the smaller events are completely missed due to the loss of data. The duration of the focal MHW was almost always negatively impacted by missing data (**Figure 3E**). The decrease in duration follows a linear trend of a reduction ranging from 1 to 3% per 1% of missing data. At 26% missing data at least 5% of the time series had their focal MHW removed entirely from the time series, as seen by a reduction in maximum intensity of 100% (**Figure 3F**). At 41% missing data at least 25% of the time series had their focal MHW removed.

The effect of missing data on a MHW depends largely on their shape, which is the area above the threshold climatology

and below the observed anomaly. The WA event has a very pronounced peak (**Figure 1A**), so when more data are missing it becomes increasingly likely that this peak is not recorded. The maximum intensity measured in the control time series is 6.5°C , but because very few days of this MHW were so intense, increases in missing data become more likely to remove these large values and the maximum intensity of the WA event begins to decrease more rapidly than either the NWA or Mediterranean MHWs. The global patterns in missing data are unremarkable and generally consistent across the oceans (**Supplementary Figure S3**).

Long-Term Trend

The effect of a long-term trend on MHW detection was the most linear of the three tests and resulted in the largest changes in the results. An added linear trend can lead to a reduction in the count of average MHWs in a time series, but generally it causes a linear increase at roughly 3% additional average MHWs detected for every $0.01^{\circ}\text{C}/\text{decade}$ added (**Figure 2G**). The effect that these additional MHWs had on the sum of average MHW days was an increase, ranging from 1.7 to 11.5% for every $0.01^{\circ}\text{C}/\text{decade}$

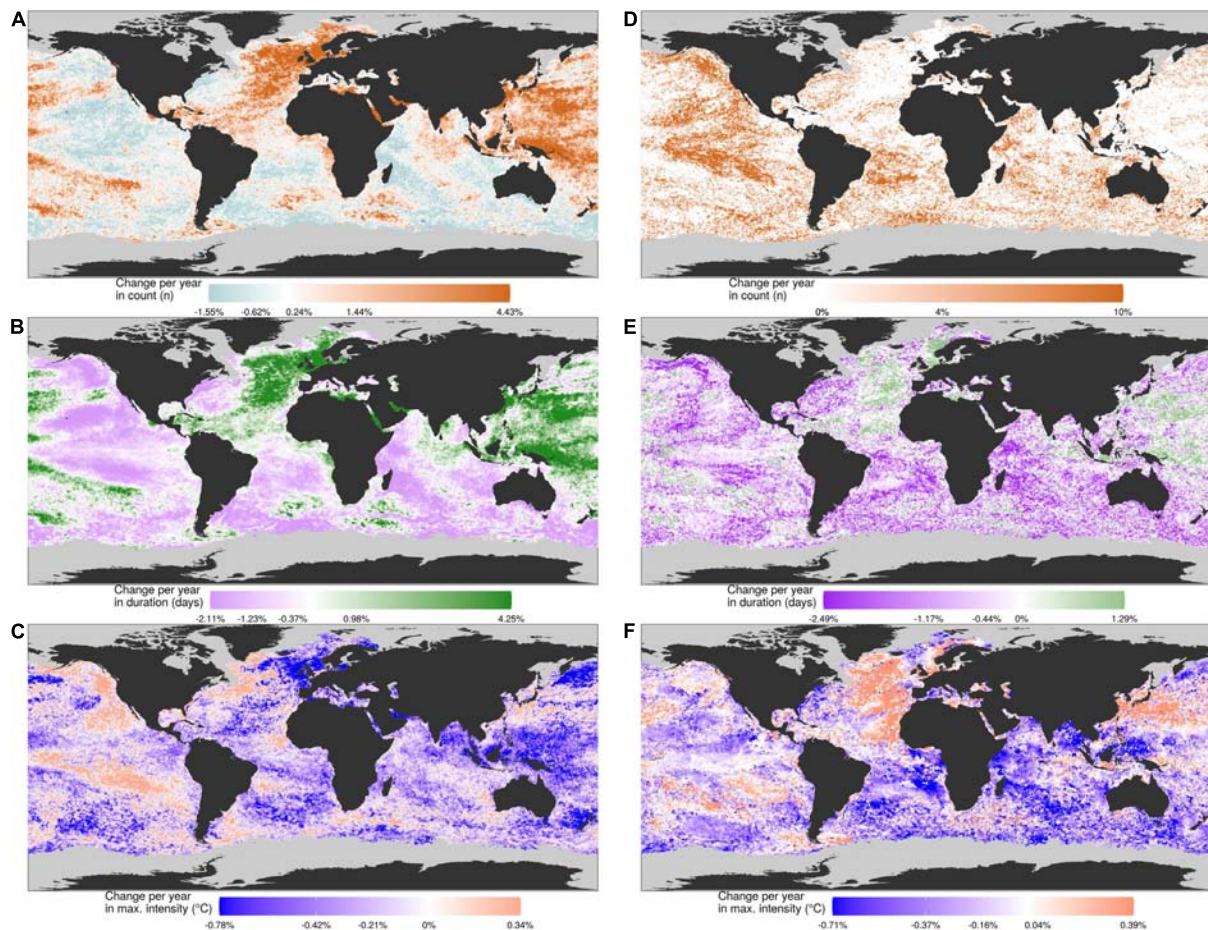


FIGURE 4 | Global map showing changes in MHW detection as the time series at each pixel is shortened from 30 to 10 years. The left column shows the effect of time series length on the average MHWs detected, while the right column shows the effect on the focal MHW. Panels (A,D) show the change in the count of MHWs as the time series are shortened, (B,E) show the change in the duration (days) of the detected MHW(s), and (C,F) show the change in the maximum intensity ($^{\circ}\text{C}$). The labels on the color bars at the bottom of each panel show what the global values are at the 5th, 25th, 50th, 75th, and 95th quantiles. Any values smaller/larger than the 5th/95th quantile were rounded to prevent the very long tails of the distribution from interfering with the visualization of the results.

added (Figure 2H). This means that the average MHWs detected in a time series with a long-term trend of $0.30^{\circ}\text{C}/\text{decade}$ could be 48–347% longer than in the same time series with no long-term trend. The effect of linear trends on the maximum intensity of the average MHWs, though generally linear, could be either positive or negative at a rate of -0.1 – 0.6°C per $0.01^{\circ}\text{C}/\text{decade}$ added.

The focal MHW in each time series was never broken into multiple events due to the added long-term trend (Figure 3G), however, the duration of the focal MHWs were affected differently. The Mediterranean MHW showed practically no increase in duration due to an added long-term trend, the WA MHW saw a large jump at $0.03^{\circ}\text{C}/\text{decade}$, and the NWA MHW had a dramatic jump at an added trend of $0.09^{\circ}\text{C}/\text{decade}$, followed by a few other increases at larger added trends (Figure 3H). Likewise, all of the other 1000 time series included in Figure 3 tend to jump up in dramatic steps, as seen by the very large range in the 90 and 50% confidence intervals (CI). These jumps in duration occur as the temperature anomalies increase more rapidly than the threshold and neighboring MHWs

in a time series connect into one event. The effect that the long-term trend had on the maximum intensity of focal MHWs was also linear and at an added trend of $0.30^{\circ}\text{C}/\text{decade}$ the 90% CI was from 8 to 35% of the control value (Figure 3I). The global patterns in added long-term trends generally show that MHW metrics increase (Supplementary Figure S4).

BEST PRACTICES

Given the effect of time series length, missing data, and long-term trends on the detection of MHWs, we can quantify the uncertainty in the results when using sub-optimal data. In Table 1 the increasing rates of uncertainty per step in the sub-optimal tests for average MHWs is shown, while Table 2 shows the uncertainty for the focal MHWs. For example, a time series that is 20 years in length (10 years shorter than optimal), will result in a median difference in the duration of average MHWs that is 3% lower, and the 90% CI will be $\pm 27\%$ around that median

difference. These rates of uncertainty at the 90% CI are large, but knowing where in the world a time series comes from it is possible to make a more accurate inference. For example, the change in the duration of average MHWs in the North Sea as the time series are shortened is very consistently positive and near the high end of the global distribution (**Figure 4B**). This means that one can be more confident that the upper range of the 90% CI is an appropriate choice when estimating the possible change in results if they had been calculated with an optimal time series (30 years). One final point of consideration in the application of this information for judging uncertainty is to consider how linear the response of the results to the sub-optimal tests is. The values in parentheses in **Tables 1, 2** show the R^2 (coefficient of determination) for each linear model that was used to determine the change in uncertainty as time series become more sub-optimal. More examples, as well as a step-by-step walk through for how to use the numbers in these tables, are provided in each sub-section below. The *a priori* and *post hoc* fixes proposed in the methods are also covered in more detail in the following sub-sections. It must be stressed here that the methods proposed below for working with sub-optimal data do not address the issues that remotely sensed data have near coastlines.

Correcting for Time Series Length

The *a priori* fix proposed for shorter time series, creating a smoother seasonal signal by expanding the window half-width of the moving average, was not a reliable option and this should be left as the standard 5 day period. Increasing the window half-width to as much as 30 days has very little effect on the 50% (interquartile) and 90% CI ranges for the count of average MHWs, the effect on individual time series is inconsistent (**Figure 5**, top row). The effect of this change to the detection algorithm on the duration of average MHWs was negligible at all window half-widths tested (**Figure 5**, middle row). The effect of wider window half-widths on the maximum intensity of the average MHWs appeared to help keep the results comparable (**Figure 5**, bottom row), but upon closer inspection this was found to be misleading. The effect of widening the window half-widths was similar for the results of the focal MHWs (**Supplementary Figure S5**). The widening of the window half-widths affects MHW detection by flattening the shape of the sinusoidal seasonal climatology. The overall mean value does not change, but the peaks and troughs are pulled closer to the mean while the slopes between them become more gradual. Because the mean of the seasonal signal does not change, the total anomalous observations remain similar, but where along the seasonal signal those anomalies are detected may shift dramatically. This is particularly noticeable for MHWs that occur at the peak of summer because the seasonal and threshold climatologies are lowered the most here, making these events appear more intense.

Although an *a priori* fix for time series length is not effective, the known rates of uncertainty can be used to provide the *post hoc* uncertainty to detected MHWs. Using the focal MHW uncertainty rates as an example, the first six rows of **Table 2** show the rate of uncertainty introduced into results for a focal MHW for each year less or more than 30 years. The “Range” column in **Tables 1, 2** indicate which direction from the 30 year control

the slope in uncertainty is moving. The focal MHW detected in a 10 year time series will have a median (50th quantile) difference in maximum intensity of -3% from that same MHW in a 30 year time series (**Table 2**, row 5, column “q50,” value = $-0.15\%/year$ shorter than 30). This may be estimated by taking the value found in the corresponding cell of the table and multiplying it by the number of years that the time series is shorter (or longer) than the 30 year optimal length. It is unlikely that results will match the median difference. It is more likely that the detected MHW will fall somewhere within the 50% CI (**Tables 1, 2**, column “q25” to “q75”), or the 90% CI (**Tables 1, 2**, column “q05” to “q95”) range. To determine these ranges in uncertainty, an approach is to use the slope found in the respective columns and multiply each slope by the number of years that the time series is shorter or longer than the 30 year control. This provides the full range of uncertainty within the 50% CI or 90% CI as well as the median change. For example, the 50% CI in the change in the maximum intensity of a focal MHW in a 10 year time series is found by multiplying the 25th and 75th quantiles of change. Using the 10 year time series example described above, this means that the overall range of uncertainty around the median change is: $0.38\% \times 20$ (difference in years) = 7.6% , the change in the 25th quantile is $-0.36\% \times 20 = -7.2\%$, and the change in the 75th percentile is $0.02\% \times 20 = 0.4\%$. The final estimate of the 50 CI around the median change in maximum intensity is therefore: -7.2 , -3.8 , and 0.4% . This means that in a 10 year time series one can assume that the focal MHW detected has a 50% chance of having a maximum intensity that is somewhere between -7.2 and 0.4% of the same MHW estimated using a 30 year times series.

Correcting for Missing Data

Linear interpolation was proposed as an *a priori* fix to address the issue of missing data and was effective. This fix could allow the use of time series missing more than 50% of their data (**Figure 6**), assuming that there is not so much missing data that the period of time during a MHW is completely missing. The rates of uncertainty that missing data introduce into detected MHWs may be found in rows 7–10 of **Tables 1, 2**, but we will focus on the use of the rates of uncertainty for interpolated data here as this is an effective fix. Note that rows 7 and 8 of **Tables 1, 2** show rates of change in the count of MHWs for missing data between different ranges of missing data. This is because the change in the count of MHWs due to missing data is not linear. If one cuts the data at roughly 25% this provides the highest R^2 values for the two slopes (most linear fit).

As an example for the use of linear interpolation over missing data in a time series we show how to calculate the 90% CI around the average MHW duration in a time series missing 30% data. The median rate of change in average MHW duration per 1% missing data after linear interpolation is 0.3% (**Table 1**, row 12, column “q50”), the rate of change for the 5th quantile is 0.09% (**Table 1**, row 12, column “q05”), and for the 95th quantile it is 0.85% (**Table 1**, row 12, column “q95”). At 30% linearly interpolated data one may assume a 90% CI around the average MHW duration to be $2.7\% - 9.0\% - 25.5\%$. In other words, there is a 90% chance that the average duration of the MHWs detected in a time series with 30% interpolated data are between 2.7 and

TABLE 1 | The degree of uncertainty introduced into the average marine heatwave (MHW) results as time series become increasingly sub-optimal.

Test	Variable	Range	q05	q25	q50	q75	q95
Length	Count	30–10	–1.00% (0.76)	–0.39% (0.65)	0.32% (0.65)	1.39% (0.94)	3.77% (0.93)
Length	Count	30–37	–2.89% (0.80)	–1.29% (0.87)	–0.35% (0.22)	0.52% (0.31)	1.97% (0.64)
Length	Duration	30–10	–1.62% (0.95)	–0.96% (0.89)	–0.29% (0.44)	0.86% (0.87)	3.80% (0.93)
Length	Duration	30–37	–2.86% (0.86)	–1.24% (0.83)	–0.33% (0.28)	0.52% (0.43)	1.67% (0.68)
Length	Max. intensity	30–10	–0.72% (0.98)	–0.42% (0.99)	–0.23% (0.97)	–0.06% (0.40)	0.21% (0.67)
Length	Max. intensity	30–37	–0.45% (0.55)	–0.11% (0.33)	0.10% (0.81)	0.36% (0.95)	0.83% (0.86)
Missing	Count	0.00–0.25	–1.45% (0.97)	–0.92% (0.95)	–0.44% (0.59)	0.24% (0.15)	1.53% (0.74)
Missing	Count	0.26–0.50	–1.67% (0.99)	–1.95% (1.00)	–2.16% (1.00)	–2.48% (1.00)	–3.10% (0.99)
Missing	Duration	0.00–0.50	–1.80% (0.97)	–1.81% (0.99)	–1.80% (0.99)	–1.76% (1.00)	–1.65% (0.99)
Missing	Max. intensity	0.00–0.50	–0.60% (0.99)	–0.42% (0.98)	–0.31% (0.96)	–0.19% (0.89)	0.01% (0.00)
Interp	Count	0.00–0.50	–0.17% (0.85)	0.00% (1.00)	0.17% (0.90)	0.35% (0.98)	0.70% (0.98)
Interp	Duration	0.00–0.50	0.09% (0.83)	0.19% (0.97)	0.30% (0.99)	0.44% (0.99)	0.85% (0.99)
Interp	Max. intensity	0.00–0.50	–0.22% (0.99)	–0.16% (1.00)	–0.12% (0.99)	–0.07% (0.91)	–0.02% (0.21)
Trend	Count	0.00–0.30	0.71% (0.95)	1.74% (1.00)	2.69% (1.00)	3.97% (1.00)	7.44% (0.99)
Trend	Duration	0.00–0.30	1.66% (1.00)	2.87% (1.00)	3.97% (1.00)	5.66% (1.00)	11.47% (1.00)
Trend	Max. intensity	0.00–0.30	–0.12% (0.40)	0.14% (0.79)	0.29% (0.97)	0.42% (0.99)	0.61% (0.99)

Starting from the left, the “Test” column shows which of the three sub-optimal tests the results are for. The rows labeled “Interp” are for the interpolation fix for the missing data tests. The “Variable” column shows the different MHW results that were focussed on in the sub-optimal tests. The “Range” column shows the range of values over which the various uncertainty rates were measured. Note that there are two entries for each variable in the length test. This is done to show the difference in the uncertainty that increasing OR decreasing a time series past the 30 year standard affects the results. Also note that there are two rows for the effect of missing data on the count of MHWs, this is because the response is made more linear, and therefore a better predictor, if broken in half from 0–25% and 26–50%. The final five columns show the rate of uncertainty as a percentage difference caused by each test on each variable at the five different quantiles used in the boxplot figures: “q05” = the 5th quantile, “q25” = the 25th quantile, “q50” = the 50th quantile, “q75” = the 75th quantile, and “q95” = the 95th quantile. The R^2 value (coefficient of determination) of the slope in each cell is given in parentheses.

TABLE 2 | The degree of uncertainty introduced into the focal marine heatwave (MHW) results as time series become increasingly sub-optimal.

Test	Variable	Range	q05	q25	q50	q75	q95
Length	Count	30–10	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	3.51% (0.33)	9.59% (0.78)
Length	Count	30–37	–8.93% (0.67)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)
Length	Duration	30–10	–2.16% (0.95)	–1.12% (0.94)	–0.34% (0.66)	0.00% (1.00)	1.05% (0.71)
Length	Duration	30–37	–2.58% (0.87)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	2.06% (0.82)
Length	Max. intensity	30–10	–0.65% (0.98)	–0.36% (0.98)	–0.15% (0.97)	0.02% (0.23)	0.29% (0.91)
length	Max. intensity	30–37	–0.40% (0.82)	–0.13% (0.66)	0.04% (0.42)	0.19% (0.89)	0.44% (0.84)
Missing	Count	0.00–0.25	0.00% (1.00)	0.00% (1.00)	5.23% (0.67)	8.75% (0.78)	19.12% (0.86)
Missing	Count	0.26–0.50	–0.85% (0.07)	–5.47% (0.70)	–5.64% (0.72)	–8.41% (0.81)	–12.12% (0.85)
Missing	Duration	0.00–0.50	–1.80% (0.81)	–2.17% (0.97)	–2.07% (0.99)	–1.95% (0.99)	–1.59% (0.93)
Missing	Max. intensity	0.00–0.50	2.66% (0.86)	2.17% (0.74)	0.70% (0.74)	0.20% (0.54)	0.01% (0.10)
Interp	Count	0.00–0.50	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)
Interp	Duration	0.00–0.50	–0.12% (0.91)	0.00% (1.00)	0.02% (0.32)	0.20% (0.88)	1.26% (0.97)
Interp	Max. intensity	0.00–0.50	–0.31% (0.98)	–0.09% (0.81)	–0.01% (0.77)	0.00% (0.02)	0.01% (0.98)
Trend	Count	0.00–0.30	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)	0.00% (1.00)
Trend	Duration	0.00–0.30	0.00% (1.00)	0.35% (0.92)	1.07% (0.98)	2.70% (1.00)	5.66% (0.98)
Trend	Max. intensity	0.00–0.30	0.27% (1.00)	0.44% (1.00)	0.59% (1.00)	0.79% (1.00)	1.19% (1.00)

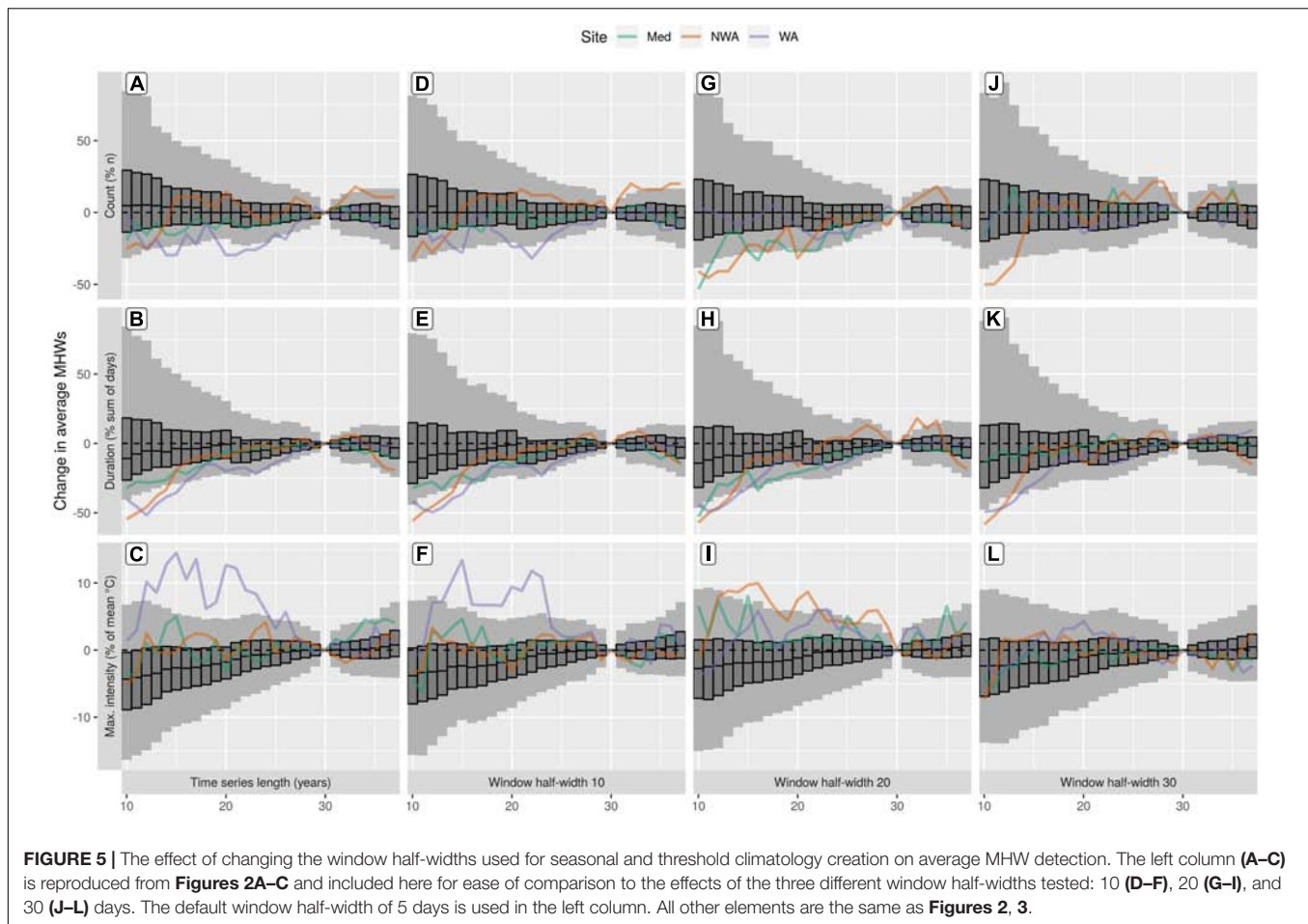
All elements of this table are the same as **Table 1** and are used the same in the calculation of uncertainties introduced into MHW results from sub-optimal data.

25.5% that of the MHWs detected in the same time series without any missing data.

Correcting for Long-Term Trend

There was no *a priori* fix proposed for the correction of an added linear trend. Rather, by knowing the trend in a time series *a priori* we have been able to model the effect that it has on detected MHWs. The effect that long-term trends have on the results are much greater than for time series length or missing data, and

the effects are more linear, therefore; we can be more confident in the uncertainty we assign to the detected MHWs. However, the ranges of uncertainty introduced by long-term trends are also much greater than for the other two tests. To illustrate how long-term trends affect the count of average MHWs we use a time series with a known linear trend of 0.25°C/decade. The median rate at which a long-term trend in a time series affects the count of average MHWs is 2.69% per 0.01°C/decade (**Table 1**, row 14, column “q50”), the 5th quantile is 0.71% (**Table 1**, row



14, column “q05”), and the 95th quantile is 7.44% (**Table 1**, row 14, column “q95”), therefore; the count of average MHWs detected in a time series with a long-term trend of $0.25^{\circ}\text{C}/\text{decade}$ is likely (90% CI) 17.75% – 67.25% – 186%. This is a very large effect that supports the argument for using a 10 year long or 50% interpolated data time series. There are long-term trends present in most time series being used and these effects on the MHWs therein are almost certainly greater than using short time series with missing data. If one is comfortable detecting MHWs in a time series before detrending it, one should be comfortable with the use of time series shorter than 30 years or missing some data.

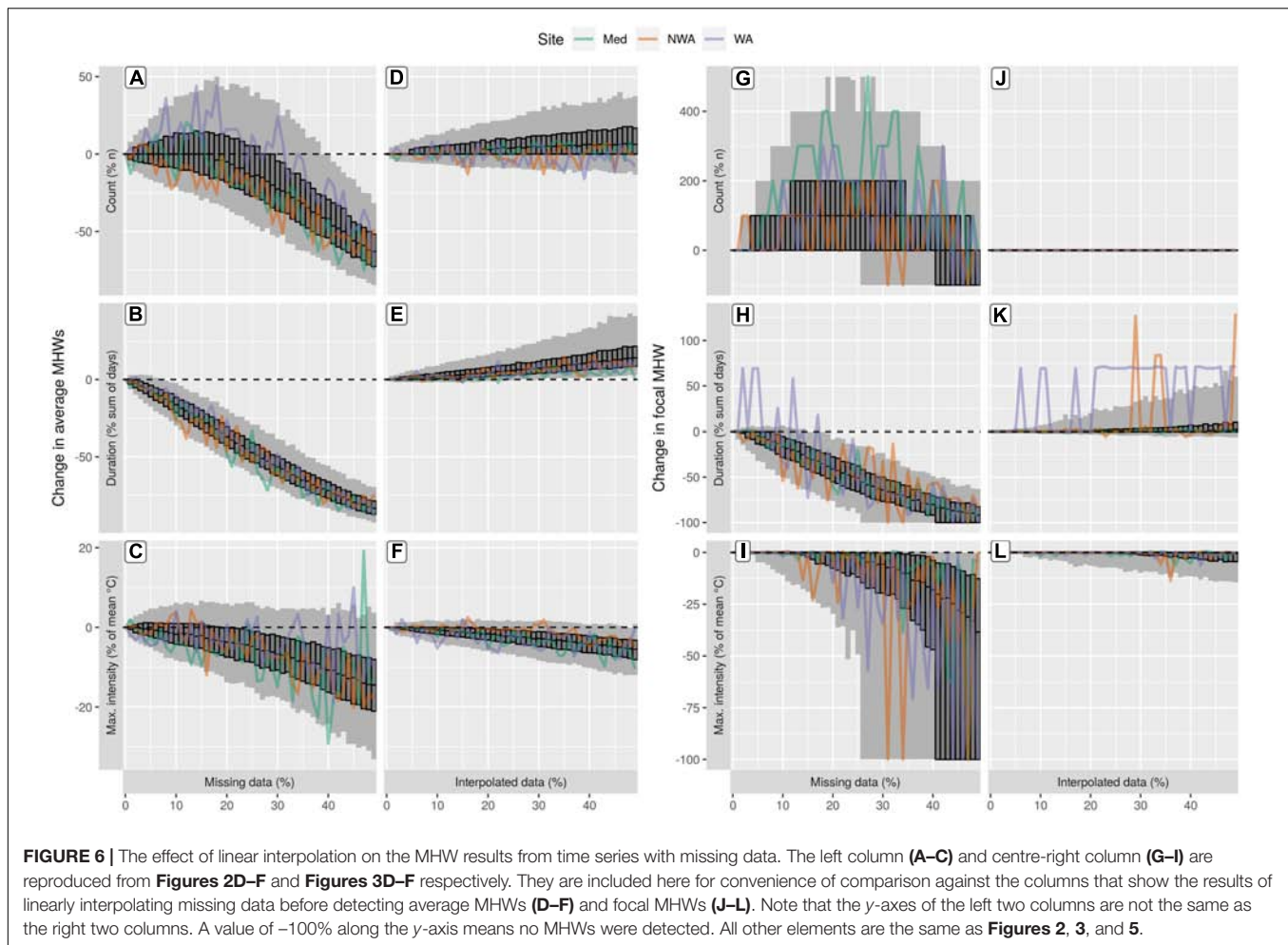
DISCUSSION

This investigation into the effects of sub-optimal data on MHW detection revealed that there are no clear statistical thresholds at which the outputs of the MHW algorithm diverge from optimal data. The ranges of uncertainty that sub-optimal data introduce into MHW results could be determined and users may now decide their acceptable level of uncertainty. It must be noted that having used only SST data for these investigations the results may not accurately represent the properties of sub-surface MHWs,

which may last longer and be more intense than those at the surface (Schaeffer and Roughan, 2017; Darmaraki et al., 2019).

The MHW results from time series with 10 years of data are not appreciably different from the MHWs detected with 30 years of data. The rates at which the count, duration, and maximum intensity of MHW change from year-to-year within a single time series may vary wildly, but a global sampling showed that the increasing range in the uncertainty of the results one may expect are roughly linear. The rates of uncertainty in **Table 1** may therefore be applied *post hoc* to MHWs detected in shorter time series to provide the uncertainty range within which the results are comparable to those from an optimal time series.

An unexpected result was that increasing the base period used for climatology creation to longer than 30 years reduced the probability that the outputs would be comparable by as much as shortening the base period did. This means that the common (often unspoken) assumption that using 30 years of data is the same as using >30 years of data for a base period is incorrect. In other words, a 30 year time series is often thought of as the minimum length needed to constrain the climatology but we have shown here that using a climatology period greater than 30 years may create outputs as different as using fewer than 30 years. This is due to the decadal and multi-decadal variability in an environmental time series. In time series with less decadal to



multi-decadal variability there will be no appreciable difference between results calculated with a 30 year base period versus the 30+ years. In a time series with large decadal to multi-decadal variability, a base period of 30 years is not long enough to remove this variability. It is therefore important to stress the adherence to the WMO standards for climatology periods as closely as possible to ensure results are comparable to other studies (Hobday et al., 2018). Increased smoothing of the climatologies derived from shortened time series was not an effective fix so it is recommended that the default climatology method in Hobday et al. (2016) also be followed to maximize comparability between studies.

The MHW algorithm proved to be resilient to missing data. Time series missing up to 25% of their data resulted in a count of MHWs comparable to using a 10 year time series and the rate of increase in uncertainty can be modeled with some accuracy. Time series missing more than 25% were affected too much and too unpredictably for the results to be reliable, while focal MHWs were sometimes not detected with 26% or more missing data. Fortunately, the effect that missing data has on the duration of average MHWs in a time series is predictable and can be corrected (**Table 1**). A simple correction for missing data in a time series is to linearly

interpolate over the gaps – for more than 50% missing data, the results will have less uncertainty in them than using a 10 year time series. This advice assumes that missing data is distributed through the time series, if the period of time during a MHW is missing large sections of data, interpolation will not be effective.

The long-term temperature trends in times series have the largest potential effect on the MHWs detected. These effects are the most predictable of the three issues examined but also introduce the largest ranges of uncertainty. The increase in duration from added long-term trends led to temperatures in the time series usually increasing “faster” than the 90th percentile threshold. So as the slope of the added trend increases, the length of a given MHW increases. MHWs with a slow onset/decline (e.g., the NWA event) will increase in duration more rapidly, while those with a more rapid onset/decline (e.g., the Mediterranean event) will not appreciably change in duration with a larger long-term trend. A series of MHWs separated by short periods of time may merge into a single larger event (e.g., the WA event). This reduces the overall count of the MHWs detected in a time series while increasing the mean duration of the events detected.

CONCLUSION

The acceptable sub-optimal data limits, their proposed corrections, and the amount of uncertainty they introduce into the results are as follows:

(1) Time series length:

- A length of 10 years produces acceptable MHW metrics that may be used with some caution.
- Smoothing the climatology before detecting MHWs does not improve the results and should not be done.
- The largest uncertainty that shorter time series introduce into average or focal MHWs is duration:
 - Average MHW duration changes by -1.62 – -3.8% /year shorter than 30 (90% CI).
 - Focal MHW duration changes by -2.16 – -1.05% /year shorter than 30 (90% CI).

(2) Missing data:

- The effect of missing data up to 25% on MHW results is comparable to the effect of a 10 year time series.
- Focal MHWs may begin to disappear from time series missing 26% or more data.
- Linear interpolation is an excellent fix for missing data up to 50%, assuming that the time period of interest is not completely missing.
- The largest uncertainty that linearly interpolated missing data introduce into MHW results is duration:
 - Average MHW duration changes by 0.09 – 0.85% per% interpolated (90% CI).
 - Focal MHW duration changes by -0.12 – 1.26% per% interpolated (90% CI).

(3) Long-term trends.

- Long-term trends had the greatest effect on MHWs of the three sub-optimal tests and had the greatest range of uncertainty around those effects.
- Long-term trends in excess of those tested in this paper occur naturally and are rarely controlled for so no limit is proposed here.
- The duration of MHWs is what is affected most by a long term trend in the data:
 - Average MHW duration changes by 1.66 – 11.47% per $0.01^{\circ}\text{C}/\text{decade}$ (90% CI).
 - Focal MHW duration changes by 0.00 – 5.66% per $0.01^{\circ}\text{C}/\text{decade}$ (90% CI).

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Researchers need not avoid using sub-optimal time series, such as might be the best available for coastal research or sub-surface analyses. Time series length may have an unpredictable effect on MHW results, but this may be corrected, and time series lengths as short as 10 years are still useful for MHW research. Missing data has a larger effect on MHW detection, but linear interpolation can compensate for up to 50% missing data. Lastly, the effect of long-term trends on MHW detection are the largest and most linear but also have the largest uncertainties. The MHW detection algorithm is robust and researchers may be confident in the inter-comparability of results when using time series within a generous range of sub-optimal data challenges.

DATA AVAILABILITY STATEMENT

The code and datasets generated for this study may be found at <https://github.com/robwschlegel/MHWdetection>. A detailed outline of the code used in this methodology may be found at <https://robwschlegel.github.io/MHWdetection/>.

AUTHOR CONTRIBUTIONS

RS prepared the majority of the text, figures, synthesized the comments, and uploaded the manuscript. AS prepared a large portion of an early version of the text and a number of initial figures. AH, EO, and AS provided several rounds of comments on the manuscript as it was developed.

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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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Projected Marine Heatwaves in the 21st Century and the Potential for Ecological Impact

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Marine heatwaves (MHWs) are extreme climatic events in oceanic systems that can have devastating impacts on ecosystems, causing abrupt ecological changes and socioeconomic consequences. Several prominent MHWs have attracted scientific and public interest, and recent assessments have documented global and regional increases in their frequency. However, for proactive marine management, it is critical to understand how patterns might change in the future. Here, we estimate future changes in MHWs to the end of the 21st century, as simulated by the CMIP5 global climate model projections. Significant increases in MHW intensity and count of annual MHW days are projected to accelerate, with many parts of the ocean reaching a near-permanent MHW state by the late 21st century. The two greenhouse gas (GHG) emission scenarios considered (Representative Concentration Pathway 4.5 and 8.5) strongly affect the projected intensity of MHW events, the proportion of the globe exposed to permanent MHW states, and the occurrence of the most extreme MHW events. Comparison with simulations of a natural world, without anthropogenic forcing, indicate that these trends have emerged from the expected range of natural variability within the first half of the 21st century. This discrepancy implies a degree of “anthropogenic emergence,” with a departure from the natural MHW conditions that have previously shaped marine ecosystems for centuries or even millennia. Based on these projections we expect impacts on marine ecosystems to be widespread, significant and persistent through the 21st century.

Keywords: marine heatwave, climate change, extreme events, global climate models, ecosystems

INTRODUCTION

Marine heatwaves (MHWs) – prolonged periods of anomalously warm seawater (Hobday et al., 2016) – have increased significantly in frequency and duration since the early twentieth century (Oliver et al., 2018a). Individually, these extreme events can have significant impacts on marine ecosystems, including effects on biodiversity (Cavole et al., 2016; Wernberg et al., 2016; Jones et al., 2018), fisheries (Mills et al., 2012), and aquaculture (Oliver et al., 2017). Ecological responses to prominent MHWs have been observed across a range of processes, scales, taxa and geographic regions (Smale et al., 2019). Collectively, and over time, an increase in the exposure of marine ecosystems to extreme temperatures may lead to irreversible loss of species or foundation habitats, such as seagrass (Thomson et al., 2015), coral reefs (Hughes et al., 2019) and kelp forests (Wernberg et al., 2016; Thomsen et al., 2019). Therefore, estimating how MHWs are projected to change globally is important for understanding their ecological impacts in a warming world.

The count of annual MHW days has increased globally by over 50% from 1925 to 2016 (Oliver et al., 2018a). In addition, MHW intensity – the associated sea surface temperature (SST) anomaly – has increased significantly since the start of the satellite era in 1982 (Oliver et al., 2018a). The physical processes driving MHWs are varied and include air-sea heat fluxes coinciding with atmospheric heat waves and/or horizontal temperature advection due to changes in ocean circulation (Sparnocchia et al., 2006; Chen et al., 2014; Oliver et al., 2017; Holbrook et al., 2019). Regardless of the physical mechanisms driving individual MHWs, consensus is emerging that anthropogenic climate change has significantly increased the likelihood of recent MHWs including the 2015/16 Tasman Sea MHW (Oliver et al., 2017), the 2016 Northern Australia MHW (Lewis and Mallela, 2018; Oliver et al., 2018b), the 2016 Gulf of Alaska and Bering Sea MHW (Oliver et al., 2018b; Walsh et al., 2018), the 2016 California Current MHW (Jacox et al., 2018), and the 2017/18 Tasman Sea MHW (Perkins-Kirkpatrick et al., 2019). Further, Frölicher et al. (2018) suggested that by the year 2100 anthropogenic climate change is projected to increase the probability of MHWs nearly everywhere, regardless of variations in emissions scenarios.

Here we use a suite of global climate models to estimate projected future MHWs to 2100. We focus on two globally projected response metrics, the annual count of MHW days and the annual maximum MHW intensity, that represent the time spent in a MHW state and the magnitude of the temperature anomaly reached, respectively (Hobday et al., 2016), as well as the intensity-based “category” of these events (Hobday et al., 2018a). These metrics are useful as they are proxies for exposure of marine ecosystems to chronic heat stress and acute heat stress, respectively. We consider two greenhouse gas (GHG) emissions scenarios in order to compare the projected futures arising from strong GHG mitigation versus a “business as usual” trajectory. We compare the projected future trajectory of MHWs against the historical trajectory and against bounds of natural variability derived from simulations without anthropogenic forcing. Finally, we discuss the likely implications

of the projected changes for marine biodiversity and ecosystem structure and function.

MATERIALS AND METHODS

CMIP5 Sea Surface Temperatures

We examined outputs from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor et al., 2012) global climate model simulations of historical and projected future climates. Daily sea surface temperature (SST) outputs were taken from the “historical” simulation, representing historical conditions with anthropogenic influence. Historical simulations were forced using anthropogenic GHG and aerosol forcing in addition to natural forcing and cover the period 1850–2005. In addition we consider two future climate projection experiments that represent the evolution of the climate system subject to two different anthropogenic emissions scenarios covering 2006–2100: “RCP4.5” which assumes anthropogenic GHG emissions peak in the year 2040 and then stabilize at a radiative forcing of 4.5 W m^{-2} , and “RCP8.5” which assumes these emissions continue to rise throughout the 21st century with radiative forcing reaching 8.5 W m^{-2} by the end of the century. We also used the “historicalNat” simulation, representing historical conditions without anthropogenic influence where models are forced by natural volcanic and solar forcing only, with greenhouse gases and aerosols held at pre-industrial levels, spanning 1850–2005. We obtained data for these experiments from six models, chosen due to the availability of daily SST outputs, each with varying numbers of ensemble members (see Table 1 for details of the models).

Marine Heatwave Definition and Categories

Marine heatwaves were identified from daily SST time series and a set of metrics were calculated to characterize their frequency, intensity and duration. Following (Hobday et al., 2016) a MHW was defined as a discrete prolonged anomalously warm water event. “Discrete” means an identifiable event with recognizable start and end dates, “prolonged” implies a duration of at least 5 days, and “anomalously warm” measures temperatures relative to a baseline climatology and threshold (see below for period

TABLE 1 | CMIP5 models used in the analysis.

Model	Historical	HistoricalNat	RCP4.5	RCP8.5
ACCESS1.3	3	3	1	1
CanESM2	1	3	5	5
CSIRO Mk3.6.0	10	9	10	10
HadGEM2-ES	2	2	4	4
IPSL-CM5A-LR	6	3	4	4
IPSL-CM5A-MR	3	3	1	1
Total	25	23	25	25

The number of ensemble members for each model experiment is listed for each model.

used). Periods when daily temperatures were above a threshold based on the seasonally varying 90th percentile for at least five consecutive days were identified as MHW events. Events with a break of less than 3 days were considered a single event. The climatological mean and threshold were calculated for each calendar day from the pool of daily SSTs within an 11-day window centered on the calendar day of interest across all years (within the climatology period). The climatology and threshold were smoothed by applying a 31-day moving average. The 11-day sample window size was chosen to ensure sample sizes were sufficient for the estimation of means and percentiles. Furthermore, by using seasonally varying thresholds, rather than a fixed mean annual threshold, this methodology allows for detection of MHWs at any time of the year, such as distinguishing summer and winter MHWs (with potential ecological implications, as summer MHWs might be expected to have larger ecological effects).

A set of properties was defined for each MHW event. We considered metrics for duration (time between start and end dates) and maximum intensity (maximum temperature anomaly, relative to the seasonally varying climatological mean, over the event duration). Noting that a 90th percentile threshold is relatively easy to exceed, providing a liberal definition for what counts as a MHW, we also examine the intensity-based MHW category. Each event was classified as being a Moderate (category I), Strong (II), Severe (III), or Extreme (IV) MHW. These categories are defined by the maximum intensity of the event scaled by the threshold temperature anomaly exceeding the climatology, defined as a “unit” (Hobday et al., 2018a). For example, events between the threshold and one unit above it are classified as Moderate (I), between one and two units as Strong (II), etc. As detailed in Hobday et al. (2018a) the impacts of relatively common Moderate MHWs are mild (or non-existent) while the impacts of rarer Severe and Extreme MHWs are much greater. Despite initially defining only four categories, this system allows for higher categories according to the recorded temperature anomaly (“extreme extremes” e.g., Category V, VI, etc.).

We calculated time series of the annual average duration and annual maximum intensity across all events in each year. Events which spanned multiple years contributed to the annual time series for each year they spanned. We also calculated the total number of MHW days in a year and the total number of days belonging to each of the four MHW categories in a year. The MHW definition (Hobday et al., 2016, 2018a) is implemented as software modules in Python¹, R², and MATLAB³.

Model Simulated Marine Heatwaves

Marine heatwaves were identified from the daily CMIP5 SSTs as described above. For all model experiments, the climatology used to define anomalies was calculated from the historical experiment, from that model, using a base period of 1982–2005. For each model/experiment and MHW metric, the

annual time series’ were re-gridded (spatially averaged) onto a common 2° × 2° grid. Then time-slice averages of the various MHW metrics were calculated over 1961–1990 and 2031–2060, as well as global-mean time series [applying a sea ice mask following (Oliver et al., 2018a)]. Individual model results represent an ensemble mean across all members for that model and experiment. Multi-model mean (MMM) results represent an average across the ensemble means for all seven models. Individual models results, indicative of the inter-model spread, are shown in the **Supplementary Material**.

We examined the change in probability of occurrence of MHW days globally by calculating the following probability ratio (*PR*; Allen, 2003; Stott et al., 2013):

$$PR(y) = \frac{P_{hist}(y)}{P_{histNat}}$$

where $P_{hist}(y)$ is the probability of a MHW day occurring in a particular year y in the historical experiment, defined as the global mean annual count of MHW days in that year divided by the total number days in that year. $P_{histNat}$ is the total number of global-mean MHW days across all years divided by the total number of days across all years from the historicalNat experiment. A *PR* value of >1 or <1 indicates that the probability of a MHW day in that year is greater than or less than that expected in the natural world, respectively. The probability ratio was also calculated for projected future years using the RCP4.5 and RCP8.5 experiments instead of the historical experiment in the numerator of *PR*. Please note that these calculated *PR* values are specific to the model ensemble used and may not as such apply to the real-world climate, due to systematic model errors often resulting in overconfident model ensembles (Bellprat et al., 2019) – a characteristic also apparent in the model ensemble used here (**Supplementary Figures 1C,F**).

Here, we define a “permanent MHW state” to be when SST exceeds the MHW threshold continuously over a full calendar year (365 days). From this definition, we calculated the year when the permanent MHW state occurs for each grid cell, for all the model ensemble members and for the MMM.

An evaluation of the model simulations of MHW intensity and total days was performed by comparing MHW statistics over the 1982–2005 period between the models and observations (**Supplementary Figure 1**). The observations used were daily SST fields from the 1/4° NOAA OI SST V2 dataset (Reynolds et al., 2007; Banzon et al., 2016). The model bias for MHW intensity was within ±0.5°C over most of the ocean, except in the highly variable western boundary current regions where the models were up to 2°C less intense than the observations. The model bias for MHW days was within ±10 days over most of the ocean except in the tropical parts of the Indian, western Pacific, and Atlantic oceans where the models simulated up to 25 more MHW days than the observations. This type of bias, where the models produce too many MHW days, is consistent with the limitations of coarse resolution models. Specifically, these models underestimate the SST anomaly produced by very small-scale features, simulate SST time series that are too smooth (high serial autocorrelation) and thus produce longer MHWs and too few heat spikes (SSTs exceeding the threshold for less

¹<http://github.com/ecjlover/marineHeatWaves>

²<https://robwschlegel.github.io/heatwaveR>

³https://github.com/ZijieZhaoMMHW/m_mhw1.0

than 5 days duration). Note that in this study we are primarily concerned with the model simulated changes in MHW metrics. Even though the models simulate a mean state in which MHWs are slightly less intense and slightly longer lasting than observed we expect that long-term changes in MHWs should not be affected by such biases in regions where mean temperature warming is the primary driver of MHW changes (Oliver, 2019). However, model-simulated MHW changes may be less realistic in regions where relevant dynamical features (such as western boundary currents) are not sufficiently resolved by the models, and changes in such dynamical features may contribute to changes in MHW properties.

RESULTS

Over the 21st century, projected MHWs show increases in intensity and duration in most regions around the globe. During the 1961–1990 period the time-averaged MHW intensity is relatively high primarily in western boundary current regions and the eastern equatorial Pacific (**Figure 1A**), consistent with the observed record (**Supplementary Figure 1**; see also Oliver et al., 2018a). From the RCP8.5 experiment, the pattern of change showed increased MHW intensity nearly everywhere by 2031–2060 (**Figure 1B**, inter-model robustness of change is indicated by hatching when all models agree on the sign of the change). Increases are particularly high (+2–4°C) in the Mediterranean Sea, the subpolar North Pacific, the Gulf Stream extension region, the East Australian Current Extension, and several disparate small tropical regions. Notably, the higher latitude portions of the North Atlantic and Southern Oceans exhibit no significant projected change in MHW intensity. This pattern is broadly consistent with that of the MMM change in annual mean SST between the same two time periods (not shown). This is also consistent with the historical record which indicates low rates of warming, and even cooling, in parts of the Southern Ocean south of the Antarctic Circumpolar Current (Armour et al., 2016; Sallée, 2018) and in the North Atlantic Subpolar Gyre (Rahmstorf et al., 2015; Menary and Wood, 2018).

Annual mean time series from the historical experiment (**Figure 1C**) indicated that, globally, the intensity of MHWs has increased over the historical period (1850–2005; **Figure 1C**, black line and gray shading) and is projected to increase significantly from 2006 to 2100 for both the RCP4.5 and RCP8.5 experiments (**Figure 1C**, red and brown lines and shading, respectively). The increase of ca. +1.5°C for RCP4.5 and ca. +3°C for RCP8.5 by 2100 compared with the 1961–1990 historical period, and that the change is largely related to a shift in the mean SST rather than a change in the variability (not shown), indicates that changes in MHW intensity co-vary with changes in mean SST. Importantly, the inter-model range of global mean MHW intensity (**Figure 1C**, gray shading) exceeds the expected range of natural variability (**Figure 1C**, blue shading) in the year 2044 for RCP4.5 and by 2033 for RCP8.5.

The mean annual count of MHW days over the 1961–1990 period is relatively uniform across the globe, with most regions experiencing 27.5–35 days (**Figure 1D**). Exceptions include the

eastern tropical Pacific (up to 40 days) and a band along ~30°S as well as part of the Western Boundary Current regions in the Northern Hemisphere (as low as 25 days). If the MHW definition was narrowed to exceedance of the 90th percentile for a single day, then we expect a climatological count of annual MHW days of 36.5 (10% of the year). However, the criterion of a 5-day minimum duration reduces this frequency and introduces some spatial heterogeneity in the mean fields (see Oliver et al., 2018a for detailed discussion of this point). Sustained warming after the climatological period would then be expected to increase the annual count into the future.

From the RCP8.5 experiment, the pattern of change in MHW days indicates an increased count nearly everywhere by 2031–2060 (**Figure 1E**). Robust increases across models are ca. +150–300 days over most of the ocean except in the far North Atlantic and the highest latitudes of the Southern Ocean where at least one model simulates changes of opposite sign. Annual mean time series from the historical experiment indicate that, globally, the annual count of MHW days has increased since 1850 (**Figure 1F**, black line and gray shading), most strong after ca. 1980, and is projected to increase significantly under both future scenarios (RCP4.5 and RCP8.5, 2006–2100; **Figure 1F**, red and brown lines and shading, respectively). Consequently, in the RCP8.5 experiment, by 2100 the entire globe is projected to approach a permanent MHW state (365 days per year; **Figure 1F**, dashed line). Importantly, the inter-model range of global mean count of annual MHW days (**Figure 1F**, gray, red, and brown shading) exceeds the expected range of natural variability (**Figure 1F**, blue shading) in the year 2009 for RCP4.5 and by 2010 for RCP8.5.

The proportional change in MHW occurrence probability in the historical and RCP simulations can be quantified by comparing outputs to simulations of a historically natural world – that is, a world where the Earth's atmosphere had not been historically subjected to anthropogenic increases in GHG concentrations (historicalNat, 1850–2005) (**Figure 2A**). During most of the historical period, the probability of a MHW day occurring was similar to 'the natural world' simulation, i.e., the ratio of the former to the latter was close to 1 (**Figure 2A**). However, by the end of the historical run this probability ratio had increased to 5.4 [inter-model range (Range): 4.1–6.9]. This result implies that globally averaged the probability of a MHW day occurring in the present day simulations is typically five times higher than in simulations with pre-industrial levels of greenhouse gases. For MHWs of at least category "moderate," this probability ratio increases to 24 for RCP4.5 (Range: 22–26) and 27 for RCP8.5 (Range: 26–28), by the end of the 21st century. This result is not strongly influenced by emissions scenario (RCP4.5 vs. RCP8.5) since MHW days come close to saturation shortly after mid-century in both scenarios (**Figure 1F**).

However, the emission scenario has a strong effect on the projected intensity of events (**Figure 1C**) and therefore the exposure to the most extreme events (**Figure 3**). Historically (1850–2005), the majority of MHW events were categorized (Hobday et al., 2018a) as being moderate (**Figure 3**, yellow) with relatively few strong events (**Figure 3**, orange) and very few severe or extreme events (**Figure 3**, red and brown, respectively). Under the RCP4.5 scenario, future projections suggest that

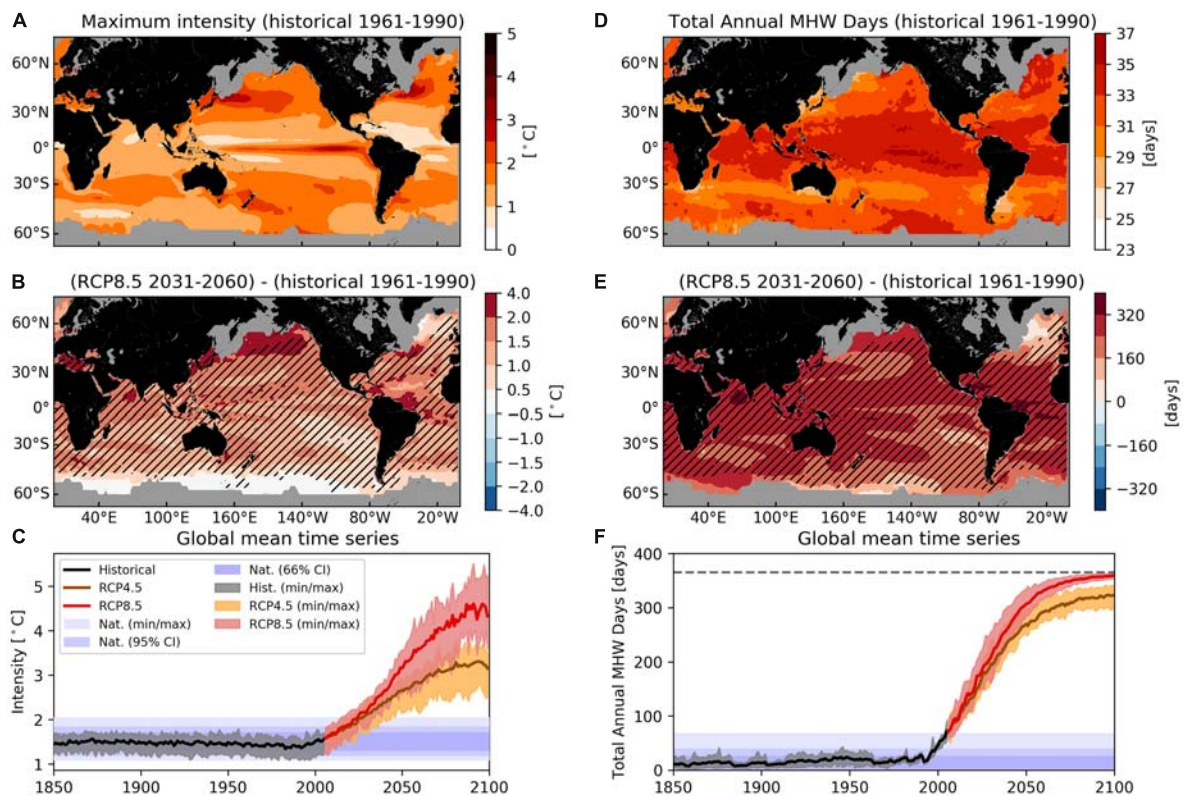


FIGURE 1 | Projected changes to marine heatwaves (MHWs). **(A,D)** Multi-model mean MHW properties from the historical runs over 1961–1990. **(B,E)** Change between RCP8.5 run (averaged over 2031–2060) and historical run (averaged over 1961–1990). Hatching indicates that all models agree on the sign of change (corresponding to a 1% significance level based on binomial distribution). **(C,D)** Annual time series for historical (black), RCP4.5 (brown), and RCP8.5 (red) runs. The gray, red and brown shaded regions show the maximum range between individual model runs. The blue shaded areas show the expected range of natural variability based on a 66% confidence interval (darkest blue), 95% confidence interval (medium blue), and full min-to-max range (lightest blue) of the historicalNat runs (1850–2005). Results for intensity are shown on the left **(A,B,C)** and for total MHW days on the right **(D,E,F)**. Equivalent figures for each individual model can be found in **Supplementary Figures 2–7**.

there will be a more even partition between the four categories (ratio of moderate:strong:severe:extreme = 27:33:24:16) by 2100 indicating a dramatic increase in strong, severe and extreme events. By comparison, under the RCP8.5 scenario, extreme MHWs make up the majority of all events (70%) by the end of the 21st century, whereas moderate events are projected to be rare (4%; ratio of moderate:strong:severe:extreme = 4:10:16:70). We also found increasing separation between the two emissions scenarios in raising the occurrence probability of the more intense MHW categories (**Figures 2B–D**). By 2100, the probability ratio for MHWs of strong (and larger) category is 160 (Range: 130–180; RCP4.5) and 240 (Range: 230–250; RCP8.5); for MHWs of severe (and larger) category is 810 (Range: 550–920; RCP4.5) and 2000 (Range: 1800–2100; RCP8.5); and for extreme MHWs is 1900 (Range: 1100–2400; RCP4.5) and 9500 (Range: 7800–11000; RCP8.5).

Under anthropogenic climate change, we see the emergence of “permanent MHW states” (based on what is considered a MHW in the 1982–2005 base period). The first year of a permanent MHW state occurs at different times over the globe, ranging from 2000 to 2020 in parts of the tropical Atlantic and Pacific, to 2020–2040 over most of the tropical and mid-latitude oceans. At higher

latitudes and within some regions (North Atlantic and parts of the Southern Ocean) this state is not reached until the end of the 21st century (**Figure 4A**). While the proportion of global grid cells experiencing a permanent MHW state increases steadily through the 21st century under both scenarios, the permanent state is approached much faster in RCP8.5 (**Figure 4B**). More specifically, under the RCP4.5 scenario about 50% of the ocean is in a permanent MHW state by 2100 (**Figure 4B**, brown line and shading), while >90% is in a permanent MHW state under the RCP8.5 scenario by the end of the century (**Figure 4B**, red line and shading).

The emergence of a permanent MHW state implies that “extremes” in the “traditional” sense (i.e., compared to the 1982–2005 climatological baseline) are no longer “extreme,” suggesting that the baseline period to maintain a 90th percentile definition into the future, could perhaps also be shifted or shifting, if understanding the “true extremes” for any time period was the focus of study. Alternatively, the use of ‘new and more extreme’ categories would address this concern, for example, by allowing for identification of increase in “extreme extremes,” as Category V, Category VI, etc. (Hobday et al., 2018a). The choice of baseline depends on the application. For understanding

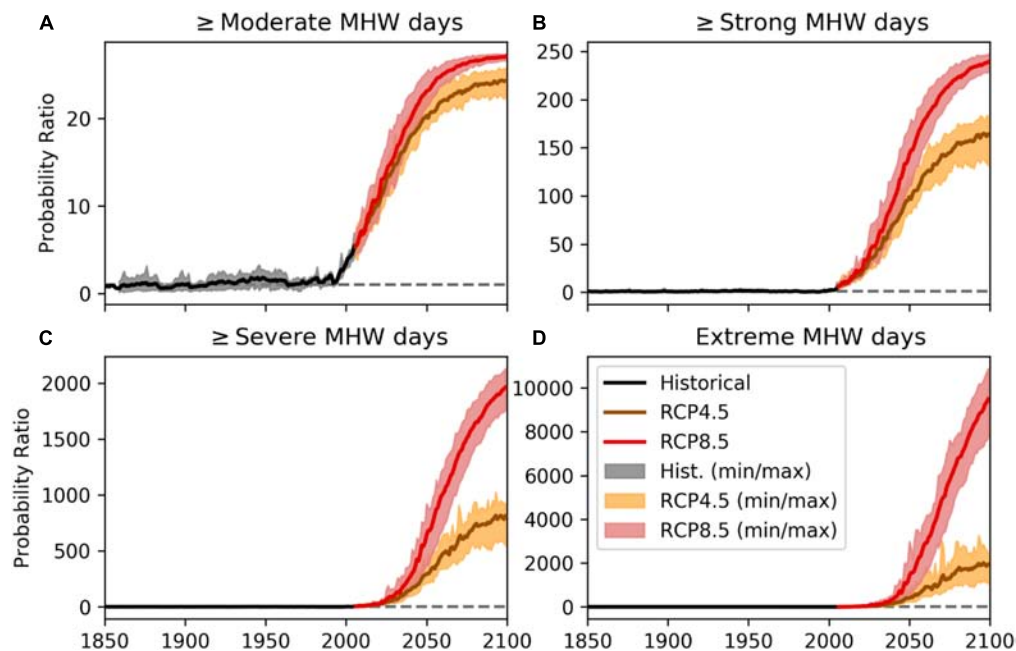


FIGURE 2 | The role of anthropogenic forcing in increasing the probability of MHW days. Each panel shows the globally aggregated probability ratio of a MHW day occurring in a given year from the historical (black), RCP4.5 (brown), and RCP8.5 (red) experiments relative to the probability of a MHW day occurring in the historicalNat experiment (calculated from the full 1850–2005 time series). The panels show the probability ratio but for only MHW days that are (A) at least category moderate, (B) at least category strong, (C) at least category severe, and (D) category extreme. The shaded regions indicate the minimum and maximum values based on individual ensemble members. The dashed line indicates a value of one (i.e., the probability in the historical or projected experiment is the same as in the historicalNat experiment).

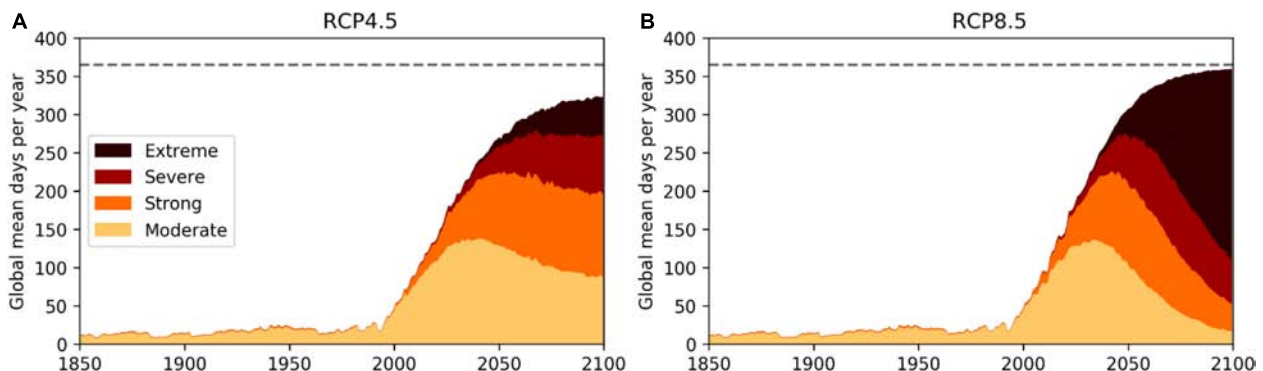


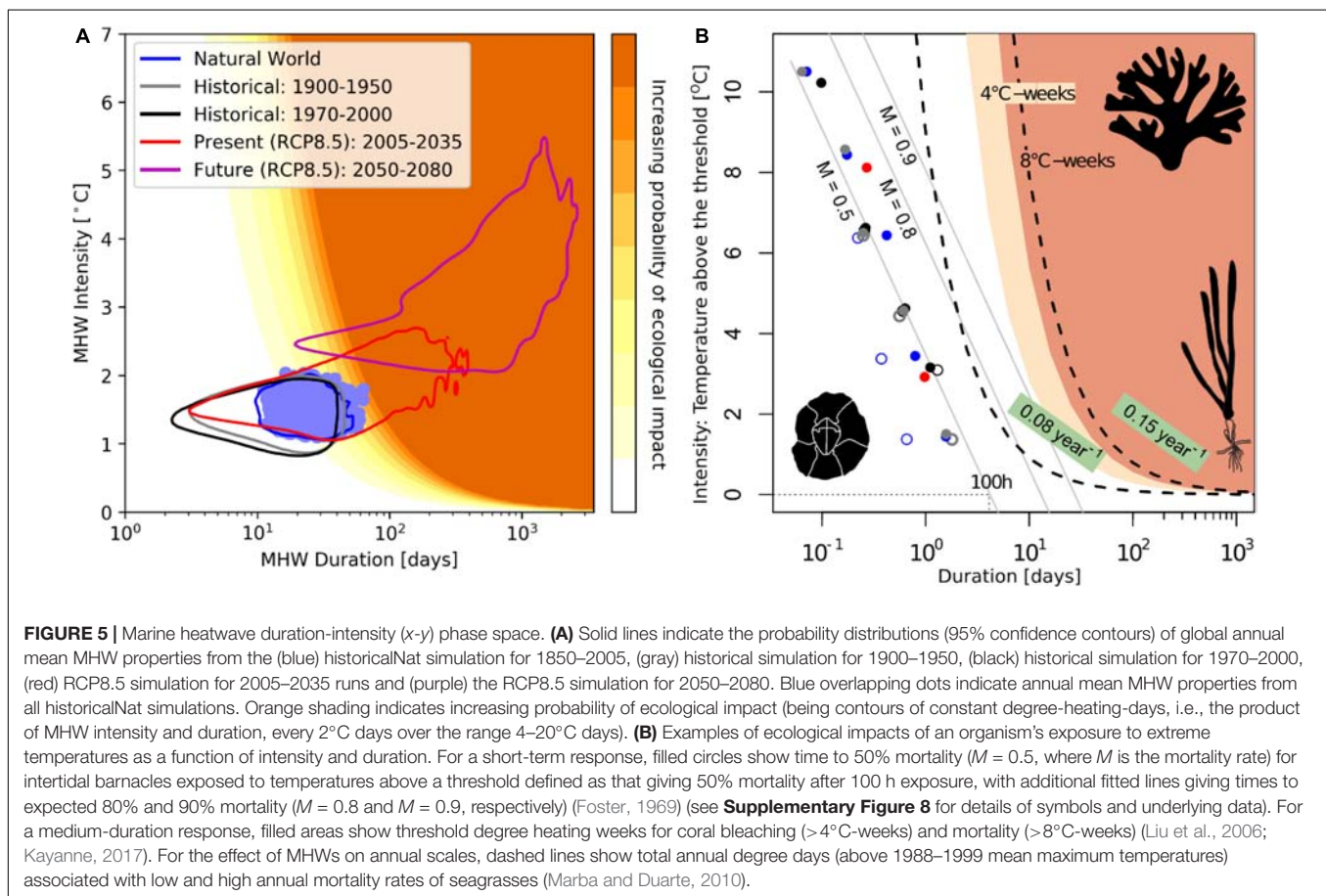
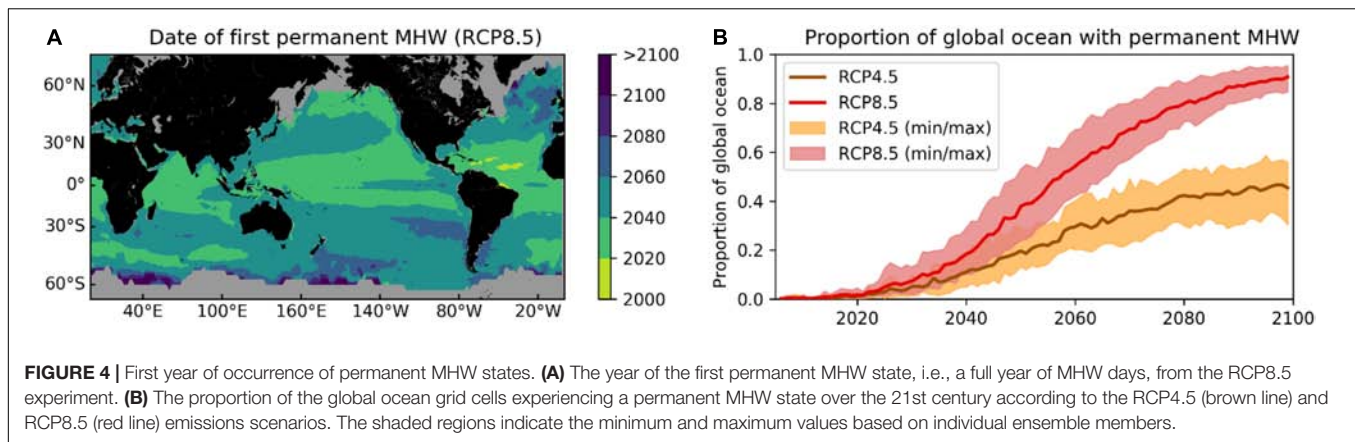
FIGURE 3 | Historical and projected evolution of global mean MHW days, by category. Annual time series of the global mean count of moderate (yellow), strong (orange), severe (red), and extreme (dark brown) MHW days are shown for (A) historical and RCP4.5 experiments and (B) historical and RCP8.5 experiments. Note that the total stacked amount is equivalent to the total MHW days, i.e., the lines shown in Figure 1F. The dashed line indicates a full year (365 days).

impacts on species that adapt slowly (perhaps on evolutionary timescales) a fixed baseline is appropriate. If a species can adapt over decadal timescales to changing temperatures then a sliding baseline would be more appropriate, although there would presumably be limits to the degree of adaptation that might be possible. Similarly, from a sociological point of view, maintaining a consistent baseline period highlights that the ocean enters an entirely new state, for which we may need to adapt our socio-economic systems (or socio-ecological systems, e.g., Serrao-Neumann et al., 2016). In the next section, we discuss

potential ecological implications of future MHWs and cover briefly some potential impacts for marine resource users.

POSSIBLE ECOLOGICAL IMPACTS

To illustrate ecological impacts, modeled MHW properties were plotted in a “MHW Intensity-Duration phase space” for different time periods and for the RCP8.5 emission scenario (Figure 5A, where lines represent 95% confidence contours of the probability



distribution of the sample of all global- and annual-mean MHW intensity and duration for the experiment and time period indicated). These are the same data as shown in **Figures 1C,F** but plotted against each other. In this representation, the trajectory of anthropogenic climate change can be followed from the first half of the 20th century (1900–1950; **Figure 5A**, gray line), to the late 20th century (1970–2000; **Figure 5A**, black line), early 21st century (2005–2035; **Figure 5A**, red line) and finally to the late 21st century (2050–2080; **Figure 5A**, purple line). Notably, the overlap with the natural range of MHW metrics (**Figure 5A**,

blue) decreases over time, and by 2050–2080 there is no overlap between the 95% confidence contours from the RCP8.5 experiment and the 20th century conditions. This divergence can be interpreted as the time when the MHW climate has changed completely from the range that species have previously experienced, and represents a qualitatively different climate.

The projections indicate that future climate will continue to diverge from historical MHW conditions throughout the 21st century, with MHWs becoming longer and more severe. Based on dramatic ecological effects observed following recent

MHWs (Smale et al., 2019), we expect that MHWs will emerge as forceful agents of disturbance to marine ecosystems in the near-future (see also Frölicher and Laufkötter, 2018), as has already occurred on land during terrestrial heatwaves, with reported mass mortality of birds and mammals (Welbergen et al., 2007; Saunders et al., 2011) and significant effects on human health (Poumadere et al., 2005; Nairn and Fawcett, 2015; Mitchell et al., 2016). In the most comprehensive synthesis of MHW impacts conducted to date (Smale et al., 2019), MHWs irrespective of their climatological attributes, all exerted negative impacts across taxa (including seaweeds, corals, birds, and mammals) and processes (such as growth, reproduction, and survival). Marine populations are most susceptible to MHWs when they live in regions close to their maximum thermal limit, because temperature anomalies here are more likely to exceed organismal physiological thresholds and hence increase mortality rates (Smale et al., 2019). With increased MHW activity, we predict dramatic losses of marginal populations at equatorward range edges, as documented for seaweeds (Smale and Wernberg, 2013; Wernberg et al., 2016; Thomsen et al., 2019), seagrasses (Thomson et al., 2015) and invertebrates (Garrahou et al., 2009). Where local extinctions and range contractions involve “foundation species,” ecosystem effects are expected to be particularly severe, as habitats are lost, and food web dynamics and species-interactions are altered. Finally, as populations, species and entire communities respond to intensifying MHWs, provision of ecological goods and services to human societies, such as fisheries and aquaculture production, natural carbon storage, nutrient cycling and coastal defense, will likely be severely compromised (Arias-Ortiz et al., 2018; Ruthrof et al., 2018; Smale et al., 2019).

How projected increases in MHW properties will induce specific ecological change will depend, in part, on the physical attributes of the MHWs themselves, as changes in intensity and duration will affect different organisms in different ways. Short, high intensity MHWs are likely to induce acute stress, as physiological tolerances are exceeded, resulting in reduced growth and possible mortality (Garrahou et al., 2009; Smale and Wernberg, 2013). Effects of MHWs on mortality rates can be expressed through the combination of intensity and duration used to define the heatwaves themselves. For extreme short-term effects, inferences can be drawn from laboratory experiments on temperature tolerance. Here increasing mortality rates reduce survival times with increasing temperature. Intertidal barnacles exhibit this, for example see Foster (1969) (**Supplementary Figure 8**), such that the log of the 50% survival time decreases linearly with temperature (**Figure 5B**, dots and gray lines), giving a quantitative expectation for survival in short, extreme MHWs. Slightly less intense but longer-lasting events may change reproductive outputs and induce behavioral changes, such as movement toward less stressful conditions (Wismer et al., 2019). Medium intensity and longer lasting events over several months, are more likely to affect organismal performance by altering rates of feeding, growth, reproduction and other key processes (Mills et al., 2012). Over this timescale, effects of MHWs on coral reefs are predicted using degree heating weeks above set thresholds

(Liu et al., 2006; Kayanne, 2017), with $>4^{\circ}\text{C}$ -weeks associated with the onset of bleaching and $>8^{\circ}\text{C}$ -weeks with widespread bleaching and some mortality (**Figure 5B**, shading). Longer-term cumulative effects of MHWs can be seen in interannual changes in mortality rates. For Mediterranean seagrasses, annual mortality correlated strongly with total degree-days above the average maximum yearly temperature in preceding decades (Marba and Duarte, 2010; **Figure 5B**, dashed lines). The three examples of combined intensity and duration effects on survival show the potential for quantitative prediction of future specific MHW effects where the responses to current extreme events is understood.

Ultimately, long-lasting MHW conditions could lead to changes in population structure (Smale et al., 2017) and the geographic distributions of species (Smale and Wernberg, 2013; Cure et al., 2018). Moreover, higher temperatures experienced during MHWs may increase the prevalence of pathogens and diseases and thereby reduce the health of organisms and populations (Rubio-Portillo et al., 2016). However, not all impacts will be “negative,” as warm-adapted species and organisms living near their colder poleward ranges should experience improved growth conditions under future MHWs and are therefore likely to increase in abundance (Smale and Wernberg, 2013).

Marine heatwave-induced changes at the organism, population and species levels will also result in changes to the structure of communities, ecosystems and food webs. Where populations of foundation species are affected, indirect effects on other dependent species can be expected (Thomson et al., 2015; Wernberg et al., 2016). For example, recent MHWs have disrupted food webs by changing prey availability, resulting in mass mortality at higher trophic levels (Jones et al., 2018). Additionally, MHWs can drive changes in the distribution and activity of key grazers, such as finfish and sea urchins, with indirect consequences for primary producers, such as seaweeds and seagrasses (Bennett et al., 2015). Clearly, rapid reconfiguration of communities, ecosystems and food webs will almost certainly have ramifications for ecological functioning, and the provision of ecosystem goods and services (Smale et al., 2019).

Major knowledge gaps in our current understanding of how intensification of MHWs will affect marine organisms and communities are associated with whether species can acclimatize and adapt to warmer conditions, and if so how (Donelson et al., 2019; Fox et al., 2019). In other words, facing increasing MHWs, species will either “adapt, move or die.” Under the various “adaptation” scenarios, species may (i) change behavior, (ii) acclimatize, (iii) experience epigenetic effects across generations, or (iv) experience “true” adaptations through natural selection. Experimental, observational, and modeling studies are needed to understand the relative contribution of each strategy to persistence, and the likely success of each in the future (Fox et al., 2019). For example, behavioral change, such as fish that move to deeper and colder water, may be a short-term strategy to avoid localized stress from a specific MHW but may thereby reduce growth and reproductive performance. Similarly, epigenetic variation may constrain the coping range

of a species, leaving selective adaptation as the only viable long-term strategy for a species to cope with the projected increase in MHWs. The rate of selective adaptation will likely vary widely between different species, complicating ecological predictions across space and time.

For human users of marine resources, such as fishers, aquaculture managers, and tourism operators, species persistence and performance are critical for long-term sustainable usage. For example, users in regions that lose iconic species or habitats as a result of global warming and MHWs, such as on the Great Barrier Reef, will have to accept modified natural systems (Hughes et al., 2018) that are likely to impact our society and economy (Marshall et al., 2019). Fisheries and aquaculture industries will need to take a risk-based approach (Hobday et al., 2018b), as prediction of MHWs will be challenging in some regions. There will continue to be surprises associated with MHWs, such as emergence of new diseases (Oliver et al., 2017) and arrival of new species (Pearce and Feng, 2013). Efforts are therefore underway in several regions to climate-proof fisheries management (Creighton et al., 2016), and the impact of extreme events such as MHWs should be considered in this planning (Hobday and Cvitanovich, 2017).

SUMMARY AND CONCLUSION

In this study, we used a suite of global climate models to examine the projected changes in MHWs globally. We found that both the intensity of MHWs and the annual count of MHW days are projected to increase significantly over the 21st century. The emission scenario strongly affects the projected intensity of events, with MHW increases following the high-emission scenario (RCP8.5) nearly double (by 2100, compared to the 1982–2005 baseline period) those projected under the lower-emission scenario (RCP4.5). The difference between emission scenarios is smaller when considering the total annual MHW days, since both saturate to near-permanent MHW states by 2100. However, the high-emission scenario dramatically increases the frequency of MHW days for the most extreme events. Overall, our analysis suggests that anthropogenic forcing will increase the likelihood of MHW occurrence in comparison to a climate with only natural forcing, especially for the more extreme category events. The models suggest that we have departed from the natural background of MHW occurrence – conditions that over millennia have shaped the distribution of marine species and the structure and function of ecosystems. Given several recently observed rapid impacts on marine ecosystems, additional ecosystem changes are likely to be widespread, significant and persistent throughout the 21st century.

An important point that the research community must consider is how to treat the baseline climatological period when performing MHW analyses for rapidly changing climates. Here we have chosen a fixed baseline, while others have advocated for a moving baseline (Jacox, 2019). In our opinion, there is no certain answer to the question of whether baselines should be fixed in time or if they should be allowed to move in time. The use of fixed versus moving baselines should in fact be dictated by the specific question of the study, and if impacted ecosystems are

likely to be able to adapt over time or not. The use here of a fixed baseline implies that the results around ecosystem impacts are of primary relevance for ecosystems with little to no ability to adapt on timescales that are fast relative to the warming rate. However, the occurrence increases strongly with the mean warming rate (Alexander et al., 2018; Oliver, 2019; Pershing et al., 2019) leading to future “permanent MHW states,” exposing to society that the paradigm of MHWs as “transient” extreme events will need re-examination. Of course, the most extreme category events will still be transient – even if new categories need to be defined. Conversely, the advantage of shifting the baseline in time is that one can more clearly partition to what extent MHWs are related to a mean background warming or non-seasonal temperature variance, which may be useful in communicating to the public why an event is occurring. Defining a fixed baseline period for developing climatologies has been questioned by some scientists (e.g., Jacox, 2019) who suggest a moving frame of reference is more appropriate. This issue needs to be guided by ecological adaptation time scales and the nature of the scientific question being asked, but a fixed baseline is currently standard across climate studies.

One limitation of the present study is the use of global models to make inferences about ecological impacts which are likely to be very coastal. These coastal zones may be poorly resolved by the model. In fact, this is one of the biggest issues facing coastal ecologists concerned with temperature-related ecosystem impacts. Here we have considered MHWs occurring at a particular location, i.e., at the pixel level, and we have neglected to acknowledge the spatial coherency of most MHWs. MHWs likely to lead to ecosystem impacts, including past “major events” such as the 2003 Mediterranean event, 2011 Ningaloo Niño and the 2012 NW Atlantic event, span far beyond the closest coastal pixel. Their spatial scale extends over hundreds to thousands of kilometers, which are resolved by global ocean and climate models. A similar correspondence can be seen in coarse resolution satellite SST products where studies have used remotely sensed satellite, surfer-captured and kelp forest temperature logger data showing a good correspondence across the data sources (Brewin et al., 2018), as well as a general consistency between satellite and benthic/coastal temperature loggers (Stobart et al., 2016), and between satellite SSTs and *in situ* benthic temperatures (Smale and Wernberg, 2009). While there certainly would be many empirical and theoretical exceptions to this correspondence, these studies indicate that there is utility in these global products at inferring coastal temperatures and ecosystem impacts.

Our study contributes to the growing body of literature examining long-term changes in MHWs. Importantly, we build directly on knowledge of changes in observed MHW characteristics over the past century estimated from daily satellite observations, daily *in situ* measurements, and gridded monthly *in situ*-based SSTs (Oliver et al., 2018a) – where it was found that global averages of annual MHW days increased by 54% from 1925 to 2016 (Oliver et al., 2018a). Here, we show that this historical trend is projected to continue and accelerate throughout the 21st century. Other studies have also modeled projected changes in MHWs, either globally (Frölicher et al., 2018) or regionally

(Alexander et al., 2018; Darmaraki et al., 2019). Here, we have provided additional critical information on the effect of anthropogenic climate change on different categories of MHW events and discussed the potential ecological impacts of changes to MHWs in the future. Specifically extreme temperature events can drive abrupt changes in the structure and functioning of entire ecosystems, with major consequences for marine resource users that depend on the ocean for ecological goods and services (Smale et al., 2019). Given that global mean warming is the principal driver of the projected increase in MHWs (Oliver, 2019), reductions in GHG emissions combined with adaptive management of marine systems is needed to minimize the impacts of MHWs on marine biodiversity and ecosystems.

DATA AVAILABILITY STATEMENT

We have made use of publicly available data only; no new data were generated as a result of this study. NOAA High Resolution SST data provided by the NOAA/OAR/ESRL PSD, Boulder, CO, United States, from their website at <https://www.esrl.noaa.gov/psd/>. CMIP5 model output data were provided by the ARC Centre of Excellence for Climate Extremes and Australia's National Computing Infrastructure. These data are available publicly via the Earth System Grid Federation's CMIP5 project data website <https://esgf-node.llnl.gov/projects/cmip5/>. The Python code used to perform the analyses is available here: https://github.com/ecjoliver/Global_MHW_Projections.

AUTHOR CONTRIBUTIONS

EO led and coordinated the various components of the study throughout. EO, MD, AS, LA, and SP-K developed the methodology for analysis of the climate model output. MB led the section on ecological impacts and AH, PM, MT, DS,

and TW contributed to its development. All authors discussed the results, aided in their interpretation, and contributed in 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.2019.00734/full#supplementary-material>

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Resistance, Extinction, and Everything in Between – The Diverse Responses of Seaweeds to Marine Heatwaves

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Globally, anomalously warm temperature events have increased by 34% in frequency and 17% in duration from 1925 to 2016 with potentially major impacts on coastal ecosystems. These “marine heatwaves” (MHWs) have been linked to changes in primary productivity, community composition and biogeography of seaweeds, which often control ecosystem function and services. Here we review the literature on seaweed responses to MHWs, including 58 observations related to resistance, bleaching, changes in abundance, species invasions and local to regional extinctions. More records existed for canopy-forming kelps and bladed and filamentous turf-forming seaweeds than for canopy-forming fucoids, geniculate coralline turf and crustose coralline algae. Turf-forming seaweeds, especially invasive seaweeds, generally increased in abundance after a MHW, whereas native canopy-forming kelps and fucoids typically declined in abundance. We also found four examples of regional extinctions of kelp and fucoids following specific MHWs, events that likely have long term consequences for ecological structure and functioning. Although a relatively small number of studies have described impacts of MHWs on seaweed, the broad range of documented responses highlights the necessity of better baseline information regarding seaweed distributions and performance, and the need to study specific characteristics of MHWs that affect the vulnerability and resilience of seaweeds to these increasingly important climatic perturbations. A major challenge will be to disentangle impacts caused by the extreme temperature increases of MHWs itself from co-occurring potential stressors including altered current patterns, increasing herbivory, changes in water clarity and nutrient content, solar radiation and desiccation stress in the intertidal zone. With future increases anticipated in the intensity, duration and frequencies of MHWs, we expect to see more replacements of large long-lived habitat forming seaweeds with smaller ephemeral seaweeds, reducing the habitat structure and effective services seaweed-dominated reefs can provide.

Keywords: temperature extremes, temperature anomalies, climate variability, extreme climatic events, macroalgae, foundation species, habitat formers, range contraction

INTRODUCTION

Anthropogenic stressors have resulted in widespread changes in coastal marine ecosystems (Perry et al., 2005; Sorte et al., 2010; Pecl et al., 2017), with increased temperature being one of the most pervasive environmental drivers of change (Hoegh-Guldberg and Bruno, 2010; Wernberg et al., 2011a; Smale et al., 2019). It is estimated that >70% of the world's coastlines have experienced significant warming in the past four decades (Lima and Wethey, 2012), with predicted near-surface warming in the order of 2–7°C by the end of the century (Christensen et al., 2007; Lima and Wethey, 2012). As a consequence of continued ocean warming, 46% of the world's coastlines have experienced a significant decrease in the frequency of cold days, whereas 38% of coastlines have experienced an increased frequency of extremely hot days when sea surface temperature (SST) exceed the 95th percentile of standardized anomalies of the raw SST between 1982–2010 (Lima and Wethey, 2012). Recently, Hobday et al. (2016) proposed a framework for describing anomalously warm water events as “marine heatwaves” (MHWs), which included a quantitative definition of periods when SSTs exceed the 90th percentile of the climatological mean for at least five consecutive days. Using this approach, Oliver et al. (2018) empirically showed that MHWs have increased in both frequency and duration since the early 20th century, by 34 and 17%, respectively. The underlying driver of this trend was primarily increased mean ocean temperature (Frölicher et al., 2018; Oliver et al., 2018, 2019), with projections of MHWs under a range of climate change scenarios showing they will likely increase in intensity, frequency and duration with ongoing climate change (Frölicher et al., 2018). Furthermore, MHWs are the direct result of local-scale processes (e.g., ocean heat advection, vertical mixing) which can be suppressed or enhanced by remote influences (e.g., climate modes such as ENSO) (Holbrook et al., 2018). Often, there are multiple drivers that significantly influence the occurrence of a MHW, resulting in temperature extremes being generally accompanied by a multitude of altered environmental factors such as ocean currents, wave action, solar radiation and in the intertidal zone, desiccation stress. This co-occurrence of changes in many environmental conditions makes it difficult to disentangle the interactive effects of different factors during MHWs.

Some MHWs have had significant impacts on marine ecosystems, with substantial ecological and socio-economic consequences (Madin et al., 2012; Pecl et al., 2017; Frölicher and Laufkötter, 2018; Smale et al., 2019). Responses include coral bleaching (Couch et al., 2017; Hoegh-Guldberg and Poloczanska, 2017; Le Nohaïc et al., 2017), loss of kelp forest (Wernberg et al., 2016; Thomsen and South, 2019; Thomsen et al., 2019), increased surface layer stratification (Bond et al., 2015; Schaeffer and Roughan, 2017), mass mortalities of marine invertebrates (Garrahou et al., 2009; Oliver et al., 2017), rapid range shifts (Smale and Wernberg, 2013), restructuring of communities (Wernberg et al., 2013a; Bennett et al., 2015b), and fisheries closures (Caputi et al., 2016, 2019; Oliver et al., 2017). In contrast to the impacts of long-term gradual warming, MHWs can outpace adaptive capabilities and cause sudden and dramatic

regime shifts that are more difficult to predict and manage (Scheffer and Carpenter, 2003; Andersen et al., 2009; Wernberg et al., 2016). Moreover, biological responses to MHWs can have devastating consequences for local economies, in particular affecting commercial fisheries, which rely on healthy ecosystem functioning for their productivity (Mills et al., 2013; Bennett et al., 2016; Caputi et al., 2016; Wernberg et al., 2019). Observations of these extreme events show that MHWs are key drivers of ecosystem-scale change, and demonstrate the drastic consequences MHWs can have on the structure and function of marine communities and ecosystems (Dayton and Tegner, 1983; Pearce and Feng, 2013; Wernberg et al., 2013a).

Seaweeds (marine macroalgae) are large, multicellular algae which often dominate shallow-water rocky ecosystems where they can form extensive marine forests (Wernberg and Filbee-Dexter, 2019). Seaweeds represent essential components of coastal habitats and underpin highly diverse ecosystems (Wernberg et al., 2013a; Bennett et al., 2016; Teagle et al., 2017). As important primary producers and habitat formers, seaweeds influence shallow-water communities on rocky reefs globally (Dayton, 1985; Tegner et al., 1997; Bertness et al., 1999; Wernberg et al., 2003; Buschbaum et al., 2006; Tuya and Thomsen, 2009; Egan et al., 2014). Kelp forests, extensive reef systems dominated by large laminarian and fuclean seaweeds (Steneck and Johnson, 2013; Wernberg and Filbee-Dexter, 2019; Wernberg et al., 2019), are especially important for local communities as they directly modify the environment surrounding them and influence adjacent habitats (Gaylord et al., 2007; Wernberg et al., 2018b). Most canopy-forming seaweed species are adapted to thrive in cool, clear, nutrient-rich waters, which makes them vulnerable to anthropogenic stressors influencing water clarity and to ocean warming in warmer parts of their distributions (Fernandez, 2011). Consequently, substantial changes in seaweed distribution and abundance have been observed in various ecoregions over the last five decades due to global change (Lima et al., 2007; Wernberg et al., 2011b; Krumhansl et al., 2016; Filbee-Dexter and Wernberg, 2018; Casado-Amezúa et al., 2019) as well as recent changes due to MHWs (Carballo et al., 2002; Vergés et al., 2014a; Mathiesen, 2016; Reed et al., 2016; Wernberg et al., 2016; Thomsen et al., 2019).

Ocean warming threatens seaweeds as the performance of populations and individuals are affected both directly and indirectly by warming. Warming can directly affect the physiology of seaweeds (Van den Hoek, 1982; Kordas et al., 2011; Tuya et al., 2012; Wernberg et al., 2013b) through sublethal stress leading to reduced performance and increased vulnerability to other stressors (Wernberg et al., 2010). Indirect effects include changes in species interactions, such as shifts in competitive hierarchies and over-consumption by range-shifting herbivores (Haraguchi et al., 2009; Ling et al., 2009; Vergés et al., 2014a; Bennett et al., 2015b; Franco et al., 2015). Pervasive warming of long duration and magnitude, with potential interaction with additional stressors such as solar radiation, desiccation stress and eutrophication, can ultimately exceed a species' lethal thermal limits (Van den Hoek, 1982). Exceeding the sublethal thermal threshold of a species leads to failure to reproduce in marginal populations (causing population

attrition), and can result in local to regional extinctions and ultimately range contractions (O'Brien and Scheibling, 2016; Wernberg and Straub, 2016; Wernberg et al., 2016; Smale et al., 2019).

Overall, increasing temperatures and MHWs directly and indirectly alter the distribution and abundance of seaweeds, their associated species and interactions between species with cascading effects on ecosystem functions and the provision of ecosystem services (Harley et al., 2012; Vergés et al., 2014a; Wernberg and Straub, 2016; Filbee-Dexter and Wernberg, 2018; Thomsen and South, 2019). Given the expected increase in the frequency and duration of MHWs, it is crucial to understand MHW impacts on underlying biological mechanisms which lead to changes in the abundance, distribution and function of foundation species such as seaweeds (IPCC, 2007; Kirtman et al., 2013; Oliver et al., 2018). Recent MHWs have caused substantial ecological changes with economic consequences across marine systems globally (Frölicher and Laufkötter, 2018; Smale et al., 2019). However, little is known about how these extreme events have impacted seaweeds and comprehensive overviews are lacking (but see Smale et al., 2019). Here, we review documented impacts of MHWs on seaweeds, highlighting the diversity of observed responses.

MATERIALS AND METHODS

We conducted a literature search using the library search portal at the University of Western Australia, ResearchGate, Google Scholar and the reference lists of papers returned in the search. We included only MHWs observed in natural ecosystems, not experiments that aimed to mimic MHWs (e.g., Gouvea et al., 2017). Keywords used in the literature search included “marine heatwave*,” “marine heat wave,” “unusually warm,” “abnormally warm,” “abnormal temperature,” “positive temperature event*,” “extreme event*,” “hot summer” in combination with “marine,” “seaweed*,” “macroalga*,” “turf” and “crustose coralline alga*.” The cut-off date for this general search was 15th of February 2019. News articles were only included where no peer-reviewed journal articles could be found.

The identified literature was screened using the MHW definition (Hobday et al., 2016) for occurrence of an unusual extreme temperature event. Due to the nature of MHWs, the extreme temperature anomalies which define these events (Hobday et al., 2016) co-occur with multiple alterations in the affected ecosystems such as current patterns, increased surface layer stratification, increased desiccation stress in the intertidal zone, altered wave activity and likelihood of strong storms. Contribution of these factors to observed impacts on organisms cannot be disentangled with certainty yet. Hence for the purpose of this paper, reported effects are discussed and categorized as MHW effects on the study organisms and ecosystems.

The observations of seaweed responses to MHW events identified through the literature search were assigned to five

broad categories based on the severity of their biological response (**Figure 1**): responses were not observable or confined to negligible sublethal stress (group 1, resistance); visible signs of sublethal stress (group 2, physiological performance, e.g., tissue bleaching); altered ecological interactions (group 3, ecological performance, e.g., changes in reproduction or herbivory affecting competition and consumer pressure); altered abundance (group 4, changes in abundance of native species or arrivals of invasive species), and; widespread seaweed mortality (group 5, range shifts and local to regional extinction).

The observed seaweed species were also categorized into functional groups based on their growth forms: crust (CCA: crustose coralline algae); turf-forming seaweeds (bladed, filamentous and GCA: geniculate coralline algae) and canopy-forming seaweeds (kelp, fucoids). Information was combined to determine how many observations existed per broad response group for each functional group.

RESULTS

A total of 58 observations of seaweed responses to MHWs were identified, reported in 17 peer-reviewed papers and three additional news articles (**Table 1**), often with multiple observations per seaweed group. Resistance ($n = 3$) and extinctions ($n = 4$) were least frequently reported, and bleaching was observed in only one event for six turf-forming red seaweeds and one brown kelp ($n = 7$). The majority of records were changes in abundance; turf-forming seaweeds typically increased in abundance ($n = 18$) whereas large canopy-formers declined in abundance ($n = 17$; **Figure 2**). Overall, 25 observations were found for canopy-forming seaweeds, 29 observations for turf-forming seaweeds and only four observations for CCA. However, there could be a bias in reported observations toward large, conspicuous canopy-formers, with better baseline data availability or because changes are easier to detect for larger species. Additionally, publication bias is likely against reporting resistance or negligent effects with increased likelihood of publication for studies that detect and report large-scale changes.

Physiological Performance

Tissue bleaching is a good primary indicator of experienced sublethal stress (Hawkins and Hartnoll, 1985). Changes to seaweed condition was categorized as visible discoloration (whitening or turning greenish) of the blade tissue due to loss of surface integrity. This indicates loss or reduction in pigmentation, which in turn is associated with reduced photosynthetic performance (Marzinelli et al., 2015; Xiao et al., 2015). Although changes in physiological performance should be relatively easy to identify, observations for multiple species have only been reported for one MHW and only for turf-forming seaweeds as well as one kelp. During the 1982/83 El Niño in California, changes in coloration from red to unusually green were evident for *Porphyra perforata*, *Iridaea cordata*, *Laurencia spectabilis*, *Prionitis lanceolata*, *Gastroclonium subarticulatum*, and *Gigartina canaliculata* near Point Piedras

Response Group	Response	Examples	MHW
Severity	1 Resistance	Not detected <i>Ecklonia radiata</i> ^(10;12) , CCA ⁽¹²⁾ , turf forming algae ⁽¹²⁾ <i>Macrocystis pyrifera</i> ⁽¹⁶⁾	2011 Ningaloo Niño, WA (Hamelin Bay) 2013/14 the blob, Southern California
	2 Health	Bleaching <i>Egregia menziesii</i> ⁽³⁾ <i>Porphyra perforata</i> ⁽⁴⁾ , <i>Iridaea cordata</i> ⁽⁴⁾ , <i>Laurencia spectabilis</i> ⁽⁴⁾ , <i>Prionitis lanceolata</i> ⁽⁴⁾ , <i>Gastroclonium subarticulatum</i> ⁽⁴⁾ , <i>Gigartina canaliculata</i> ⁽⁴⁾	1982/83 ENSO California
	3 Ecological performance	Increased recruitment potential <i>Pelvetia fastigiata</i> ⁽³⁾ , <i>Sargassum muticum</i> ⁽³⁾	1982/83 ENSO California
		Increased herbivory Range-expansion of sub-tropical and tropical herbivores ^(5, 10)	1997/98 ENSO 2011 Ningaloo Niño; WA
	4 Abundance change to altered biodiversity indices	Increased abundance natives <i>Ulva spp.</i> ⁽²⁾ , <i>Enteromorpha spp.</i> ⁽²⁾ , <i>Iridaea spp.</i> ⁽²⁾ Geniculate coralline algae ^(8; 9) CCA ⁽⁴⁾ and turf-algae cover ^(7-10; 13;15) <i>Chorda filum</i> ⁽¹⁴⁾	1982/83 ENSO, Chile 2009/10 ENSO, California 2011 Ningaloo Niño; WA
		Increased abundance invasives <i>Giffordia mitchelliae</i> ⁽¹⁾ <i>Agardhiella tenera</i> ⁽⁶⁾ , <i>Amphiroa misakiensis</i> ⁽⁶⁾ , <i>Caulerpa sertularioides</i> ⁽⁶⁾ , <i>Padina durvillaei</i> ⁽⁶⁾ , <i>Jania capillacea</i> ⁽⁶⁾ , <i>Jania mexicana</i> ⁽⁶⁾ <i>Undaria pinnatifida</i> ⁽¹⁷⁾	1982/83 ENSO; South America 1997/98 ENSO, Mexico 2017/18 Tasman Sea MHW
		Declined abundance natives <i>Sargassum sp.</i> ⁽¹⁾ , <i>Blossevillea galapagensis</i> ⁽¹⁾ , <i>Ulva spp.</i> ⁽¹⁾ , <i>Spermothamnio spp.</i> ⁽¹⁾ , <i>Centroceras spp.</i> ⁽¹⁾ <i>Lessonia nigrescens</i> ⁽²⁾ , <i>Macrocystis integrifolia</i> ⁽²⁾ <i>Egregia menziesii</i> ⁽³⁾ , <i>Eisenia arborea</i> ⁽³⁾ <i>Mastocarpus papillatus</i> ⁽⁴⁾ <i>Lessonia trabeculata</i> ⁽⁵⁾ , <i>Macrocystis pyrifera</i> ⁽⁵⁾ <i>Ecklonia cava</i> ⁽⁷⁾ CCA ⁽¹⁴⁾ <i>Saccharina latissima</i> ⁽¹⁵⁾	1982/83 ENSO; South America 1982/83 ENSO; Chile 1982/83 ENSO; California 1997/98 ENSO; Chile 2011 Ningaloo Niño; WA 1997, 2002, 2006 hot summers, Norway
	5 Extinction	Range shift, local to regional extinction <i>Ecklonia radiata</i> ^(10, 11) , <i>Scytothalia dorycarpa</i> ^(10, 11) <i>Macrocystis pyrifera</i> ⁽⁴⁾ <i>Durvillaea poha</i> ⁽¹⁷⁾	2011 Ningaloo Niño; WA 2015/16 Tasmanian MHW 2017/18 Tasman Sea MHW
		Global extinction Not yet observed	

FIGURE 1 | Schematic of different responses of seaweeds with examples to MHWs grouped by severity of the observed response, from no observed effect (e.g., resistance) and less severe impact (e.g., tissue bleaching) at the **top**, to more severe impacts (e.g., local to global extinctions) at the **bottom**. Number/letter in brackets refer to **Table 1**. Several species have multiple observations as their responses differed between locations, e.g., resistance, abundance decline, and regional extinction were observed for *Ecklonia radiata* and *Scytothalia dorycarpa* along the latitudinal gradient in Western Australia.

(Murray and Horn, 1989) and at La Jolla many adult individuals of the kelp *Egregia menziesii* became reddish due to stress (Gunnill, 1985).

Ecological Performance

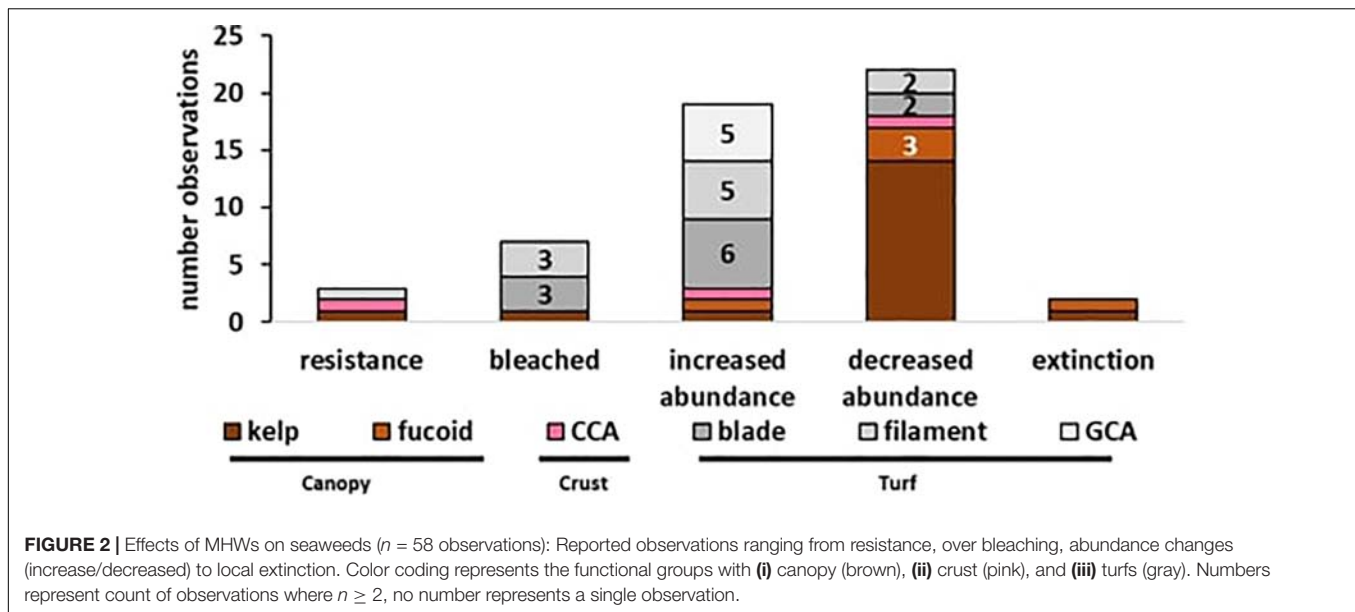
Reproduction potential and early life-history stages of many seaweeds are temperature-sensitive (Bartsch et al., 2013;

Andrews et al., 2014), and increased temperatures can both suppress or enhance reproduction and recruitment success (de Bettignies et al., 2018; Muth et al., 2019). Following the 1982/83 El Niño, the turf-forming *Pelvetia fastigiata* and the canopy-forming furoid *Sargassum muticum* showed increased recruitment success at La Jolla, California (Gunnill, 1985), which led to elevated abundances and likely shifted competitiveness

TABLE 1 | Details of studies ($n = 20$; 17 journal articles^{1–17}, three news articles^{a,b,c}) and species/genera ($n = 58$) found with recorded impacts of MHWs on algae.

MHW	Species	Classification	Functional group	Study number	References
1982/83 ENSO South America	<i>Sargassum</i> sp.	Phaeophyceae	Canopy	1	Laurie, 1990
	<i>Blossevillea galapagensis</i>	Phaeophyceae	Canopy		
	<i>Ulva</i> spp.	Chlorophyta	Turf		
	<i>Spermothamnion</i> spp.	Rhodophyta	Turf		
	<i>Centroceras</i> spp.	Rhodophyta	Turf		
1982/83 ENSO Chile	<i>Giffordia mitchelliae</i>	Phaeophyceae	Turf	2	Soto, 1985
	<i>Lessonia nigrescens</i>	Phaeophyceae	Canopy		
	<i>Macrocystis pyrifera</i>	Phaeophyceae	Canopy		
	<i>Ulva</i> spp.	Chlorophyta	Turf		
	<i>Enteromorpha</i> spp.	Chlorophyta	Turf		
1982/83 ENSO California	<i>Iridaea</i> spp.	Rhodophyta	Turf	3	Gunnill, 1985
	<i>Egregia menziesii</i>	Phaeophyceae	Canopy		
	<i>Ecklonia arborea</i>	Phaeophyceae	Canopy		
	<i>Pelvetia fastigiata</i>	Phaeophyceae	Turf		
	<i>Sargassum muticum</i>	Phaeophyceae	Canopy		
1982/83 ENSO California (Piedras Blancas)	<i>Porphyra perforata</i>	Rhodophyta	Turf	4	Murray and Horn, 1989
	<i>Iridaea cordata</i>	Rhodophyta	Turf		
	<i>Laurencia spectabilis</i>	Rhodophyta	Turf		
	<i>Prionitis lanceolata</i>	Rhodophyta	Turf		
	<i>Gastroclonium subarticulatum</i>	Rhodophyta	Turf		
	<i>Gigartina canaliculata</i>	Rhodophyta	Crust		
	CCA	CCA	Turf		
	<i>Mastocarpus papillatus</i>	Rhodophyta			
1997/98 ENSO Chile	<i>Macrocystis pyrifera</i>	Phaeophyceae	Canopy	5	Alonso Vega et al., 2005
	<i>Lessonia trabeculata</i>	Phaeophyceae	Canopy		
1997/98 ENSO Pacific Mexican Coast	<i>Agardhiella tenera</i>	Rhodophyta	Turf	6	Carballo et al., 2002
	<i>Amphiroa misakiensis</i>	Rhodophyta	Turf		
	<i>Caulerpa sertularioides</i>	Chlorophyta	Turf		
	<i>Padina durvillaei</i>	Phaeophyceae	Turf		
	<i>Jania capillacea</i>	Rhodophyta	Turf		
1997/1998 ENSO southern Japan	<i>Jania mexicana</i>	Rhodophyta	Turf	7	Serisawa et al., 2004
	<i>Ecklonia cava</i>	Phaeophyceae	Canopy		
2009/10 ENSO Southern Mexican Pacific	GCA	Rhodophyta	Turf	8	Tanaka et al., 2012
	Turf-forming algae	Turf	Turf		
2011 Ningaloo Niño Western Australia	GCA (<i>Amphiroa</i>)	Rhodophyta	Turf	9	López-Pérez et al., 2016
	<i>Ecklonia radiata</i>	Phaeophyceae	Canopy		
2011 Ningaloo Niño Western Australia	<i>Scytothalia dorycarpa</i>	Phaeophyceae	Canopy	10	Wernberg et al., 2016
	Turf-forming algae	Phaeophyceae	Canopy		
	CCA	CCA	Crust		
	CCA biofouling (on <i>E. radiata</i>)	CCA	Crust		
	CCA	CCA	Crust		
1997, 2002, 2006 hot summers	<i>Saccharina latissima</i>	Phaeophyceae	Canopy	11	Smale and Wernberg, 2013
	Turf-forming algae	Turf	Turf		
	<i>Chorda filum</i>	Phaeophyceae	Canopy		
2013/14 the blob followed by 2015/16 ENSO Southern California	<i>Macrocystis pyrifera</i>	Phaeophyceae	Canopy	12	Wernberg et al., 2013a
	understory algae	Turf	Turf		
2017/18 Tasman Sea MHW Christchurch, NZ	<i>Macrocystis pyrifera</i>	Phaeophyceae	Canopy	13	Smale and Wernberg, 2012
	<i>Durvillaea</i> spp.	Phaeophyceae	Canopy		
	<i>Undaria pinnatifida</i>	Phaeophyceae	Canopy		
	<i>Colpomenia sinuosa</i>	Phaeophyceae	Turf		
2013/14 the blob followed by 2015/16 ENSO Philippines	<i>Dictyota</i> sp.	Phaeophyceae	Turf	14	Short et al., 2015
	Seaweed production drop				
2013/14 the blob followed by 2015/16 ENSO Northern California				15	Moy and Christie, 2012
2015/16 Tasmanian MHW				16	Reed et al., 2016
2013/14 the blob followed by 2015/16 ENSO Philippines				17	Thomsen et al., 2019
2013/14 the blob followed by 2015/16 ENSO Northern California				a	Galolo, 2016
2015/16 Tasmanian MHW				b	Catton, 2016
2015/16 Tasmanian MHW				c	Mathiesen, 2016

News articles were only included if results were not yet published in peer-reviewed journals. MHW, marine heatwave, CCA, crustose coralline algae, GCA, geniculate coralline algae, ENSO, El Niño Southern Oscillation. Effects are recorded in **Figure 1**.



between species. Furthermore, grazing pressure on seaweeds is likely increased when tropical and subtropical herbivores shift their ranges (Vergés et al., 2014a; Smale et al., 2017; Zarco-Perello et al., 2017) due to MHWs. Altered grazing pressure can result in the collapse of seaweed populations and reinforcement of ecosystem transitions (Haraguchi et al., 2009; Vergés et al., 2014a,b, 2016; Bennett et al., 2015b; Franco et al., 2015). During the 1997/98 El Niño, an increase in grazing pressure occurred simultaneously at lower latitudes (10–23°S) of both hemispheres, and the combination of thermal anomalies and migration of grazers produced a synergistic effect. In northern Chile, two canopy-forming kelps were negatively affected, with local disappearance of *Macrocystis pyrifera* at shallow depths and a decreased abundance of *Lessonia trabeculata* at its depth limit (Halpin et al., 2004; Alonso Vega et al., 2005). During the following 1998–2000 La Niña event, kelp productivity was minimal due local disappearance of *M. pyrifera* and decreased densities of *L. trabeculata*, however, recovery occurred post La Niña during the mild 2002/03 El Niño event (Alonso Vega et al., 2005).

In Western Australia, the 2010/11 MHW led to increased herbivory due to the range expansion of tropical and subtropical herbivores, reinforcing the temperature-driven loss of the kelp *Ecklonia radiata*, and facilitating domination of turf algae, with no signs of recovery 8 years after the event (Wernberg, 2019). Additionally, tropical herbivorous fish expanded their range beyond the areas directly affected by the high MHW temperatures, resulting in a further decline of seaweed canopy cover by up to ~70% at localized reefs (Zarco-Perello et al., 2017). This MHW also caused heavy biofouling by CCA on *E. radiata* at the Houtman Abrolhos Islands in Western Australia (Smale and Wernberg, 2012), the only report of its kind to date. Thus, indirect effects of MHWs come in an array of forms and can act as important drivers of change within marine systems, with possible long-lasting impacts far beyond the direct MHW impacts itself.

Changes in Abundance

The most commonly recorded effect of MHWs was changes in seaweed abundances (~79% of all observations). During the extreme 1982/83 El Niño, areas of the Galapagos archipelago in South America experienced declines of fucoids and turf-forming seaweeds, followed by colonization of the invasive turf-forming seaweed *Giffordia mitchelliae*. The fucoids *Sargassum* sp. and *Blossevillea galapagensis* as well as the turfs *Ulva* spp., *Spermothamnion* spp. and *Centroceras* spp. decreased in abundance (Laurie, 1990). In comparison, the same ENSO event led to reduced abundances of the two kelps *Lessonia nigrescens* and *Macrocystis pyrifera* in Chile (Soto, 1985). After the abundance of kelp was reduced, the turf-forming seaweeds *Ulva*, *Enteromorpha* and *Iridaea* spp. all proliferated (Soto, 1985). In California, the ENSO-associated warming event resulted in no drastic changes, but led to reduced abundances of the kelps *Egregia menziesii* and *Ecklonia arborea* at La Jolla (Gunnill, 1985), and a substantial increase of CCA in the low- and mid-intertidal zone near Point Piedras Blancas (Murray and Horn, 1989). Even though there is some uncertainty attributing the effects in California to the warmer sea temperatures *per se* due to the co-occurrence of large waves, the population-level responses were similar to those that occurred due to elevated water temperatures recorded in late summer and autumn of 1976 (Gunnill, 1985).

During the 1997/98 El Niño in northern Chile kelp abundances were maintained due to the continuity of coastal upwelling buffering the warming of the ocean. However, after the 1997/98 El Niño event two kelp species were negatively affected with complete disappearance of *M. pyrifera* at shallow depths and decreased abundance of *Lessonia trabeculata* (Alonso Vega et al., 2005). Along the Pacific Mexican Coast seaweed diversity and biomass fluctuated significantly, with an initial increase in biomass caused by the rise in the abundance of warm water tolerant species such as the small turf species

Agardhiella tenera, *Amphiroa misakiensis*, *Caulerpa sertularioides*, *Padina durvillaei*, *Jania capillacea*, and *Jania mexicana* (Carballo et al., 2002). Overall, seaweed diversity decreased and net biomass increased during the ENSO, whereas diversity increased, biomass decreased and the assemblage structure were altered following the El Niño mediated MHW (Carballo et al., 2002), highlighting the complexity of impacts that MHWs exert over seaweed communities. In the southern Mexican Pacific coral reef communities, the 2009/10 ENSO increased seaweed cover from 2 to 6% due to an increase in turf-forming algae (López-Pérez et al., 2016). This increase in seaweed cover was coupled with a decrease in coral cover, coral overgrowth and changes in echinoderm and fish species composition, all of which altered the overall reef community (López-Pérez et al., 2016). Significant increases of turf-forming algae also occurred in southwestern Australia following the 2010/11 MHW, after drastic declines and range-contractions of canopy forming seaweeds (*E. radiata* and *Scytothalia dorycarpa*) at their northern range edge (Smale and Wernberg, 2013; Wernberg et al., 2013a, 2016). The same MHW in Western Australia negatively affected CCA, suppressing seasonal growth patterns and increasing mortality rates (Short et al., 2015). In comparison, a shift toward CCA dominated barrens followed widespread loss of seaweed forests (*Ecklonia cava*) in Japan after the 1997/98 ENSO and particularly poor growth of *E. cava* in 1999 and 2001 (Serisawa et al., 2004; Tanaka et al., 2012). Also, the 2017/18 Tasmanian Sea MHW resulted in mid-range extinctions and declines in abundances of bull kelp, *Durvillaea* spp. while the percent cover of the weedy macroalgae *Undaria pinnatifida*, *Colpomenia sinuosa* and *Dictyota* sp. increased in conjunction, most likely due to competitive release (Thomsen et al., 2019).

Overall, we found 22 records both of increased and decreased abundances of seaweeds as a result of MHW events. All 22 records for abundance declines were native species, whereas from the 22 abundance increases reported, 13 were native species and nine were invasive species. Given the fact that invasive species generally have broader temperature tolerances than native species (Sorte et al., 2010) these numbers suggest that the occurrence of MHW events could increase the competitiveness of invasive species.

Interesting differences were also found between growth forms, as 14 records reported a decrease in the abundance of canopy-forming kelps and three reported that fucoids experienced a decline in abundance (see **Figure 2**). For turf-forming species, only one record showed decline in two native turfs, but an invasive turf increased in abundance. In contrast, 18 observations report the increase of turf-forming bladed, filamentous or geniculate coralline algae (GCA). For CCA, no clear trend was obvious, as over four records CCA responses were ranging from resistance to increased abundance, increased abundance as biofouling but also increased mortality. Overall, large conspicuous canopy-formers generally declined following a MHW, whereas for CCA no clear pattern was evident due to a low number of observation, and for turf-forming seaweeds several cases of decreased abundances were observed, but the majority of records showed an increase in abundance.

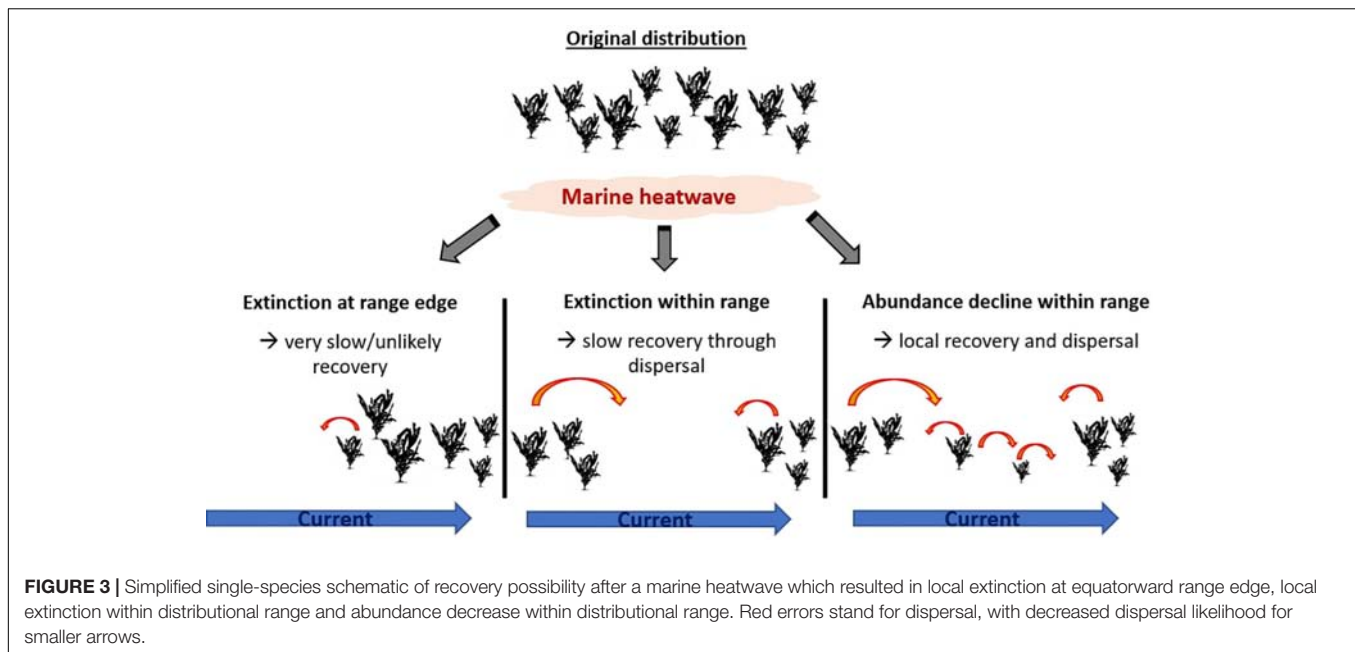
Local and Regional Extinctions

While changes in abundance have been recorded for several species in response to multiple MHWs, only in one instance have regional extinctions along the range edge been observed. The 2010/11 MHW off Western Australia led to a poleward range contraction of ~100 km for two of the main canopy-forming seaweeds, *Ecklonia radiata* and *Scytothalia dorycarpa*, as marginal populations were extirpated (Smale and Wernberg, 2013; Wernberg et al., 2013a). This contraction culminated in the loss of 43% of the marine forests along >800 km of coastline, and a regime shift toward turf-dominated reefs (Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018; Wernberg, 2019). Besides extinctions at the trailing range edge, local extinctions of range-center populations have also been observed. The 2015/16 Tasman Sea MHW was associated with localized die-off of *Macrocystis pyrifera* off Tasmania's east coast (Mathiesen, 2016). Over the last few decades, *M. pyrifera* has declined from a 250 km stretch along Tasmania's east coast to a last remaining patch in the inner coves of Munroe Bight (Mathiesen, 2016). The 2015/16 Tasmanian MHW, however, stressed *M. pyrifera* individuals which became less resilient to winter storms and were dislodged from the inner coves of Munroe Bight, leading to a local as well as regional extinction of this species along the eastern Tasmanian coast (Mathiesen, 2016). Additionally, following the Tasman Sea MHW in 2017/18, widespread declines in abundance with mid-range local extinctions of bull kelp were observed on the east coast of the South Island of New Zealand (Thomsen et al., 2019). Regional surveys showed a strong reduction in the abundance of *Durvillaea poha* in the region and smaller reductions in *D. willana*. Targeted surveys around Christchurch revealed total elimination of *Durvillaea* spp. on 12 out of 19 local reefs, with reef-wide extinctions observed on the reefs within and immediately north or south of Lyttelton Harbor (Thomsen et al., 2019). Following the elimination of *Durvillaea* spp. densities and cover of weedy macroalgae increased in the area previously inhabited by *Durvillaea* spp. with the potential to suppress future re-colonization by *Durvillaea* spp. into these areas (Thomsen et al., 2019).

Post-MHW Recovery Potential

The potential for affected seaweed populations to recover from MHWs will depend on the severity of the MHW and on species-specific traits of the seaweeds. This includes the location within a species range, species-specific thermal tolerance and reproductive traits, life history (e.g., annual versus perennial) and dispersal capacities. Additionally, recovery trajectories will depend on the severity of alterations in ecosystem structure and local patterns of oceanic currents.

When seaweed abundance declines in the center or poleward parts of the species' range, there is a high chance for population recovery after the MHW due to local reseedling as well as dispersal from adjacent areas (**Figure 3**). In contrast, when propagules are unlikely to disperse into affected areas (Molinos et al., 2017), competitive interactions are altered, or grazing pressure increased, recovery is unlikely or will be very slow. In the more extreme case of local extinctions, recovery will likely be markedly slower as it will depend on re-seeding from less



affected populations, which may be separated by considerable distances. In the extreme case of localized to regional extinctions at the equatorward range edge of a species, recovery is predicted to be very slow or unlikely to occur. The 2010/11 MHW in Western Australia demonstrates how recovery is unlikely after extinctions along the range edge. To date, the marine forests that were lost have not recovered (Wernberg et al., 2016; Wernberg, 2019) and the poleward flow of the Leeuwin Current makes natural re-seeding unlikely, as possible source populations are located “downstream.” Additionally, recovery will depend on herbivore pressure, as range-expanded as well as local herbivores may suppress any recovery and facilitate domination by turf algae (Bennett et al., 2015b; Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018).

In all cases, recovery potential is dependent on a return to suitable conditions (e.g., temperature, light, turbidity) after the MHW, competition for space (open settlement ground, species invasions) and herbivore pressure, and the distance from adjacent populations, dispersal properties and current systems (Molinis et al., 2015) for reseedling success. However, it is unlikely that a complete recovery to pre-event conditions will occur, as post-disturbance communities are generally different from the pre-disturbed communities (Sousa, 1984; Shea et al., 2004), resulting in different ecosystem structure and function. Ultimately, declines in abundance and localized extinctions within a species range may be the precursor to projected future range contractions at a species distributional limit (Martinez et al., 2018).

Attribution of Impacts to MHWs

A large proportion of the observed impacts were directly attributed to the events with extreme temperatures identified as the main or one of the key drivers of documented impacts (16 of the 19 studies). Only three studies (Gunnill, 1985; Moy and Christie, 2012; Reed et al., 2016) did not

attribute changes in seaweed performance majorly to MHWs due to the co-occurrence of interacting processes, making it difficult to disentangle the influence of each driver. In these instances, the MHWs were accompanied by storms and long-term eutrophication, or previous impacts in the area surpassed possible MHW effects (e.g., recruitment peaks in prior years, great annual variability). For example, the lack of dramatic long-term effects on seaweeds of the 1982/83 MHW in California is likely to be a consequence of strong storms and high cloud cover which reduced desiccation stress and buffered the possibly negative temperature effects (Gunnill, 1985). Furthermore, seaweed increased in abundance prior to the MHW through recruitment peaks in 1977, 1981, and 1982. As a result, seaweeds persisted during the event (Gunnill, 1985). However, it is likely that the MHW weakened the seaweeds and contributed to the severe loss during storms and strong wave action following the event (Gunnill, 1985). Similarly, multiple stressors, e.g., warm summer temperature, eutrophication and increased sedimentation have been suggested to explain ecosystem shifts in Norway, with large-scale shifts from sugar kelp forests (*Saccharina latissima*) to filamentous red algae on the Skagerrak coast and shifts to a small, functionally different kelp, *Chorda filum*, on the west coast (Moy and Christie, 2012). While the study was not designed to identify the causes of change, severe long-term eutrophication accompanied by reduced light levels was inferred to be the main driver explaining the loss of *S. latissima*. One possible trigger identified for the sudden community shifts were the unusually hot summers in 1997, 2002 and 2006 for 58, 36, and 45 days, respectively, which resulted in SSTs exceeding the thermal tolerance of *S. latissima* (Moy and Christie, 2012). Thus, it is often complicated to establish causal linkages to MHWs as multiple drivers typically occur simultaneously, resulting in complex interactive effects with studies not designed to disentangle possible drivers and

their contributions (Moy and Christie, 2012; Filbee-Dexter and Wernberg, 2018).

It is possible that the effects of MHWs may not be evident during, or immediately after the peaks in temperature, but instead have long time-lags. For example, in California, following the MHW in 1982/83, significant differences in seaweed abundance and diversity were evident in the winter of 1983/84 (Gunnill, 1985). It is possible that standing stocks of the two laminarians *Ecklonia arborea* and *Egregia menziesii* decreased as the MHW weakened the plants resulting in delayed die-offs during the summer of 1983 (Gunnill, 1985). The impact of MHWs can also vary between geographical region. This was observed following the 1997/98 El Niño which caused local extinctions of the kelp *Macrocystis pyrifera* in Peru, southern Chile and California, whereas effects in Japan and northern Chile were delayed and only detected after the event (Edwards, 2004). Similarly, in Western Australia impacts of the 2010/11 MHW ranged from catastrophic for marine temperate communities at warmer locations (Kalbarri, 28°S), severe in central locations (Jurien Bay, 30°S) to absent in cooler locations (Hamelin Bay, 34°S), even though all regions experienced similar temperature anomalies (Wernberg et al., 2013a, 2016, 2018a). Delayed impacts and differential responses over time (season) and space, is likely to depend on the spatial extent and magnitude of the MHW as well as species-specific geographical ranges and potential for local adaptation (Wernberg et al., 2018a), and may cause MHWs to go unrecognized as important drivers of ecological change.

Limitations

The majority of published information on seaweed responses to MHWs are from sites that were subjected to extreme warming conditions and experienced a multitude of ecological impacts. Notwithstanding potential publication bias that encourage reporting significant ecological changes following MHWs, but discourage reports about species resistance (no changes, i.e., non-significant effects), lack of observed impacts at some sites may be the result of limited seaweed research taking place or difficulties in determining impacts due to a lack of long-term baseline data or high natural inter-annual variability. For example, *M. pyrifera* in California showed considerable biomass variation between 2001 and 2015. Although the recorded *M. pyrifera* biomass in 2014 and 2015 during and directly after “the blob” were two of the lowest on record, the low biomass was not attributed to the MHW because its biomass is naturally variable and the monitoring sites were well within the species distribution range (Reed et al., 2016). The importance of biogeography was also evident during the 2010/11 MHW in Western Australia, where the more southern (Hamelin Bay, cool region) populations of *E. radiata*, CCA and turf-forming algae showed resistance, whereas northern populations closer to the trailing range edge (Jurien Bay, warm region) were heavily impacted by the MHW despite experiencing similar temperature anomalies (Wernberg et al., 2013a). These different responses at two locations within the area covered by the MHW highlights the need to consider the location of a population within a species range as well as species-specific thermal limits and the potential of resistance when assessing impacts from MHWs (Wernberg et al., 2013a, 2016). Moreover, recent

evidence suggests that thermal divergence, either *via* plasticity or adaptation, is common across species distributional ranges in marine macrophytes (King et al., 2017). Range-center seaweed populations could therefore be equally vulnerable to MHWs compared to range-edge populations (Bennett et al., 2015a; King et al., 2019; Thomsen et al., 2019); clearly, further work on intraspecific and inter-regional variability in susceptibility to MHWs is warranted (Bennett et al., 2019).

A key constraint of MHW impact studies is the lack of available historical information about seaweed populations and communities – a prerequisite to disentangle impacts from natural variability and to quantify the magnitude of ecological change (Southward et al., 1995; Wernberg et al., 2016). Without historical baseline data it is particularly difficult to detect resistance as well as immediate to long-term changes, and dramatic large-scale impacts have only been recognized in areas with sustained biological monitoring (Wernberg et al., 2011b; Poloczanska et al., 2013). This limitation can, however, be ameliorated, to an extent, by combining observations with MHW experimental studies. As climate change experimental studies on seaweed are still rare (Wernberg et al., 2012), and even more scarce related to MHWs (Gouvea et al., 2017), we recommend that efforts are directed toward conducting such experiments. Focus should be first on determining susceptibility of key species to different characteristics of MHWs, followed by studies disentangling the interactive nature of temperature, desiccation, solar radiation and eutrophication effect to determine when and if stressors enhance or buffer against impacts of each other. Additionally, we emphasize the invaluable knowledge that baseline data on seaweed biogeography, population structure and physiological performances can provide, both to document and assess future impacts as well as re-analyzing existing datasets to evaluate in more detail resistance and susceptibility of seaweeds to MHWs as well as assess which additional factors could have enhanced or buffered temperature effects.

CONCLUSION

Superimposed on decadal-scale increases in mean oceanic temperatures, MHWs are increasing in frequency and duration (Oliver et al., 2018), and will likely continue to do so in the future (Frölicher and Laufkötter, 2018). These MHWs have impacted marine ecosystems with well-documented effects on seaweeds ranging from resistance, to altered physiological and ecological performances, and drastic shifts in ecosystem structure and functioning and, in a few cases, regime shifts. These regime shifts have led to profound economic and environmental changes (Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018; Smale et al., 2019). In addition to directly affecting seaweeds, MHWs have facilitated poleward range shifts of subtropical and tropical herbivores, leading to increased grazing pressure (Bennett et al., 2015b; Vergés et al., 2016; Zarco-Perello et al., 2017). This compounded stress favors a shift from canopy-forming kelps and fucoids toward simplified turf-dominated systems that suppresses canopy recovery. Between canopy-formers, turfs and crustose coralline algae, turf-forming seaweeds were the only functional

group with a majority of positive responses. Ultimately, the severity of MHW effects will depend on the resilience, recovery and recolonization traits of the affected seaweeds, their position within their thermal safety margins, interaction with other stressors such as eutrophication and altered currents, modified grazing pressure, and the attributes of the MHWs. Specifically, research about the resilience of seaweeds is required to better understand species-specific sensitivity to MHWs, and to identify which coastal regions are most vulnerable to regime shifts. Further range shifts and local regime shifts in marine forests, as well as within similarly important ecosystems (e.g., coral reefs and seagrasses meadows), seem inevitable in the near future (Takao et al., 2015; Kumagai et al., 2018; Martinez et al., 2018; Smale et al., 2019). However, it remains uncertain how altered ecosystems will impact the provision of ecological services upon which human societies depend.

AUTHOR CONTRIBUTIONS

SS and TW conceived the idea for the manuscript. SS wrote the manuscript. TW, MT, PM, MB, BH, and DS

contributed to the concept and writing. All authors approved the submitted manuscript.

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Observational Insight Into the Subsurface Anomalies of Marine Heatwaves

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Marine heatwaves (MHWs) are extreme ocean warming events that can have devastating impacts, from biological mortalities to irreversible redistributions within the ocean ecosystem. MHWs are an added concern because they are expected to increase in frequency and duration. To date, our understanding of these extreme ocean temperature events is mainly limited to the surface layers, despite some of the consequences they are known to have on the deep marine environment. In this paper, using data from sea surface temperature (SST) and *in situ* observations from Argo floats, we investigate the anomalous water characteristics during MHWs down to 2000 m in the western Tasman Sea which is located off the east coast of Australia. Focusing on their vertical extensions, characteristics and potential drivers, we break MHWs down into three categories (1) shallow [0–150 m], (2) intermediate [150–800 m], and (3) deep events [>800 m]. Only shallow events show a relationship between surface temperature anomalies and depth extent, in agreement with a likely surface origin in response to anomalous air-sea fluxes. By contrast, deep events have greater and deeper maximum temperature anomalies than their surface signal (mean of almost 3.4°C at 165 m depth) and are more frequent than expected (>45%), dominating MHWs in winter. They predominantly occur within warm core eddies, which are deep mesoscale anticyclonic structures carrying warm water-mass from the East Australian Current (EAC). This study highlights the importance of MHWs down to 2000 m and the influence of oceanographic circulation on their characteristics. Consequently, we recommend a complementary analysis of sea level anomalies and SST be conducted to improve the prediction of MHW characteristics and impacts, both physical and biological.

Keywords: MHW depth, extreme temperature anomaly, warm-core eddy, western boundary current, ocean heat content, East Australian current, mixed layer depth, ENSO

INTRODUCTION

Marine heatwaves (MHWs) are extreme climate events of anomalously warm ocean temperature that can have profound impacts on marine species, ecosystem distribution and as a result, socioeconomics. Some have caused coral bleaching (Benthuisen et al., 2018), mass mortality of marine organisms (Cerrano et al., 2000; Mills et al., 2013; Short et al., 2015; Jones et al., 2018) irreversible physiological damage and species redistribution (Wernberg et al., 2016;

Smale et al., 2019), and consequently damaging impacts on fisheries management and local economies (Mills et al., 2013). Analysis of sea surface temperatures (SSTs) showed that some of these biological changes are due to anomalous, discrete and persistent warming which leads to the introduction of warm water species and causes biological changes among residing species in the affected depths (Wernberg et al., 2013).

Globally, climate change is associated with MHWs lasting longer, becoming more frequent and more intense (Frölicher et al., 2018; Oliver et al., 2018a). Oliver et al. (2018a) found that from 1925 to 2016, surface MHWs have increased globally in frequency and duration by 34 and 17%, respectively. Furthermore, Frölicher et al. (2018) found that MHW duration doubled from 1982 to 2016 and attributed 87% of MHWs to human-induced warming. The observed and anticipated increases in MHWs underscore the need for a rapid improvement in understanding MHWs and how to manage them.

Being a global warming hotspot, the western Tasman Sea (Figure 1) is a region where these effects are acutely experienced. This is due to climate change-induced shifts in the westerly winds which affect the East Australian Current (EAC) flow and strengthen the EAC extension through the Tasman Sea, generating one of the largest warming rates in the southern hemisphere (Cai et al., 2005; Wu et al., 2012; Sloyan and O’Kane, 2015; Oliver and Holbrook, 2018). The EAC is the western boundary current within the South Pacific subtropical gyre. At around 30–32°S, it splits into an eastward extension known as the Tasman Front, and a southward extension, mainly consisting of a flow of eddies (Oke et al., 2019), referred to as the “Eddy Avenue” (Everett et al., 2012). In this region, eddies are deep and centered around 300–350 m depth with temperature

anomalies detected down to 800 m (Rykova and Oke, 2015). They have greater sea-level and SST anomalies, and faster rotation in comparison to the rest of the Tasman Sea (Everett et al., 2012), playing a significant role in mass and heat transports. The anomalous southward extension of the EAC (Hill et al., 2008) causes greater thermal stratification in this region (Cai et al., 2005; Ling, 2008) and one of the observed biological results of this more frequently occurring, warm, nutrient-poor water on the coast is an increase in sea-urchin over-grazing which leads to the formation of “barrens” habitat and shifting of the marine ecosystem in the eastern Tasmanian region (Ling, 2008; Johnson et al., 2011).

It has been established that MHWs are not restricted to the surface but rather exhibit vertical warming that can have great effects in the subsurface. This was emphasized through response impacts like the coral bleaching during the Austral 2015/16 summer which occurred with no depth dependence, from 9 m down to 30 m (GBRMPA, 2016) and the large-scale decline of giant kelps (Oliver et al., 2017) given their sensitivity and direct response to ocean temperatures (Marzinelli et al., 2015). Jackson et al. (2018) also showed that abnormally warm water still lingered at depth in the Northeast Pacific Ocean and in river inlets on British Columbia’s central coast, 2 years after the end of the “Blob” MHW event at the surface. While this event was one of the most significant in the region, driven by anomalous air-sea heat flux and weak cold advection (Bond et al., 2015; Chen et al., 2015), Jackson et al. (2018) used Argo floats to show how subsurface warming (~150 m depth) was delayed by about a year.

Few studies have focused on the depth structure of MHWs, due to the lack of sustained high-resolution temperature records below the surface. In the coastal Tasman Sea off Sydney, Schaeffer and Roughan (2017) studied the depth extent of warming (down to 100 m depths) during MHW events from long-term mooring observations. They found persistent extreme warming down the full extent of the water column at least 30% of the time, with maximum temperature anomalies occurring below the surface around the thermocline. Some deep MHW events did not have a surface signature hence SST variability was not representative of the vertical propagation of the MHW. Due to the coastal nature of the site, the major driver of deep MHW was downwelling favorable winds which depress the stratification enabling deeper mixing of warm surface waters. Conversely, upwelling events tend to suppress warm water anomalies with the intrusion of cold water. Further south, near Tasmania, Oliver et al. (2018b) used self organizing maps on modeling outputs to characterize the regional MHWs. They found that the average MHW depth was 90–185 m, with delays between the maximum anomalies at different depths. Types of MHWs were linked to a combination of anomalous EAC extension, offshore anticyclonic eddies, warm-air temperatures and wind anomalies from the north-westerly to easterly direction. Around the tropical Australia region, the longest MHW on record occurred in the Austral 15/16 summer and was documented by a range of regional observations (Oliver et al., 2017; Benthuyssen et al., 2018) including *in situ* ocean gliders, Argo floats and moorings. The maximum anomalies occurred in March (end of the Austral summer) and at depth

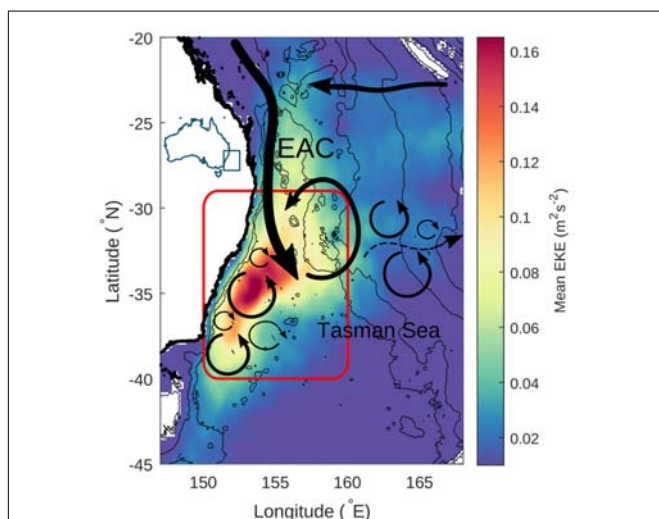


FIGURE 1 | A schematic showing the boundaries of the region analyzed (red box). The mean eddy kinetic energy (EKE, 01/09/1981 to 30/12/2018) is shown with bathymetry contours (0, 200, and 2000 m). Inset shows the map of Australia and the location of the region in context. Arrows indicate the schematic of the mean circulation in the region. EAC stands for the East Australian Current.

(~60 m at a shelf mooring site), consistent with coral bleaching below the surface layer. A nearby Argo float measured positive temperature anomalies down to 300 m, showing the substantial depth extent of the MHW event. The authors attribute the record warming to surface heat flux anomalies (reduced cloud cover and weakened winds) during extreme El Niño and reduced Madden-Julian Oscillation conditions.

Despite these few studies, a full description of the depth extent of MHWs is still lacking. Furthermore, the factors affecting these subsurface extreme temperatures are still speculative, which together make it difficult to anticipate and prepare management responses to these extreme events.

The purpose of this paper is to provide the needed insight into MHW depth extent and the subsurface properties during a MHW. Here, we identify Argo floats during MHWs using SST time-series and utilize float observations extending down to 2000 m depth. We focus on the profiles of temperature and salinity anomalies and relate them to the ocean circulation in the western Tasman Sea, seasons, regions and drivers. Specifically, we address four aims: quantify “MHW depth” (see section “MHW Depth and Maximum Temperature Anomalies”), relate surface parameters and the subsurface extension (see section “Subsurface Properties in a MHW”), identify spatial or seasonal patterns (see section “Spatial and Seasonal Variability”), and drivers of the vertical structure of the MHW (see sections “Relationships Between MHW Depths and Profile Characteristics and Influence of Mesoscale Eddies”).

MATERIALS AND METHODS

SST and MHW Identification

As in Benthuyssen et al. (2018), Hobday et al. (2016), and Oliver et al. (2017) amongst others, SST observations were used to identify MHW events due to the lack of other daily *in situ* long time-series of temperature. SST was obtained from the daily National Oceanic and Atmospheric Administration Optimum Interpolation dataset gridded on a 0.25° grid (NOAA OI SST; Reynolds et al., 2007; Banzon et al., 2016), covering the period 01/09/1981–30/12/2018.

Applying the Hobday et al. (2016) definition of a MHW, as a discrete, prolonged and anomalous warm water event, MHWs were identified as events where temperatures exceeded the daily 90th percentile over five or more days. The climatology of the 90th percentile was calculated based on data for the period 01/09/1981–31/12/2018 for each day of the year using an 11-day window centered on that day, then smoothed with a 31-day moving average.

In situ Measurements and Climatology

Our defined study region is bounded by (150°E–160°E) and (40°S–29°S), covering the EAC extension area as indicated by the high kinetic energy (Figure 1). Mean eddy kinetic energy (EKE) is calculated using, $EKE = \frac{1}{2}(u'^2 + v'^2)$, where u' and v' are the zonal and meridional anomalous surface geostrophic velocities (Richardson, 1983), calculated from gridded sea-level anomaly (GSLA). The data was sourced

from the Integrated Marine Observing System (IMOS) for the period of 01/01/2004–30/12/2018 at 0.2° grid resolution which combines satellite altimeters and tide gauge observations (Deng et al., 2011).

In situ measurements were collected from available Argo float data within the region between 01/01/2004–31/12/2018. The processed data were obtained from the Australian Ocean Data Network portal (AODN) and include temperature, salinity and pressure profiles down to 2000 m depth. A total of 6550 Argo profiles were extracted.

Argo profiles were identified as MHW profiles if they were compiled during a MHW, otherwise, they were identified as NoMHW profiles. This was applied through the following process: all MHW event duration were identified from SST time-series for each profile location. If the temperature profile date (from Argo) fell within the MHW time-intervals, then it was determined a MHW water profile. Surface MHW events, their duration, intensity and category (as defined in Hobday et al. (2018)) were then extracted along with the Argo profile's URL. This resulted in 894 water profiles in MHWs, providing a sufficient basis for analysis (Supplementary Figure S1).

Mean climatological profiles of temperature and salinity were obtained from the CSIRO Atlas of Regional Seas (CARS 2009) (Ridgway et al., 2002). Using linear interpolation, the gridded climatology profiles were calculated for each Argo profile by location and day of year. The CARS climatology encompasses mean ocean properties from all available quality-controlled historical subsurface measurements mapped to a 0.5° grid resolution. This climatology is used to compute the temperature anomaly $T'(z) = T(z) - \bar{T}(z)$, where $T(z)$ is the temperature at depth z in the profile and $\bar{T}(z)$ is the climatological average. A similar procedure is employed for salinity ($S'(z)$) and density anomaly profiles.

A selection of the extracted MHW Argo water profiles was achieved by applying tests to remove any inconsistent profiles that either had missing fields or showed negative surface anomalies, which would contradict the positive anomaly indicated by the SST. Further, only profiles that contained observations extending down to 900 m depths or more were retained. Consequently, 39 out of the 894 MHW profiles were rendered unusable. Despite the different temporal periods for the SST (NOAA OI SST) and *in situ* climatology (CARS) datasets, no statistically significant difference was detected between the two surface averages in the datasets (mean square error of 0.15°C²).

Moreover, the surface temperature from Argo profiles and the extracted NOAA OI SST used to detect MHW events show a reasonable mean square error of 0.3°C², most likely due to the different product resolutions. Additionally, residuals are found to be normally distributed and the correlation between the two parameters is $r = 0.98$ (Supplementary Figure S2). That is, no statistically significant difference was detected between the two measures and the assumptions of residual normality and constant variance are reasonable, justifying the link between SST and Argo float measurements.

Mixed Layer Depth

Climatological mixed layer depth (MLD) is also available from CARS and further calculated from Argo profiles, following the Condie and Dunn (2006) definition based on variations from surface temperature and salinity measurements at 10 m depths.

As such, MLD was determined as the minimum depth at which either (1) or (2) occur.

$$T(z) < T(10) - 0.4^{\circ}\text{C} \quad (1)$$

$$S(z) > S(10) + 0.03\text{PSU} \quad (2)$$

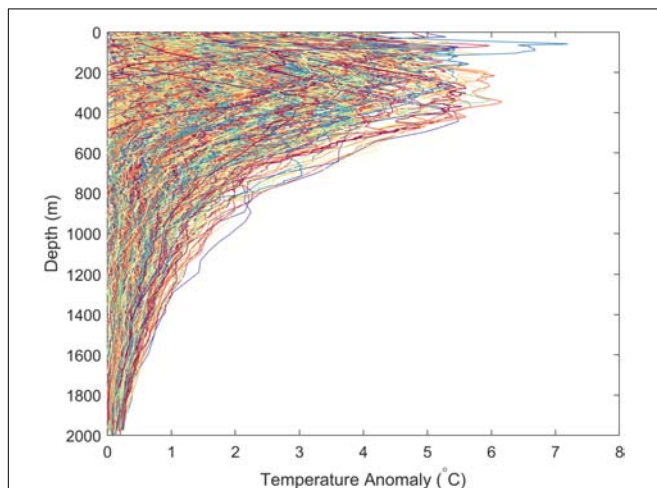


FIGURE 2 | Temperature anomaly profiles in MHWs cut off at their respective Positive Threshold Depths.

MHW Depth

All Argo MHW water column profiles were truncated at the first instance of a negative or zero temperature anomaly from the surface. The depth at which this occurs is defined as the positive threshold depth (denoted Z_N hereafter), as follows,

$$\text{Positive Threshold Depth: } Z_N = \text{Min}(z(T'(z) \leq 0)). \quad (3)$$

The temperature anomaly profiles are long-tailed and positive anomalies are detected down to 2000 m in some profiles. However, the temperature is often almost homogenous (small vertical gradients) over 100 s of meters at depth (**Figure 2**). On this basis, we focus on vertical cumulative temperature anomaly (CTa) for each profile from the surface ($z = 0$) to its positive threshold depth ($z = Z_N$) summed at 1 m spacing ($\Delta z = 1$) (Eq. 4). This measure also represents a scaled version of the anomalous heat content in the MHW (Willis et al., 2004; Dijkstra, 2008).

$$\text{CTa}(Z_N) = \sum_{z=0}^{Z_N} T'(z) \Delta z, \quad (4)$$

In order to reduce the effect of the insignificant warming at depths per water profile, we define the MHW depth as the depth where a proportion (ϵ , varied between 0.85–0.95) of the cumulative temperature anomaly is reached (Eq. 5).

$$\text{MHW depth} = \text{Max}(z(\text{CTa}(z) \leq \epsilon * \text{CTa}(Z_N))) \quad (5)$$

Figure 3 illustrates this application on a single profile (top row) and on the mean profile (bottom row) with ϵ values of 0.85, 0.9, and 0.95. In this particular example, positive anomalies are detected down to 2000 m and therefore the positive threshold depth is 2000 m. It is clear, however, that the profile changes at

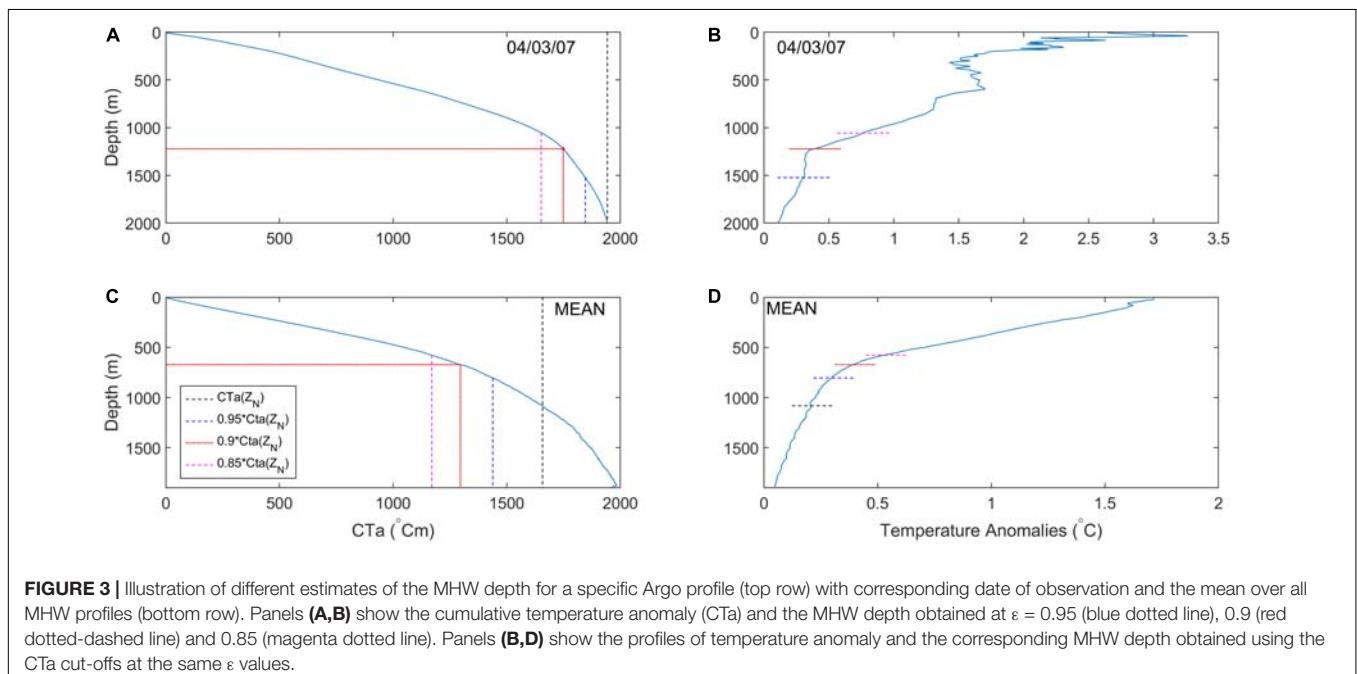


FIGURE 3 | Illustration of different estimates of the MHW depth for a specific Argo profile (top row) with corresponding date of observation and the mean over all MHW profiles (bottom row). Panels (A,B) show the cumulative temperature anomaly (CTa) and the MHW depth obtained at $\epsilon = 0.95$ (blue dotted line), 0.9 (red dotted-dashed line) and 0.85 (magenta dotted line). Panels (B,D) show the profiles of temperature anomaly and the corresponding MHW depth obtained using the CTa cut-offs at the same ϵ values.

~1200 m with incrementally diminishing temperature anomalies toward the bottom of the profile (**Figure 3B**). In this case, $\varepsilon = 0.9$ (90% of the total warming in the water column up to its positive threshold) detects the onset of the small variation range in the profile that corresponds to a cumulative warming of 1749°Cm, which occurs at 1221 m depth and 0.39°C temperature anomaly in the profile. On the mean of all MHW profiles, $\varepsilon = 0.9$ produces an average MHW depth of 672 m occurring at an anomaly of ~0.31°C and retains much of the significant warming while reducing the effect of the characteristic long tail in temperature anomaly profiles (**Figure 3D**). This is the desired outcome and is therefore chosen as the optimal threshold value for MHW depth.

A sensitivity analysis is conducted to test the robustness of different methods for measuring MHW depth cut-offs. The monthly variability of the MHW depth is used as a dependent variable and its sensitivity to the different methods is depicted in **Figure 4**. These methods include an arbitrary absolute temperature anomaly cut-off measure at 0.5°C, a cut-off value corresponding to the 10th percentile of the temperature anomaly profile (the depth below which 10% of the temperature observations are found), the positive threshold depth (Z_N) and the above-mentioned thresholds with ε varied over the range of 0.85–0.95. The monthly means show that all MHW depth definitions exhibit similar monthly variability, but the signal is noisier with the methods using thresholds on absolute temperature anomalies (Z_N and 0.5°C). In terms of magnitude, the MHW depths found vary over 100s of meters. The shallowest depths are found with the CTa threshold with $\varepsilon = 0.85$, and is very similar to the 0.5°C temperature anomaly cut-off. The deepest MHW depths are obtained when considering positive temperature anomalies (Z_N) or the 10th percentile of the profile. For this study, we choose to consider the CTa with $\varepsilon = 0.9$, as it allows for the extraction of the depth where the abnormal heat significantly decreases (**Figure 3**) and it produces a meaningful (depth at which 90% of the abnormal cumulative heat is contained) and conservative MHW depth cut-off.

Eddies

Using the framework expressed in Rykova and Oke (2015) for eddy detection and classification, GSLA was mapped around a 250 km radius of each water profile. Cyclonic (anticyclonic) eddies were detected within the radius if the minima (maxima) sea-level anomalies (SLA) were less (more) than -0.2 (0.2 m). Profiles are identified as being in neither eddies if no eddies were detected within their radius. Otherwise, profiles are in cyclonic (anticyclonic) eddies if the SLA at the Argo profile location is less than -0.02 (greater than 0.02) m and is monotonically decreasing (increasing) to the eddy extremum.

RESULTS

MHW Depth and Maximum Temperature Anomalies

The calculated depths of the MHWs were highly variable, ranging from 10 m to 1522 m. Based on the distribution of the temperature profiles and the relationship with surface MHW

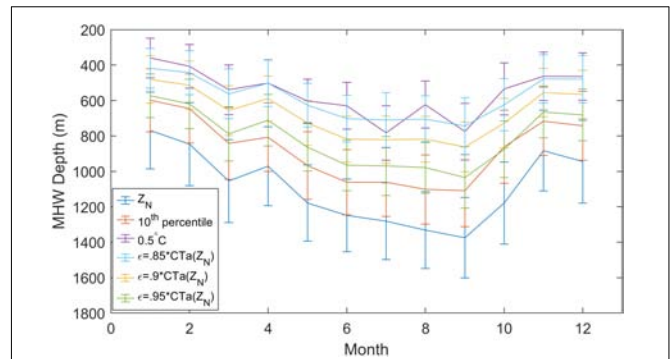


FIGURE 4 | Sensitivity analysis: Mean MHW depth per month used as a dependent variable for testing the effect of different MHW depth cut-off methods. Positive Threshold Depth, 10th percentile (the value below which 10% of the observations are found), absolute value of temperature anomaly at 0.5°C and the CTa cut-off with $\varepsilon = 0.95, 0.9, 0.85$. Bars represent the standard errors.

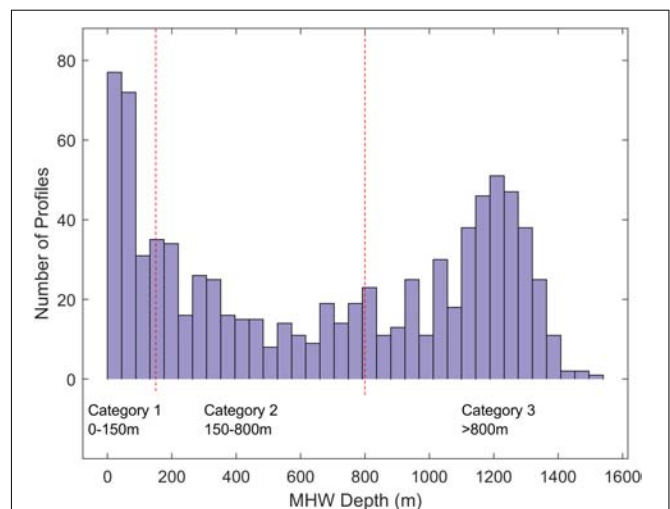


FIGURE 5 | Marine heatwave depth for Argo float profiles. Three categories were identified: 0–150 m (shallow), 150–800 m (intermediate) and >800 m (deep). Depths bins have 50 m spacing.

properties (see section “Relationships Between MHW Depths and Profile Characteristics”), MHWs are divided into three categories (**Figure 5**), namely category 1 (shallow, 0–150 m deep), consistent with the heat capacity of the ocean mixed layer (Schwartz, 2007), category 2 (intermediate, 150–800 m deep) and category 3 (deep, depth >800 m). Note that the peak for MHW depth that occurs in the higher range depths is likely due to the influence of the profiles which are warmer than climatology all the way down to the deepest (2000 m) Argo measurement. This, however, does not have an implication on our results given that these characteristics are captured within the category thresholds.

Only 23% of the total MHWs are restricted to the surface layers (category 1, average of 63 m deep, **Table 1**), while almost half (~45%) show a significant temperature anomaly deeper than 800 m (category 3, average of 1146 m deep, **Table 1**).

Although, the highest frequency of MHW depth is less than 50 m deep (~ 80 profiles, **Figure 5**). The three categories also have different MHW durations with the deepest MHWs lasting longest on average (27 days compared to 20 days) (**Supplementary Figure S3, Table 1**).

The temperature anomaly profiles within each MHW category are distinctively different and suggest that varying mechanisms are driving these extreme events (**Figure 6**). Shallow MHWs (category 1) tend to show a decreasing warming in the top 100 m. The maximum temperature anomaly is close to the surface (24 m) around 1.6°C , similar to the SST anomaly of 1.5°C (average across all profiles). It is notable that many profiles are anomalously cooler below the MHW depth in this category (**Figure 6A** and **Supplementary Figure S4**), however, for the purpose of this study we focus on the warming depths in a MHW. In contrast, the mean profile of deep MHWs (category 3) has a greater subsurface temperature anomaly of 3.4°C , twice the maximum anomaly in category 1 and peaks at depth (mean of 165 m). Interestingly, the magnitudes of the surface temperature anomalies across all categories are similar ($1.5\text{--}2^{\circ}\text{C}$), suggesting that distinct intense MHW patterns cannot be differentiated when only looking at the surface (**Table 1**). Category 2 shows a mix of the previous characteristics, with a slight increasing temperature anomaly in the top 93 m in the mean, where the maximum anomaly occurs before decaying.

Subsurface Properties in a MHW

Using CARS climatology, characteristics of density and salinity anomalies during a MHW at depth are also investigated. In the top 100 m, MHWs are on average fresher than climatology (**Figure 7A**) most likely due to the long-term trends identified by Rykova and Oke (2015). They showed using Argo *in situ* measurements and models, that since 2005 the Tasman Sea surface region has freshened in response to increased precipitation off Eastern Australia. Below 100 m, MHWs have various signatures which appear related to the overall depth of the extreme warming. Category 1 freshens below the MHW depth reaching a maximum at ~ 250 m and decaying to ~ 700 m. This freshness is consistent with the aforementioned cooling found below the MHW depth in this category, leading to an unchanged density (**Figure 7B**).

TABLE 1 | Mean characteristics of MHWs in categories 1 (0–150 m), 2 (150–800 m), and 3 (800–2000 m) from Argo data: depth extent, mixed layer depth, duration, sea-surface temperature anomaly (Surface, from SST and Argo floats), maximum temperature anomaly (Max) and the depth where it occurs (Depth of Max).

MHW depth (m)		MLD (m)	Duration (days)	Temperature anomaly		
				Surface (°C)	Max (°C)	Depth of max (m)
Category 1	63	45	20	1.5	1.6	24
Category 2	432	73	23	2	2.7	93
Category 3	1146	94	27	1.9	3.4	165

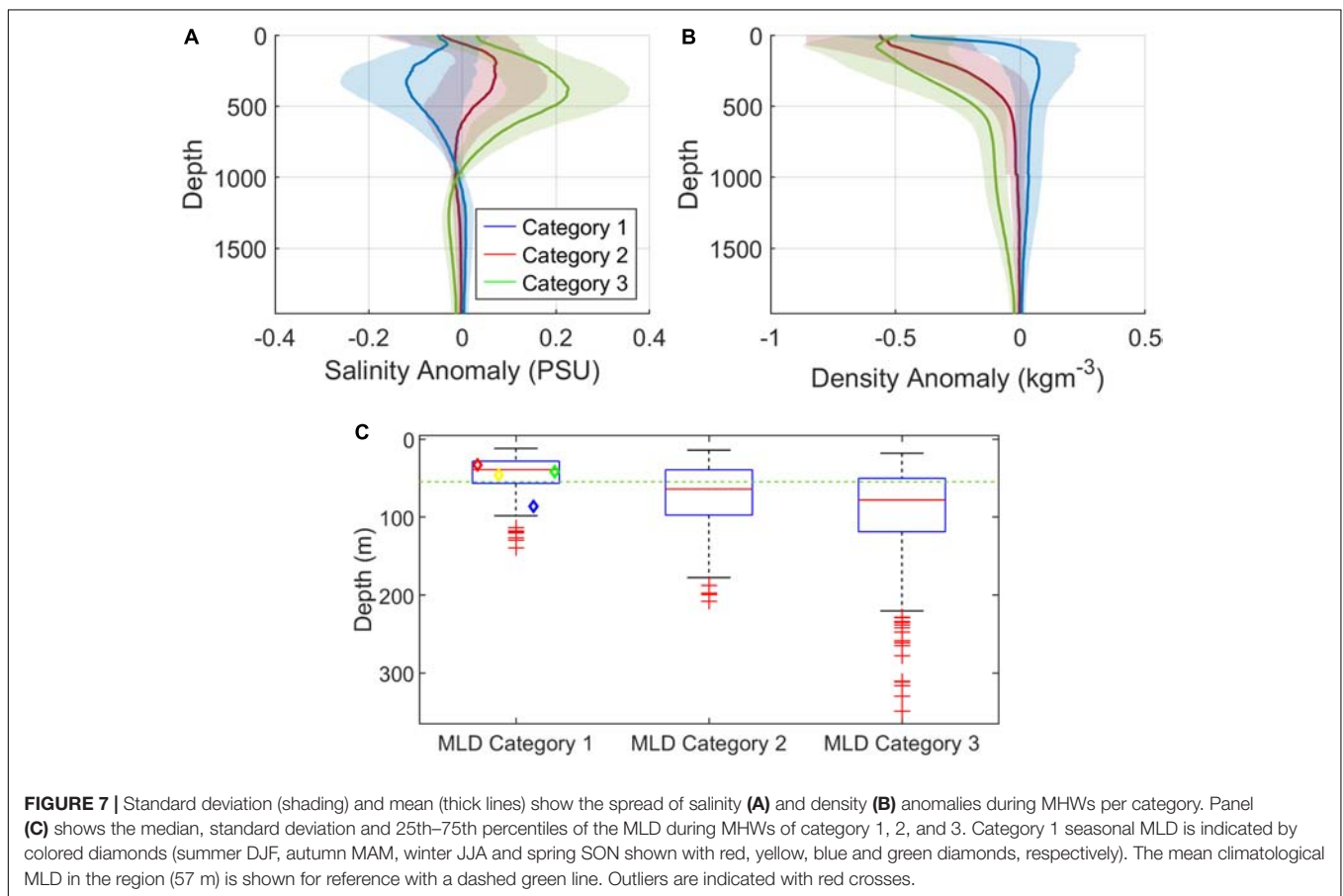
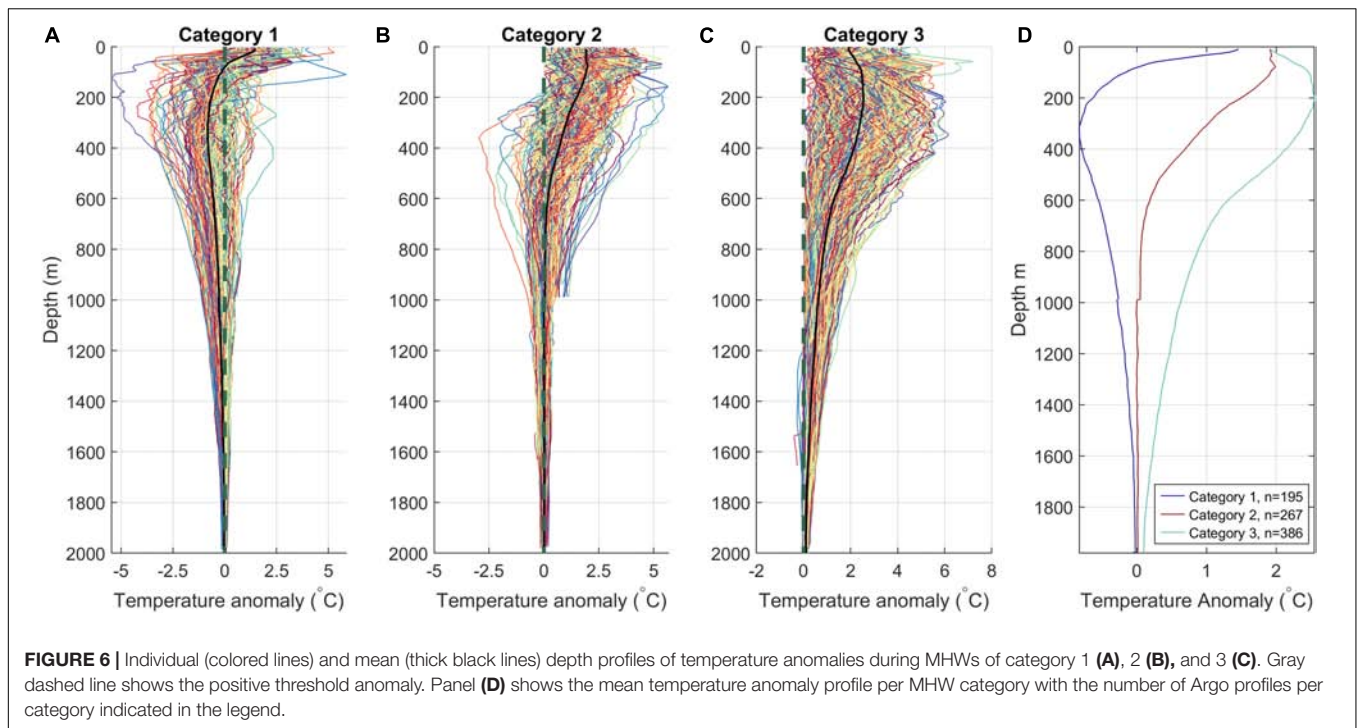
Whereas categories 2 and 3 become saltier down to ~ 650 m and ~ 900 m, respectively, with anomalies peaking at 0.26 PSU on average for the latter. In terms of density (**Figure 7B**), the profiles are similar to the temperature profiles due to the predominant influence of temperature on density variability in the region, characterized by lighter water-mass in the range of warm temperature anomalies for the intermediate and deep MHWs.

Compared to climatology, the MLDs (**Figure 7C**) for category 1 MHWs are shallower with a median at 39 m compared to climatological MLD at 57 m, meaning the water column is more stratified. Category 1 seasonal MLDs (as shown by colored diamonds) appear to behave as expected in this region with the seasonal variation centering around the median and category 1 matching the most stratified months. Category 3 median MLD is much deeper at 78 m, showing more mixing and less stratification in the water columns while category 2 is almost equivalent to that of climatology. That is, shallow MLDs correspond with shallow MHWs and progressively deepen with MHW depth.

Spatial and Seasonal Variability

Spatially, the incidence of category 2 and 3 MHWs varies with latitude. Southward of 32°S , all three categories occur whilst the deepest MHWs dominate the region between 32°S and 38°S (**Figure 8A**), corresponding to the area of maximum EKE (**Figure 1**). Northward of 32°S , deep MHWs (category 3) become less frequent with category 2 dominating the region, which coincides with the mean location of the eastward extension of the EAC (Tasman Front) which occurs at around 32°S (Oke et al., 2019 and **Figure 1**). Shallow MHWs are the most frequent below 38°S , south of the maximum EKE.

In terms of temporal variability, MHWs occur all year round but their depth and intensity in the region vary seasonally (**Figure 8B**). Note that CARS climatology includes seasonality, that is, the anomalies investigated here are with respect to the characteristic seasonality of water profiles. Shallow MHWs tend to occur preferentially in the austral summer and autumn (October–April) when the water column is the most stratified. MHWs are deeper in spring and winter, although categories 2 and 3 still occur year round. Looking at the mean profiles of all MHWs per season (**Figure 9**), winter is characterized by warmer and deeper anomalies that are consistent with mostly deep MHW events. The mean anomalies reach a maximum intensity of 1.9°C at 200 m and 0.14 PSU at 384 m in winter, with July being the most intense reaching a temperature anomaly of 2.7°C . The depth structure in MHWs in spring and summer behave similarly whereby temperature anomalies decay from near the surface, with summer having warmer surface temperatures and cooling more quickly with depth than spring. Autumn shows a subsurface temperature maximum similar to winter with slightly less intensity of $\sim 1.8^{\circ}\text{C}$ and at a shallower depth of ~ 100 m. MHWs in summer and autumn are fresher at the surface, whilst there is no significant surface salinity signal in spring. The most saline surface occurs in winter. The composite plot in **Figure 9C** shows the annual cycle of temperature



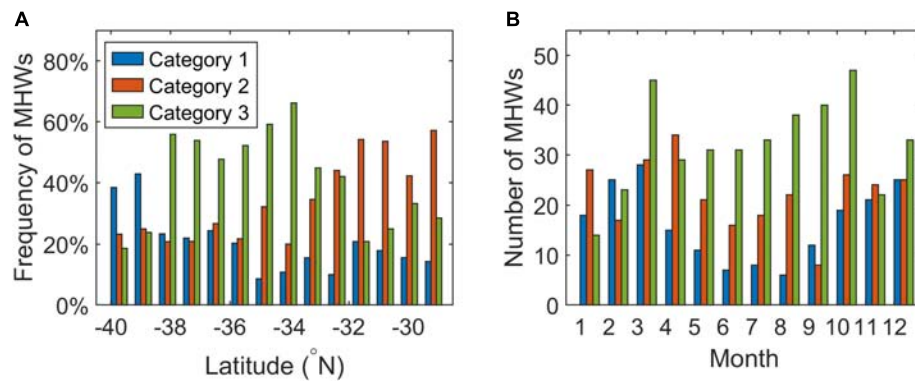


FIGURE 8 | Latitudinal (A) and monthly (B) distribution of Argo float profiles during MHWs for shallow (category 1), intermediate (category 2) and deep (category 3) events.

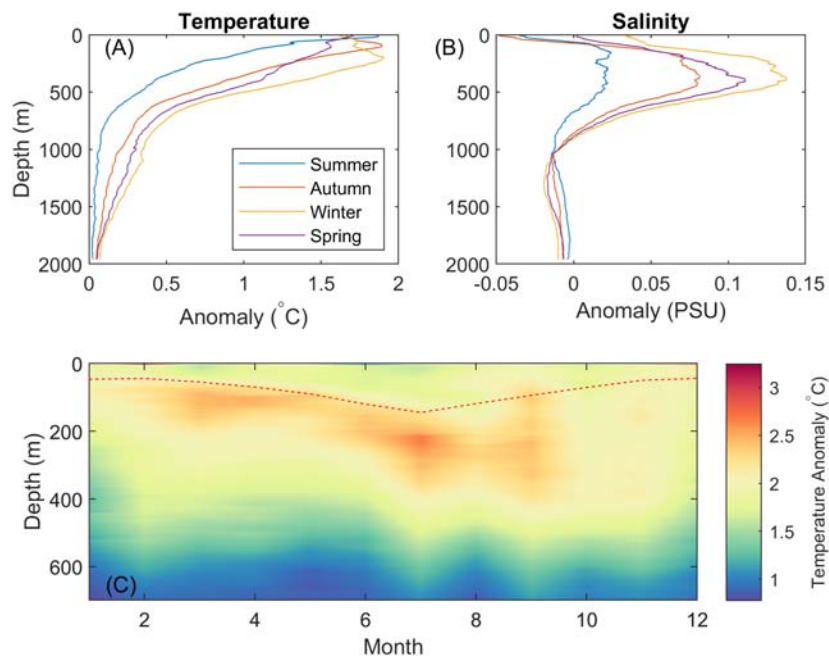


FIGURE 9 | Mean seasonal depth profiles of temperature (A) and salinity (B) anomalies during MHWs. (C) Monthly composites of temperature anomaly during MHWs. The monthly mean MLD (red dashed line) is overlaid.

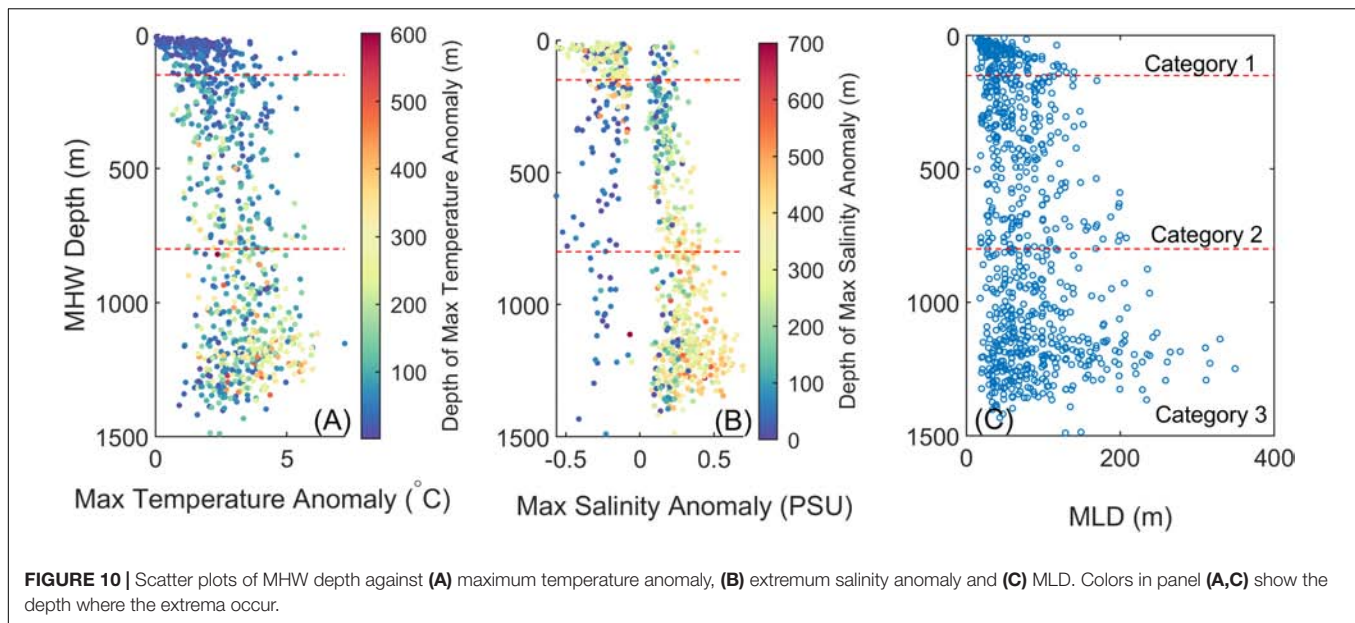
anomalies versus depth, illustrating the deepening intensity in temperature anomalies in particular around the July and September months and the link between MLD and the depth of maximum temperature anomalies.

Relationships Between MHW Depths and Profile Characteristics

Statistically, the MHW depth is only related to the surface temperature in the case of shallow MHWs. For category 1 (MHWs shallower than 150 m) we find a positive, statistically significant relationship between the surface temperature anomaly and the MHW depth penetration with a correlation of 0.3 (p -value < 0.00001) showing that the more intense the surface

warming is, the deeper it penetrates (**Supplementary Figure S5**). However, the depth of categories 2 and 3 is not related to the surface temperature anomaly, thus this relationship only holds for shallow MHWs. That is, the intensity of surface warming is limited to indicating shallow MHWs depths to some extent and is not a prognostic tool for MHWs that extend deeper than ~150 m in the water columns.

Significant relationships are, however, found between MHW depth and the characteristics of the water's vertical profile for all MHW categories (**Figure 10**). The deeper the MHW is, the deeper and greater the maximum temperature anomaly is (correlation of 0.5 and 0.52 with p -value < 0.0001, respectively). It is interesting to note that salinity exhibits distinct behavior across the MHW categories. Consistent with the previously



described characteristic of cooling and freshening below category 1 MHWs (see section “MHW Depth and Maximum Temperature Anomalies”), shallow MHWs are distinctively freshest at depth but show no relationship between freshness (negative salinity anomalies) and MHW depth. On the other hand, deep MHWs tend to be anomalously saltier with a strong relationship to MHW depth over all categories ($r = 0.67$, p -value < 0.0001). MLD has a slightly weaker relationship with MHW depth but still shows a significant correlation at $r = 0.4$ (p -value < 0.0001). A principal component analysis (PCA), following the Emery and Thomson (2001) framework, also confirms the relationships found here, with the strongest being the maximum salinity anomaly and the weakest being the SST anomaly (**Supplementary Figure S6**). Therefore, subsurface characteristics are a more reliable indicator of the vertical warming extent, with salinity being a strong discriminator.

Influence of Mesoscale Eddies

Consistent with the western Tasman Sea being an eddy-dominated region (**Figure 1**), 84% of the MHWs studied were found in eddies with 88% of those in warm core eddies (WCE). **Figure 11** shows an example of three individual Argo profiles sampling MHWs within a WCE (anticyclonic), a cold core eddy (CCE) (cyclonic) and no eddy. The profile sampling in a WCE (column 1) has the deepest MHW depth at 771 m while the CCE (column 3) is shallowest at 125 m.

In fact, the MHW depth is strongly correlated to the corresponding SLA extracted from altimetry (**Figure 12A**, $r = 0.62$ and $p < 0.0001$) consistent with the findings of Rykova and Oke (2015) on the relationship between SLA intensity, the temperature anomaly intensity and depth of the eddy core. **Figure 12A** shows the breakdown of eddy conditions per category and while most category 2 and 3 MHWs (deeper than 150 m) were found within anticyclonic eddies, it is interesting to see that category 1 MHWs occur across a mix of ocean conditions,

suggesting different drivers for the shallow MHWs. In particular, vertical warming during MHWs also occurs in cyclonic eddies, meaning their cold characteristic does not necessarily suppress the extreme warming during the MHW, although they do occur at a lesser frequency of 5% as opposed to 21% in WCEs. Note, the hollow circles in **Figure 12A** are of those profiles that were detected in eddy conditions and failed the monotonically increasing/decreasing test to the eddy extremum. Failing this test, however, does not prove that the profiles are in neither eddy conditions and therefore their statistics are not included in the eddy condition categories.

It has been shown that WCEs have a deeper MLD especially in winter based on their seasonality (Tranter et al., 1980; Brenner et al., 1991; Kouketsu et al., 2011). Given the predominance of MHWs occurring in WCE, this effect is evident in the MHW MLD (**Figure 7C**). In the region, WCEs typically have a warm core of 2–4°C at depths of around 300–350 m while the mean CCEs have a cold core centered around 250–350 m with –1.5 to –4°C temperature anomalies (Rykova and Oke, 2015). These eddy characteristics are consistent with the mean profile in eddies found here. **Figure 12B** illustrates the differences between mean temperature profiles in MHWs (solid lines) and NoMHWs (dashed lines) in the various eddy conditions. The influence of the MHW within eddies is clear with a significant warming in the top ~600 m on average overlaid to the typical structures. This additional warming leads to positive anomalies in the surface layers for CCEs and duplicates the positive temperature anomaly in WCEs at higher temperature intensities (~1.5°C warmer down to ~300 m). Profiles outside of eddies tend to show a warming in the top ~200 m during MHWs and a slight cooling at greater depths.

Seasonality of eddy conditions and profiles within (**Figure 13A**) and out of MHWs show that most of the NoMHW profiles are found within WCE and CCE (**Figure 13B**),

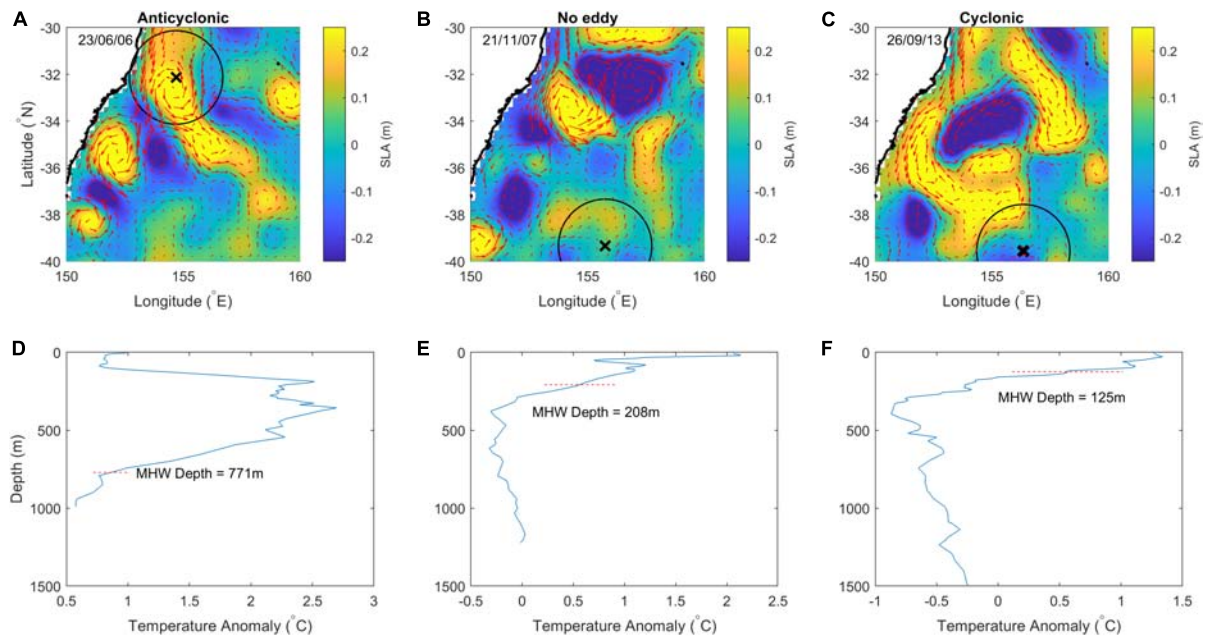


FIGURE 11 | Examples of Argo floats in an anticyclonic (A,D), no eddy (B,E), and cyclonic (C,F) eddy for specific dates. Top panels show the corresponding sea level anomaly (SLA) and geostrophic currents with the location of the Argo float (black cross). Bottom panels show the Argo float temperature anomaly profile and the corresponding calculated MHW depth. The marked circle around the Argo float outlines the 250 km radius used to search for nearby eddies.

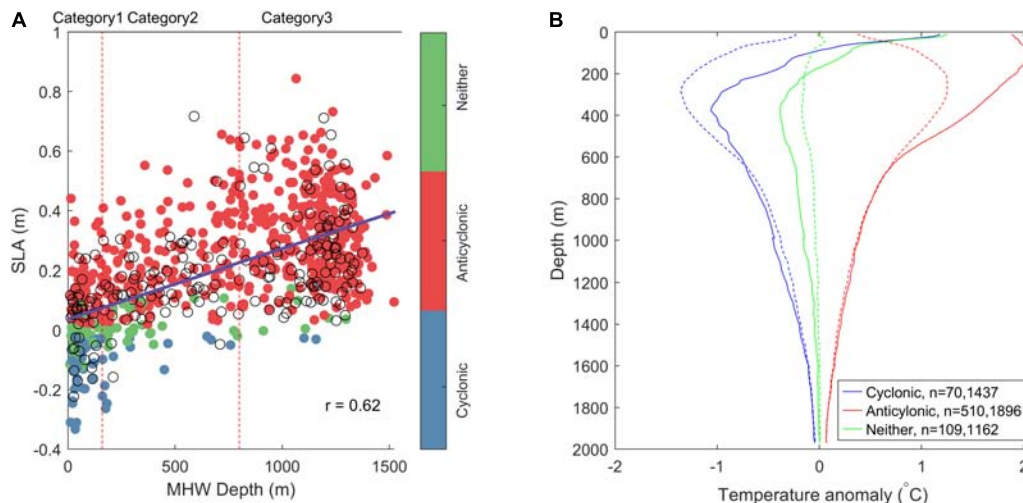


FIGURE 12 | (A) Scatter plot of sea level anomaly (SLA) and MHW depth. Colors indicate whether the water profile is in a cyclonic eddy (blue) an anticyclonic eddy (red) or not in an eddy (green). Hollow circles represent non-significant SLA. The regression line between SLA and MHW depth and correlation coefficient are indicated. Category thresholds are depicted by the top x-axis. **(B)** Mean temperature anomaly profiles per eddy type: cyclonic (blue line), anticyclonic (red line) and not in an eddy (green line) averaged for MHW (solid) and NoMHW (dashed) Argo floats. Number of profiles per category are indicated in the legend for MHWs and NoMHWs, respectively.

confirming that eddies are not the sole contributors to warm anomalies at depths but rather function as a catalyst to drive warm anomalies deeper during an existing MHW event. MHWs in CCEs exhibit a seasonal cycle predominantly occurring in summer and spring while MHWs in WCE are more frequent in the first half of the year.

DISCUSSION

This study reveals that, contrary to common understanding, MHWs in the Tasman Sea can extend to 1500 m. MHWs frequently extend much deeper than the MLD, regardless of the definition used for the MHW depth. When applying the

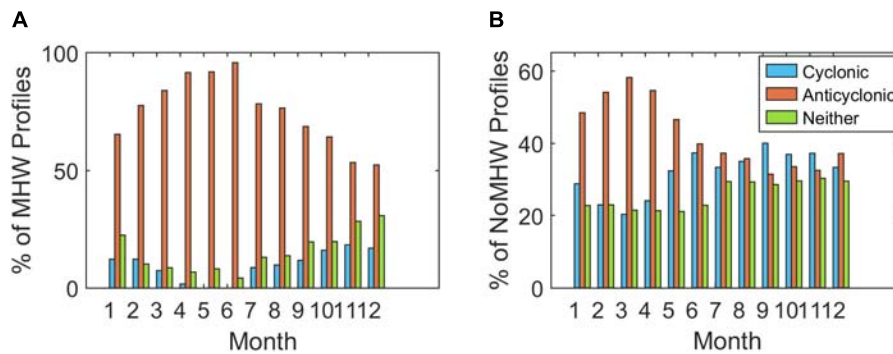


FIGURE 13 | Monthly distributions of Argo profiles in cyclonic (blue), anticyclonic (yellow) eddies or neither (red) during MHWs (A) and NoMHWs (B).

cumulative temperature anomaly threshold, we have showed that MHWs have a mean depth of 672 m with anomalous warming reaching down to 1522 m. In comparison, focusing on positive anomalies leads to warming detected down to >2000 m. The definition using a percentage threshold for the CTa appears to be most fitting because it is more conservative and meaningful than an absolute value (or percentile) of positive temperature anomaly. Moreover, the application of the CTa threshold reduces the potential risk of bias that can be associated with a positive threshold anomaly given its sensitivity to measuring the very gradual warming effect expected in the deep ocean (Roemmich et al., 2015).

Shallow MHWs restricted to the surface layers (<150 m) only represent 23% of the Argo profiles. They occur predominantly in summer/autumn in various mesoscale structures (cyclonic, anticyclonic or no eddies) and their depth is correlated with the SST anomaly. These events are characterized by stratified and fresh surface waters, suggesting that there is a predominant air-sea flux forcing whereby anomalous solar radiation and decreased wind stress act on latent heat-flux to reduce evaporation (Chen et al., 2014, 2015; Bond et al., 2015; Benthuyssen et al., 2018). Interestingly, when the domain is restricted to the high eddy field region only [(150°E, 157°E) and (37°S, 29°S)], the correlation coefficient between surface temperature anomalies and shallow MHW depth increases to 0.6 (as opposed to 0.3), that is, shallow MHWs are more sensitive to the region's characteristics.

In contrast, deep MHWs (>800 m) almost exclusively occur in anticyclonic warm core eddies, all year round but predominantly in winter south of the Tasman Front. They are characterized by a deeper MLD, a freshening in the top 100 m under which the water-mass is more saline (between 100 and 900 m), which is consistent with WCEs in the Tasman Sea (Rykova and Oke, 2015). Depth for deep MHWs is not related to surface conditions, however, it is directly related to the water-mass's anomalies, where the deeper the MHW extends, the deeper and more intense the temperature and salinity anomalies become. The lack of correlation between MHW surface temperature and depth characteristics is consistent with Brenner et al. (1991) who found a similar result for eddies in summer. By comparison, a strong relationship exists between SLA and MHW depth due to the steric height of the warm water column. It should, however, be noted

that MHWs in eddies are still rare events since most of the Argo float profiles in WCEs sampled regular temperatures.

Due to a lack of long-term *in situ* observations, this study is limited to the analysis of the vertical extensions of MHWs that are identifiable by anomalous SST. As Schaeffer and Roughan (2017) showed on the Sydney continental shelf, not all MHWs are detectable at the surface. The signatures of such MHWs are of great interest and further studies in this topic using subsurface detection methods are essential to grasp a more complete picture of MHW dissemination. Since *in situ* daily observations over decades [as recommended by Hobday et al. (2016)] do not exist in the open ocean, ocean modeling is necessary to investigate the full three-dimensional dynamics of the heat flux budgets.

In terms of inter-annual variability, our study's 14 year span (limited by the Argo era) is too short to draw conclusions; however, a deepening trend can be seen in both the yearly averaged maximum temperature anomalies and MHW depth (Figure 14). In this region, the El Niño Southern Oscillation (ENSO) index is only weakly related to local SST (Holbrook

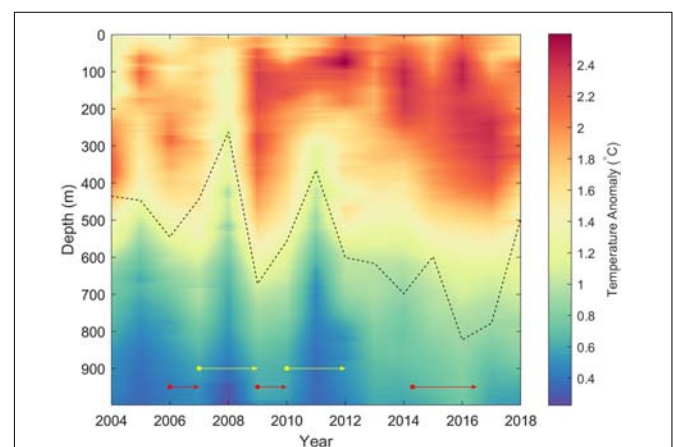


FIGURE 14 | Yearly composite of temperature anomaly in MHWs. The annual mean of MHW depth (thick black line) is overlaid. Arrows indicating major El Niño (red) and La Niña (yellow) events are shown. ENSO events are identified using SOI monthly (BOM) where maxima exceed ± 7 .

and Maharaj, 2008; Shears and Bowen, 2017), however, some of the more intense MHWs further south occurred during simultaneously strong El Niño events like the Austral Summer 2015/16 MHW (Oliver et al., 2017). Despite the coexistence of these events, the authors found that the El Niño had only a modest role on the MHW event in the Tasman Sea region due to its limited influence on EAC transport (Oliver et al., 2017). On the other hand, Heidemann and Ribbe (2019) recently found significant correlations (~ 0.35) between SST anomalies and ENSO (with a 7-month lag) in Southern Queensland, leading to more MHW days during El Niño years. While the link between the EAC, its eddies, the Tasman Sea SST and ENSO is still unclear, **Figure 14** suggests a deepening of MHWs during strong El Niño years [2006, 2009, 2014–2016, defined as a sustained Southern Oscillation Index (SOI) exceeding +7, BoM (2017)]. This potential connection needs to be considered through additional investigation where longer time-series are available for the dynamical link to be understood.

It is reasonable to posit that the discernible links between MHW depth and their drivers presented here are likely to apply mostly in the case of short term events (the mean duration here is around 3 weeks) and when MHWs are located offshore as opposed to year-long or coastal. In fact, in coastal areas like the ones considered by Schaeffer and Roughan (2017) and Oliver et al. (2018b), short term (days-weeks) events were found to be driven by wind stress anomaly, in particular downwelling winds that influenced the vertical mixing and MLD, resulting in deeper MHWs. In the case of long-term events the connection between MHW depth and single drivers is most likely less detectable. Studies on year-long record events (as opposed to a mean duration of 20–27 days as found in this study) find a broad range of interactions since a broader range of processes are likely to interact while overlapping with the inter-annual variability expected (Feng et al., 2013; Benthuyssen et al., 2014, 2018; Oliver et al., 2017). In this case, the depth of the extreme warming may vary locally during the event and the relationship we identified may not be applicable.

Given that intermittent warming can have a more damaging effect on the marine habitat than gradual ocean warming (Oliver et al., 2018a), the detection of warm anomalous waters at extreme depths found here suggests that the mesopelagic habitat could also be impacted. Temperature is one of the main environmental drivers influencing shark abundance (Lee et al., 2018) and we can expect deep extreme temperatures to affect the behavior of some of the local megafauna. Climate change has already been established to cause irreversible redistribution in the coastal benthic species (Ling, 2008; Johnson et al., 2011) and on this basis, it is conceivable that the intermittent warming brought about by MHWs causes comparatively more damage within the anomalous warming depth range.

In summary, this paper finds MHWs extending to extreme depths with no detectable surface signal and substantial eddy influence on warming extensions. The results highlight the fact that the surface characteristics of MHWs based on SST only inform anomalies in the water column if the MHW is

shallow and most likely surface-forced, independent from the ocean circulation. This has been the primary indicator for most studies to date, however, in light of our results, SST is an insufficient proxy for anomalous warming at depth. Further, given the eddy abundance in the Tasman Sea region, mesoscale ocean dynamics need to be considered to allow meaningful supposition as to the water-mass profile at great depths. As such, we recommend a simultaneous analysis of SST and SLA to investigate and potentially predict future MHWs particularly in eddy-dominated regions such as the Western Boundary Current extensions, e.g., off the Gulf stream (Leterme and Pingree, 2008) and the Kuroshio–Oyashio Confluence region (Sugimoto et al., 2017). Ultimately, this will improve our understanding of subsurface biological impacts and the management actions necessary to work toward preventing irreversible impacts on the ocean ecosystem.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: <https://portal.aodn.org.au/>, <https://www.esrl.noaa.gov/psd/>, www.cmar.csiro.au/cars and www.bom.gov.au. The Argo data were downloaded from the Australian Ocean Data Network portal (<https://portal.aodn.org.au/>) and Argo GDAC Data Browser (https://www.usgodae.org/cgi-bin/argo_select.pl), and these data are collected and made freely available by the International Argo Program and the national programs that contribute to it (<http://www.Argo.ucsd.edu>, <http://Argo.jcommops.org>). The Argo Program is part of the Global Ocean Observing System. Data for altimetry was obtained through the Australian Ocean Data Network portal (<https://portal.aodn.org.au/>) from the Integrated Marine Observing System (IMOS) – IMOS is a national collaborative research infrastructure, supported by the Australian Government. CARS2009 Climatology data were obtained from CSIRO Marine Laboratories from www.cmar.csiro.au/cars. NOAA_OI_SST_V2 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, United States, from their Website at <https://www.esrl.noaa.gov/psd/>. The Southern Oscillation Index (SOI) for ENSO events shown in **Figure 14** were obtained from the © Bureau of Meteorology, www.bom.gov.au.

AUTHOR CONTRIBUTIONS

YE performed the analysis and wrote most of the manuscript as part as her Master research project. AS supervised, proposed and guided the project, and took part in the writing.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00745/full#supplementary-material>

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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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