THE FUTURE OF CORAL REEFS SUBJECT TO RAPID CLIMATE CHANGE: LESSONS FROM NATURAL EXTREME ENVIRONMENTS

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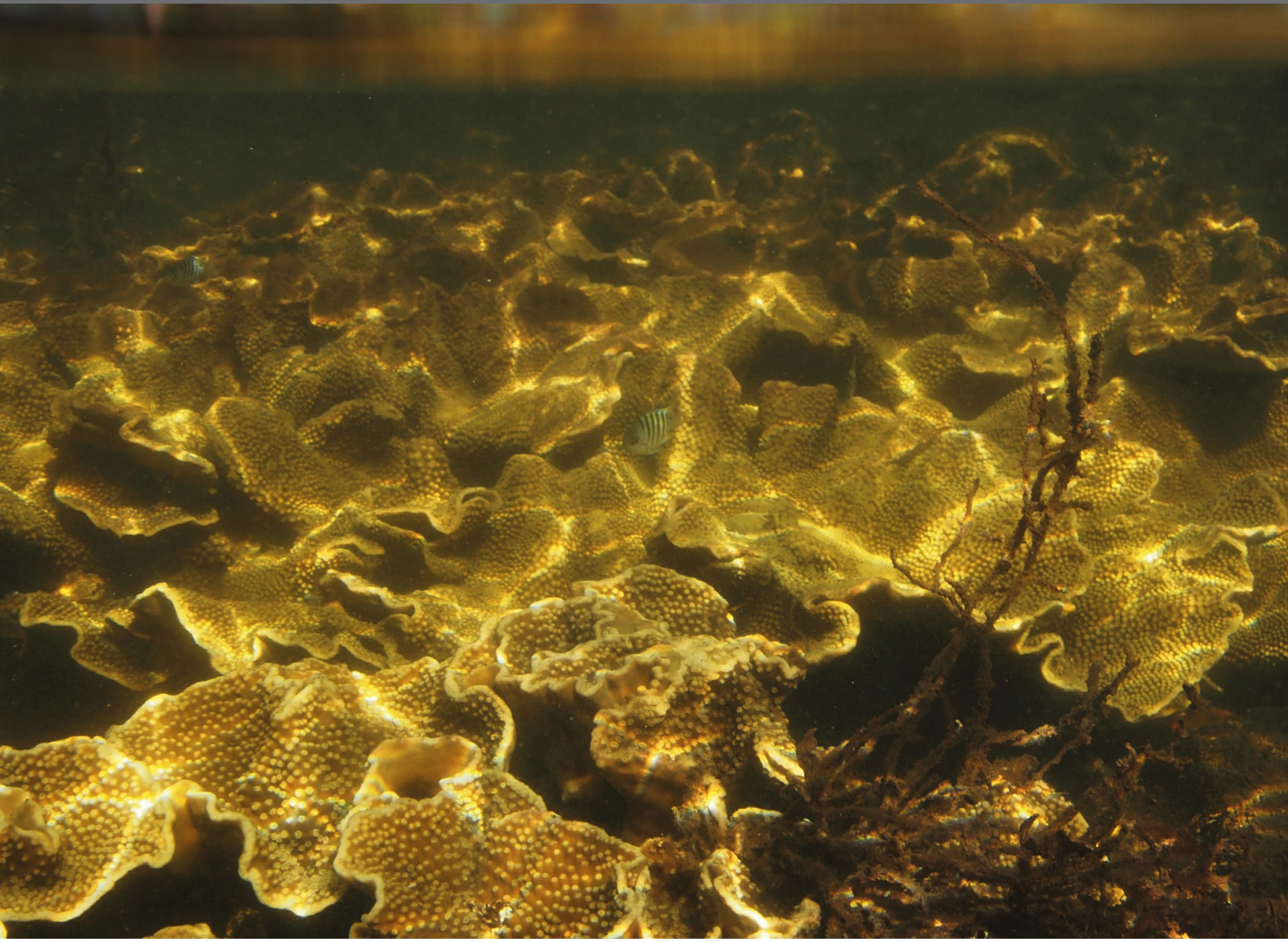

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THE FUTURE OF CORAL REEFS SUBJECT TO RAPID CLIMATE CHANGE: LESSONS FROM NATURAL EXTREME ENVIRONMENTS

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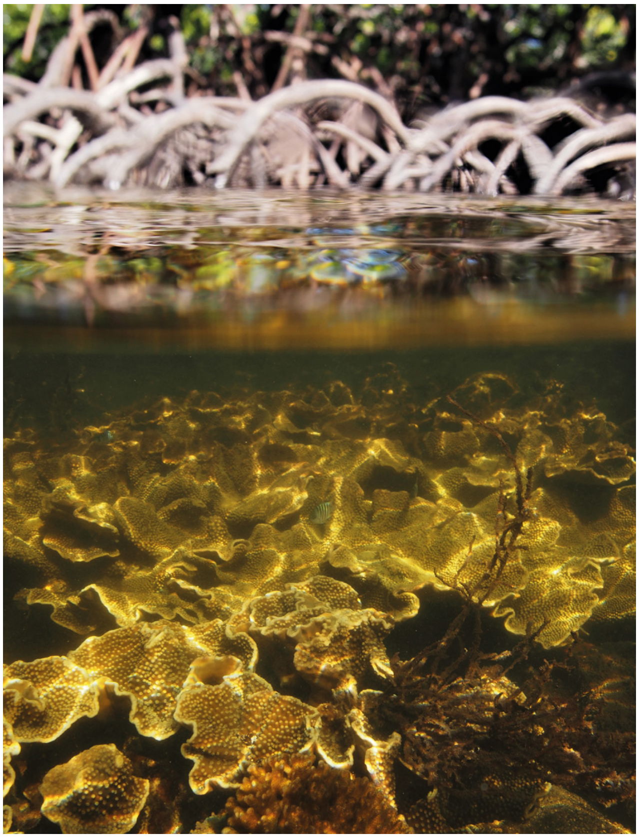

Extreme mangrove corals of the Great Barrier Reef by Emma Camp.

Examination of corals and reef-associated organisms which endure in extreme coral reef environments is challenging our understanding of the conditions that organisms can survive under. By studying individuals naturally adapted to unfavorable conditions, we begin to better understand the important traits required to survive rapid environmental and climate change. This Research Topic, comprising reviews, and original research articles, demonstrates the current state of knowledge regarding the diversity of extreme coral habitats, the species that have been studied, and the knowledge to-date on the mechanisms, traits and trade-offs that have facilitated survival.

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EDITORIAL
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Editorial: The Future of Coral Reefs Subject to Rapid Climate Change: Lessons From Natural Extreme Environments

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Keywords: marginal, extreme, coral reefs, climate change, suboptimal

Editorial on the Research Topic

The Future of Coral Reefs Subject to Rapid Climate Change: Lessons From Natural Extreme Environments

Coral reefs globally have to contend with increasing environmental impacts and rapid climate change (Hoegh-Guldberg et al., 2014). Understanding if, and how, coral reefs and their associated biodiversity will persist is a central question for scientists, reef managers, and policy makers worldwide. An important emerging research area shaping our understanding of how coral reef ecosystems might adapt and/or acclimate to environmental and climate change, has been through the study of naturally extreme coral environments.

The 15 contributions assembled in this Research Topic consider corals and reef fishes persisting in marginal or extreme reef environments. The opening article of this Ebook is a review by Camp et al. that provides a global synthesis of 285 research articles. The review indicates clearly that corals, in particular, exhibit a great deal of plasticity in their realized niche, yet no single taxon appears consistently successful across extreme environments examined to date. Common survivorship traits expressed by corals within such extremes include phenotypic plasticity, maintenance of energy reserves (e.g., enhanced heterotrophy), and genetic diversity. However, the review highlight significant knowledge gaps in our understanding of the multitude of abiotic factors that affect the persistence of coral reefs, and identifies priorities for future research.

Thomas et al. also contributed a review article, targeting the mechanisms that facilitate coral survivorship within the back-reef pools of Ofu, American Samoa. This unique system in Ofu has generated a wealth of research, which has shown both acclimation and adaptation processes occurring to support coral survival under high temperatures. The authors conclude in their review that corals may, in fact, have the tools required to cope with future climate change through their genetic diversity, phenotypic plasticity, dispersal abilities, and prevalence across large temperature gradients. At what spatial scale these traits can support survival remains to be observed and will ultimately depend on other local interacting abiotic parameters. For example, Bahr et al. found that the duration and magnitude of high temperatures were the primary factors determining coral bleaching susceptibility at Kāneʻohe Bay, Hawaii. However, differing local irradiance, precipitation, and turbidity within the bay created spatial variation in bleaching prevalence.

Severe marine heatwaves are an increasingly conspicuous component of climate change that catastrophically impact coral reefs (Frölicher et al., 2018; Oliver et al., 2018). Elevated turbidity is considered suboptimal for coral growth, yet an abiotic factor that could aid corals' ability to survive

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marine heatwave events. Morgan et al. report higher coral bleaching tolerance of reef corals in nearshore, turbid waters along the Great Barrier Reef, Australia, during the 2015–2016 warming event. Only 1.5% of studied colonies showed partial bleaching, and coral cover after the warming event remained unchanged from pre-event measures. Their findings suggest that the increased ability of corals in turbid environments to attenuate solar irradiance that can otherwise compound thermal stress (a stressor's antagonism; Brown et al., 2013), may provide refuge for native corals. Furthermore, the high organic matter of turbid reefs can support elevated coral heterotrophy that can facilitate energy maintenance during periods of stress (Anthony and Fabricius, 2000). Van Woesik and Mccaffrey drew similar conclusions based on their study of corals on the Florida Reef Tract from 2005–2015, where they suggest under a warming ocean that corals capable of surviving in turbid waters will potentially be preferentially selected for.

For corals not living in turbid environments, protection during marine heatwaves events could be provided through local micro-refugia. Hoogenboom et al. report variation in bleaching susceptibility of *Acropora* spp. on the Great Barrier Reef during the 2015–2016 thermal stress event. Corals living in shaded microhabitats, created by the crevices and overhangs of the coral reef three-dimensional structure, experienced less coral bleaching due to reduced irradiance. These findings reinforce the importance of studying local abiotic conditions needed to inform and reconcile biological observations of patchiness of coral survival.

The tolerance of corals to temperature anomalies is not restricted to marine heatwave events, as corals can also be subjected to marine cold spells. Tuckett and Wernberg describe a marine cold spell event in 2016 off the coast of Perth, Western Australia that saw temperatures fall below 15.5°C, and remain below 17°C for 19 days. Despite the extreme cool waters, native corals of these subtropical reefs showed minimal (<5%) visual signs of bleaching. Whether exposed to extreme high or low temperatures, corals that are not protected through environmental refuge will be required to adapt and/or acclimate to the prevailing environmental conditions, or risk potential extirpation. Riegl et al. use the Persian Arabian Gulf (PAG) to explore the demographic mechanisms that can lead to winnowing of coral species poorly adapted to changing environmental conditions. They report variable species susceptibility to winnowing following environmental stress. Losses in coral cover, coral size, and population fecundity will be crucial in determining the future connectivity of a species population, and ultimately, whether it declines following environmental disturbances.

Fecundity, larvae settlement, and post-settlement processes are clearly important contributors to the ecological success of any coral species, particularly under environmental stress and climate change (Richmond et al., 2018). The ability of corals to recover from stress events will depend, in part, on their reproductive capacity and the availability of suitable substrate to colonize. What space remains available for coral recruitment depends on how other taxa have been impacted by the stress event (Mumby and Van Woesik, 2014), and which taxa colonize an environment first. Bento et al. investigated recruitment success of different taxa at three regions within north-east Arabia that experienced different environmental disturbances. Using unglazed terracotta tiles as an artificial substrate to study recruitment, they observed low coral recruitment, and high recruitment of non-coral taxa across the regional sites. Regional differences were reported in the initial recruiting taxa, which could be an important factor in determining the future colonization success of corals at these impacted reefs.

For corals to survive climate-induced stressors, such as ocean warming and acidification, may require migration into new habitats (Pandolfi and Kiessling, 2014). Lohr et al. investigated the ability for corals to recruit into seagrass meadows in the Cayman Islands. Seagrass habitats have been proposed as potential ocean acidification refugia due to their ability to off-set the negative impacts associated with ocean acidification (Manzello et al., 2012). Fourteen coral taxa were able to recruit into the seagrass meadows investigated, with recruit populations comparable in composition to those established in the local seagrass meadows. Interestingly, some coral species abundant on the fringing back-reef were absent from the adjacent seagrass meadows. Further studies are required to understand the drivers that might prevent the recruitment of some species into the marginal seagrass habitat.

Increasing evidence of the ability of corals to tolerate environmental stress and survive in extreme environments suggests that all members of the coral holobiont (animal host, algal symbiont and associated microbes) are important. Grottoli et al. investigated the response of the coral holobiont to temperature stress in thermally tolerant corals from the northern Red Sea. Their findings demonstrated species-specific responses, but that maintenance of energy reserves and heterotrophic capacity appear to be important traits to support thermal tolerance. Hume et al. investigated algal symbionts of corals from the world's hottest sea to better understand the genetic diversity of the *Symbiodinium thermophilum* group that has been associated with native corals' thermal tolerance. Their findings reveal a genetic boundary (as small as 20 km) structuring genetically distinct populations of *S. thermophilum*. While this may, in part, result from limited connectivity, the authors hypothesize that other factors are likely important in establishing local symbiont populations. The flexibility of corals to adjust their associated microbes when experiencing environmental change has been postulated as a major aid to coral survival (Torda et al., 2017). Rothig et al. report distinct microbiomes for the Red Sea deep coral *Eguchipsammia fistula in situ* compared to *ex situ*. In under a year, corals kept *ex situ* under increased oxygen and food availability experienced very different microbiomes compared to *in situ* populations. Corals exhibiting a flexible microbiome may therefore have greater phenotypic plasticity to persist across different environmental conditions.

While the majority of articles received as part of this Research Topic focused on corals, two articles considered the persistence of fishes in marginal reef environments. Shraim et al. studied the stomach content of fishes living in the southern Arabian Gulf where temperatures are extreme. They found *Pomacanthus aquilus* and *P. trichrourus* had seasonal variation in their diet that corresponded to changes in food availability. However, *P. maculosus* had a diet dominated by coral and sponge over both seasons. Such findings highlight the species- specific responses that will potentially occur for reef associated taxa as coral cover declines worldwide. Booth et al. also reported species-specific responses in the capacity of coral reef associated fishes to move into temperate waters of New South Wales, Australia. Their 18-years dataset revealed over 150 coral reef fish species recruiting to temperate reefs of Sydney (latitude 34°S) and 60 species to Merimbula (latitude 37°S). The ability of species to tolerate temperature drops during winter was found to be a good general indicator of predicting coral reef associated fishes range expansion. Habitat availability and local predators are also important considerations. More research into fishes and non-coral taxa of extreme and marginal systems is clearly an important area for future research.

As climate change alters reef landscapes globally, focused research into coral reef taxa persisting within suboptimal systems becomes increasingly important, as it can provide important insights into the biological mechanisms taxa require to survive. While no single suboptimal system provides a perfect analog to future reef conditions, investigations carried out in extreme environments can elucidate complex abiotic, ecological and biogeochemical processes inherent to reef systems. The insights garnered can, in turn, shed important light on the potential responses of corals, coral reefs and associated organisms to a changing ocean environment. The papers collated in this Research Topic provide a renewed appreciation for the diversity of mechanisms coral reef taxa are able to utilize to survive in extreme and marginal reef environments and highlight the value of studying these underexplored ecosystems.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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REVIEW
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The Future of Coral Reefs Subject to Rapid Climate Change: Lessons from Natural Extreme Environments

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Global climate change and localized anthropogenic stressors are driving rapid declines in coral reef health. *In vitro* experiments have been fundamental in providing insight into how reef organisms will potentially respond to future climates. However, such experiments are inevitably limited in their ability to reproduce the complex interactions that govern reef systems. Studies examining coral communities that already persist under naturally-occurring extreme and marginal physicochemical conditions have therefore become increasingly popular to advance ecosystem scale predictions of future reef form and function, although no single site provides a perfect analog to future reefs. Here we review the current state of knowledge that exists on the distribution of corals in marginal and extreme environments, and geographic sites at the latitudinal extremes of reef growth, as well as a variety of shallow reef systems and reef-neighboring environments (including upwelling and CO_2 vent sites). We also conduct a synthesis of the abiotic data that have been collected at these systems, to provide the first collective assessment on the range of extreme conditions under which corals currently persist. We use the review and data synthesis to increase our understanding of the biological and ecological mechanisms that facilitate survival and success under sub-optimal physicochemical conditions. This comprehensive assessment can begin to: (i) highlight the extent of extreme abiotic scenarios under which corals can persist, (ii) explore whether there are commonalities in coral taxa able to persist in such extremes, (iii) provide evidence for key mechanisms required to support survival and/or persistence under sub-optimal environmental conditions, and (iv) evaluate the potential of current sub-optimal coral environments to act as potential refugia under changing environmental conditions. Such a collective approach is critical to better understand the future survival of corals in our changing environment. We finally outline priority areas for future research on extreme and marginal coral environments, and discuss the additional management options they may provide for corals through refuge or by providing genetic stocks of stress tolerant corals to support proactive management strategies.

Keywords: extreme, ocean acidification, marginal, refuge, review

INTRODUCTION

Coral reef ecosystems and the services they provide sustain half a billion people on Earth, but are deteriorating under the effects of climate change (Cinner et al., 2016; Hughes et al., 2017). Accumulation of greenhouse gases in the atmosphere (primarily carbon dioxide, CO_2) is resulting in warmer sea surface temperatures (SST) and rising seawater acidity; processes that are predicted to intensify under current climate change projections (van Hooidonk et al., 2014). Even if carbon emissions were to stabilize today, the world's oceans will experience prolonged warming and inevitable change in carbonate chemistry, due to the lag time that oceans re-equilibrate with the atmosphere (IPCC, 2014). Further changes in other physicochemical conditions, such as reduced oxygen levels (Schmidtko et al., 2017), are accompanying ocean warming, creating a complex suite of environmental factors that coral reefs will need to overcome in order to persist into the future. Understanding whether and how corals can physiologically or genetically adjust to keep pace with environmental change, has therefore become a global research priority.

A key challenge for researchers studying how future projected climates will impact reef form and functioning, is to consider the influence of local scale environmental conditions, including natural diel and seasonal fluctuations (Guadayol et al., 2014). It is imperative to understand the ecological limits to coral distributions by resolving their fundamental niche (the range of conditions an organism can physiologically survive and reproduce under in the absence of biotic interactions, Hutchinson, 1959), relative to their realized niche [determined by other biological pressures, such as competition, (Morin and Thuiller, 2009)], thereby addressing the impact of climate stressors on community reorganization in response to the prevailing conditions (Doney et al., 2012). Natural environments where corals live at the periphery of their environmental tolerance, such as CO_2 vent sites, have therefore become increasingly popular to study corals free of the constraints imposed by *in vitro* experimentation. Such natural extreme and marginal environments have conditions close to the perceived thresholds of coral growth (Kleypas et al., 1999), but support corals that have clearly acclimated and/or adapted to more extreme environments (e.g., Palumbi et al., 2014). Thus, an important role of these environments is that they can offer insight into how corals and coral reefs may survive into the future (Perry and Larcombe, 2003), as they are continuously subjected to more extreme environmental conditions through climate change. The insight provided by these environments will depend in part on the dispersal of adults and juveniles, with sessile brooding species more likely to exhibit adaptation to extreme environments over multiple generations, compared to broadcast spawning species that may recruit into the extreme environment as progeny from "parents" in less stressful environments. Ultimately, no single site studied to date provides a "perfect" analog to future environmental conditions projected for coral reefs. However, a collective assessment of such sites can provide essential information on the ability of corals and coral reefs to persist according to different scenarios, in terms of intensity of stressor and/or combination of stressors at play. Until now, no such collective assessment has been undertaken.

Here, we review and synthesize information across a range of extreme and marginal coral environments, to: (i) demonstrate the extent of abiotic scenarios under which corals can persist, (ii) explore whether there are commonalities in coral taxa able to persist in such extremes, (iii) provide evidence for key mechanisms required to support survival and/or persistence under sub-optimal environmental conditions and, (iv) evaluate the potential of current sub-optimal coral environments to act as potential refugia under changing environmental conditions. We undertake a synthesis of the abiotic variability documented for the different extreme environments, to provide a collective assessment of these systems. Finally, we draw on the findings from the review to explore how these systems may support corals tolerant of stress that could be utilized in proactive reef management, and outline key areas for future research.

MATERIALS AND METHODS

To begin, we review the current state of knowledge of coral environments that are considered marginal or extreme in relation to one or more abiotic factor, notably, seawater pH, temperature, low light (including highly turbid environments), and oxygen. We use case studies of some well-documented sites within each environment to quantify the extreme abiotic conditions experienced and provide examples of the mechanisms that have been reported to support coral survival. We also consider the ability of these different environments to act as potential coral refugia. Refuge environments are areas that maintain favorable conditions being lost elsewhere (*sensu* Keppel and Wardell-Johnson, 2012). These could vary across temporal scale, with some environments providing short-term refuge against acute stress (e.g., turbid reefs reducing irradiance during a bleaching event) vs. long term chronic changes (e.g., the potential buffering ability of seagrass systems). As coral reefs globally are forced to acclimatize to changing environmental conditions, utilization of refuge environments becomes an important alternative solution to aid survival.

We then conduct a quantitative synthesis of information from 285 studies (**Supplementary Table 1**) that have considered extreme, marginal or refuge coral environments. To parameterize the literature included in the quantitative synthesis, only studies that considered scleractinian corals or the physicochemical conditions of coral systems were included. Studies were collected for analysis until the 3rd August 2017. The collection of studies was identified from ISI Web of Science database or Google Scholar searching relevant keywords, e.g., the type of extreme coral environments (high-latitudinal, CO_2 vent, mangrove system, seagrass, macro-tidal, ojos (low pH springs), upwelling, turbid reefs, mesophotic, deep reefs, hot seas, tide-pools) with the following words: refuge, coral, thermal tolerance, bleaching, ocean acidification. We also searched the literature cited in all studies identified during that search. Review of this current literature quickly demonstrated that there were not enough data available to compare biological metrics (e.g., calcification rates) across these environments, and as such, we used the quantitative synthesis to: (i) identify knowledge gaps, and (ii) compare the range of abiotic conditions corals are currently able to persist under.

To identify knowledge gaps, the work undertaken in each study was grouped into eight categories: community composition, experimentation, health, holobiont community, physicochemical conditions, physiology, population biology and structural properties, each of which had sub-categories that are illustrated in a heat-map (**Figure 1**). The heat-map is based on the proportion of studies within a given environment that measured any given parameter.

To compare the abiotic parameters (pH, temperature, oxygen, total alkalinity (A_T) and salinity) of sites within different environments, studies that included the maximum and minimum abiotic values for a minimum of one seasonal period (dry season/wet season) were included. Due to the limited data available across temporal scales (e.g., day, week, month, season, years), data were used as long as a minimum of one diurnal cycle was available for that season. Once additional high-resolution abiotic datasets are available for these environments, comparisons across different temporal scales should be conducted (**Table 1**). Raw data were used or extracted from primary literature using WebPlot Digitizer (Rohatgi, 2017). Unfortunately, the synthesis quickly revealed that the comparison of multiple abiotic variables across all extreme and marginal coral environments would not be possible due to a lack of data. As such, abiotic comparisons were made across environments on the most commonly reported abiotic variables: pH and temperature. A further Principle Component Analysis (PCA) was conducted on pH (total scale), temperature (°C), total alkalinity (A_T; μmol kg^{-1} SW), salinity and oxygen (mg L^{-1}) for 14 studies, spanning five environments to demonstrate the need to consider multiple abiotic variables within these systems. The PCA was performed in R (R Core Team, 2017) using the prcomp function. To avoid scale change sensitivity in the PCA (Everitt and Hothorn, 2011) variables were rescaled (Härdle and Simar, 2012) to have a mean of zero and a standard deviation of one.

REVIEW OF THE CURRENT STATE OF KNOWLEDGE

Low pH/High CO$_2$ Environments

Absorption of excess atmospheric CO$_2$ by the world's oceans lowers seawater pH and re-organizes the composition of carbonate species of seawater, resulting in reduced saturation states of calcium carbonate minerals [e.g., aragonite (Ω_{arag})]. This phenomenon, termed ocean acidification, threatens to impact many marine processes (Kroeker et al., 2013) notably through reduced growth and physical integrity of marine

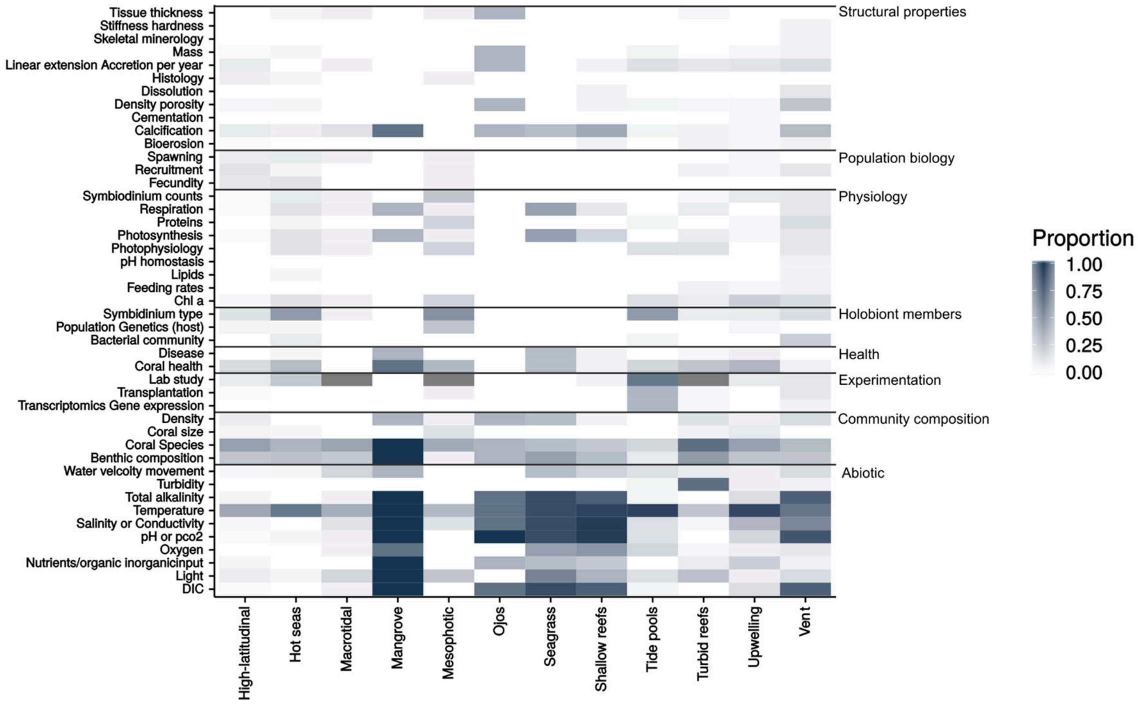

FIGURE 1 | A heat-map showing the research parameters measured within the 285 studies reviewed for the quantitative synthesis. The heat-map is based off the proportion of studies for each environment that researched the given parameter. Number of studies contained in the synthesis per environment: High-latitudinal = 70, Hot seas = 34, Macrotidal = 17, Mangrove = 3, Mesophotic reef = 15, Ojos = 3, Seagrass = 6, Shallow reefs = 21, Tide pools = 21, Turbid reefs = 40, Upwelling = 35, Vent = 20.

calcifiers (Guinotte and Fabry, 2008). CO_2 vent sites and ojos (low pH springs) are natural extreme environments where the seawater carbonate chemistry (low pH and low Ω_{arag}) provides comparative conditions to ocean acidification scenarios.

CO_2 Vents

Underwater volcanic vents emit CO_2 (along with other trace gases, e.g., N_2, O_2, CH_4, **Figure 2**) into the adjacent seawater, reducing the Ω_{arag} and creating seawater conditions similar to those predicted to occur under ocean acidification. Local hydrology and variations in gas release can create large diel oscillations in pCO_2 at vent sites relative to adjacent control sites (Enochs et al., 2015). Even so, vent sites offer a unique natural environment to study ecosystem changes in response to frequent, low pH (Hall-Spencer et al., 2008). In the Mediterranean, the release of CO_2 at vent sites has been shown to alter a variety of ecosystems, including seagrass beds (Martin et al., 2008), rocky-reef systems (Hall-Spencer et al., 2008), and vermetid reefs (Milazzo et al., 2014). These temperate studies all report adverse effects of elevated pCO_2, including loss of diversity of marine calcifiers (Martin et al., 2008; Kroeker et al., 2011), reduced calcification (Milazzo et al., 2014), shifts from calcareous dominated systems to a state lacking scleractinian corals (Hall-Spencer et al., 2008) and reductions in trophic groups (Kroeker et al., 2011).

To date, there have only been three regions where vent systems have been described adjacent to coral reefs: Iwotorishima Island, Japan (Inoue et al., 2013), Papua New Guinea (PNG; Fabricius et al., 2011) and Maug, in the Commonwealth of the Northern Mariana Islands (Enochs et al., 2015). Findings from these vent sites have been variable, likely due to site-specific pH gradients, hydrology and conditions such as nutrient availability (Enochs et al., 2015). For example, in Iwotorishima, communities shifted from hard coral to soft coral as seawater acidified, with all corals absent from the highest pCO_2 zone (1,465 µatm, Inoue et al., 2013). In contrast, coral dominated sites at Maug (mean pH $= 8.04 \pm 0.016$, min pH $= 7.98$) transitioned to macroalgal dominance (mean pH $= 7.94 \pm 0.051$, min pH 7.72).

A common feature across the various vent sites are changes in community structure, where only a few acidification-tolerant species thrive under high pCO_2 (e.g., Hall-Spencer et al., 2008; Fabricius et al., 2011, 2015; Kroeker et al., 2011, 2013). There is also evidence that the structural integrity of any reef framework is compromised due to a loss of architectural complexity (Fabricius et al., 2011), increased rates of bioerosion (Enochs et al., 2016a,b), reductions in coral growth (Fabricius et al., 2011) and reduced skeletal density (Fantazzini et al., 2015; Strahl et al., 2015b).

The ability of corals around vent sites to maintain calcification under elevated pCO_2 appears to be species-specific (Rodolfo-Metalpa et al., 2011; Inoue et al., 2013). Both in laboratory work (Venn et al., 2011; McCulloch et al., 2012) and field investigations (Wall et al., 2016) species-specific abilities to buffer internal-pH have been recorded. There do appear to be defined physiological limits under which calcification can occur (McCulloch et al., 2012; Wall et al., 2016), and physiological plasticity appears important in supporting calcification at high pCO_2. For example,

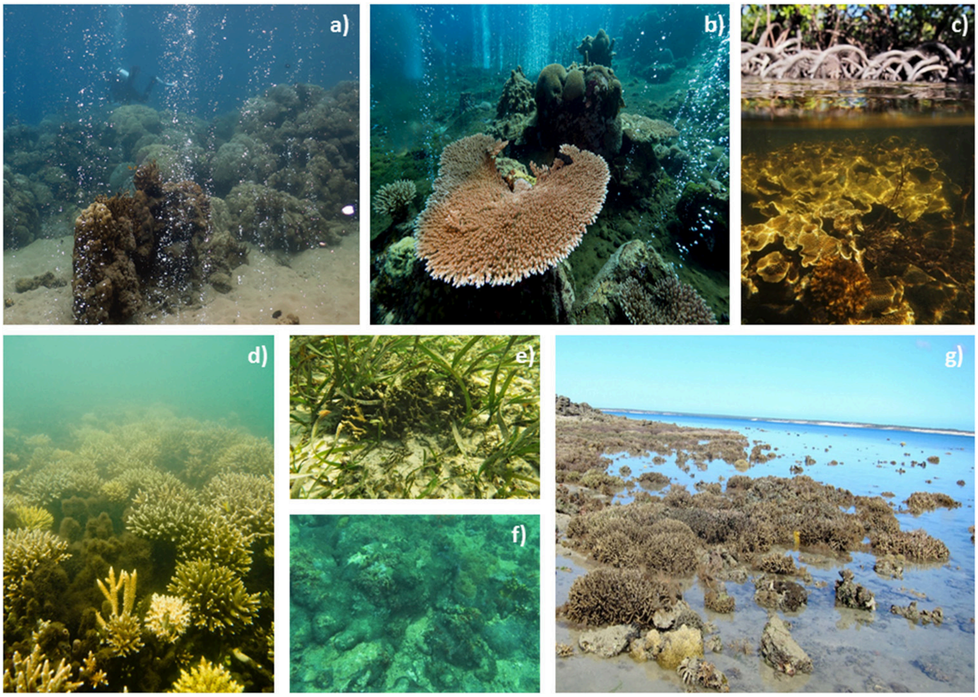

FIGURE 2 | Photographs from different extreme and marginal coral environments. **(a,b)** Vent sites in Papua New Guinea (photo credit R. Rodolfo-Metalpa and J.M. Boré), **(c)** mangrove system Great Barrier Reef (photo credit E. Camp), **(d)** mangrove system New Caledonia (photo credit E. Camp), **(e)** seagrass bed the Cayman Islands (photo credit E. Camp), **(f)** turbid reef Salvador Brazil (photo credit E. Camp), **(g)** Kimberley reef flat (photo credit V. Schoepf).

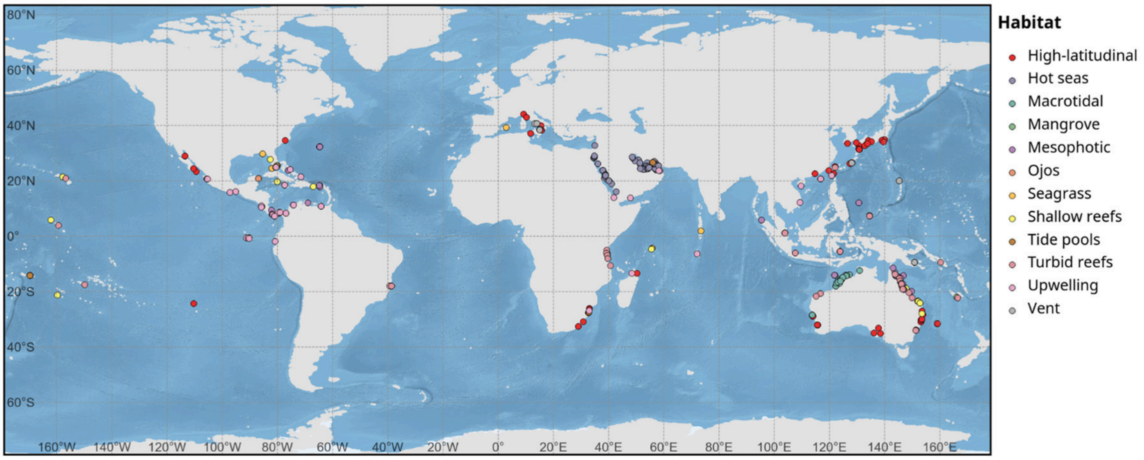

FIGURE 3 | A global map showing the study locations of the extreme and marginal coral environments.

increased rates of calcification (Rodolfo-Metalpa et al., 2011), or the utilization of elevated external dissolved inorganic carbon (DIC) can fuel photosynthesis (Inoue et al., 2013; Strahl et al., 2015a) and offset the higher energetic cost of calcification under acidification. For soft corals (Inoue et al., 2013), sea anemones (Suggett et al., 2012a), and scleractinian corals (Strahl et al., 2015a), success at high $p\mathrm{CO}_2$ seems to be driven by their capacity to enhance, or at least sustain, photosynthesis under elevated $p\mathrm{CO}_2$. Other physiological processes such as higher cell protective capacities, total lipid content, tissue biomass (Strahl et al., 2015b) and changes in fatty acid metabolism (Kenkel et al., 2017) may also promote resistance to environmental stress at low pH.

Alongside physiological plasticity, live-tissue coverage (Rodolfo-Metalpa et al., 2011), and changes in microbial taxa (Morrow et al., 2014) can support species survival under elevated $p\mathrm{CO}_2$. Variable changes in gene expression of *Symbiodinium* at the PNG vent system suggest population-specific responses to low pH (Kenkel et al., 2017). The collective response of the animal host, symbiotic algae and other microbial taxa demonstrate that fully considering the holobiont (i.e., the coral host, algal symbionts and microbiome) is important in determining success and survival under high $p\mathrm{CO}_2$.

Low pH Springs (ojos)

Underwater seeps (ojos) of the Yucatan Peninsula (Mexico) have physicochemical conditions entirely unique to the local area. Here, water that has associated with soil and limestone mixes with high CO_2 groundwater resulting in seawater that has a low pH (6.70–7.30), low Ω_{arag} (0.3–0.97 at the center of the seep), and high DIC, A_T, Ca^{2+} and nutrients (Crook et al., 2012). Although the combined physicochemical conditions differ from potential future ocean acidification scenarios and vent environments (e.g., low pH accompanied by high DIC, A_T, and Ca^{2+}), the site provides insight into how coral diversity and growth are impacted when corals are exposed to low pH for an extended period of time [high CO_2 water has discharged for millennia, (Beddows et al., 2002)]. Crook et al. (2012) found that only three coral species (*Porites astreoides, P. divaricata,* and *Siderastrea radians*) persisted close to the ojos where the Ω_{arag} was <2.5. Further analysis of the growth rates of *P. astreoides* showed no change in linear extension rates, but a fall in skeletal density (*ca.* 40%) and calcification (*ca.* 30%) when Ω_{arag} was below 2.0, relative to an adjacent control site where Ω_{arag} was >3.5 (Crook et al., 2013). The ojos sites can experience changes in temperature, salinity and light that may in part explain the reduced calcification rates (Iglesias-Prieto et al., 2014), although the collective assessment from the laboratory and field experimentation suggests low pH is largely responsible for the reductions in calcification measured (Paytan et al., 2014). To date for this site, no molecular data or information on other life-history traits (e.g., metabolic properties) have been published, making it difficult to assess whether this reduction in density does indeed demonstrate a lack of acclimation ability for *P. astreoides* (Crook et al., 2013) or rather highlights a potential survival process to persist in adverse conditions (e.g., phenotypic or metabolic plasticity, see Pigliucci et al., 2006). Either way, these findings corroborate results from the vent sites that coral calcification will likely be compromised under low pH.

Highly Variable pH/CO_2 Environments

Similar to corals, seagrasses (**Figure 2**) are ecosystem engineers given that they modify their local physical and geochemical conditions (Duarte et al., 2013). During daylight hours, seagrass photosynthesis removes CO_2 lowering DIC, while at night, respiration dominates in the absence of photosynthesis, increasing DIC. This metabolic activity in seagrass meadows has been documented to cause large diurnal variation in local seawater carbonate chemistry conditions that can alter the saturation state of carbonate minerals (Schmalz and Swanson, 1969). For example in the Cayman Islands, pH varied by 0.3 units over a diel-cycle (Camp et al., 2016b). Daytime drawdown of CO_2 has resulted in seagrass meadows having elevated pH during the day across several regional locations, e.g., Spain

(Invers et al., 1997), Florida (Manzello et al., 2012), the Cayman Islands, Indonesia, and the Seychelles (Camp et al., 2016a) that can create an inshore-to-offshore carbonate chemistry gradient (Manzello et al., 2012; Camp et al., 2016a). The capability of seagrasses to elevate local mean pH has led to them being described as potential refugia under ocean acidification (Manzello et al., 2012), since they buffer resident species from rising seawater acidity (Hofmann et al., 2011; Manzello et al., 2012; Hendriks et al., 2014). Unsworth et al. (2012) proposed that the photosynthetic activity of seagrass meadows in the Indo-Pacific could enhance seawater physicochemical conditions to increase coral calcification downstream by as much as 18%. However at night, high respiration rates can lead to seagrass meadows becoming a source of CO_2 (Schmalz and Swanson, 1969), causing large drops in local seawater pH, that at several locations have caused pH to fall below 7.8 (Camp et al., 2016a,b), creating conditions predicted under future ocean acidification (Feely et al., 2004).

The ability of seagrasses to modify the local environment may result in non-genetic ecological inheritance (Bonduriansky and Day, 2009), influencing the evolutionary selection pressure on themselves and other local taxa (Mumby and Van Woesik, 2014). Seagrass meadows have not typically been considered important coral habitats due to a lack of solid substrate (Jackson, 1986; Manzello et al., 2012). However, corals can recruit into seagrass systems; for example in the Cayman Islands where 14 coral taxa (primarily *P. astreoides* and *Siderastrea* sp.) were found to recruit into seagrass beds (Lohr et al., 2017). The ability of seagrasses to moderate the local seawater carbonate chemistry has resulted in an increased interest in their role as a coral habitat and potential coral refugia, although, the latter role is still unclear. Increased availability of CO_2 and HCO_3^- under ocean acidification is predicted to enhance photosynthetic rates of carbon limited seagrasses (Durako, 1994; Buapet et al., 2013; Hendriks et al., 2014) and increase the growth and biomass of seagrass beds (Zimmerman et al., 1997). Research from high CO_2 systems has provided compelling evidence that seagrasses will flourish (Hall-Spencer et al., 2008; Fabricius et al., 2011; Duarte et al., 2013), sustaining their ability to modulate pH (Duarte et al., 2013). Furthermore, low night-time pH could result in chemical conditions where carbonate-sediment dissolution occurs (Yamamoto et al., 2012), increasing local A_T and pH, thus creating a self-buffered system (Andersson et al., 2014). However the shallow nature of seagrass systems means they also experience variability in other parameters such as oxygen (Hendriks et al., 2014), salinity (Manzello et al., 2012), temperature (Manzello et al., 2012; Camp et al., 2016a,b), and light (Hendriks et al., 2014). Work from seagrass habitats in the Cayman Islands suggests that if future diel-oscillations in pH and temperature change at an equivalent magnitude as predicted for the open-ocean, seagrass systems could be limited in their ability to buffer resident species, due to the extreme low night-time pH and elevated daytime temperatures they experience (Camp et al., 2016b). Consequently, the interactive effect of local physicochemical conditions, and the magnitude of diurnal and seasonal variance, will likely control whether any protective services are provided by seagrass systems in the future.

High Temperature Environments

Tropical corals live close to their upper thermal limits and are therefore highly sensitive to periods of elevated SST and ocean warming (Heron et al., 2016). Coral bleaching occurs when corals lose a significant portion of their algal endosymbionts and/or photosynthetic pigments in response to heat stress, and can result in widespread coral mortality on regional-to-global scales. Global interest in elevated temperature effects on corals has peaked recently due to the increasing frequency and intensity of thermally-induced mass bleaching events (Hughes et al., 2017). This has led to research efforts that focus on identifying maximum, and variations in thermal tolerance across coral species and regions, as well as identifying potential coral refugia to future ocean warming.

During the summer season, the Persian-Arabian Gulf (PAG) experiences the highest sea temperatures in the world, yet still houses a significant number of coral species (55–60 species) despite the most extreme temperature conditions ever recorded for extant coral reefs (Sheppard, 2009; Riegl and Purkis, 2012). Shallow (generally <30 m) water depth and restricted water exchange with the Indian Ocean, requires that resident corals must not only endure the highest maximum SSTs ($>35°C$ in summer) recorded for extant coral reefs, but also the largest seasonal range of $>20°C$ (Sheppard, 2009; Riegl and Purkis, 2012). In addition, high evaporation rates in the PAG result in unusually high salinity, regularly exceeding 40 psu (Sheppard, 2009; Riegl and Purkis, 2012). Since the PAG was only formed about 15,000 years ago, and shifted toward the present temperature regime only 3–6,000 years ago (Sheppard, 2009; Purkis et al., 2010), Gulf corals have adapted to these extreme environmental conditions over only the last few millennia. As such, the PAG has become a popular area to better understand the mechanisms corals have evolved to thrive under warmer climates.

Corals within the PAG have the highest upper temperature thresholds for bleaching (~35–36°C; Riegl and Purkis, 2012; Coles and Riegl, 2013), but still remain highly susceptible to bleaching when temperatures exceed their local maximum summer temperatures (Coles and Riegl, 2013; Kavousi et al., 2014). For example, five times from 1995 to 2010, temperatures exceeded normal summer temperatures, reaching 35–37°C for extended periods of time, which resulted in extensive bleaching and mortality (Coles and Riegl, 2013; Kavousi et al., 2014). These disturbances resulted in a decline of branching species and rise of massive favid corals. It is well-known that massive coral species are typically more tolerant to light and heat stress, and such shifts from more heat-sensitive, branching coral communities to more heat-tolerant, massive communities are commonly observed after bleaching (e.g., Loya et al., 2001). In contrast to branching corals, massive corals have skeletons that are less efficient in enhancing the internal light field of the coral (Enríquez et al., 2017), which appears to be a key factor in enabling their higher tolerance to light and heat stress. Although less diverse and spatially complex, the new poritid- and faviid-dominated communities in the PAG appear to be relatively resilient to ongoing disturbances in the region (e.g., Bento et al., 2016) and could represent future coral communities under continued climate change and increasing anthropogenic stressors.

Extensive research into the biology of corals surviving in the warm waters of the PAG has revealed mechanisms for survival, such as metabolic trade-offs (e.g., reduced fecundity Howells et al., 2016a), and unique physiological and genetic signatures, notably a regionally prevalent heat-specialist algal endosymbiont, *Symbiodinium thermophilum* (Hume et al., 2015; Smith et al., 2017a) belonging to a highly diverse ancient group of symbionts cryptically distributed outside the PAG (Hume et al., 2016). *S. thermophilum* occurs in high temperature, high saline environments, and as such, the benefit of a temperature stress-resistant phenotype, comes with a fitness-trade off of existing in high saline systems (D'Angelo et al., 2015). In addition to the algal endosymbiont species, PAG corals appear to have evolved genetic hardware at both the level of host and host associated bacteria in heat stress resistance, for example, the coral *Platygyra daedalea* exhibits superior ability to cope with oxidative stress in the PAG compared to conspecifics from the cooler Gulf of Oman (Howells et al., 2016b). Unusual patterns in the coral microbiome of PAG corals were also recently observed, as bacterial microbiome composition was found to be similar in bleached and healthy *Porites lobata* corals (Hadaidi et al., 2017), which is in contrast to studies from other coral reef regions (e.g., Bourne et al., 2007).

The PAG is arguably the world's hottest sea supporting coral reefs; however, other hot seas exist (e.g., the Red Sea) that support corals potentially more tolerant of thermal stress events (Fine et al., 2013; Grottoli et al., 2017; Krueger et al., 2017). The hot, southernmost end of the Red Sea acts as a selective thermal barrier favoring heat-resistant genotypes; once these genotypes spread to the northern, cooler Red Sea, they live well below their bleaching threshold (Fine et al., 2013). Consequently, elevated temperatures of 2°C above average thermal maxima did not result in any coral bleaching in northern Red Sea corals in laboratory studies (Fine et al., 2013; Krueger et al., 2017), and for three coral species, *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia favus*, coral bleaching did not occur until 6°C above average thermal maxima (Krueger et al., 2017). Furthermore, the coral *S. pistillata* has shown resistance to the combined effects of ocean acidification (pH 7.8) and elevated temperatures (Krueger et al., 2017). The unique evolutionary history of northern Red Sea corals highlights the key role of broad latitudinal temperature gradients in promoting adaptation to high temperatures and providing genetic rescue via the exchange of heat-resistant genotypes across latitudes. However, high connectivity across latitudes is critical for the establishment of high temperature high-latitude coral reef environments as refugia from climate change.

Highly Variable Temperature Environments

Alongside environments that experience persistently high temperatures, environments that have variable temperature regimes can provide information on the heat-tolerance, and acclimation/adaptation potential of coral species. Variations in temperature regimes can occur due to local (e.g., tide pools) conditions, or can result from temporal differences (e.g., high-latitudinal corals).

Back Reef Tide Pools

Elevated temperatures become particularly pronounced as reefs shallow and flushing becomes restricted. One key system that has been extensively studied since the early 2000s is the back reef tide pools on Ofu Island, American Samoa. The back reef pools harbor diverse coral communities (Craig et al., 2001) and feature distinct thermal regimes, governed by the thermal dynamics of pools of different sizes (Smith et al., 2007; Oliver and Palumbi, 2011b; Koweek et al., 2015); specifically, smaller high-variance (HV) pools where SST can briefly reach 35°C during strong noontime low tides (exceeding the local critical bleaching temperature of 30°C) and fluctuate by up to 6°C daily, vs. larger moderately variable (MV) pools, where SSTs rarely exceed 32°C and exhibit a more stable thermal environment.

Corals within the HV pool appear to have acquired putative heat tolerance through genetic, physiological, and ecological adaptations. For example, phenotypic plasticity of skeletal characteristics (Smith et al., 2007) that could potentially be linked to optimization of skeletal optical properties (Enríquez et al., 2017), a switch in symbiont type that is considered more heat-tolerant (Smith et al., 2008; Oliver and Palumbi, 2009, 2011a,b), enhanced thermal tolerance when exposed to heat stress (Oliver and Palumbi, 2011b; Palumbi et al., 2014), higher transcription of heat responsive genes than MV corals (Barshis et al., 2013) and a reservoir of alleles pre-adapted to high temperatures (Bay and Palumbi, 2014). Changes in the microbiome have also been demonstrated with bacterial communities changing in response to transplantation between the MV and HV pools (Ziegler et al., 2017). Higher heat tolerance of HV corals was found to be the result of both local acclimatization and fixed effects such as adaptation, with acclimatization in <2 years achieving the same heat tolerance that would be expected from strong natural selection over multiple generations (Palumbi et al., 2014). This unique system has thus provided critical insights into the mechanisms underlying coral heat tolerance, particularly of host-based contributions to holobiont heat tolerance. Nevertheless, it is currently unclear whether even naturally heat tolerant corals can continue to improve their heat tolerance fast enough to keep pace with global warming, with locations within American Samoa recently experiencing severe bleaching (Eakin et al., 2016).

High-Latitude Environments

Corals from high-latitude environments are functionally different to tropical corals, having traits that may facilitate their survival under climate change (Beger et al., 2014). High-latitude, cooler water (sub-tropical) coral environments have received increasing attention as potential refugia from climate change and ocean warming for tropical coral reef organisms (Beger et al., 2014; Muir et al., 2015b). They currently exist at the environmental limits for growth, in terms of temperature, salinity and Ω_{arag}, where conditions are also highly seasonally variable (Kleypas et al., 1999; Guinotte et al., 2003). Well-studied locations include: Lord Howe Island and the Solitary Islands (30–32°S), Sydney Harbour (34°S) in eastern Australia, the Abrolhos Islands (28°S) and Rottnest Island (32°S) in Western Australia, Sodwana Bay in South Africa (28°S), several islands in temperate Japan (32–34°N), and Bermuda (32°N). Due to the marginal environmental conditions (particularly at more extreme high-latitudes), they can be considered natural extreme coral reef environments which differ from their tropical counterparts in many aspects. For example, the unique diversity of high-latitude reefs is due to the overlap of tropical and temperate species ranges, species that are rare or absent at lower latitudes and species endemic to these environments (Beger et al., 2014 and references therein). Species temporal turnover can be high depending on larval supply and recruitment from lower latitudes and fluctuations in environmental conditions. Whilst coral cover (Harriott et al., 1994; Thomson and Frisch, 2010; Denis et al., 2013) and even coral growth rates can be high (e.g., Ross et al., 2015), reef accretion and development are nevertheless often limited, with corals sometimes only forming living veneers on rocky substrate (Beger et al., 2014 and references therein). Furthermore, future reef accretion could become increasingly challenged with the percent changes in Ω_{arag} predicted to be greater at high-latitude reefs relative to their tropical counterparts (Hooidonk et al., 2014).

Greater fluctuations in environmental conditions at high-latitude coral reefs have been hypothesized to increase the environmental tolerance of high-latitude species as observed in tropical corals (Oliver and Palumbi, 2011b; Schoepf et al., 2015), thus potentially increasing their ability to cope with climate change. In high-latitude corals, phenotypic plasticity may support their survival, through diverse coral symbiont communities (Wicks et al., 2010b), enhanced symbiont tolerance to extreme (low) temperatures (Wicks et al., 2010a), enhanced heterotrophic plasticity (Bessell-Browne et al., 2014) and evidence of shifted thermal optima for calcification at cooler temperatures (Ross et al., 2015). High-latitude coral communities around the world have also been found to reproduce sexually and are therefore not solely dependent on recruitment from tropical region coral stocks (e.g., Babcock et al., 1994; van Woesik, 1995; Wilson and Harrison, 2003; Miller and Ayre, 2004; Madsen et al., 2014).

As predicted, corals have already extended their latitudinal range pole-wards in several locations such as Japan and eastern Australia (Booth et al., 2007; Yamano et al., 2011; Baird et al., 2012), although range expansion can be accompanied by reduced symbiont diversity (Grupstra et al., 2017). The ability and rate of this range expansion will be key in determining the ability of high-latitude locations to act as refugia. Furthermore, high-latitudinal corals themselves are increasingly threatened by climate change and ocean warming, as bleaching events have also occurred in many high-latitude locations in recent years (Celliers and Schleyer, 2002; Harrison et al., 2011; Thomson et al., 2011; Abdo et al., 2012; Smale and Wernberg, 2012). In addition, several other factors specific to high-latitude coral reefs, such as latitudinal light attenuation (Muir et al., 2015a), geographic isolation and small population sizes combined with greater predicted ocean warming and generally lower Ω_{arag} of cooler waters, could make high-latitude coral communities particularly susceptible to climate change (Beger et al., 2014). It is therefore currently unclear whether and to what extent high-latitude corals can in fact serve as refugia from continued climate change, despite evidence for some adaptations to their marginal, more extreme environments.

Broad Temperature Gradients

Reef systems that extend across broad latitudes and temperature gradients have provided evidence of juvenile (Woolsey et al., 2015) and adult corals with enhanced thermal tolerance (Ulstrup et al., 2006; van Oppen et al., 2011; Howells et al., 2012, 2013). On the Great Barrier Reef (GBR), mean summer maximum temperatures have been reported to have nearly 2°C difference at reefs 250 km apart (South Molle Island to Magnetic Island; Howells et al., 2013). Different thermal histories on the GBR have been found to influence bleaching susceptibility (Ulstrup et al., 2006; Ainsworth et al., 2016) and the physiological performance of a generalist coral symbiont (Howells et al., 2012). Warmer latitudes have also been shown to enhance heritable thermal tolerance, up to 10-fold in *Acropora millepora* from the GBR (Dixon et al., 2015). Such latitudinal gradients thus provide important information over the spatial scales through which thermal tolerance can be achieved, and opens discussion on the ability for more "tolerant" species to provide "genetic rescue" through the exchange of more tolerant larvae across latitudes (Ingvarsson, 2001). That said, studies of the coral *Oculina patagonica* in the Mediterranean across locations with different thermal temperature regimes demonstrated limited capacity to acclimate to conditions comparable to future warming (Rodolfo-Metalpa et al., 2014). Thus, the ability for corals to inherit thermal tolerance is likely to be species-specific, and highly-dependent on the dynamics of local temperature regimes. Costs may also be associated with greater thermal tolerance, for example, a thermo-tolerant symbiont, *Symbiodinium trenchii* (D1a), has been shown to reduce host mortality rates by 30% under thermal stress; however, that is accompanied by a reduction in growth rates of 50–60% (Little et al., 2004; Smith and Iglesias-Prieto, 2010; Pettay et al., 2015). Energetic trade-offs need to be considered alongside the benefit of tolerance to assess whether coral reef form and function can be maintained.

Low Light Environments

Limitations in light availability can be fundamental in restricting scleractinian coral distribution (Yentsch et al., 2002; Muir et al., 2015a). However, during thermal stress events, solar radiation can act synergistically to intensify the impact on corals (Mumby et al., 2001; Anthony et al., 2007). Consequently, shaded (Coelho et al., 2017) and low-light environments (e.g., turbid reefs and mesophotic reefs) that are typically considered marginal for coral growth, could become increasingly valuable for corals under climate change and ocean warming.

Turbid Reefs

Inshore turbid environments (**Figure 2**) often have a suite of extreme conditions, such as low light and elevated water temperatures, and thus have historically been overlooked as important coral environments. Corals employ physiological plasticity to persist in turbid waters, including flexible photosynthetic properties, which may include a change of algal endosymbiont genetic type, and/or enhanced host heterotrophy (Anthony, 2000; Anthony and Fabricius, 2000; Hennige et al., 2008, 2010; Suggett et al., 2012b). Morgan et al. (2016) recently described over 21 genera of coral surviving in muddy waters on the inshore GBR suggesting that turbid systems may afford important range (niche) extension beyond that currently considered for many key "blue water" tropical oligotrophic reef-forming coral taxa.

High irradiance exacerbates susceptibility to coral bleaching, and thus turbid reef environments where irradiance is reduced could act as potential refugia during bleaching events. Cacciapaglia and van Woesik (2015) predicted that 9% of coral environments previously considered uninhabitable under ocean warming, due to the combination of elevated temperatures and high irradiance, would be protected by the mitigating effect of shading in high turbid sites. Studies in Palau (van Woesik et al., 2012), Florida (van Woesik and McCaffrey, 2017), and on the GBR (Morgan et al., 2017) have all provided compelling evidence that coral bleaching can be reduced at high-turbidity sites. Consequently, as the oceans warm and bleaching events become more frequent, there could be a direct selection of corals able to survive in inshore turbid environments (van Woesik and McCaffrey, 2017). Potts and Jacobs (2000) propose that turbid inshore habitats have provided ecological and evolutionary continuity and refugia for scleractinian corals during non-reefal periods when environmental conditions have been too extreme for reef growth.

Mesophotic Reefs

High-anthropogenic stress experienced by shallow reefs has seen deeper reefs proposed as potential refugia (Glynn and Morales, 1997; Riegl and Piller, 2003; Armstrong et al., 2006). Under this hypothesis, deeper reefs are able to: (i) protect or reduce the disturbances faced on shallower reefs, and (ii) provide a genetic stock of corals that can re-seed shallower reefs after a disturbance. Supporting this theory are studies evidencing reduced bleaching on deeper coral reefs (e.g., Riegl and Piller, 2003; Bridge et al., 2014). However, this bleaching pattern is not always observed; for example, with deeper corals in the Seychelles bleaching first, and more severely, than shallow corals during the 1997–1998 bleaching event (Spencer et al., 2000). Smith et al. (2016) demonstrated that deep (30–75 m) coral reefs have lower bleaching threshold temperatures than shallow-reefs, and that any increase in temperature above the local mean can result in stress and bleaching. Furthermore, deepwater generally has lower pH and Ω_{arag} than shallow-water, complicating the ability of these systems to act as refugia.

Capacity for deep reefs to act as potential refugia remains debated and depends in part on the connectivity of shallow and deep coral populations (Bongaerts et al., 2011). van Oppen et al. (2011) found evidence of deep-to-shallow coral recruitment for some reefs (Scott's Reef) on the GBR, but not others (Yonge Reef). Similarly, Serrano et al. (2014) found geographic differences in vertical connectivity due to local geophysical conditions. Species-specific differences in population connectivity with depth have also been reported in the Caribbean (Bongaerts et al., 2017).

Low-light conditions of deeper reefs are considered sub-optimal, and may select against some corals that do not have the physiological plasticity to survive. For example, Smith et al. (2017b) identified the importance of photoconvertible red fluorescent proteins (pcRFPs) to support coral adaptation/acclimation to deeper waters, while Cooper et al. (2011) showed that both the host and symbiont needed to have photobiological flexibility to survive across light regimes. Similarly, Lesser et al. (2010) found for the coral *Montastrea cavernosa* in the Bahamas that both physiological and morphological adaptation was required to survive in depths down to 91 m. Changes in the endosymbiont community (e.g., Frade et al., 2008; Lesser et al., 2010; Bongaerts et al., 2015) and density (Frade et al., 2008) have also been reported with depth. Specialization of deeper coral communities suggests plasticity will be required for species to survive across depths and ultimately utilize these systems as potential refugia.

Multiple Stressor Environments

Under climate change, multiple environmental factors such as temperature, pH, and oxygen, are predicted to co-vary (Bijma et al., 2013). Understanding how these changes will co-occur and influence biological processes is one of the hardest challenges facing researchers. Natural extreme environments where multiple factors co-vary, e.g., mangrove systems (Yates et al., 2014; Camp et al., 2016a), shallow reef habitats (e.g., Price et al., 2012), macrotidal reef environments (e.g., Schoepf et al., 2015) and upwelling environments (Riegl and Piller, 2003) offer natural laboratories to address these more complex environmental questions. Notably in these systems it can be difficult to assess the relative importance of individual factors for the observed response; thus, a collective assessment with systems where one abiotic variable primarily changes is essential to advancing our understanding of how corals will survive into the future.

Mangrove Habitats

Mangroves are widespread reef-associated environments that have recently received attention for their potential services to corals threatened by climate change (e.g., Yates et al., 2014; Camp et al., 2016a). Mangrove systems have dynamic temperature, pH and oxygen profiles, and as such, expose resident corals to very different physicochemical conditions than neighboring reefs (Camp et al., 2017). Mangroves are highly heterogeneous in nature, with freshwater input, organic content, system size and consequently water residency time, along with other benthic components (e.g., seagrass composition) influencing the local physicochemical conditions. As such, mangrove systems appear to offer a range of potential services to corals, dependent on local spatial and temporal biogeochemical conditions. For example, work in the Caribbean (Yates et al., 2014) suggested that mangroves could act as a potential refuge for corals, through physical shading and the elevation of downstream A_T as a result of carbonate-sediment dissolution (i.e., buffering potential similar to seagrass habitats), as well as frequent exposure to more variable temperatures. In other locations [e.g., the Seychelles, Indonesia (Camp et al., 2016a) and New Caledonia (Camp et al., 2017)] mangrove systems have exposed corals to simultaneously low pH, low oxygen and warmer waters relative to adjacent reefs. As such, these mangrove systems may precondition corals to future climates (Camp et al., 2016a) or house corals more resilient to future climate conditions (**Figure 2**, Camp et al., 2017). In New Caledonia, over 20 coral species were regularly exposed to pH as low as 7.3, temperature 1–2°C higher than adjacent reefs, and oxygen levels below 3 mg L^{-1} (Camp et al., 2017). Initial research at this site suggests that physiological plasticity (e.g., enhanced respiration indicative of increased heterotrophy) is facilitating survival of diverse coral communities, which include numerous species typically thought to be more sensitive to stress, e.g., *Acropora* spp.

Shallow In-shore Variable Reef Habitats

Physicochemical conditions of shallow reef systems are dynamic and highly influenced by their coastal interface, ecosystem structures and local metabolic activity. Across global locations, there are reports of shallow in-shore reef systems being regularly exposed (albeit for different durations) to conditions predicted for the open-ocean under climate change by the end of the century (e.g., Hofmann et al., 2011; Price et al., 2012; Albright et al., 2013; Guadayol et al., 2014; Kline et al., 2015). The shallow water depth and reduced residency time of inshore waters can create an inshore to offshore carbonate chemistry gradient (Manzello et al., 2012; Shamberger et al., 2014; Camp et al., 2016a). Nutrient run-off and freshwater input can influence A_T, while the metabolic activity of local benthos can change $p\text{CO}_2$ levels. Sites in Palau (Shamberger et al., 2014; Barkley et al., 2015), Puerto Rico (Gray et al., 2012), Florida (Millero et al., 2001; Yates et al., 2007), and the GBR (Santos et al., 2011; Shaw et al., 2012, 2015; Kline et al., 2015) have all been characterized as having extreme in-shore low pH reef systems. In the in-shore low pH bays of Palau, coral cover and richness remained similar to control areas, but community composition shifted, with replacement of *Acropora*, *Montipora*, and *Pocillopora* with *Porites* (Barkley et al., 2015). For the abundant *Porites* sp. skeletal extension and density remained unchanged but macrobioerosion increased at the lower Ω_{arag} sites (Barkley et al., 2015). Interestingly, one of the low pH Palau communities was not dominated by *Porites* but instead, *Leptastrea*, *Platygyra*, *Favites*, and *Dipsastrae*a, contributing to the emerging evidence that a range of species are tolerant to low pH conditions. These findings suggest that acidification conditions are not deterministic, and that other local factors are also important in shaping coral community composition under low pH and low Ω_{arag} (Barkley et al., 2015).

Along with environments that have persistently low pH (e.g., Palau), there are highly variable pH habitats that routinely, through tidal and diurnal cycles, experience low pH beyond what is predicted for coastal systems by 2100 (Duarte et al., 2013). For example, the Heron Island reef flat can experience a seasonal range in temperature of 8.1°C (17.9–26°C) and pH of 1.04 (7.57–8.61; Kline et al., 2015). Daytime photosynthesis, and night-time respiration in the absence of photosynthesis, create large diel cycles in pH (0.75 units, Santos et al., 2011) and Ω_{arag} (5.4 units, Shaw et al., 2012). At these highly variable in-shore sites, carbonate chemistry conditions can be optimal (elevated pH and Ω_{arag}) or sub-optimal (low pH and Ω_{arag}), and the presence of diverse and abundant coral communities at these sites indicates that corals can tolerate, at least periodic, short-term exposure to low pH. It remains unclear whether exposure to periodic low pH and low Ω_{arag} enhances resistance to future ocean acidification. In the Cayman Islands, corals from a naturally variable inshore pH environment experienced no enhanced tolerance when exposed to conditions predicted for 2100 (Camp et al., 2016b). Similarly, three corals species in Florida Bay regularly exposed to seasonal and diel variance in $p\text{CO}_2$ and Ω_{arag} showed no reduced sensitivity to low $\Omega_{\text{arag,}}$ with calcification rates equivalent to corals from a more stable physicochemical environment (Okazaki et al., 2013). However, the natural oscillations of $p\text{CO}_2$ in these in-shore environments may reduce the negative effects of elevated $p\text{CO}_2$, by ensuring at least periodic conditions for optimal calcification. For example, Comeau et al. (2014) observed calcification rates for *Acropora hyacinthus* that were increased by 21% under 400 to 2,000 μatm oscillatory $p\text{CO}_2$ vs. 1,000 μatm constant $p\text{CO}_2$ treatment. Such heterogeneity of in-shore reef systems, means that some locations dominated by photoautotrophs could in fact see an elevation in mean pH relative to offshore, due to the daytime consumption of CO_2 elevating pH and local Ω_{arag}, as observed for the back reefs of the Cayman Islands (Camp et al., 2016a) and in seagrass dominated environments.

Macrotidal Coral Reef Environments

Coral reefs subjected to large tidal ranges are similarly exposed to extreme environmental conditions. The most extreme macrotidal reef site examined to date is the Kimberley region in northwest Australia, which features the world's largest tropical tides (up to 12 m). Corals on the reef flat of the Kimberley region have to cope with extended aerial exposure during spring low tides (up to several hours, **Figure 2**) and periods of stagnant water alternating with strong tidal currents (>10 knots). These physical conditions create extreme fluctuations in environmental parameters, such as temperature (e.g., the well-studied Shell Island where temperature can fluctuate by up to 7°C daily, Dandan et al., 2015; Schoepf et al., 2015), pH (e.g., Tallon Island where pH can fluctuate from 7.6 to 8.8 units over a spring low tide, Pedersen et al., 2016), dissolved oxygen (Pedersen et al., 2016; Gruber et al., 2017), unusually turbid waters, and monthly SST exceeding 30°C for several months a year. Despite these extreme conditions, highly diverse coral reefs exist throughout the Kimberley of up to 225 species (Rosser and Veron, 2011; Richards et al., 2015), which are comparable to inshore reefs in the central GBR ~2 decades ago (Richards et al., 2015).

Research is just beginning to uncover the biological properties that allow corals to thrive in this extreme macrotidal environment. Firstly, algal endosymbionts appear to be locally adapted with clade C dominating northern Kimberley *Acropora* assemblages (Thomas et al., 2014) and southern *Acropora* and *Dipsastraea* corals (Schoepf et al., 2015); however, further research is required to determine how *Symbiodinium* diversity within clade C is linked to environmental gradients in this region. Furthermore, thermal history has been shown to influence bleaching susceptibility of corals harboring the same symbiont type, with more variable temperature environments enhancing heat resistance (Schoepf et al., 2015). During the first documented regional-scale bleaching event in the Kimberley in the austral summer of 2016 (Hughes et al., 2017), corals were more severely bleached (Le Nohaïc et al., 2017) and experienced much greater mortality (V. Schoepf, unpublished data) at the less-variable subtidal site on Shell Island.

Reef flat communities of the Kimberley appear to have adapted their physiology to maintain metabolic balance of photosynthesis-to-respiration (P:R) despite the extreme physicochemical conditions of the reef-flat (Gruber et al., 2017). Furthermore, a seasonal calcification study revealed high resilience of coral calcification to both intertidal and subtidal temperature conditions as branching and massive corals calcified at rates that were comparable to those of similar species at a more typical coral reef 1,200 km to the southwest (Ningaloo Reef; Dandan et al., 2015). Given that rising sea levels are expected to reduce extreme temperature variation on macrotidal reef flats such as Tallon Island (Lowe et al., 2016), reef flat communities might have more time than other reef types to acclimatize and/or adapt to ongoing ocean warming. However, further research is needed on these systems to disentangle the complex interactions of acclimation/adaptation processes that support coral survival under such extreme physicochemical conditions.

Upwelling Environments

Dispersed across the world's oceans are sites where deep, nutrient-rich, cooler ocean water wells-up to the surface through local water circulation. Such waters have been proposed as potential localized coral refugia under times of thermal stress (Riegl and Piller, 2003); however, the cool water is also high in CO_2 and low in Ω_{arag}; consequently, upwelling environments have the potential to be ocean acidification hot-spots (Feely et al., 2008; Manzello, 2010). Upwelling sites clearly comprise a complex mix of abiotic stressors, with any refuge potentially limited by upwelling time (Chollett et al., 2010). In regions such as the Eastern Tropical Pacific (ETP) and Arabian Sea, marginal coral reef formation has been attributed to the cool upwelled waters creating a "pseudo-high-latitude effect" (Sheppard and Salm, 1988) by reducing reef-building processes (Benzoni et al., 2003). Here, corals do not form a true reef structure, but instead form low-relief coral carpets (often monospecific) or remain as isolated coral colonies that are generally small in size. These locations can illustrate the changes in coral community composition when reef formation ceases, as is predicted to occur in a high CO_2 world.

A unique upwelling system exists in the ETP where high CO_2 water upwells to the surface, resulting in coral reef and coral communities off the coast of the Galápagos Islands having some of the lowest Ω_{arag} documented for modern coral reefs (<2.5, (Manzello et al., 2008)). Corals of the Galápagos Islands and neighboring Panamá reefs also contend with frequent exposure to the El Niño-Southern Oscillation (ENSO, + 3–4°C during ENSO events for >2 months), creating a unique opportunity to study the long-term effects of low pH and thermal stress events on corals (Manzello et al., 2014). Only one coral reef exists within the low Ω_{arag} waters of the Galápagos archipelago and it is dominated by *P. lobata* (Manzello et al., 2014). High bioerosion rates (>25 kg $CaCO_3$ m^{-2} yr^{-1}) and low reef cementation are characteristic of sites within the Galápagos region (Manzello et al., 2008).

Upwelled waters of the ETP are also high in nutrients, which may in part have enhanced coral growth rates for four coral species of the ETP (Jiménez and Cortés, 2003). Elevated nutrient levels have the potential to alleviate some of the negative impacts of decreased coral calcification associated with the low Ω_{arag} of the upwelled waters, by potentially enhancing heterotrophy (Langdon and Atkinson, 2005; Cohen and Holcomb, 2009), or increasing inorganic nutrients that can enhance cell growth and proliferate abundance of the algal symbiont (see review by Fabricius, 2005). However, enhanced heterotrophy may not always be an advantage for corals around cooler upwelling sites, with zooplankton feeding rates of three coral species reduced under cooler upwelling conditions in Panamá (Palardy et al., 2005). High nutrients, in particular phosphates, can also reduce skeletal density (Dunn et al., 2012), and may explain why corals around the Galápagos Islands maintain their linear extension rates, but experience reduced skeletal density (Manzello et al., 2014). Increased exposure to nitrogen levels has also been documented to enhance bleaching susceptibility when exposed to heat and light stress (Wiedenmann et al., 2013) and could add to the potential bleaching susceptibility of corals at upwelling sites (D'Croz and Maté, 2004). Clearly the net-gain or cost of elevated nutrients for corals around upwelling sites remains debated and is an area for further investigation. An important consideration with upwelling sites is that the severity or even presence of upwelling is often seasonal (as occurs for sites of the ETP), meaning the physicochemical conditions representative of future scenarios may be limited in duration. Timing of assessment at these sites is therefore important, with seasonal differences having large impacts on the biodiversity recorded (e.g., Diaz-Pulido and Garzón-Ferreira, 2002; Witman and Smith, 2003).

DISCUSSION

What Are the Extreme Abiotic Scenarios Extant Corals Persist under?

Review of the current literature on extreme and marginal coral environments demonstrated that coral populations presently thrive under different combinations of extreme abiotic conditions that are comparable to, or even exceed, predictions for the open-ocean under future climate change (**Figures 3**, **4**). For example, corals around ojos experienced persistently low pH below 7.7 (Crook et al., 2013), while corals of the PAG in summer experienced temperatures exceeding 35°C (Sheppard, 2009); these are conditions that are not predicted for the tropical open-ocean to well beyond 2100 (IPCC, 2014). The predictability and duration of the extreme environmental conditions experienced by corals are important considerations when assessing the role these environments can play in coral reef research and management. For example, regular exposure, rather than periodic pulses of extreme conditions may be required to facilitate acclimation and/or adaptation (e.g., Oliver and Palumbi, 2011a; Howells et al., 2012). Alternatively, fluctuating abiotic conditions, such as pH, may offer periods of time when physiological processes (e.g. calcification) can occur at less of an energetic cost. A key question is therefore how species will respond to stress according to different exposure time-frames (Mumby and Van Woesik, 2014). To better resolve how environmental history influences the survival of extreme and marginal corals, continuous, multi-physicochemical data sets are required that show both the mean and range of environmental conditions. As demonstrated in **Figure 4**, clustering of sites varied depending on the metric considered, e.g., mean or range. When reporting environmental conditions, there is also a need to provide both the immediate and historical context. As such, it is recommended that actual abiotic measurements (both mean and variance) are reported alongside historical datasets.

The current review highlighted that few studies reported multiple physicochemical conditions. For example, a seasonal comparison of pH, temperature, A_T, salinity, and oxygen was only possible at a total of 14 sites spanning five environments (**Figure 4**). The limited data collected on multiple abiotic parameters fundamentally restricts our ability to: (i) determine how extreme some coral environments are, and (ii) understand the different biogeochemical responses reported across sites. The PCA highlights that for many environments multiple parameters interact within these extreme systems (**Figure 4**), thus emphasizing the need to collect a full suite of abiotic parameters to provide context for biological assessments (**Table 1**). Whilst such a recommendation is not trivial, it becomes increasingly important as we begin to resolve the complex abiotic interactions that regulate many biological processes.

Are There Commonalities in Coral Taxa of Extreme Environments?

Review of the current literature suggests that the capacity for coral taxa to persist in sub-optimal environments is species-specific, and largely dependent on local factors, e.g., nutrient availability. Despite a lack in common coral taxa across extreme environments, critical thresholds in community structure do appear to exist as abiotic conditions become increasingly less optimal: (i) an initial reduction in species diversity (e.g., Craig et al., 2001; Fabricius et al., 2011; Enochs et al., 2015) with specialist species often able to survive and potentially even thrive within the new environmental niche (e.g., Kroeker et al., 2011; Fabricius et al., 2014; Dandan et al., 2015; Schoepf et al., 2015), followed by, (ii) a "lethal" threshold beyond which survival ceases (e.g., Inoue et al., 2013). For example, in the vent sites of Japan, hard corals dominate at 225 μatm, become limited at 831 μatm and are absent at the highest $p\text{CO}_2$ sites (1,465 μatm, Inoue et al., 2013). Similarly, in the Kimberley region, diverse coral communities dominated by branching *Acropora* exist in tide pools characterized by large diurnal temperature but not pH fluctuations (Dandan et al., 2015), whereas coral cover drops to $<10\%$ and *Acropora* ceases to exist on reef flats where extreme temperature, pH and oxygen fluctuations create a much more extreme environment (Gruber et al., 2017).

Changes in the ecological success of coral taxa can result in shifts in coral community composition that can change the entire reef function. For example, the reduction in coral diversity and dominance by a single taxa, *Porites* of the PNG vent site have reduced architectural complexity compared to adjacent reefs, where multiple coral species with a range of growth forms are present. A loss of reef structure and architectural complexity will compromise the ecological services provided (Rogers et al., 2015). The ability for coral taxa to provide reef accretion is a clear difference between several of the extreme and marginal coral environments; some have diverse coral reef systems e.g., the reef flats of Kimberley (Richards et al., 2015) and American Samoa (Craig et al., 2001), deep-reefs (Glynn and Morales, 1997) and reefs of the PAG (Sheppard, 2009). These environments demonstrate that the realized niche for many corals can in fact span a broad range of abiotic conditions (Schoepf et al., 2015). However, in some environments, non-framework building coral populations are described, e.g., in seagrass habitats of the Cayman Islands and the mangroves of the Seychelles and Indonesia (Camp et al., 2016a,b).

Understanding the interaction of physicochemical factors that result in critical thresholds is required to better predict, and ultimately manage changes in coral community structure, e.g., from accreting reef structures to isolated coral populations. Greater environmental characterization, along with information on the fitness trade-offs for coral populations to survive in sub-optimal environments (see **Figure 2**), will be needed to better resolve the thresholds and patterns underpinning survival (**Table 1**). Ultimately, it is likely that moving to a framework that considers the key functional traits conferring fitness (Madin et al., 2016; Suggett et al., 2017) may be required to overcome the limitations and complexities in attempting to reconcile commonalities based on taxonomic identity. Understanding mechanisms that confer survival will be necessary to identify the traits of interest (Suggett et al., 2017).

Mechanisms That Support Corals Surviving in Extremes

Some naturally extreme environments are well-studied with regards to the mechanisms that support survival, while other sites have only recently been discovered (**Figure 2**). Nevertheless, across environments various adaptive mechanisms seem evident. For example, genetic and physiological characterization across environments where corals have acquired high heat tolerance have shown it is typically the result of acclimatization and/or adaptation in both the coral host and algal symbionts. For example, many PAG corals host an endemic *Symbiodinium* species with high heat tolerance (Hume et al., 2015), but the coral host also contributes to heat tolerance via a superior ability to cope with oxidative stress (Howells et al., 2016b). Similarly, prevalence of clade D *Symbiodinium* is linked to heat tolerance in corals from American Samoa (Oliver and Palumbi, 2011b), but follow-up genomic and transcriptomic work has again highlighted the critical role of the coral host in terms of higher transcription of heat responsive genes and alleles pre-adapted to high temperatures (Barshis et al., 2013; Palumbi et al.,

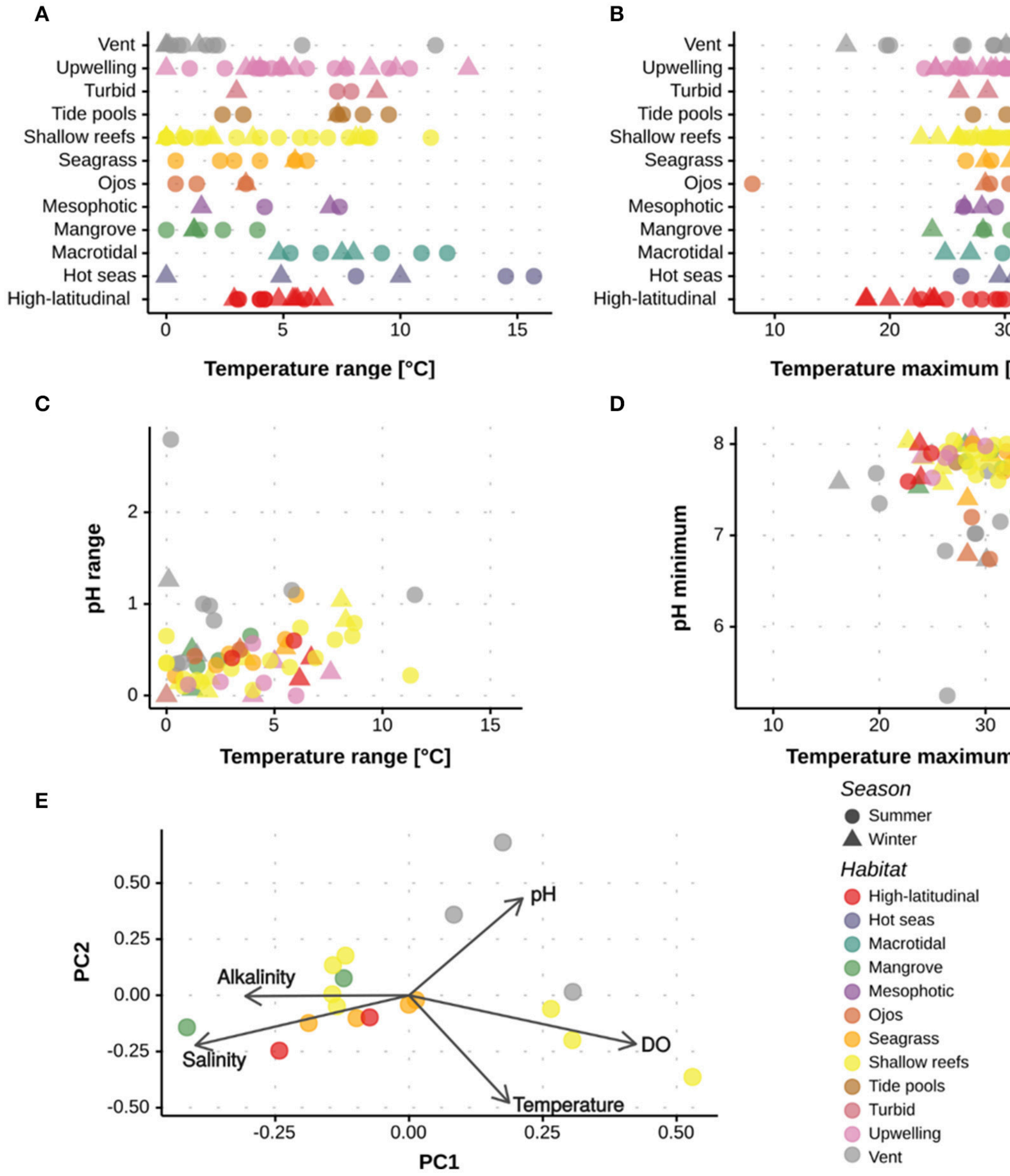

FIGURE 4 | Quantitative assessment of the abiotic conditions experienced at the different extreme and marginal environments. Data are shown for studies out of the 285 assessed that reported the maximum, minimum or range in **(A,B)** temperature, **(C,D)** temperature and pH, and **(E)** temperature, pH, A_T, salinity and oxygen. Data are shown per season and environment. **Supplementary Table 1** and **Supplementary Figure 1** have the references for the data used.

2014; Bay and Palumbi, 2015). Around the vent sites of PNG, changes in gene expression of *Symbiodinium* were highly variable across populations of *A. millepora*, whereas the host-response remained consistent (Kenkel et al., 2017). These findings suggest population-specific responses may exist, driven by differences in the holobiont community.

Capacity for phenotypic plasticity is also clearly critical in response to naturally extreme environmental conditions. For example, corals across high temperature, low pH, and multi-stressor sites were able to maintain high calcification rates (e.g., Dandan et al., 2015; Wall et al., 2016), enabled via mechanisms such as unimpaired pH-homeostasis at the site of calcification (Wall et al., 2016) or increased photosynthesis rates to supply the required energy demand (Strahl et al., 2015a). Although this is sometimes associated with trade-offs such as lower skeletal density and increased bioerosion (Smith et al., 2007; Crook et al., 2013), other corals are able to do so without indication of compromised energy budgets (Strahl et al., 2015a). Similarly, corals in mangrove habitats appear to enhance respiration rates indicative of increased heterotrophy, to facilitate survival in this challenging habitat (Camp et al., 2017). Traits that can facilitate energy acquisition appear beneficial across environments as

TABLE 1 | Future research priorities.

- Collection of longer-term, high-resolution abiotic data sets that include multiple parameters, across different temporal scales.
- Reporting of both mean and variance, and the time-frames over which data were collected to allow better cross-comparison between studies and environments.
- Utilization of multi variant analysis to consider the influence of several abiotic variables on the biological responses reported for corals in extreme systems.
- Ground truth satellite data by deployment of *in situ* loggers.
- Research that considers multiple members of the coral holobiont.
- Research on physiological traits beyond photosynthesis and calcification rates, particularly related to energy budgets.
- Research into the fitness trade-offs associated with surviving in sub-optimal conditions.
- Research into the connectivity of extreme coral populations relative to adjacent, optimal reef environments.
- Understanding the interaction of multiple-stressors, across varying temporal scales.

corals persist toward the tails of their fundamental niche (Sommer et al., 2014). Currently it is still being resolved how the long-term ability to cope with one stressor could impact the ability of corals to deal with other chronic stressors. For example, in the coral *A. millepora* at the PNG vent site, a downregulation of chaperones could increase its vulnerability to temperature stress (Kenkel et al., 2017). Understanding the interaction of multiple-stressors, across varying temporal scales, should be a research priority (**Table 1**).

For many environments significant knowledge gaps exist regarding the adaptive capacity of their coral population (**Figure 2**), and further research is required to identify how widespread phenotypic plasticity is across these extreme systems. In particular, it is poorly understood whether high physiological plasticity is ultimately an inheritable trait and thus reflects adaptation of specialist populations. In the PAG for example, the algal endosymbiont *S. thermophilum* demonstrated superior heat tolerance but only within the high saline waters of the PAG (D'Angelo et al., 2015), thus demonstrating that adaptation can constrain the acclimatization potential of well-adapted populations. Similar evidence comes from heat tolerant corals in American Samoa, where the genotype of the coral host limits the plasticity of physiological responses when faced with new environmental conditions (Barshis et al., 2010). Such "specialist" restrictions carry critical implications for the ability of naturally stress-resistant corals to cope with future climate change superimposed on already extreme physicochemical conditions. As a consequence, protecting existing biodiversity by maintaining the largest possible pool of potentially stress-tolerant genotypes, rather than solely the best adapted genotypes, will be crucial to provide sufficiently diverse genetic material for evolution to act on, and thus promote rapid adaptation to climate change (Hume et al., 2016).

The Potential of Refuge Environments

Refuge environments are likely to become increasingly important, particularly for species that are less capable of acclimating to environmental change. The current review shows that there are systems that could off set single stressors; for example, turbid reefs can provide refuge for corals during thermal stress events (van Woesik et al., 2012; Morgan et al., 2017; van Woesik and McCaffrey, 2017) whereas high-latitude reefs can provide refuge from rising ocean temperatures (Beger et al., 2014; Muir et al., 2015a). However, with the exception of the northern Red Sea (Fine et al., 2013), most refuge environments are highly debated, with inconsistent findings across geographic locations. This, in part, results from the heterogeneity of coral environments on the scale of individual reefs. For example, local hydrography likely explains why some deep reefs, but not others, are capable of seeding shallow reefs (van Oppen et al., 2011; Serrano et al., 2014). Similarly, differences in local physicochemical conditions see mangroves of the U.S. Virgin Islands considered a coral refuge, while mangrove systems in the Seychelles, Indonesia and in New Caledonia are not (Camp et al., 2016a, 2017).

Timing of buffering is also an important consideration at these potential refuge environments. Upwelling sites, for example, can only offset thermal stress if the pulse of cool upwelled water coincides with a stress-event, yet this is frequently not the case (Chollett et al., 2010). Similarly, seagrass environments can only positively enhance local seawater pH and Ω_{arag} during the day, with the opposite occurring at night due to the dominance of respiration in the absence of photosynthesis (Schmalz and Swanson, 1969). Furthermore, environments that operate as a refuge against one abiotic variable may also enhance stress from another; for example, cool upwelled water often has a lower Ω_{arag}, which can increase the threat of ocean acidification (Manzello, 2010). Similarly, lower light levels and Ω_{arag} characteristic of high-latitude reefs, particularly during winter, could potentially become limiting for many physiological variables (Beger et al., 2014; Muir et al., 2015a,b).

A further complication of refuge environments is that we currently have only limited information on the ability of non-native coral populations to move into these systems. Although poleward range expansion of tropical coral has been documented in several geographically different locations (e.g., Yamano et al., 2011; Baird et al., 2012), such information for other potential refuge environments is currently lacking. Thus, we do not know if all corals could utilize potential refuge services as they may lack the traits needed to survive. For example, there is evidence that corals surviving on deep reefs require physiological plasticity to survive (Lesser et al., 2010; Cooper et al., 2011; Smith et al., 2017b). An ultimate unknown on the potential of refuge environments is how they will themselves change in the future, and ultimately whether favorable physicochemical conditions can be sustained (Shaw et al., 2013). What we do know is that our understanding of conditions optimal for refugia is increasing, but that the heterogeneous nature of reef systems challenges the ability for environments to act as refuge against multiple abiotic parameters. Effective refugia have recently been described by Kavousi and Keppel (2017) as needing to provide long-term buffering to multiple-stressors. As such, consideration could be given to environmental engineering to facilitate the suite of conditions required for effective refugia, e.g., artificial shading (Coelho et al., 2017).

CONCLUSIONS

The future structure and composition of coral communities will be shaped by the vulnerability of different species to climate change and local stressors. Protection of existing biodiversity must be a priority to help maintain the greatest pool of stress-resistant genotypes (Hume et al., 2016). Critical thresholds appear to be a commonality for coral populations within extreme coral environments, which could provide valuable information on the tipping-points beyond which coral reefs or coral populations cease to exist. Importantly, corals will need to be ecologically competitive despite the extreme prevailing conditions to maintain their form and function. This could be increasingly challenging if they experience reductions in growth, while other taxa they compete for space with flourish, e.g., photoautotrophs (Durako, 1994; Buapet et al., 2013; Hendriks et al., 2014). Slower growth not only limits reef formation, but it can also compromise recruitment success (Ortiz et al., 2014). The interaction between taxa will be important in shaping the realized niche of corals into the future as environmental conditions change. As such, caution should be taken in making simple projections on future reef form and function when only a limited number of species are considered (Mumby and Van Woesik, 2014).

Our collective assessment of extreme and marginal coral environments highlights that multiple factors appear important to coral survival in sub-optimal conditions, particularly phenotypic plasticity and ecological fitness traits that can facilitate energy acquisition. Consequently, unless corals can be protected by refuge environments, it will be the collective suite of available traits of the coral holobiont that determine its adaptive capabilities and ultimate survival. As such, understanding the full suite of traits available for corals to trade-off for survival is imperative to assessing the future vulnerability of species, and ultimately shifts in community structure and function (**Table 1**) (van Woesik et al., 2012). Caution must therefore be taken in assessing single traits and using these to make statements on acclimation and/or adaptive potential (e.g., Suggett et al., 2017).

While no single environment is a perfect analog to projected future climates (which themselves are uncertain), they consistently provide evidence of corals tolerant to stress conditions that could become the "norm" in the future, and that plasticity is often required to survive. Extreme coral populations provide key additional tools for researchers to use alongside laboratory studies and modeling, to better understand the future survival of coral reefs. Beside the value extreme coral environments offer for research, they may also provide additional management options for corals through refuge systems or by providing genetic stocks of corals preconditioned to extreme physicochemical conditions (Camp et al., 2016a). Current information on coral refuge environments remains highly-debated, but evidence suggests the northern Red Sea could provide some refuge for corals in the future (Fine et al., 2013). Reduction of emissions, in particular carbon dioxide, is undoubtedly required to preserve the future form, function and ecosystem services of coral reefs (Gattuso et al., 2015; Hughes et al., 2017). But there is also an increasing debate over the need to facilitate coral survival through proactive reef management, e.g., reef restoration and/or assisted evolution processes (e.g., Coles and Riegl, 2013; van Oppen et al., 2015; Oppen et al., 2017). The use of proactive reef management is highly debated and beyond this synthesis (see van Oppen et al., 2015; Oppen et al., 2017), but what is evident from these extreme environments is the presence of corals that have traits highly favorable for future survival. For many environments we still do not know how these traits may be conserved or lost as corals are moved to new environments, however evidence of heritable heat-tolerance (Palumbi et al., 2014) and conserved thermal tolerance (Hume et al., 2013) has been reported.

Despite current knowledge gaps, extreme coral environments may have an unrecognized (and disproportionally) high conservation value, due to the trait selection of resident coral populations adapted to extremes. Furthermore, extreme environments may offer genetic rescue (e.g., heat-tolerant genotypes across latitudes), which again gives them a high research and conservation value. As we move to identifying areas of high conservation priority to better target limited management resources, encompassing areas that have extreme elements may be crucial in maximizing diverse genetic populations.

AUTHOR CONTRIBUTIONS

EC, DSu, and VS conceived the manuscript. EC and VS led the review and quantitative synthesis. LH conducted the data analysis and figure production. EC and VS led the writing of the manuscript with all authors contributing to the final manuscript preparation.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00004/full#supplementary-material

Supplementary Table 1 | Literature used in the quantitative synthesis for each environment.

Supplementary Figure 1 | Quantitative assessment of the abiotic conditions experienced at the different extreme and marginal environments. Data is shown for studies out of the 285 assessed that reported the maximum, minimum, or range in **(A,B)** temperature, **(C,D)** temperature and pH, and **(E)** temperature, pH, A_T, salinity, and oxygen. Data is shown per season and environment. Numbers correspond to the studies where data was obtained (detailed in **Supplementary Table 1**).

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REVIEW
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Mechanisms of Thermal Tolerance in Reef-Building Corals across a Fine-Grained Environmental Mosaic: Lessons from Ofu, American Samoa

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Environmental heterogeneity gives rise to phenotypic variation through a combination of phenotypic plasticity and fixed genetic effects. For reef-building corals, understanding the relative roles of acclimatization and adaptation in generating thermal tolerance is fundamental to predicting the response of coral populations to future climate change. The temperature mosaic in the lagoon of Ofu, American Samoa, represents an ideal natural laboratory for studying thermal tolerance in corals. Two adjacent back-reef pools approximately 500 m apart have different temperature profiles: the highly variable (HV) pool experiences temperatures that range from 24.5 to 35°C, whereas the moderately variable (MV) pool ranges from 25 to 32°C. Standardized heat stress tests have shown that corals native to the HV pool have consistently higher levels of bleaching resistance than those in the MV pool. In this review, we summarize research into the mechanisms underlying this variation in bleaching resistance, focusing on the important reef-building genus *Acropora*. Both acclimatization and adaptation occur strongly and define thermal tolerance differences between pools. Most individual corals shift physiology to become more heat resistant when moved into the warmer pool. Lab based tests show that these shifts begin in as little as a week and are equally sparked by exposure to periodic high temperatures as constant high temperatures. Transcriptome-wide data on gene expression show that a wide variety of genes are co-regulated in expression modules that change expression after experimental heat stress, after acclimatization, and even after short term environmental fluctuations. Population genetic scans show associations between a corals' thermal environment and its alleles at 100s to 1000s of nuclear genes and no single gene confers strong environmental effects within or between species. Symbionts also tend to differ between pools and species, and the thermal tolerance of a coral is a reflection of individual host genotype and specific symbiont types. We conclude the review by placing this work in the context of parallel research going on in other species, reefs, and ecosystems around the world and into the broader framework of reef coral resilience in the face of climate change.

Keywords: phenotypic plasticity, polygenic adaptation, coral reefs, thermal tolerance, acclimatization, *Acropora*

INTRODUCTION

Species are often spread across heterogeneous environments, and populations that experience different temperature regimes can have markedly different responses and thresholds to thermal stress (Somero, 2010; Pereira et al., 2016). This is particularly true for marine organisms that have large geographic ranges that encompass strong gradients in temperature (Sorte and Hofmann, 2004; Sagarin and Somero, 2006; Dong and Somero, 2009; Kuo and Sanford, 2009). Understanding the mechanisms underlying variation in thermal tolerance within and among species has been a central focus of ecology for decades and is becoming increasingly urgent as climate change intensifies environmental stressors and alters species distributions (Somero, 2010; Wernberg et al., 2016).

Thermal tolerance arises primarily through two mechanisms: acclimatization and adaptation (Chevin et al., 2010; Foo and Byrne, 2016). Acclimatization refers to the physiological plasticity that allows an individual to maintain performance across a range of environments. It represents a physiological response within an organism's lifespan, resulting in a phenotypic shift that is plastic and often reversible. By contrast, adaptation is the result of environmental selection on beneficial genotypes in a population (Barrett and Schluter, 2008; Savolainen et al., 2013). Selection is acting on specific alleles, so these changes are heritable and passed on to the next generation. Thus, while acclimatization can occur within a single individual, adaptation acts between generations.

Coral reefs are dynamic yet fragile ecosystems and are particularly vulnerable to the impacts of climate change (Hoegh-guldberg, 1999; Hughes et al., 2003; Hoegh-guldberg et al., 2007). Bleaching sparked by an increase of ocean water temperature has triggered widespread coral mortality over the past decades, including global die-offs in the recent 2015, 2016, and 2017 El Niño years (Hughes et al., 2017). Yet coral reefs occur in a variety of different temperature regimes, with corals in one area able to withstand the same warm temperatures that cause bleaching in their conspecifics from other areas. As the climate warms, natural variation in thermal tolerance will be a key driver in the capacity of corals to cope with rapid environmental change (Palumbi et al., 2014; Dixon et al., 2015; Kleypas et al., 2016); however, there is still much to learn about the underlying mechanisms driving thermal tolerance in reef-building corals.

Environments that are characterized by high levels of temperature variation at fine-spatial scales are ideal settings to unravel the relative roles of phenotypic plasticity and adaptation in thermal tolerance while minimizing the impacts of demographic processes that can confound patterns across broader spatial scales (e.g., latitude). Furthermore, corals thriving in present day extreme thermal environments can offer important insight into the mechanisms of elevated thermal tolerance and the future capacity for reef corals in general to cope with a rapidly warming planet. In this review, we summarize the findings of over a decade of research into the mechanisms of thermal tolerance in corals of the back-reef pools on Ofu, within the Manu'a Islands Group of American Samoa. The corals in these back-reef pools are exposed to a range of tidal temperature fluctuations that give rise to significant physiological differences between conspecific corals inhabiting different pools. Focused on the important reef-building genus *Acropora*, this work has shown us that the variation in thermal tolerance among pools arises from a combination of acclimatization and adaptation and that there are 100's of genes involved in each mechanism. While acclimatization can greatly elevate the thermal tolerance of individuals at remarkably fine temporal scales, fixed genetic differences facilitate a level of bleaching resistance that cannot be achieved through acclimatization within a single generation. To conclude, we place this work in the context of parallel research going on in other species and in the broader framework of resilience in the face of rapid climate change.

THE SETTING

Ofu Island

The natural temperature mosaic in the lagoon of Ofu, in the Manu'a Islands Group of American Samoa, is an ideal natural laboratory for studying thermal tolerance in coral. The fringing reef along the southern coast of Ofu lies in the National Park of American Samoa and forms a series of back-reef pools with diverse coral assemblages with ~80 scleractinian species (Craig et al., 2001). During low tides the prominent reef crest obstructs circulation, and water in the back-reef pools becomes stagnant and heats up. On high tides, the pools experience extensive flushing (Koweek et al., 2015). As a result, the corals in these back-reef pools are exposed to wide swings in temperature and irradiance throughout the tidal cycle (Craig et al., 2001; Smith and Birkeland, 2007). The most variable of these pools reach ≥34°C during summer low tides and exhibits daily thermal fluctuations up to 6°C. Corals in these variable back-reef pools have higher stress protein biomarker levels (Barshis et al., 2010) and faster growth rates (Smith et al., 2007) than exposed fore-reef populations.

Within the back-reef, two adjacent pools ~500 m apart have different temperature profiles (**Figure 1**). The smaller of the two pools (~4,000 m^2, 1.1 m depth at low tide) experiences temperatures that range from 24.5 to 35°C, whereas the larger pool (~27,000 m^2, 1.9 m depth at low tide) is characterized by more moderate variation in temperature (25–32°C) (Craig et al., 2001). These pools will hereafter be referred to as the highly variable (HV) pool and the moderately variable (MV) pool, respectively. Both pools harbor diverse coral assemblages that are nearly identical in species diversity and percent live coral cover (Craig et al., 2001).

Standardized Stress Tests

Exploring variation in thermal tolerance among coral populations from the two pools requires a standardized assay to measure bleaching resistance. In order to do this, a portable stress tank system was developed that provides accurate (within 0.2°C) controllable temperature profiles that can mimic field recordings of reef temperatures (Palumbi et al., 2014). Each tank is made of a 5-gallon cooler equipped with two Peltier chillers and a 200-watt aquarium heater powered by a custom-built interface based on a Newport controller. The typical heat stress profile ramps water temperature from 29 to

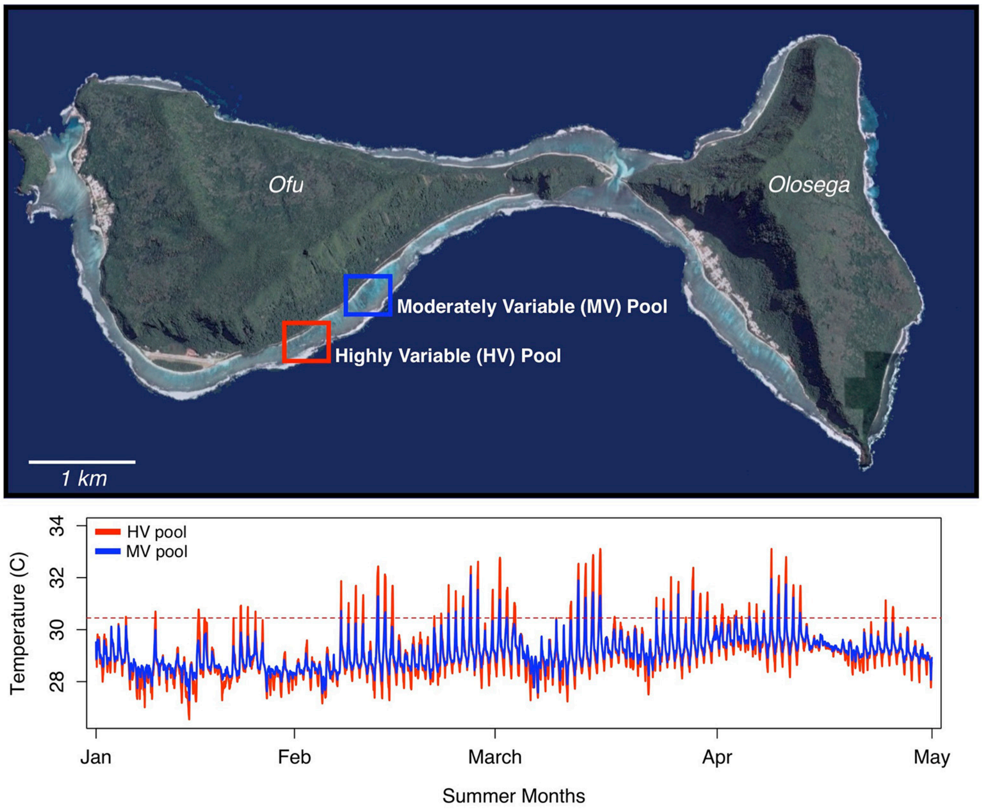

FIGURE 1 | Location of the highly variable (HV) and moderately variable (MV) pools on Ofu, in the Manu'a Islands Group of American Samoa. The plot below shows the temperature profiles over the summer months for the two adjacent back-reef pools.

34°C over 3 h starting about 10 a.m. The tanks hold at 34°C for 3 h, before cooling back down to 29°C within an hour. For each heat stress experiment, several coral branches 1–2 cm in length are collected from a set of colonies and placed in control (29°C) and heated experimental tanks in the morning. The temperature ramp is conducted from 10:00 to 16:00, and bleaching is recorded the next morning, 20 h after the onset of heat stress. Bleaching levels seen 20 h after heating in *Acropora* corals remained stable in subsequent days of incubation at 29°C. Heated branches are then compared to branches from the same colonies from control tanks, visually scored on a 1–5 scale (Seneca and Palumbi, 2015; Rose et al., 2016), and placed in 3 ml of 95% ethanol for chlorophyll spectrophotometric analyses (Ritchie, 2008). Samples used for genomic analyses are preserved in RNAlater. It is important to note that different profiles are needed for species with different heat responses. For example, *Porites* corals often require multiple days of treatment; heat levels high enough to cause a reaction in 1 day often kill the coral outright.

The Acute Heat Stress Response

Whole transcriptome analysis offers insight into the entire physiology of an organism under stress and is an emerging tool used to explore the stress response in natural populations (Franssen et al., 2011). By combining the portable stress assay with RNA sequencing technologies, Seneca and Palumbi (2015) showed that colonies of *Acropora hyacinthus* from both pools mount a large and dynamic physiological response to heat stress that involves thousands of transcripts. These results showed that acute heat stress broadly affects protein processing, cell cycle, and metabolism at first, while the later bleaching response is associated with activity in RNA transport, extracellular matrix, calcification, and DNA replication and repair (Seneca and Palumbi, 2015). In addition, high-resolution temporal sampling every 30 min indicated that components of the transcriptome are significantly upregulated within 90 min following the onset of heat stress (Traylor-knowles et al., 2017a). Spatial gene expression visualization using histological techniques showed that this stress response is a complex mix of responses from different cell types (Traylor-Knowles et al., 2017b). The data suggest that heat responsive genes occur widely in coral tissues outside of symbiont containing cells and that an expression response to bleaching conditions does not itself signal that a gene is involved in bleaching, but rather may be a component of a generalized stress response (Traylor-Knowles et al., 2017b).

The environmental stress response in organisms often consists of a large and dynamic transcriptome response that involves thousands of transcripts. As a result, sorting through the swaths of gene expression data for genes that are more important than others in driving thermal tolerance can be extremely difficult. One solution to this problem is to focus on groups of co-expressed genes rather than looking at genes individually. Co-regulated gene sets, or transcriptional modules, can represent distinct physiological units with individual functional enrichments, environmental responses, and relationships to physiology that simplify interpretations of the stress response.

The acute heat stress response in *A. hyacinthus* involves changes in thousands of transcripts that can be explained as variation in the expression of a small number of co-regulated transcriptional modules (Rose et al., 2016). These modules have various functional enrichments, and the expression of two modules (Module 10 and Module 12) at the onset of heat stress predicted bleaching outcome at the 20-h time point. Module 10 was negatively correlated with bleaching and enriched for extracellular matrix proteins and Module 12 was positively correlated with bleaching and enriched for sequence-specific DNA-binding proteins such as transcription factors and zinc-finger proteins. Focusing on co-regulated gene sets instead of individual genes revealed that the most abundant classes of stress responsive genes (e.g., apoptosis genes) are not the most strongly related to variation in bleaching outcomes. Instead, the expression of other less abundant classes of genes (e.g., ETS-family transcription factors) is more strongly related to differences in coral bleaching (Rose et al., 2016). These results point to the fact that less abundant classes of genes occupy a potentially pivotal place in coral bleaching gene networks. Extending these analyses to different species and time-points after the onset of heat stress will help further elucidate the true relevance of these transcriptional modules in a generalizable bleaching response.

Pool Differences

Corals native to the HV and MV pools vary in thermal tolerance. Under experimental heat stress, corals from the HV pool had higher rates of chlorophyll retention (Palumbi et al., 2014), photosystem II photochemical efficiency and survivorship (Oliver and Palumbi, 2011) than the MV pool corals. In addition, variation in thermal tolerance is reflected in differences in gene expression. Corals from both pools mounted a broad transcriptomic response to experimental heat stress (Seneca and Palumbi, 2015); however, corals from the MV pool had greater increases in expression of hundreds of genes (Barshis et al., 2013). A large portion of the genes that are differentially responsive between pools are constitutively upregulated under control conditions in corals from the HV pool, suggesting that these genes may start off with a higher level of expression before heat stress (Barshis et al., 2013). Transcripts with higher constitutive expression under ambient conditions in HV corals included classic heat stress genes such as Hsp70, TNFRs, peroxidasin, and zinc metalloproteases (Barshis et al., 2013). This constitutive frontloading in HV pool corals may enable individual colonies to maintain physiological resilience during frequently encountered environmental stress.

ACCLIMATIZATION

Phenotypic plasticity can play an important role in the response of marine organisms to rapid environmental change (Chevin et al., 2010). This phenomenon can be defined as the capacity of a single genotype to exhibit a range of phenotypes in response to environmental variation (Fordyce, 2006). Limits to acclimatization, the short-term phenotypic adjustment within an individual's lifespan, are set by species-specific physiological constraints (Somero, 2010). Acclimatization is particularly relevant for long-lived organisms such as corals in the context of global climate change because this mechanism operates within a single lifespan of an organism and does not require a population-level shift in allele frequencies over multiple generations as is the case with evolutionary adaptation.

Capacity for Acclimatization

Through reciprocal transplantation, acclimatization can be quantified using the equation $I = I_F + I_A$. Here, I represents the cumulative phenotypic change between two native populations living in different habitats, measured as the average phenotypic difference divided by the standard deviation. This value is comprised of fixed effects (I_F) that are determined by the location of origin of an individual and acclimation effects (I_A) that are determined by an organism's response to its local environment. *A. hyacinthus* colonies from the HV Pool had higher chlorophyll retention after stress tests than did colonies from the MV Pool (**Figure 2**). The difference in chlorophyll retention between populations was $I = 2.45$, measured as the difference in means divided by the standard deviation. Following a 12-month reciprocal transplantation experiment, colonies of *A. hyacinthus* from the MV pool transplanted to the HV pool showed significantly ($p < 0.001$) higher chlorophyll retention during heat stress than the same colonies native to the MV pool (**Figure 2**). Acclimatization also works in the opposite direction, and HV pool corals transplanted to the MV pool dropped their chlorophyll retention to the same level as MV pool natives within 12 months. The overall change in phenotype due to acclimatization ($I_A = 1.56$ SD) was higher but similar to the estimated change caused by fixed effects between pools ($I - I_A = I_E = 0.94$ SD). Monitoring phenotypes in native populations and the same colonies after transplants indicated that both fixed effects between pools and acclimatization ability is a primary feature of coral adaptability to heat extremes (Palumbi et al., 2014).

Mechanisms of Acclimatization

Transcriptome-wide gene expression analyses via RNA-seq on reciprocally transplanted *A. hyacinthus* colonies revealed 74 genes that were differentially expressed between the two pools when comparing genetically identical coral fragments (Palumbi et al., 2014). These acclimatization genes had annotations for several transcription factors, cell signaling proteins, heat shock and chaperonin proteins, TRAF-type proteins, cytochrome P450, and fluorochromes. Loci with strong components of acclimatization include the Tumor Necrosis Factor Receptor-Associated Factors, the signaling transducers for TNFRs, as well as *Ras* and *Rab* proteins, transcription factors and heat shock proteins. Overall, 15 out of the 23 transcriptional modules that comprise the *A. hyacinthus* stress response system showed

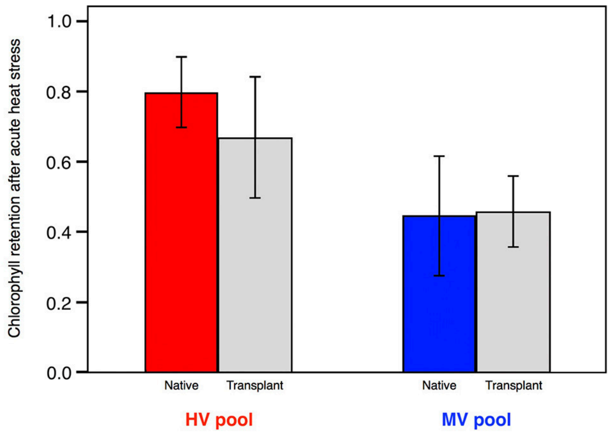

FIGURE 2 | Thermal tolerance, measured as chlorophyll retention following acute heat stress, in *A. hyacinthus* following 14 months of reciprocal transplantation between the HV and MV pools.

signs of acclimatization after reciprocal transplantation (Rose et al., 2016). These data suggest that acclimatization is in part accomplished through the regulation of co-expressed gene modules.

Rates of Acclimation

To test the rapidity of acclimation, and determine if it was equally sparked by daily variation in temperature as it is by constant temperatures, Bay and Palumbi (2015) exposed colonies of *Acropora nana* to experimental acclimation treatments mimicking local heat stress conditions (i.e., a stable 31°C and a variable 29–33°C acclimation treatment). In both sets of conditions, colonies achieved significant gains in thermal tolerance within 7–11 days (Bay and Palumbi, 2015): nubbins acclimated to heat treatments had significantly higher chlorophyll retention than nubbins from the same colonies held at 29°C prior to acute heat stress. After 7 and 11 days, acclimatized and control coral nubbins showed different transcriptomic responses to acute heat stress. Expression patterns in the absence of acute heat stress did not change compared to the original value after acclimation; coral nubbins had the same baseline transcriptional profiles regardless of whether they were exposed to a short-term heated acclimation treatment. However, almost 900 contigs showed differences in expression levels between acclimated and control corals after acute heat stress, the majority of which could be clustered into two gene modules that were significantly enriched for gene ontology (GO) terms related to carbohydrate metabolism and ribosomal RNA processing (Bay and Palumbi, 2015). These data show that rapid acclimation did not change the normal expression levels of any gene. Instead, rapid acclimation sparked the sensitivity of many genes to heat exposure—it adjusted the heat response system, not the normal daily physiology of these corals. This is in contrast to the front loading mechanism seen by Barshis et al. (2013) in *A. hyacinthus*. Those results were from corals native to either pool, suggesting that frontloading is either a longer-term acclimation response or is a reflection of genetic adaptation between pools.

Transcriptome analysis also has shown the impact of very short term environmental stresses on reefs. High-resolution transcriptomic and environmental profiling show that regular exposure to strong tidal cycles triggers a large but transient transcriptional response in *A. hyacinthus* (Ruiz-Jones and Palumbi, 2017). During a 17-day period of daily monitoring, extreme low tides on days 7 and 8 caused temperatures to spike to above 31.5°C, eliciting a transcriptional response in *A. hyacinthus* that involved hundreds of genes (Ruiz-Jones and Palumbi, 2017). These genes could be organized into three co-regulated gene sets that were enriched for gene products essential to the unfolded protein response, an ancient cellular response to endoplasmic reticulum (ER) stress. The response was transient and returned to normal expression levels after the temporary heat pulse passed, suggesting a return to homeostasis in the ER when temperatures drop below 30°C. Under experimental heat stress, the expression of these modules increases to levels above that observed during the extreme low tide, suggesting that the unfolded protein response becomes more intense during severe stress.

Symbiodinium and Host Thermal Tolerance

A well-documented driver of thermal tolerance in corals is based on the flexible association of individual colonies with *Symbiodinium* types with inherent differences in thermal tolerance (Lajeunesse et al., 2004; Rowan, 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008; Hume et al., 2015). Sequencing of the chloroplast 23s rDNA from colonies collected from both Ofu pools showed that corals from the HV pool had significantly higher proportions of *Symbiodinium* clade D than those from the MV pool in five of the seven species examined (Oliver and Palumbi, 2010). The clade D haplotype recovered was shown to be heat resistant elsewhere (Rowan, 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008). Symbiont type alone, however, could not explain differences in bleaching resistance between pools: colonies from the MV pool that also harbored high levels of clade D experienced declines in photosystem II photochemical efficiencies that were not statistically different from the MV colonies predominantly harboring clade C (Oliver and Palumbi, 2011). In addition, there was little evidence for symbiont switching in *A. hyacinthus*. Following the 12-months of reciprocal transplantation, MV pool corals transplanted to the HV pool showed an increase in thermal tolerance without a shift in symbiont clade (Palumbi et al., 2014). It is important to note, however, that these studies focused on clade-level differences between pools, which remains too course a resolution for studies of thermal tolerance in corals, as sub-cladal differences in thermal tolerance have been widely documented (Tchernov et al., 2004; Jones et al., 2008; Sampayo et al., 2008; Fisher et al., 2012; Hume et al., 2015).

The Microbiome

The coral microbiome is a far less explored realm of the holobiont than *Symbiodinium*. Bacteria have been well-documented to contribute to the health of other marine organisms and

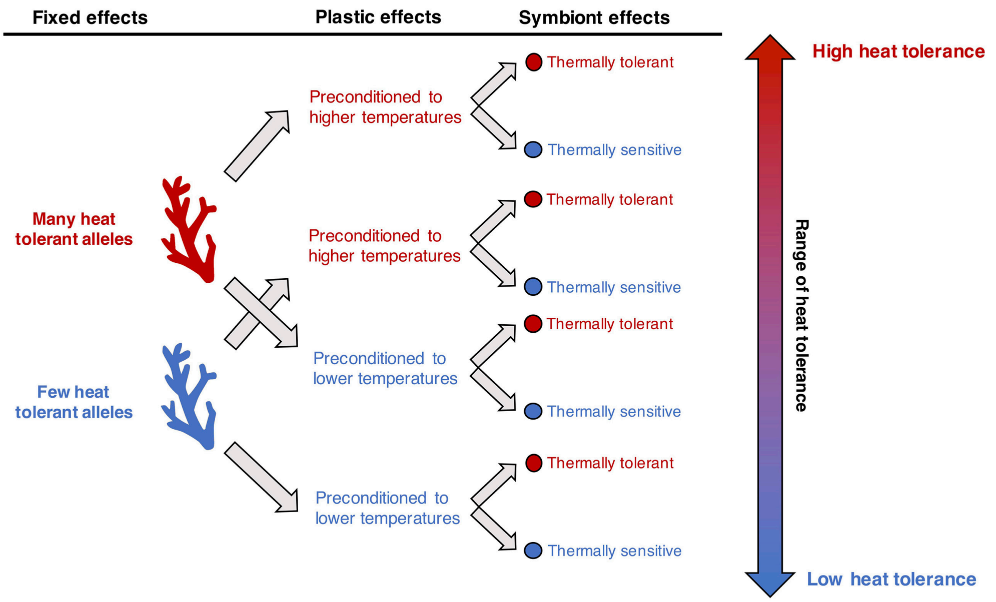

FIGURE 3 | Conceptual model for adaptation and acclimatization in generating thermal tolerance.

ecosystems, and metabarcoding approaches have begun to chart the diverse community of bacteria associated with reef corals (Ritchie, 2006; Rosenberg et al., 2007; Lema et al., 2012; Ainsworth et al., 2015; Hernandez-Agreda et al., 2017). Yet, the relative role of the microbiome in thermal tolerance remains largely unknown. In Ofu, metabarcoding of the 16S rRNA gene showed that the microbiome of *A. hyacinthus* is different between the HV and MV pools (Ziegler et al., 2017). Additionally, following 17 months of reciprocal transplantation, transplanted colonies shifted their microbial communities to reflect that of the native colonies. In subsequent short-term heat stress experiments, the microbial community shifted as a result of temperature stress in colonies transplanted to the MV pool, but colonies living in the HV pool bleached less and maintained their microbial communities. The robust and stable microbiome of corals from the HV pool was characterized by a consistent set of microbial taxa that were rare in the corals transplanted to the MV pool (Ziegler et al., 2017). These results scratch the surface of the dynamics of coral-microbial interactions. In particular, they are based on microbial observations at one point in time. As a result, even though the sampling among pools clearly shows spatial differences, and the transplant experiments allow microbial dynamics to be strongly inferred, the dynamics of microbial communities over space and time is still poorly explored.

ADAPTATION

Selection favors specific combinations of alleles that confer beneficial phenotypes (Savolainen et al., 2013) and patterns of local adaptation often reflect the thermal history of a given environment. Local adaptation, however, is a balance between selection and gene flow. When gene flow is high, gene swamping can replace locally-adapted alleles with maladaptive ones, and genetic differences between populations are eroded (Tigano and Friesen, 2016). If selection is strong enough to overwhelm the homogenizing effects of gene flow, then locally adapted alleles maintain moderate levels of frequency in the population, and genetic variation is maintained. This kind of population genetic model may be common in long lived, sessile organisms such as redwood trees or corals. Once an individual settles into a location, its survival, growth, and reproduction may depend upon the match of its inherent genetics and its habitat. In these cases, a kind of local lottery selection ensues, in which natural selection generated on a very local scale determines fitness.

Fixed Effects

Layered on top of the plastic physiological responses are sets of fixed effects that distinguish populations in the two pools. Following the 12-month reciprocal transplant experiment, corals native to the MV pool increased their thermal tolerance but could not achieve the levels of the HV pool natives (Palumbi et al., 2014). MV pool corals transplanted to the HV pool retained significantly less chlorophyll in bleaching experiments than corals native to the HV pool (68 and 80%, respectively). These differences reflect limits on the ability of acclimatization to alter thermal tolerance of a colony, and are ascribed to fixed effects between localities (**Figure 3**). Additionally, HV natives have higher survivorship (22% higher than MV natives) regardless of where they are transplanted (Bay and Palumbi, 2017), further evidence of fixed differences between the two pools.

Transcriptome-wide gene expression also identified expression differences depending strictly on the pool of origin and not on the final transplant site. Seventy-one contigs were identified that differed in expression levels depending on the origin of the colonies, including TNFRs, galaxin, superoxide dismutase, immunoglobin e-Fc receptors, and pinin (Palumbi et al., 2014). For example, TNFR genes showed a 10-fold difference in expression in colonies native to the HV pool, regardless of whether they were living in the HV pool or transplanted to the MV pool 12-months prior. These results indicate that mediators of coral thermal tolerance have constitutive expression levels that represent signs of genetically based local adaptation. They represent expression polymorphisms that differ between pools. These differences are also amplified in the transcriptional modules, where genetic differences between colonies from the two pools result in constitutive differences in expression of transcriptional modules (Rose et al., 2016). For example, corals transplanted from the MV pool to the HV pool had significantly lower expression for Rose Module 12 under heat stress, but MV pool colonies transplanted to the HV pool could not achieve the expression levels of the HV natives. These data suggest that adaptation to thermal stress is in part driven by fixed genetic differences that regulate the coordinated expression of groups of genes.

Expression Quantitative Trait Loci

Some of these differences in gene expression can be driven by higher expression of one allele over another. Expression quantitative trait loci (eQTLs) are regions of the genome that contain sequence variants that alter the expression of a gene associated with a quantitative trait (Gilad et al., 2008). Individuals that are homozygous for this region—sometimes demarcated by only a single SNP—have different expression compared to individuals homozygous for the alternate allele in that region. Heterozygotes are intermediate, with one allele being expressed more than the other. In this way, expression variation and SNP differences are functionally linked. Because they have such a clear phenotypic effect, expression polymorphisms are a class of variants on which selection can quickly act.

eQTLs that explain gene expression are common in *A. hyacinthus* and clustered in non-coding regions and among amino-acid changing positions (Rose et al., 2017). Some of these eQTLs showed differences in allele frequencies between pools that could be driving the observed expression polymorphisms. For example, individuals with a putative transcription factor *Rab*-1b ortholog showing a TT genotype at position 292 had twice the expression level of this contig compared with individuals with the AA genotype. Furthermore, AT heterozygotes show intermediate expression. These alleles were present at different frequencies in the HV and MV pools. The A allele was present at ∼50% frequency in the MV pool but was almost entirely absent from the more thermally stressful HV pool. As a result, coral colonies in the MV pool had lower *Rab*-1b expression compared to colonies in the HV pool.

These analyses are likely to underestimate eQTL occurrence because they are based on RNASeq data which ignore several important regions controlling gene expression, especially gene promoter regions and introns. However, the data show that adaptive differences in gene expression between different coral populations may be related to selection for differences in the frequencies of gene regulatory variants. Future research will benefit from utilizing complete gene models (when available) and focus more closely on regions controlling gene expression, such as promoters, to build a more complete understanding of mechanisms driving differences in gene expression associated with gains in thermal tolerance.

Multi-locus Adaptation

Population differentiation based outlier analyses have shown that thermal tolerance in *A. hyacinthus* is associated with 100's of genes of small effect (Bay and Palumbi, 2014). Genome-wide patterns of differentiation between pools is low and non-significant; however, population differentiation based genome outlier scans have identified hundreds of SNPs putatively under divergent selection (FDR-corrected $p < 0.05$, $F_{ST} > 0.05$ and bootstrap-resampling tested). Further filtering of these loci for only those that correlated with individual temperature measurements (i.e., time spent above 31°C for each colony) resulted in more than a hundred loci as likely candidates for directional selection. Minor allele frequencies for these candidate loci were higher in the HV pool, instead of having been evenly distributed among populations as were the non-candidate SNPs. Across all candidate SNPs, each HV pool coral had higher frequencies of minor alleles, on average, compared to the MV pool corals. These results suggest that a large number of loci, each with individually small effect, are contributing to the fixed effects we see between pools in thermal tolerance.

SYNTHESIS

Local Adaptation Amidst High Gene Flow

Gene flow is high among back-reef pools in Ofu, yet populations maintain significant differences in allele frequency at hundreds of loci (Bay and Palumbi, 2014). This pattern of local adaptation amidst high gene flow is consistent with the Levene (1953) model of spatially varying selection, where recruits from a mixed larval pool are exposed to different selective forces that drive subtle shifts in allele frequencies between micro-environments (**Figure 4**). Local adaptation is a balance between selection and migration (gene flow), and spatially varying selection develops into patterns of genetic differentiation only when selection is strong enough to counteract the effects of gene flow (Savolainen et al., 2013). Simulation studies show that even alleles that are not maintained at intermediate frequencies by balancing selection can contribute to local adaptation; under some circumstances this could lead to persistence of locally adapted populations with a shifting set of genomic variants underlying adaptive differentiation between populations (Yeaman, 2015). The existence of significant F_{ST} outliers which do not appear to be at stable equilibrium among eel populations that show a Levene-type system may provide evidence for the importance of non-equilibrium processes in local adaptation involving polygenic traits (Gagnaire et al., 2012).

A key question that arises from this research is whether the spatial patterns of thermal tolerance and local adaptation identified in the back-reef lagoons of Ofu are ubiquitous across a range of coral reef systems. Do all reef systems

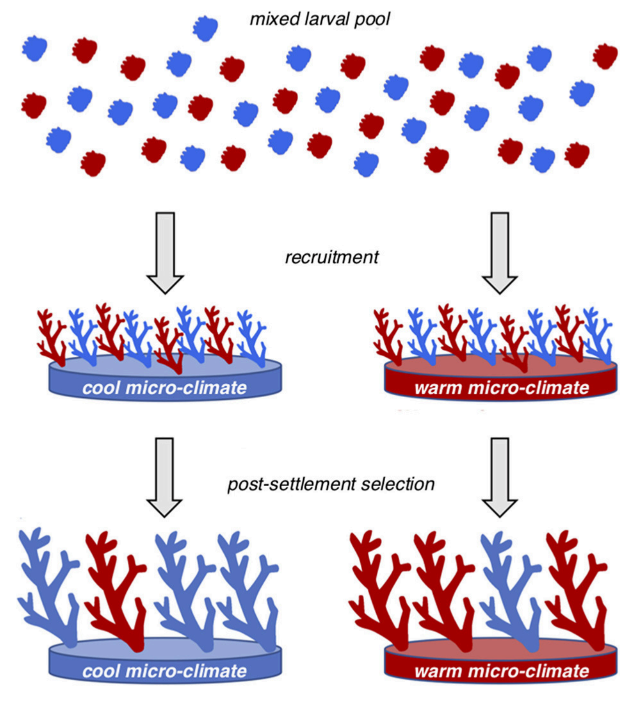

FIGURE 4 | The Levene (1953) model of spatially varying selection to explain patterns of local adaption between pools amidst high gene flow.

harbor thermally resilient locally adapted populations? What environmental conditions are associated with the presence of heat adapted alleles? Certainly, the extreme temperature profiles of the HV pool are not unique to Ofu; corals are found in a variety of extreme environments and are exposed to temperatures that would cause bleaching in their conspecifics from other areas (Coles and Riegl, 2013; Kline et al., 2015; Richards et al., 2015; Camp et al., 2017). Wide variation in thermal tolerance and genetic divergence has been reported across latitudes and at large-spatial scales (Middlebrook et al., 2008; Howells et al., 2013; Dixon et al., 2015; Thomas et al., 2017), and it is becoming increasingly clear that locally adapted thermally tolerant pockets of corals exist at fine-spatial scales within a variety of coral reef systems (Goreau and Macfarlane, 1990; Smith et al., 2007; Barshis et al., 2010; Castillo et al., 2012; Kenkel et al., 2013b, 2015; Schoepf et al., 2015). For example, *Porites astreiodes* colonies from the thermally variable inshore patch reef environment of south Florida have greater thermal tolerance than offshore populations less than 10 km away (Kenkel et al., 2013a). These populations exhibit significant spatial genetic structure (Kenkel et al., 2013b) and reciprocal transplantation experiments confirmed that the physiological differences observed between inshore and offshore populations can be attributed to local adaptation (Kenkel et al., 2015). Similarly, *Sideerastrea sidera* and *Montastrea annularis* populations from the warmer and more variable back-reef environment of the Mesoamerican Barrier Reef System have greater thermal tolerance than colonies from the more thermally stable fore-reef environment (Castillo and Helmuth, 2005; Castillo et al., 2012). This functional variation has also been reported at extremely fine-scales; intertidal corals of the remote Kimberley region in Western Australia experience aerial exposure and large daily swings in temperature and populations of *Acropora aspera* and *Dipsastraea* sp. have greater thermal tolerance than their subtidal conspecific counterparts 10's of meters away (Schoepf et al., 2015); however the genetic mechanisms remain unknown. Expanding our portfolio of known "thermally resilient" populations will help fine tune our understanding of molecular mechanisms governing thermal tolerance, thereby creating a more robust and potentially predictive understanding. Common garden experiments show that once identified, heat tolerant corals can be used in transplants to generate bleaching tolerant populations and can significantly improve the success of reef restoration efforts (Morikawa MK, personal communication).

Local adaptation requires a fitness trade-off, and alleles that confer thermal tolerance in one environment must confer lower fitness in the other environment, otherwise a locus would reach fixation for the allele with the higher fitness (Savolainen et al., 2013). This is known as reciprocal home site advantage, where adaptation to one environment comes at a cost of adaptation to other environments (Hereford, 2009). Fitness related trade-offs associated with local adaptation appear to be widespread in corals (Howells et al., 2013; Kenkel et al., 2015; Bay and Palumbi, 2017). A reciprocal transplantation experiment of *Acropora millepora* between central and southern Great Barrier Reef found signals of local adaptation in fitness related traits including thermal tolerance, reproduction, and growth (Howells et al., 2013). In addition, growth trade-offs exist between inshore and offshore populations of *P. astreoides* (Kenkel et al., 2015) and *M. annularis* (Hudson, 1981) in Florida. Similar fitness tradeoffs exist in Ofu, and colonies with the highest survivorship in the HV pool grow less when transplanted to the MV pool (Bay and Palumbi, 2017). These studies highlight the fact that although some corals are locally adapted to thermally extreme environments, costs to other fitness related traits can be high and may impede survival in foreign environments.

The Genetic Architecture of Thermal Tolerance

Accurately modeling the adaptive capacity of coral populations to climate change relies on a concrete understanding of the genetic architecture of thermal tolerance (Bay et al., 2017a). Genetic architecture refers to the number, effect size, and distribution of genes that control a phenotypic trait (Gagnaire and Gaggiotti, 2016) and can range from a few genes of large effect (oligogenic) to many genes of small effect (polygenic) (Jain and Stephan, 2017). Data from Ofu indicate that thermal tolerance is a polygenic trait, where a number of alleles of small effect across many different cellular pathways are responsible for elevated thermal tolerance of the HV pool corals (Bay and Palumbi, 2014; Palumbi et al., 2014). Polygenic traits are a common feature of high gene flow species and occur widely in marine populations (Limborg et al., 2012; Hale et al., 2013; Pespeni et al., 2013; Laporte et al., 2015; Barney et al., 2017).

When selection acts on a phenotype that is driven by a large number of loci, then large allelic shifts may not be evident and alleles will rarely reach fixation. Instead, subtle coordinated changes in allele frequencies across many loci will occur (Berg and Coop, 2014; Yeaman, 2015; Wellenreuther and Hansson, 2016). Outlier detection software that scan the genome for large effect loci are thus not capable of providing a complete picture of the genetic architecture of thermal tolerance in corals. However, when gene flow is high, as in most broadcast-spawning corals, adaptation favors the tight clustering of these small effect loci into regions of reduced genetic distance and into areas under low recombination (Thompson and Jiggins, 2014; Samuk et al., 2017). In this case, even though a large number of genes may contribute to phenotypic variation, specific chromosomal regions may play a particularly important role in driving evolutionary change. Experimental designs taking advantage of phenotypic variation within and among populations spread across variable environments may help identify these regions. The best example of this in natural populations comes from a recent meta-analysis on threespine stickelbacks, where genomic data from 52 populations showed statistically that adaptive alleles tend to cluster together on chromosomal regions of low recombination (Samuk et al., 2017).

Recently, Dixon et al. (2015) used inter-latitudinal reciprocal back crossing to identify two genomic regions of ∼100 cM in size that strongly respond to heat selection in larval populations of *A. millepora* from the GBR. This study paves the way for future research that explores the genetic architecture of thermal tolerance in corals; however; it is important to note that studies on model systems with large sample sizes often exceeding a thousand individuals still struggle to identify genes of significant impact for certain phenotypes, representing a cautionary tale for this pursuit in corals (Rockman, 2012).

Thermal History and Bleaching Susceptibility

Data from Ofu show that corals have a remarkable capacity to shift their physiology in response to environmental variation (Palumbi et al., 2014; Bay and Palumbi, 2015). Early examples of this phenotypic plasticity come from work on photo-acclimation, where individual colonies showed shifts in morphology and physiology in response to changes in solar radiation (Dustan, 1973; Willis, 1985; Brown, 1997). For example, reciprocal transplant studies of *Turbinaria mesenterina* along a depth gradient revealed significant changes in morphology depending on transplant site; colony growth became more vertical in transplants from deep to shallow water, presumably to reduce light attenuation (Willis, 1985).

More recently, focus has shifted toward understanding the plasticity of thermal tolerance in corals, and numerous studies have identified a direct link between thermal preconditioning and bleaching susceptibility from both field observations (Castillo and Helmuth, 2005; Maynard et al., 2008; Thompson and van Woesik, 2009; Castillo et al., 2012; Shuail et al., 2016) and experimental manipulation (Brown et al., 2000, 2002; Dove et al., 2006; Middlebrook et al., 2008; Bellantuono et al., 2012b; Bay and Palumbi, 2015). For example, *Acropora*, *Pocillopora,* and *Porites* from the Great Barrier Reef showed lower rates of bleaching during the 2002 bleaching event than the 1998 event, despite more intense conditions during the 2002 event (Maynard et al., 2008). Bellantuono et al. (2012b) showed that short-term experimental preconditioning to sub-bleaching temperatures results in gains in thermal tolerance without shifts in symbiont type (Bellantuono et al., 2012b).

Acclimatization as a mechanism for increased thermal tolerance, however, is most effective if the rates and limits match the dynamics of the environment. In the context of coral bleaching events, heat stress from extreme climatic events that generally drive bleaching occurs on the time-scale of weeks, so acclimatization would need to occur within this time-scale in order to be effective against warming water temperatures. Indeed, data from Ofu show that significant gains in thermal tolerance can be achieved within roughly a week of preconditioning (Bay and Palumbi, 2015). Similarly, studies from other regions and on other coral taxa have revealed significant gains in thermal tolerance after days of preconditioning (Brown et al., 2002; Dove et al., 2006; Middlebrook et al., 2008; Bellantuono et al., 2012b). For example, Middlebrook et al. (2008) showed that gains in thermal tolerance in *A. aspera* can occur in as little as 48 h of preconditioning. A similar response was observed in *A. millepora* following 8 days of experimental preconditioning to sub-bleaching temperatures (Bellantuono et al., 2012a). That corals can increase their thermal tolerance this quickly suggests that short term acclimation may be a key mechanism for resilience in the face of warming waters.

In *A. hyacinthus*, elevated thermal tolerance following thermal preconditioning is in part achieved through transcriptome dampening, where preconditioned colonies show a lesser-magnitude response to acute heat stress in certain stress response genes. This is accomplished through two fundamentally different pathways depending on the duration of preconditioning (**Figure 5**). Short-term acclimation is attained through reduced expression of stress response genes under acute heat stress (Bay and Palumbi, 2015), whereas long-term acclimatization involves a shift in baseline expression under control conditions, referred to as "frontloading" (Barshis et al., 2013; Palumbi et al., 2014). The dampening of stress response genes following short-term preconditioning has also been reported in studies on *A. millepora* from the Great Barrier Reef, which showed a lesser magnitude response of genes associated with apoptotic signaling to acute heat stress following 10 days of preconditioning (Bellantuono et al., 2012a). Moreover, Gates and Edmunds (1999) showed that exposure to heat stress triggers upregulation of heat shock proteins in *Montastrea franksi* but a return to normal expression at 12 h despite continued exposure to heat stress, indicative of acclimatization to elevated temperatures. In addition, an organism's physiological response to environmental change reflects the intensity and frequency of the stressor. For example, elevated thermal tolerance of inshore *P. astreoides* in Florida is achieved through a varying capacity for gene expression plasticity, where colonies from the more variable and warmer inshore environment show a higher capacity for shifting expression of stress response genes than colonies from

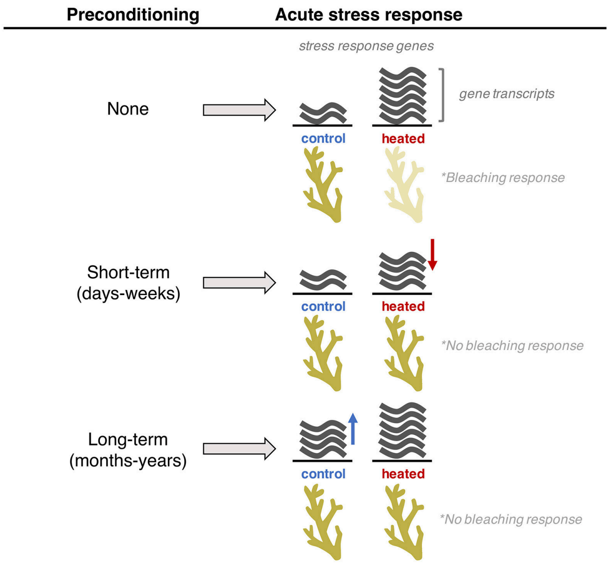

FIGURE 5 | Pathways of acclimatization to elevated temperatures. Short-term preconditioning results in the reduced expression of stress response genes during acute heat stress. Long-term preconditioning results in a fundamental shift in baseline expression of stress response genes ("frontloading").

offshore sites (Kenkel and Matz, 2016). In Ofu, daily variation in temperature is frequent enough to spark fundamental shifts in baseline expression (Barshis et al., 2013), while seasonal differences in South Florida are not frequent enough to alter baseline expression but is instead achieved through short-term expression plasticity (Kenkel and Matz, 2016).

Although phenotypic plasticity of the coral animal is one mechanism of acclimatization to environmental stress, the dynamic symbiotic relationship with dinoflagellates of the genus *Symbiodinium* offers an additional pathway to elevated thermal tolerance (Berkelmans and van Oppen, 2006; Jones et al., 2008; Cooper et al., 2011; Hume et al., 2016). In Ofu, subtle differences in temperature among pools give rise to differences in *Symbiodinium* communities between habitats, with clade D occurring at higher frequencies in HV pool corals (Oliver and Palumbi, 2010; Palumbi et al., 2014). This is consistent with a wide range of literature that have reported high proportions of clade D in colonies from more thermally extreme environments or in those that have historically encountered high levels of heat stress (Baker et al., 2004; Berkelmans and van Oppen, 2006; Jones et al., 2008; Keshavmurthy et al., 2012). Although there are clear differences in symbiont communities between pools in Ofu, colonies of *A. hyacinthus* show a limited capacity to shuffle their symbionts when transplanted to a different environment (Palumbi et al., 2014). Furthermore, the type of symbiont a coral harbored did not explain differences in thermal tolerance among pools (Palumbi et al., 2014). These data suggest that the higher prevalence of clade D in HV corals does not occur primarily because of symbiont shifts in adult corals as the external environment changes. Instead, clade C or D dominance may occur during early settlement stages or at young colony ages. As is the case with the coral host, however, adaptation and acclimatization of the symbiont represent additional pathways to rapid acclimatization and is a rapidly growing area of research (Howells et al., 2011; Baums et al., 2014; Hume et al., 2016).

Evolution in the Face of Environmental Change

As the climate warms, changes to the physical and chemical properties of the ocean pose serious challenges to the future health of marine populations. This is particularly true for corals living close to their upper thermal thresholds. Rapid adaptive responses to climate change are wide-spread in the terrestrial literature and are predominantly associated with timing of reproduction and activity (Hoffmann and Sgrò, 2011). Marine fishes have also shown a high capacity for rapid adaptation (Bernatchez, 2016; Reid et al., 2016; Vera et al., 2016). For corals, however, it remains unclear whether populations are capable of keeping up with the pace of environmental change.

Although reef-building coral populations are experiencing wide-spread die offs in the Anthropocene (Hughes et al., 2017), in many ways corals have the necessary tool-kit to cope with near-future climate change. Firstly, corals generally have large effective populations sizes with high levels of genetic diversity. Standing genetic variation is a key component of the adaptive capacity to environmental change as higher levels of genetic diversity provide a greater probability of achieving allelic combinations that confer beneficial phenotypes in the new environment (Barrett and Schluter, 2008). Secondly, coral species span strong temperature gradients and as a result likely have an abundance of genetic variation in traits associated with thermal tolerance. Thirdly, the main reproductive mode of corals is via broadcast spawning (Baird et al., 2009), with larvae capable of dispersing large distances (Ayre and Hughes, 2000; Miller and Ayre, 2008; Davies et al., 2014). This means that coral populations are generally characterized by high levels of gene flow, so the exchange of beneficial genetic variants among populations spread across large areas is high. Furthermore, a high dispersal capacity means that they have a high capacity for colonizing novel habitats that become suitable as isotherms shift poleward. The rate of expansion of leading edge-populations in the ocean on average is an order of magnitude higher than that observed on land (Poloczanska et al., 2013). Fourthly, coral populations show a remarkable capacity for phenotypic plasticity and can rapidly shift their physiology to cope with repeated stress events. Phenotypic plasticity can also be adaptive, and recent studies show that this trait provides resilience to frequently encountered environmental variation (Kenkel and Matz, 2016).

Such mechanisms set the stage for short-scale local adaptation over space but can also allow rapid evolution over time. Unlike on land where many long-lived animals have limited capacity for rapid evolution because of long generation times and low genetic diversity (Romiguier et al., 2014), even long-lived corals may show adaptability. Bay et al. (2017b) estimated evolutionary rates in *A. hyacinthus* in the face of warming ocean temperatures by examining a high latitude population in the Cook Islands for the same putative warm-adapted alleles found in the more equatorial Samoa archipelago. Under a multi-locus model in which a colony's inherent thermal tolerance was proportional to the number of heat tolerant alleles it had inherited, they could project the Cook Island population's level of heat adaptation under various climate scenarios. Under this evolutionary model, they predicted successful adaptation under mild buildup of atmospheric CO_2, but failure under more extensive CO_2 emissions. Such predictions are sensitive to the evolutionary models used and the genomic architecture of adaptation—for example if thermal tolerance alleles are clustered in short genomic regions as in Dixon et al. (2015), then evolutionary adaptation might be more rapid. There is also an interaction between acclimatization and adaptation. An acclimated individual experiences less environmental stress than a non-acclimated individual, and stress induced fitness loss may be less. This has been called the "Beneficial Acclimation Hypothesis" (Kingsolver and Huey, 1998), and the process of natural selection on tolerance of extremes may be slower in such cases (Seebacher et al., 2014). This increases population fitness in the short term, but may decrease it in the long term. Such a situation may be observed on the Great Barrier Reef when protective pulses of short-term, warm water occur before bleaching events (Ainsworth et al., 2016).

These overlapping mechanisms of adaptability will play a key role in the future of coral populations as they encounter climate change over the next century. Whether they are sufficient to allow populations to persist, and over what spatial scales, is a key question. The layered capacity of adaptability in corals is a major asset to their population persistence under some future climate scenarios. Research on the capacity of corals to persist despite local, global, and existential threats will require multi-species, multi-stressor, and multi-disciplinary efforts.

AUTHOR CONTRIBUTIONS

LT and SRP conceived the study and drafted the manuscript. All authors edited the manuscript and gave final approval.

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frontiers in Marine Science

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Impact of Three Bleaching Events on the Reef Resiliency of Kāne‘ohe Bay, Hawai‘i

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Coral bleaching events have been increasing in frequency and severity worldwide. The most prolonged global bleaching event began in 2014 and continued into 2017 impacting more reefs than any previous occurrence. Here we present the results of coral bleaching and mortality surveys conducted in Kāne‘ohe Bay O‘ahu, Hawai‘i and compare them to the only other widespread bleaching events to impact the main Hawaiian Islands in 1996 and 2014. Results from these surveys along with associated environmental factors were used to compare these events to gain a baseline understanding of the physical processes that influence localized bleaching dynamics under these extreme environmental conditions. Survey results show extensive variation in bleaching (1996–62%, 2014–45%, 2015–30%) and cumulative mortality (1996—<1%, 2014–13%, 2015–22%) between years. Bleaching prevalence was observed to decrease in certain reef areas across events, suggesting some acclimation and/or resilience, but possible increase susceptibility to mortality. Long-term monitoring sites show a similar temporal pattern of coral mortality and decline in coral cover, but revealed some reefs remained relatively un-impacted by consecutive high temperature events. Across the three bleaching events, we found that although circulation patterns can facilitate heating, the duration and magnitude of the high temperature event were the primary forcing functions for coral bleaching and mortality. Other localized primary drivers influencing water temperature such as irradiance, turbidity, and precipitation contributed to spatial variations. Recovery and resilience of this coral reef ecosystem is dependent on many factors including duration and magnitude of heating, resulting mortality levels, localized environmental factors in the bay, and coral species affected and their bleaching tolerances.

Keywords: coral reefs, resiliency, ecology and conservation, environmental monitoring, climate change impacts, coral bleaching

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INTRODUCTION

Coral reefs throughout the world are undergoing significant ecological decline due to climate change (Aronson et al., 2002; Gardner et al., 2005; Norström et al., 2009; De'ath et al., 2012). Increases in anthropogenic atmospheric gases mainly from fossil fuel burning have resulted in significant increases in global sea surface temperatures (SST) (Sabine et al., 2004). Increased SST have resulted in more severe and more frequent coral bleaching events worldwide. 2014 marked the beginning of the longest global bleaching event on record, which continued for nearly three years and has affected more reefs than any previous worldwide bleaching event (Eakin et al., 2016). As warming continued, not only was 2015 the warmest year on record, but it also saw the single largest ocean temperature increase (0.16°C) within any given year (Heron et al., 2016).

The offshore subtropical waters of the Hawaiian Islands have experienced heating over the past 58 years (+1.15°C), which appears to have accelerated the frequency and severity of bleaching events throughout the archipelago (Hoeke et al., 2009; Bahr et al., 2015a). Previously recorded bleaching events (i.e., 1996, 2002, 2004) in the Hawaiian Archipelago were relatively short in duration and resulted in high recovery; however, reefs experienced unsurpassed bleaching on a statewide scale during the multi-year bleaching events in 2014 and 2015 (Bahr et al., 2015a).

The largest sheltered body of water in the main Hawaiian Islands, Kāneʻohe Bay, contains among the highest coral cover in the State with numerous patch reefs, a fringing reef, and a barrier reef. This intensively studied estuarine coral reef ecosystem has been impacted by humans for over 700 years (Bahr et al., 2015b). Drastic modifications in the terrestrial environment (e.g., urbanization, stream channelization, extensive dredging) and direct release of primary sewage into the bay for nearly 20 years (circa 1960–1979) decreased species diversity, increased eutrophication, and altered ecosystem structure away from a coral dominated ecosystem (Bahr et al., 2015b). By 1973, Kāneʻohe Bay was declared an ecosystem under stress until sewage diversion led to natural recovery of the coral reefs. The corals in Kāneʻohe Bay have shown resilience by their capacity to respond to the numerous perturbations by recovering rapidly. Whether this is a result of a reduction in genetic diversity or that acclimatization and/or adaptations have occurred, the population has shown high resilience. Climate change now poses a significant new threat to the integrity of this unique coral reef ecosystem. Kāneʻohe Bay has experienced initial indicators of climate change with more frequent localized storm events and flooding (i.e., freshwater kill events in 1965, 1988, 2014) and three major bleaching events (i.e., 1996, 2014, 2015). Thermally stressed corals are more susceptible to disease (Miller et al., 2009; Mydlarz et al., 2009; Burge et al., 2014), predation, bioerosion, and have reduced capacity for competition, growth, reproduction, and survival (Jokiel, 2004; Baker et al., 2008; Jones, 2008). Continued exposure to bleaching stress will eventually lead to reduced reef complexity, coral cover and biodiversity; therefore, providing lower quality habitat for fishes and marine invertebrates and consequently fewer ecosystem goods and services for dependent human communities (Munday et al., 2008).

Along with the rather unnatural history of Kāneʻohe Bay, these corals are currently living at temperatures (+1–2°C) and acidification (average pCO_2 levels ∼500 µatm) regimes that will not be experienced for decades on open coastal reefs across the Hawaiian Archipelago (Bahr et al., 2015b). To determine whether these conditions increase the susceptibility of these corals to future anthropogenic and climate change stressors, we investigated the response and recovery of this coral reef ecosystem from recent bleaching events. Corals in the bay were closely monitored and documented during the previous 1996, 2014, and 2015 bleaching events. Previous work has documented the 1996 (Jokiel and Brown, 2004) and 2014 (Bahr et al., 2015a) bleaching events. The methodology and observer remained constant across all bleaching events. This presented a unique opportunity to examine all three bleaching events to determine differences in coral bleaching and mortality and their relationships with environmental factors. Furthermore, detailed long-term benthic monitoring surveys have been conducted by the Coral Reef Assessment and Monitoring Program (CRAMP) since 1999 to identify the controlling factors (i.e., natural and anthropogenic) contributing to the stability, decline, and/or recovery of the reefs in Kāneʻohe Bay (Brown et al., 2004). Together, these data reveal the impact of these bleaching events on the resiliency of this unique coral reef ecosystem. Here we present the survey findings from the 2015 bleaching event in Hawaiʻi and interpret those findings in the context of the two previously documented bleaching events. The objectives of this research were to: (1) describe the severity and extent of the 2015 bleaching event, (2) investigate the influence of the environmental drivers on bleaching variability across years, and (3) examine coral response and recovery during consecutive bleaching events to aid in understanding resiliency of the Kāneʻohe Bay reef ecosystem.

MATERIALS AND METHODS

Bay-Wide Coral Bleaching and Mortality Surveys

Documentation of the 1996 and 2014 bleaching events have been previously described in Jokiel and Brown (2004) and Bahr et al. (2015a), respectively. Here we described our detailed methods to quantify the extent of bleaching and associated mortality during the 2015 bleaching event. All bleaching surveys (1996, 2014, and 2015) were conducted using the same methodology described below.

Bay-wide coral surveys were conducted following the peak of the high temperature events for all three documented bleaching events in Kāneʻohe Bay, Oʻahu Hawaiʻi (21°28′N; 157°48′W).

The goal of our bay-wide surveys was to detect change in coral cover following the high temperature event; therefore, site selection criteria for each survey year included the same depth (1–2 m), presence of coral, and spatial coverage. Surveys were conducted between 1 and 2 m on the reef flat and slopes were coral species identification and pigmentation level could be accurately estimated without discoloration or distortion with depth. Stations were surveyed on Leeward and Windward sides of patch reefs when possible to account for potential differences in coral cover. Extent of bleaching was defined by surveying fringing, patch, and barrier reefs within Kāneʻohe Bay across bleaching years (i.e., 1996, 2014, and 2015). To define bleaching prevalence, rapid assessments of total coral cover, species composition (% of live coral cover), and coral condition (i.e., normal, pale, bleached, dead expressed as % of live coral cover) at each site were conducted using a visual estimate technique at the same sites using the same observer (Bahr et al., 2015a). Individual coral colonies were not quantified, instead conditions of live coral area (100 m^2) were estimated. These assessments were conducted from a boat at the surface under clear, calm conditions using a clear viewing box and/or snorkeling along the reef edge and across reef flats during a 5-min observation period that covered an area of 100 m^2 (Bahr et al., 2015a). This method was previously compared to eight other quantitative methods (i.e., quadrat, random, point intercept transect, CRAMP assessments, video transect, towed-diver, photographic transect, NOAA ground truth) and produces comparable results in total coral cover estimates (Jokiel et al., 2015). This visual estimate technique allowed us to rapidly evaluate bleaching severity and extent across the large sampling area but may show higher variance. Coral condition was defined by visual assessment of pigmentation: "normal" (fully pigmented), "pale" (obvious pigmentation loss but retention of color), "bleached" (loss of all color), and recently "dead" skeleton as a result of bleaching mortality. These coral condition classifications follow the same methodology and classification originally established by Jokiel and Coles (1974) and were used in previous bleaching surveys (i.e., 1996 and 2014 bleaching events) at the same reef locations by the same observers (Bahr et al., 2015a).

The 2015 Bleaching Event

Bay-wide surveys ($n = 24$) were conducted ~25 days following peak temperature on 16 October 2015 in areas of high coral cover at a depth of 1–2 m. These sites were revisited after the 2014 surveys to confirm bleaching occurrence covering the spatial extent of the Bay. Sample intensity was lower in Oct 2015 and is accounted for in our statistical approach. Coral recovery surveys were conducted on 8 December 2015 to assess coral mortality and pigmentation on the reefs previously surveyed ($n = 103$ sites) using identical methods and observer. Additional surveys of coral condition, coral cover, and species composition were conducted on 11 November 2016 to determine the degree of recovery from the 2015 bleaching event ($n = 100$ sites). Bay-wide coral surveys from 1996, 2014, and 2015 were compared to investigate variation in bleaching response across documented bleaching events. Results from bay-wide surveys were then compared to long-term CRAMP surveys (shallow sites, 2m depth) to investigate the effects of these high temperature events on long-term coral cover changes.

Long-Term Coral Reef Assessment and Monitoring (CRAMP) Sites

The Hawaiʻi CRAMP was developed in 1998 to describe changes on reefs over time in relation to natural and anthropogenic factors. This network of 62 permanent reef stations at 31 sites are stratified by depth (i.e., shallow ~3 m and deep ~10 m) across the main Hawaiian Islands. Three of these sites are located within Kāneʻohe Bay, at two depths (2 and 8 m). The shallow sites are at comparable depths to the bay-wide surveys, thus the shallow sites were used to assess the effects of bleaching impacts on long-term coral cover trends. These sites are located in three different sections of the bay, the north bay (patch reef 44, Kaʻalaea; flow regime 4), central bay (patch reef 17, Heʻeia; flow regime 5) and south bay (Moku o Loʻe Island, flow regime 6) (**Figure 1**; **Table 1**). At each station, 10 randomly selected 10 m transects and five photo quadrats within a 200 m^2 area are permanently marked with short stainless steel pins. Non-overlapping digital images estimate benthic coverage using the software program PhotoGrid (Bird, 2001). Percent coral cover, coral species richness, and coral diversity are calculated. The methodology was designed with high statistical power to distinguish an absolute change of 10% in coral cover annually within a site with statistical power increasing over time. CRAMP methodology is described in further detail in Brown et al. (2004). Coral surveys at long-term monitoring sites in 2012 and 2016 serve to provide benchmarks for the reef status before and after the consecutive bleaching events. From these data, we can deduce changes in coral cover in relation to the high temperature event rather than potential natural oscillations in coral cover. Further, CRAMP provides supporting evidence of the presence and degree of mortality and the spatial pattern documented in the bay-wide surveys.

Meteorological Data

Meteorological data [i.e., photosynthetically active radiation (PAR), ultraviolet radiation, seawater temperature, precipitation, and wind strength and direction] were monitored continuously throughout the bleaching events (1996, 2014, 2015) at an automated weather station located on Moku o Loʻe at the Hawaiʻi Institute of Marine Biology (HIMB) (http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/) (**Figure 1**). To investigate the influence of the environmental drivers on bleaching variability, meteorological data collected between Aug 1 and Nov 1 were compared across bleaching years (1996, 2014, and 2015).

Due to the unique bathymetry of the bay, water circulation and residency times vary between ~1 day in north bay to up to 1–2 months in south bay (Lowe et al., 2009). Continuous *in situ* water temperatures were recorded at 1–2 m depth at seven locations characterizing four flow regimes during the 2015 bleaching event (**Table 1**). Water temperatures were recorded in the following flow zones: Zone 2, on reef flat near Kapapa Island; Zone 4, on northern fringing reef near Channel Marker 12; Zone 5, on patch reefs 12, 19, 31; Zone 6, at three locations including fore reef slope of the HIMB reef adjacent to weather station, and on the reef flat of the south bay fringing reef near Kokokahi pier (**Figure 1**). Temperature at the HIMB weather station was recorded using a recording thermistor thermometer (Cole-Parmer Instrument Co., Vernon Hills, Illinois, USA). All other *in situ* water temperature measurements (i.e., Kapapa isle, Marker 12, PR 12, PR 19, PR 31, and Kokokahi) were recorded at 15-min intervals using replicate HOBO Water Temperature Pro v2 Data Loggers (Onset, MA, USA). All temperature loggers were placed in areas of well-developed coral communities in 1–2 m of water. The loggers were secured in 6″ × 12″ hand-poured concrete structures to mimic the benthic substrate, provide weight, and protect loggers from solar irradiance and associated heating (Bahr et al., 2016b).

Differences in cumulative heating between bleaching years (1996, 2014, and 2015) were calculated by adding number of degrees above optimal mid-day temperatures of 27°C (defined by Jokiel and Coles, 1990) using seawater temperatures from the HIMB weather station. Daily mid-day temperatures above 27°C

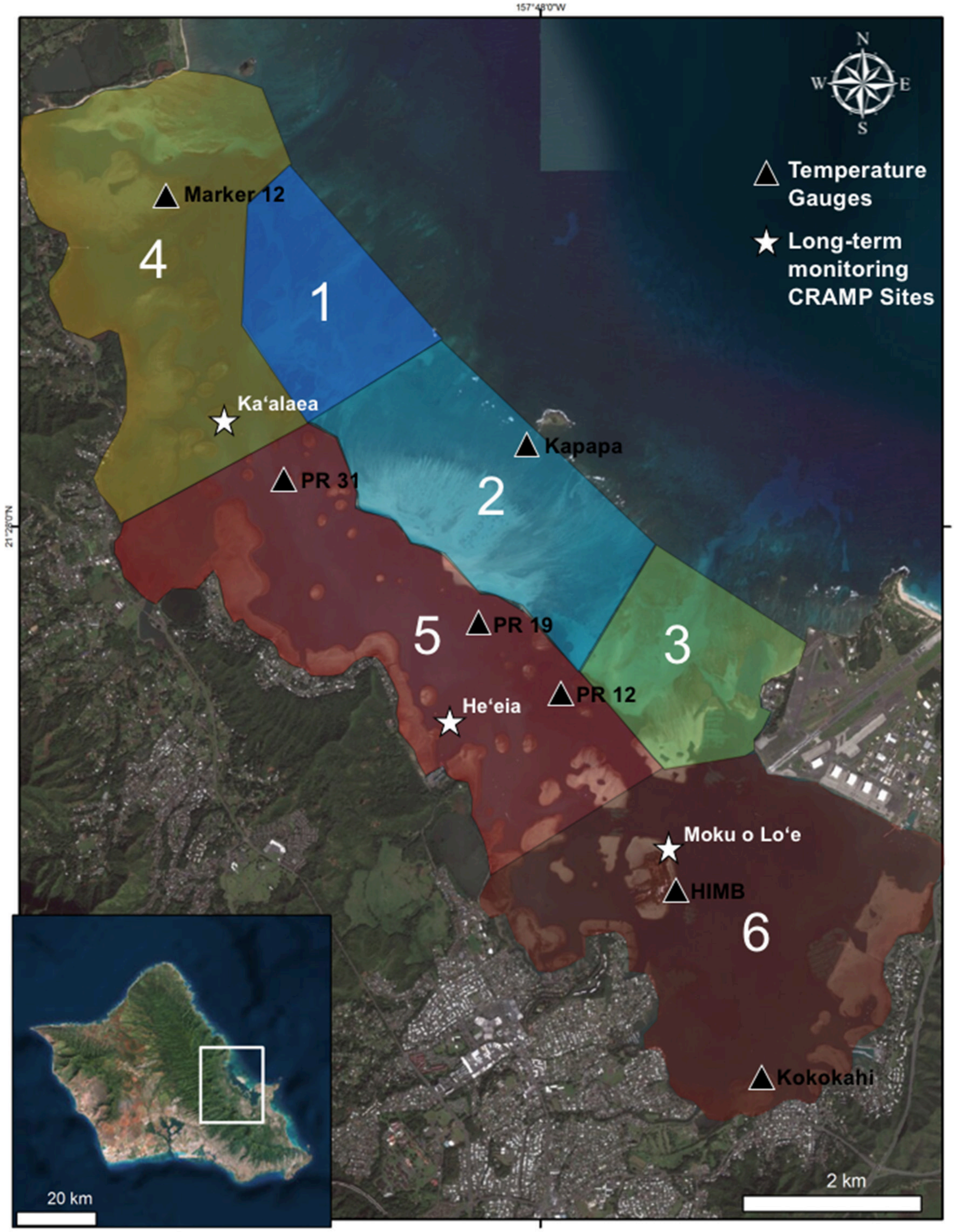

FIGURE 1 | Map of Kāne'ohe Bay, Hawai'i with flow regimes (1–6) defined by Lowe et al. (2009) (**Table 1**), *in situ* temperature loggers (triangles), and long-term Coral Reef Assessment and Monitoring (CRAMP) sites (stars). Photo credit: Quickbird Digital Globe.

were summed to determine the duration and extent of cumulative heating up to the onset of bleaching during the three documented bleaching events.

Statistical Analysis

To characterize localized temperature regimes during the 2015 bleaching event, *in situ* seawater temperatures (mean mid-day temperatures 11:00–14:00) during the peak (above 27°C) of the 2015 bleaching event (1 Aug-25 Sept 2015) were analyzed using a one-way ANOVA. *Post-hoc* Tukey tests were used to determine which sites differed from the other.

Bay-wide assessment surveys from 1996, 2014, and 2015 were compiled to investigate the influence of environmental drivers on bleaching prevalence and severity in Kāneʻohe Bay.

A Generalized Linear Mixed-effects Model (GLMM) was conducted to investigate bleaching prevalence (% live coral) across bleaching years using October bleaching surveys. Year (i.e., 1996, 2014, 2015), flow regime, and total coral cover (%) were included as predictor variables. The GLMM allows and accounts for analysis assuming unequal group variance and analysis of longitudinal data with unequal time points and missing time points. Collinearity between candidate predictor variables were assessed with Pearson correlation coefficients (<0.7) and variance inflation factors (<5). GPS location (i.e., latitude and longitude) of each surveyed area was included in the GLMM as a repeated covariance spatial isotropic spherical structure to account for spatial autocorrelation. A Principal Component Analysis was used to identify the environmental factor drove coral bleaching prevalence across bleaching years.

Average coral mortality (including zeros) by survey month during each bleaching event was compiled and analyzed using a three-way ANOVA with fixed factors of survey month, bleaching event year, flow regime, and the interaction between year and flow regime. Tukey *post-hoc* analyses were used to investigate differences across factors. Average daily mid-day temperatures (°C) (2 m depth), daily wind (mph), cumulative daily Photosynthetically Active Radiation (PAR) (μmol photons m^2), and log transformed total daily rainfall (mm) were analyzed using a GLMM by year with day as a random effect. All meteorological variables were recorded at the HIMB weather station on Moku o Loʻe.

To understand the implications of the high temperature events, comparisons of changes in coral cover at long-term CRAMP sites were analyzed using a two-way ANOVA with fixed factors of site and year and their interaction. Preplanned contrasts were used to analyze changes in coral cover before bleaching (i.e., 2012) and after (i.e., 2016). All statistical analyses and descriptive statistics were conducted using JMP Pro 12 (SAS Institute Inc., USA).

RESULTS

2015 Bleaching Event

Mean mid-day seawater temperatures varied spatially within Kāneʻohe Bay during the peak of the bleaching event (1 Aug-25 Sept 2015) [One-way ANOVA; $F_{(6,\,391)} = 32.3150$; $p < 0.0001$]. Temperatures were at least 0.60°C warmer in the sluggish waters in south bay (Kokokahi Pier; 29.78 ± 0.11°C) compared other sites. Lower water temperatures were recorded in central bay (patch reef 19, 28.66 ± 0.08°C; patch reef 12, 28.61 ± 0.07°C), Moku o Loʻe (28.49 ± 0.08°C), and the barrier reef site, Kapapa (28.40 ± 0.09°C; **Figure 2**).

Bay-wide coral surveys in Oct 2015 determined 46% of surveyed corals had signs of bleaching and paling and 13% showed recent mortality due to bleaching. Detailed surveys by location revealed the highest levels of bleaching and paling in the north bay (70%) with 18% mortality, while the highest mortality was observed in the south bay (28%) accompanied by 60% bleaching and paling. The lowest mortality (4%) and bleaching/paling (38%) levels were observed in the central bay. On the barrier reef where coral cover is low (5–10%), 50% of the surveyed corals revealed signs of bleaching or paling and recent bleaching mortality was estimated at 21% (**Figure 3d**).

TABLE 1 | Descriptions of residency times and flow regimes in Kāneʻohe Bay, Hawaiʻi by Lowe et al. (2009).

Flow regime	Dominant physical force	Reef type	Residence time (days)
1	Wave	Barrier reef	<1
2	Wave	Barrier reef	4–10
3	Tide	Barrier reef	3–7
4	Wave	Patch and fringing reef	<1
5	Wave	Patch and fringing reef	10–20
6	Tide	Patch and fringing reef	>30

By December 2015, 2 months following the initial survey, high levels of recovery (∼81% normal pigmentation) were observed (**Figure 3e**). Nearly 9% of surveyed corals in the bay exhibited signs of paling or bleaching, and recent mortality was estimated at 8%. A large proportion of coral mortality was attributed to the barrier reef (∼56%). Recovery was delayed in the south bay where 25% of the surveyed corals remained bleached and/or pale in pigmentation. The highest recovery and lowest mortality rates ($< 2\%$) were observed in central bay. Normal pigmentation levels had returned by Nov 2016 (>99%) (**Figure 3f**).

Total live coral cover of surveyed area in Kāneʻohe Bay (mean ± SE) was estimated at 59.17 ± 5.28% in Oct 2015. Higher total live coral cover was estimated during recovery surveys in December 2015 (68.95 ± 2.20%) and decreased again in November 2016 surveys (54.35 ± 1.98%; Supplementary Table 1).

Comparison of Documented Bleaching Events in Kāneʻohe Bay, HI

Results of the 1996 and 2014 bleaching events have been previously documented in Jokiel and Brown (2004) and Bahr et al. (2015a). These data were compiled with the 2015 surveys to investigate differences in bleaching prevalence and mortality across documented events.

Bleaching Prevalence

Bleaching prevalence varied by year ($p = 0.0002$) and by flow regimes ($p = 0.0003$) (**Table 2**). Bleaching prevalence was ∼27% higher in 1996 (62.00% ± 15.42) in comparison to 2014 (45.28% ± 1.91; $p = 0.0138$) even though bleaching was restricted to the inner bay and fringing reef in 1996, while bleaching extended throughout the bay to the barrier reef in 2014. Two consecutive years of bleaching revealed bleaching levels to be 15% lower in 2015 than in 2014 (**Figure 4**) (Supplementary Table 1). The highest bleaching prevalence was observed in zone 5 (48.93 ± 2.36%), zone 6 (45.24 ± 4.49%), and zone 4 (44.33 ± 4.82%).

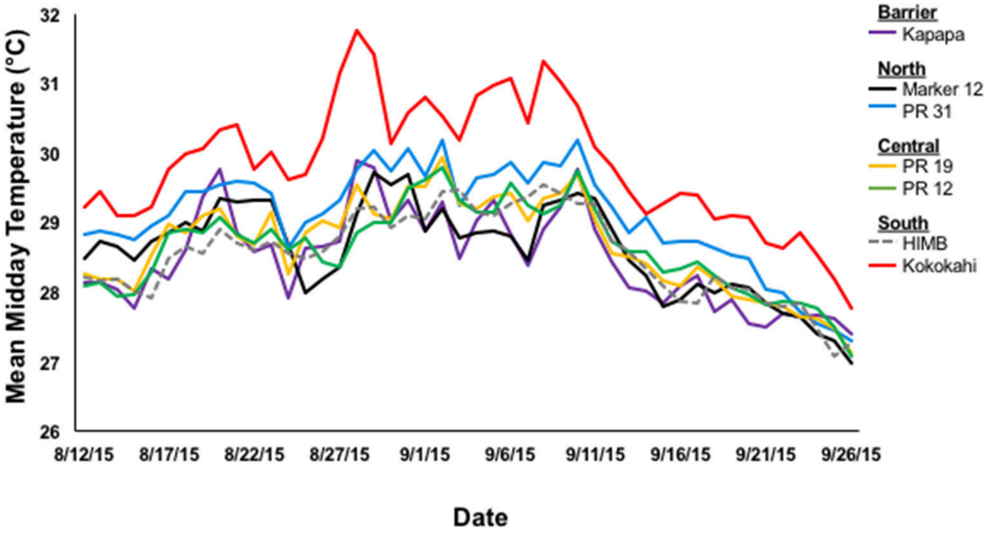

FIGURE 2 | Mean mid-day temperature (°C) by location in Kāneʻohe Bay, HI during the 2015 bleaching event collected at 15 min intervals with Onset ProV2 HOBO Temperature loggers.

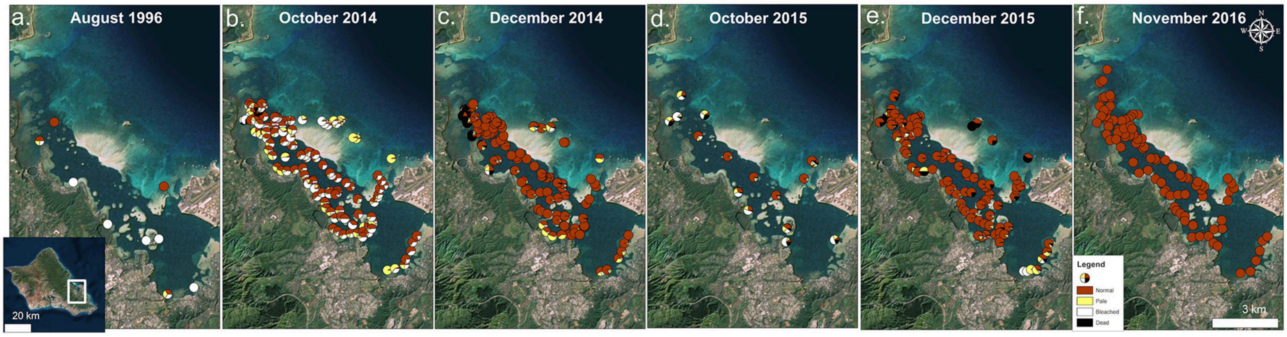

FIGURE 3 | Times series of bay-wide surveys on 31 August 1996 **(a)**, 14 October 2014 **(b)**, 1 December 2014 **(c)**, 16 October 2015 **(d)**, 8 December 2015 **(e)**, and 11 November 2016 **(f)**. Proportion of surveyed corals are shown as normal (red), pale (yellow), bleached (white), and dead (black). Survey data from 1996 (Jokiel and Brown, 2004) and 2014 (Bahr et al., 2015a) bleaching events are used with permission from authors. Photo credit: Quickbird Digital Globe.

Bleaching prevalence was lower in areas more influenced by oceanic waters (zone 1, 29.0 ± 11.87; zone 2, 29.0 ± 9.83%; and zone 3, 17.5 ± 4.55%) across years (**Figure 4B**). Bleaching prevalence did not vary by total coral cover ($p = 0.1429$; **Table 2**).

Coral Mortality

Average coral mortality increased during the documented bleaching events ($p < 0.0001$) with high mean mortality in 2015 (16.07 ± 1.53%), less in 2014 (5.58 ± 1.42), and lowest in 1996 (<1%) (Supplementary Table 1; **Table 3**). Coral mortality varied by flow regime within years (year*flow, $p = 0.0005$). High mortality levels were observed in 2014 in flow regime 4 (28.81%) due to a freshwater flooding event that interacted synergistically with the high temperature event (Bahr et al., 2015a). Mortality during 2015 was similar across all flow regimes with the highest in flow regime 2 (39.16 ± 4.91%) (**Table 3**; **Figure 5**). Cumulative mortality (sum of both October and December surveys) was lowest in 1996 (<1%) and highest in 2015 (21.66 5 ± 5.32%).

Environmental Factors

Further investigation of environmental drivers (i.e., temperature, irradiance, wind, and precipitation) during the height of bleaching (1 Aug-1 Nov) revealed significant differences between bleaching years. Average daily mid-day temperatures recorded at 2 m at the HIMB weather station varied between bleaching events [GLMM; $F_{(2,\,184)} = 7.62$; $R^2 = 0.31$; $p = 0.0007$]. 1996 had significantly higher temperatures compared to the 2015 event (**Figure 6A**). Cumulative daily solar (PAR) input was higher in 2014 than in 2015 [Mixed Model; $F_{(2,\,184)} = 4.28$; $R^2 = 0.20$; $p = 0.0153$]. Similar levels of PAR were observed in 1996 (8,019.59 ± 122.69 μmol photons m^2) compared to the 2014 (8,409.38 ± 214.92 μmol photons m^2) and 2015 (7,616.33 ± 247.38 μmol photons m^2) events (**Figure 6B**).

TABLE 2 | Model output (GLMM) of bleaching prevalence (% live coral cover) (October surveys only) by year (i.e., 1996, 2014, 2015), flow regimes (i.e., 1–6), and total coral cover (TCC).

Term	Estimate	Std. error	*t*-ratio	Prob>|t|
Intercept	43.561	4.696	9.280	**<0.0001***
Year[1996]	17.238	5.526	3.120	**0.0021***
Year[2014]	−2.091	3.443	−0.61	0.545
Year[2015]	−15.147	4.145	−3.65	**0.0003***
Flow regime[1]	−6.330	8.998	−0.70	0.483
Flow regime[2]	−11.911	7.317	−1.63	0.106
Flow regime[3]	−16.846	6.573	−2.56	**0.0113***
Flow regime[4]	10.128	4.404	2.30	**0.0227***
Flow regime[5]	15.090	3.601	4.19	**<0.0001***
Flow regime[6]	9.869	4.381	2.25	**0.0256***
TCC	−0.102	0.069	−1.47	0.143

Asterisks and bold numbers indicate a significant effect ($p < 0.05$). $R^2 = 0.192$; $p < 0.0001$; $n = 177$; $df = 168$; AICc = 1628.99.

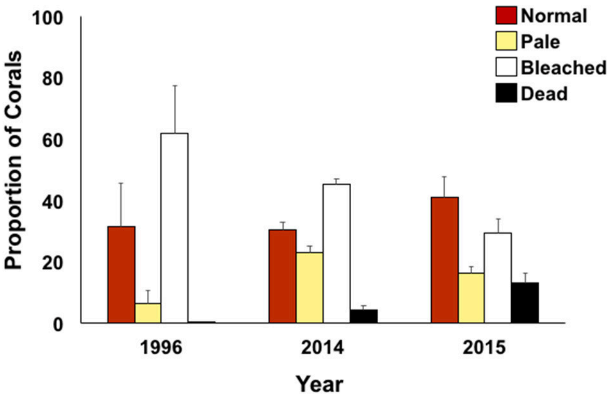

FIGURE 4 | Coral condition (proportion of surveyed area) defined as normal (red), pale (yellow), bleached (white), and dead (black) for bay-wide bleaching assessment surveys (October only) during documented bleaching events.

Average daily wind was similar among the three documented bleaching events [GLMM; $F_{(2,\,184)} = 1.17$; $R^2 = 0.25$; $p = 0.3116$] (**Figure 6C**). Total daily rainfall (mm) was higher in 2015 and 2014 compared to 1996 [GLMM; $F_{(2,\,184)} = 88.53$; $R^2 = 0.61$; $p < 0.0001$] (**Figure 6D**). Multivariate analyses reveal significant correlations between bleaching and total daily PAR ($r = 0.77$), average daily wind ($r = -0.56$), and temperature ($r = 0.77$). A Principal Component Analysis reveals average mid-day temperature was the most representative variable driving coral bleaching across years (75.6% variance explained).

Long-Term Coral Reef Assessment and Monitoring (CRAMP) Sites

Long-term CRAMP sites were surveyed before (i.e., 2012) and following (i.e., 2016) consecutive bleaching events. In 2016, the highest coral cover was observed in central bay (He‘eia, 60.66 ± 3.61%) and north bay (Ka‘alaea, 49.13 ± 13.99%). The south bay site, Moku o Lo‘e, has significantly lower coral cover compared to the other shallow CRAMP sites in the bay (28.35 ± 2.53%; **Figure 7A**). Over the 4-year period (2012–2016), significant decline in coral cover occurred at shallow (2 m) sites in central bay, He‘eia (−19.7%; $p = 0.0015$), and south bay, Moku o Lo‘e (−42.2%; $p < 0.0001$; **Figure 6**). Coral cover did not significantly change over this 4 year period at the shallow north bay site (Ka‘alaea, $p = 0.2640$) [Two-way ANOVA; $F_{(11,\,119)}$ =55.64; $p < 0.0001$] (**Figure 7**). Total coral cover was statistically similar among all CRAMP deep sites (8 m) in 2016 (Ka‘alaea = 6.45 ± 4.15%; He‘eia = 10.53 ± 2.06%; Moku o Lo‘e = 9.67 ± 2.34%) [One-way ANOVA; $F_{(2,\,29)} = 1.2131$; $p = 0.3129$] (**Figure 7B**) and did not change in response to the consecutive bleaching events [Two-way ANOVA; $F_{(11,\,119)} = 55.64$; $p < 0.0001$] (**Figure 7**).

TABLE 3 | Three-way ANOVA output of coral mortality by survey month (December and October surveys), bleaching event year (1996, 2014, and 2015), flow regime (as defined by Lowe et al., 2009), and the interaction of flow and year.

Factor	DF	SS	*F*-ratio	*p*
Month	1	6.471	0.257	0.6192
Year	2	1,452.659	30.144	**<0.0001***
Flow regime	5	957.098	7.944	**0.0005***
Year*flow regime	10	1,498.886	6.221	**0.0005***

Asterisks and bold numbers indicate a significant effect ($p < 0.05$). $F_{(18,\,34)} = 7.574$, $p < 0.0001$; $n = 35$, $df = 35$, $R^2 = 0.895$.

DISCUSSION

The occurrence and severity of mass coral bleaching has increased dramatically over the last two decades with almost every reef region in the world suffering extensive bleaching and mortality (Hughes et al., 2017). The goals of this research were to (1) describe and compare the severity, extent, and spatial variability of bleaching during documented bleaching events and (2) examine recovery at long-term monitoring sites to aid in understanding the resiliency of Kāne‘ohe Bay, HI.

The first coral bleaching event in Kāne‘ohe Bay occurred during 1996 where high levels of bleaching but little mortality occurred. This event was followed by more severe events in 2014 and 2015. Patterns of bleaching and mortality in the 1996 event did not continue during the 2014 event (**Figure 3**). Likewise, the patterns observed in 2015 diverged from the previous two events, with higher levels of coral mortality. Our data suggests that the unexpected trends of bleaching and mortality within and across documented bleaching events were due to several factors including: (1) Localized patterns of water circulation and heating within bleaching events (**Figure 2**), (2) Variation in irradiance due to different levels of cloud cover and temporal variation in turbidity (**Figure 6B**), (3) Differences due to seasonal timing and duration of the warm water events (**Figure 8**), and (4) Influence of localized fresh water flood events (2014) interacting with temperature induced bleaching (**Figure 3B**).

Temperature (seasonal timing and duration) is the chief environmental factor driving coral bleaching extent and severity.

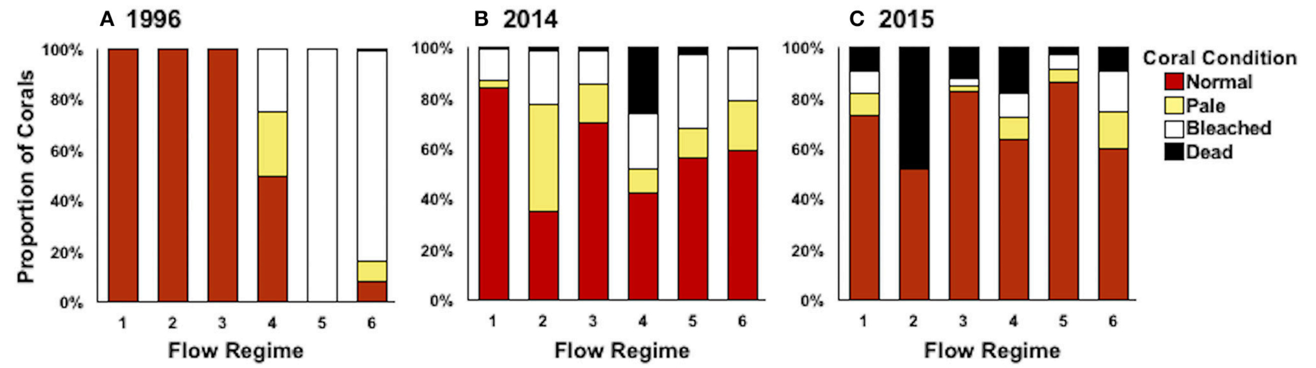

FIGURE 5 | Coral condition (proportion of surveyed area) defined as normal (red), pale (yellow), bleached (white), and dead (black) by flow regime in 1996 **(A)**, 2014 **(B)**, and 2015 **(C)**. Coral condition was averaged across survey months (October and December) for bay-wide bleaching surveys.

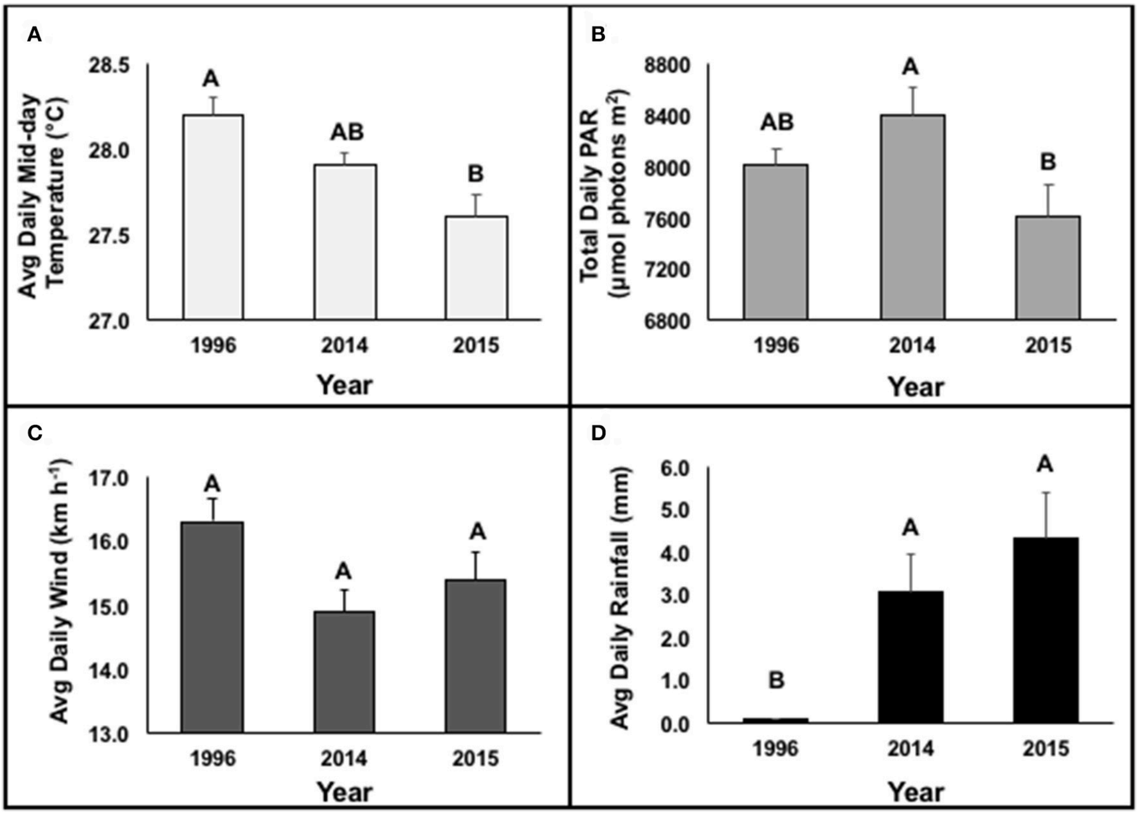

FIGURE 6 | Environmental characteristics of average daily mid-day temperature (°C) **(A)**, total daily PAR (µmol photons m^{-2}) **(B)**, average daily wind (km h^{-1}) **(C)** and average daily rainfall (mm) **(D)** between 1 Aug and 1 Nov during documented bleaching events (1996, 2014, and 2015). Levels not connected by the same letter are significantly different at $p < 0.05$. Data was obtained from Hawai'i Institute of Marine Biology Weather Station (http://www.pacioos.hawaii.edu/weather/obs-mokuoloe).

During the 2015 bleaching, reefs across the Hawaiian Islands experienced different Degree Heating Weeks (DHW). Among the highest were on the west side of Hawai'i Island, where surveyed corals experienced high levels of bleaching (up to 86%) and mortality (50%) after 18 DHW (Kramer et al., 2016). Conversely, after 12 DHW Kāne'ohe Bay had 22% mortality, while the Hanauma Bay Nature Preserve (HBNP) on O'ahu experienced high levels of bleaching (47%) and mortality (9.8%) after 10 DHW (Rodgers et al., 2017).

The 2015 Bleaching Event

Results of the 2015 bleaching event showed the influence of water circulation and localized heating on coral bleaching and mortality patterns inside Kāne'ohe Bay. Historically, circulation patterns

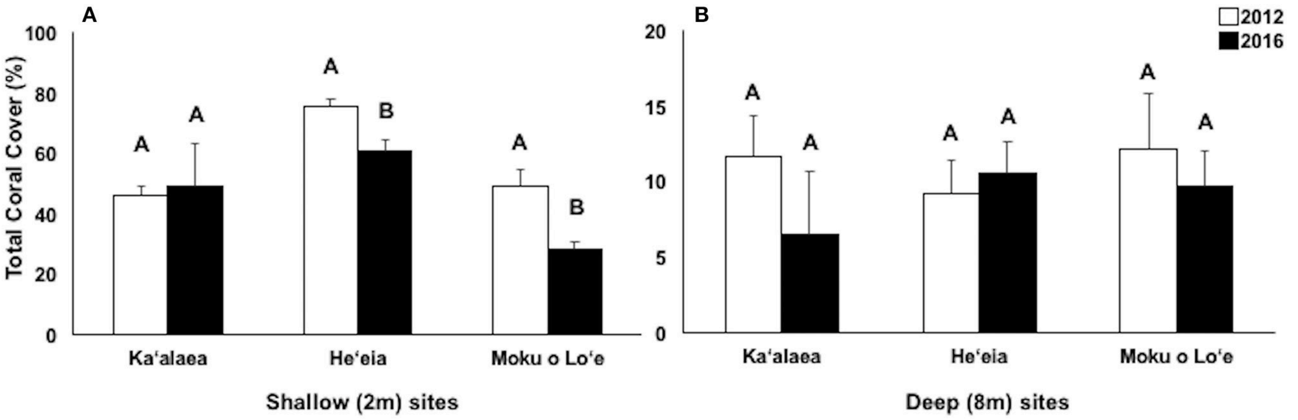

FIGURE 7 | Changes in total coral cover over time at long-term Coral Reef Assessment and Monitoring (CRAMP) sites at shallow (2 m, **A**) and deep (8 m, **B**) in North bay, Ka'alaea; Central bay: He'eia; and South bay: Moku o Lo'e. Different letters within site indicate statistically significant differences between years at $p < 0.05$.

in the bay have been described as the primary factor controlling distribution of coral species (Smith et al., 1981; Bahr et al., 2015b). Oceanic waters enter the bay over the barrier reef circulating cool water to adjacent patch reefs in central bay (Jokiel, 1991; Bahr et al., 2015b). The reef areas influenced by the movement of this cool oceanic water and low residency times had the lowest bleaching and mortality and highest recovery during the 2015 event. Net transport of water out of the bay occurs through the NW channel and the central Sampan channel (**Figure 1**). Although north bay is also characterized by high circulation, movement of warm water through the NW channel exacerbated bleaching (70%) and mortality (18%) on north bay reefs. These reefs have consistently had among the highest bleaching levels during the previous documented events (**Figure 3**). South bay has flow patterns anomalous to the rest of the bay with high residency times (∼8 to > 30 days) and heavy riverine influence (**Table 1**). The high residency time and restricted circulation patterns facilitated localized heating (+0.65°C) in south bay and delayed recovery with high mortality rates (**Figures 2**, **3F**). Although temperature was determined to be the driving factor of bleaching, reduced light penetration via wind-induced mixing and resuspension of sediments into the water column may explain lower than expected bleaching prevalence in south bay (Smith et al., 1973).

Comparison of Documented Bleaching Events in Kāne'ohe Bay, Hawai'i

Different patterns of warming (i.e., timing and duration) greatly influenced severity and extent of bleaching in Kāne'ohe Bay across documented events (**Figures 3**, **8**). Warm water approached the Hawaiian Islands from the north in 2014, while in 2015 warm water advanced from the south resulting in twice the duration of elevated temperatures as previous events with a maximum 6 DHW in 1996, 5 DHW in 2014, and 12 DHW in 2015 for Kāne'ohe Bay (**Table 4**). Seasonal timing also varied across documented events. Elevated seawater temperature began in late August in 1996 and in 2015 and in late September in 2014 (**Figure 8**). Once average water temperatures exceeded 27°C, initial signs of bleaching occurred after 28 days in 1996 (cumulative heating of 32°C), 62 days in 2014 (cumulative heating of 44°C), and just after 24 days in 2015 with the lowest cumulative heating (14°C) (**Figure 9**). Therefore, bleaching onset in 2015 occurred earlier (24 days) under lower cumulative heat stress (14°C). During the 1996 event, bleaching was restricted to the fringing and patch reefs. Conversely, bleaching during the 2014 and 2015 events extended throughout the bay onto the barrier reef. The severity of the high temperature event was lowest in 1996, where little to no mortality was recorded (Jokiel and Brown, 2004). In 2014, a freshwater kill event a month prior to the high temperature event, contributed significantly to observed mortality (nearly 60%). Areas not impacted by the freshwater flooding event experienced little to no mortality (<1%) (Bahr et al., 2015a; **Figure 3b**). The largest cumulative mortality (21%) due to high temperature was recorded in the most recent 2015 bleaching event in which warming began sooner, and corals bleached under less cumulative heating and lower irradiance regimes but experienced prolonged high SSTs at 12 DHW.

Changes at Long-Term CRAMP Sites

Our long-term CRAMP sites provide a record of change in coral cover across the three bleaching events that provides supporting evidence of the validity of our mortality results within Kāne'ohe Bay (Rodgers et al., 2015). Significant increases in coral cover were reported at Moku o Lo'e shallow (south), He'eia shallow (central), and Ka'alaea deep (north) between 1999 and 2012. During the period of the more severe bleaching events in 2014 and 2015, significant declines in coral cover were reported at the shallow site in south bay (−42%) and the shallow site in central bay (−20%). Conversely, coral cover at the shallow north bay site (Ka'alaea) and all three deeper sites (8 m) remained relatively stable. This is in concert with our bay-wide coral bleaching surveys conducted in 2014 and 2015. Additionally, bleaching prevalence was observed to decrease in certain flow regimes (4–6) across bleaching events, which may suggest some acclimation or

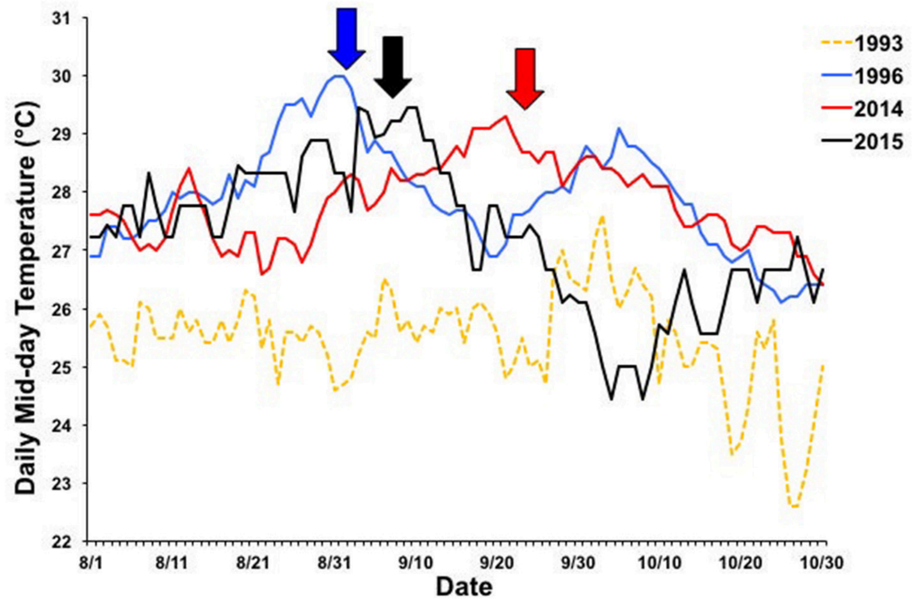

FIGURE 8 | Seasonal timing of 1996 (blue), 2014 (red), and 2015 (black) bleaching events. Daily mid-day (11:00–14:00) temperatures between 1 Aug and 1 Nov are shown for each year. Temperature data from 1993 is included as a non-bleaching reference year (yellow, dashed line). Arrows indicate when bleaching began. Temperature data collected from Hawai'i Institute of Marine Biology Weather Station (http://www.pacioos.hawaii.edu/weather/obs-mokuoloe).

TABLE 4 | Summary comparision of coral response and enviornmnental parameters for all documented bleaching events in Kāneʻohe, Oʻahu, Hawaiʻi.

		1996	2014	2015
Coral Response	Bleaching (%)	62 ± 15.42	45.28 ± 1.91	29.58 ± 4.42
	Cumulative mortality (%)	0.11 ± 0.11	12.76 ± 3.5	21.66 ± 5.32
Environmental Parameters	Degree heating weeks (DHW)	6	5	12
	Cumulative heating (°C)	32	44	14
	Midday temperature (°C)	28.16 ± 0.10	27.88 ± 0.07	27.65 ± 0.13
	Cumulative daily PAR (μmol m^{-2})	8,019.59 ± 122.69	8,409.38 ± 214.92	7,616.33 ± 247.38
	Avg daily wind	10.13 ± 0.36	9.25 ± 0.35	9.56 ± 0.45
	Total daily rainfall (mm)	0.06 ± 0.03	3.05 ± 0.89	4.34 ± 1.07

Mean ± SE environmental parameters between Aug 1-Nov 1 for each year. Cumulative mortality is the sum of average mortality in the October and December surveys.

reef resilience to bleaching in these area, but possible increased susceptibility to mortality. The large mortality coral observed in 2014 and 2015 have contributed to the decline in coral cover at these long-term monitoring sites.

CRAMP surveys conducted in 2012 revealed overall coral cover and diversity in Hawaiʻi have remained relatively stable since the initial survey in 1998 (Rodgers et al., 2015). During this period, coral cover on reefs in the Caribbean and other regions declined by as much as 50% due to climate change related bleaching events, increased storm damage and lowered coral growth (Wilkinson, 2004). Moreover, the recent longest, most widespread, and possibly the most damaging coral bleaching event on record had a significant impact on Australia's Great Barrier Reef (Hughes et al., 2017). While some reef areas in Kāneʻohe Bay remained relatively un-impacted by the consecutive bleaching events.

Offshore sea surface water temperatures in Hawaiʻi have increased by approximately 1.15°C over the past six decades (Bahr et al., 2015a). Since the establishment of bleaching thresholds in 1974 (Jokiel and Coles, 1977), there has been a regional increase in temperature of over 0.8°C with three bleaching events documented in Kāneʻohe Bay (1996, 2014, 2015). Reef recovery following disturbance has been documented at other CRAMP sites in the state (Rodgers et al., 2015); however, with projected increase in severity and frequency of bleaching events, we may see more significant declines in coral cover in the near future.

Recovery and resilience after these major disturbances not only depends on the prevailing environmental conditions but also the coral species affected. While Kāneʻohe Bay holds some of the highest coral cover (>90%) in the Main Hawaiian Islands,

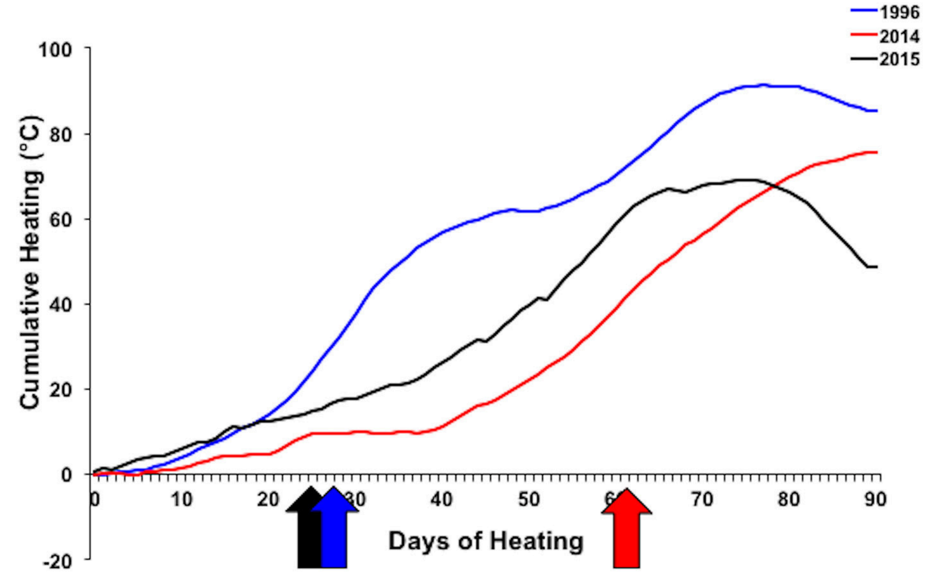

FIGURE 9 | Cumulative heating index for 1996 (blue), 2014 (red), and 2015 (black) bleaching events. Arrows indicate when bleaching began. Temperature data collected from Hawai'i Institute of Marine Biology Weather Station (http://www.pacioos.hawaii.edu/weather/obs-mokuoloe).

the majority of its reefs are comprised of two reef building species: *Porites compressa* and *Montipora capitata* (Bahr et al., 2015b). Previous experimental work has determined the endemic coral, *P. compressa*, to be the most susceptible to future climate change scenarios with the largest decreases in calcification and high partial mortality (Bahr et al., 2016c). A main factor in *M. capitata's* resilience is its ability to increase heterotrophic feeding under high temperature conditions meeting all dietary requirements without their symbiotic zooxanthellae (Grottoli et al., 2006; Rodrigues and Grottoli, 2007; Hughes and Grottoli, 2013). Cryptic species (*Fungia scutaria* and *Leptastrea purpurea*) were observed to be more resilient to climate change. These species-specific responses correlate with the bleaching susceptibility hierarchy described during the bleaching events (Jokiel and Brown, 2004; Bahr et al., 2015a). Shifts in optimal growth rates have been documented and estimated in the second dominant species, *M. capitata*. By mid-century, growth rates are expected to decline by half with further reductions in growth at the end of the century with those corals exposed to high irradiance levels (e.g., reef flats) expected to have negative growth (Bahr et al., 2016a). With these reductions, shifts in seasonal growth patterns are expected. Currently, the highest growth rates occur in the late summer (Jokiel and Coles, 1977). As we progress to mid-century, maximum growth rates will shift to spring, and at the end of the century to winter due to changes in water temperature projections (Bahr et al., 2015a). The primary factor controlling coral populations in the future will be coral mortality caused by short-term high temperature excursions (i.e., bleaching events); however, localized environmental factors as well as differences in species composition may reveal resilient coral communities.

CONCLUSION

Results of this study reveal duration and magnitude of heating are the primary factors controlling the severity and extent of bleaching in Kāneʻohe Bay. Circulation patterns in the bay facilitate localized heating and influence spatial bleaching and its associated mortality. Sectors within the bay that were influenced by cool oceanic waters had low coral bleaching and mortality and high recovery rates. Conversely, restricted water movement facilitated localized heating and therefore increased bleaching and associated mortality. Other localized environmental factors that can influence water temperature (i.e., irradiance, turbidity, rainfall) may also reduce or amplify bleaching and explain spatial variations in bleaching and mortality. Long-term monitoring sites revealed significant declines in coral cover at some sites while others recovered from the consecutive bleaching events. Having an established network of long-term monitoring sites with associated temperature loggers allows for a reliable baseline to evaluate both natural and anthropogenic factors that contribute to the stability, decline and/or recovery of coral reefs and direct targeted management actions. Further, understanding of the driving factors that influence spatial variability in coral bleaching and mortality can assist managers in identifying areas to focus efforts and resources.

AUTHOR CONTRIBUTIONS

KB conceived and designed the experiments and surveys, performed the surveys, analyzed the data, wrote the paper, prepared figures and tables. KR performed and helped design the surveys, analyzed the data, reviewed drafts of the paper.

PJ conceived and designed the experiments, provide intellectual insights, and reviewed drafts of the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2017.00398/full#supplementary-material

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frontiers in Marine Science

ORIGINAL RESEARCH
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Repeated Thermal Stress, Shading, and Directional Selection in the Florida Reef Tract

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Over the last three decades reef corals have been subjected to an unprecedented frequency and intensity of thermal-stress events, which have led to extensive coral bleaching, disease, and mortality. Over the next century, the climate is predicted to drive sea-surface temperatures to even higher levels, consequently increasing the risk of mass bleaching and disease outbreaks. Yet, there is considerable temporal and spatial variation in coral bleaching and in disease prevalence. Using data collected from 2,398 sites along the Florida reef tract from 2005 to 2015, this study examined the temporal and spatial patterns of coral bleaching and disease in relation to coral-colony size, depth, temperature, and chlorophyll-a concentrations. The results show that coral bleaching was most prevalent during the warmest years in 2014 and 2015, and disease was also most prevalent in 2010, 2014, and 2015. Although the majority of the corals surveyed were found in habitats with low chlorophyll-a concentrations, and high irradiance, these same habitats showed the highest prevalence of coral bleaching and disease outbreaks during thermal-stress events. These results suggest that directional selection in a warming ocean may favor corals able to tolerate inshore, shaded environments with high turbidity and productivity.

Keywords: corals, bleaching, disease outbreaks, climate change, directional selection

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INTRODUCTION

Predicting and responding to the effects of climate change is critical if we wish to preserve marine life in the oceans. The global effects of climate change are becoming glaringly apparent on coral reefs, where repeated thermal anomalies are forcing temperatures beyond the physiological tolerance range of many coral species. These stress events are causing widespread coral bleaching and mortality (Loya et al., 2001; Baker et al., 2008). Yet, predicting where corals are less likely to bleach, and more likely to survive thermal-stress, is an important scientific endeavor that might redirect ocean conservation efforts at both local and regional scales (Cacciapaglia and van Woesik, 2015). Here we use an 11-year dataset (from 2005 to 2015) to examine the spatial relationships between coral bleaching, coral disease, and environmental conditions at 2,398 study sites along the Florida reef tract.

Coral bleaching is a combination of irradiance and temperature stress (Takahashi et al., 2004). High seasonal irradiance causes photoinhibition of the coral symbionts, from which they can recover, unless water temperatures are high. When irradiance and water temperatures are both high, the symbiont's photosystems are compromised, and nighttime recovery from daytime photoinhibition is minimal (Warner et al., 1999; Takahashi et al., 2004). Weeks of high-water temperatures leads to chronic photoinhibition, or bleaching, that can lead to the expulsion of coral symbionts. This bleaching can be temporary and non-fatal for some coral species (Goreau, 1964; Loya et al., 2001), or fatal for other coral species that rely heavily on their symbionts as a food source (Grottoli et al., 2006).

Coral bleaching can also lower the tolerance of corals to pathogens, and bleaching can lead to disease (Muller et al., 2008; Brandt and McManus, 2009; Randall et al., 2014). The causative agents of most coral diseases are still unknown, but laboratory and field studies have shown an influence from a variety of stressors in addition to water temperatures, including population density (Bruno et al., 2007), nutrient enrichment (Bruno et al., 2003; Voss and Richardson, 2006), and irradiance (Kuta and Richardson, 2002). It is also likely that physiological and environmental parameters interact to influence the virulence of the pathogens, and the susceptibility of coral hosts (Randall and van Woesik, 2015).

By contrast, reducing irradiance during temperature-stress events relieves stress on the symbiont's photosystem, buffers corals from temperature stress, and reduces the likelihood of coral bleaching (Warner et al., 1999; Takahashi et al., 2004). Such reductions in irradiance are common on deep reef slopes (Smith et al., 2014), or nearshore, where turbidity and chlorophyll-a concentrations are high (Wagner et al., 2010; van Woesik et al., 2012). Yet, reef corals generally prefer low-nutrient waters (Tomascik and Sander, 1987), and nearshore environments support high nutrient concentrations, which in combination with high temperatures are detrimental to reef corals (Wooldridge and Done, 2009; Wagner et al., 2010; Wiedenmann et al., 2013). Still, if shading in nearshore, turbid environments provides protection to corals under thermal-stress events, then the corals that can tolerate those nearshore conditions may be selected for when thermal-stress events become frequent. We hypothesize that although shading by high turbidity and high organics are less than optimal for reef-building corals, these conditions may be physiologically beneficial for corals under thermal stress. Indeed, the benefits of shading under extreme thermal stress may override the costs of living in these less suitable nearshore environments, with high thermal variation, low irradiance, and high nutrients. We question whether global warming is progressively driving reef corals away from clear, oligotrophic waters, to more nearshore, turbid habitats.

The present study uses an extensive dataset collected between 2005 and 2015 (http://www.frrp.org) at 2,398 sites along the Florida reef tract to examine the spatial distribution of scleractinian corals and the environmental variables that cause and relieve stress. Specifically, the objectives of this study were to: (i) quantify the water-quality characteristics of the study sites, particularly temperature and chlorophyll-a concentrations, (ii) determine the spatial extent of bleaching and coral disease, and (iii) examine interactions between coral bleaching, coral disease, and water quality.

METHODS

Water-Quality Data

Water-quality data were obtained from the Southeast Environmental Research Center, Florida International University (http://serc.fiu.edu/wqmnetwork/). These data were collected at 215 sites along the Florida Keys sampled quarterly from January 2005 to December 2015. We were particularly interested in both the benthic water temperature that the corals experienced (**Figure 1**), and the chlorophyll-a concentrations, used as a proxy for primary productivity in the water column. To geographically align the water-quality data with the coral data, we spatially cropped the coral data to the same extent as the water-quality data, and then spatially interpolated the water-quality data using ordinary kriging with the R package "gstat" (Pebesma, 2004). The interpolated data were combined to reflect patterns (i) over the entire study period, (ii) from 2005 to 2009, and (iii) from 2010 to 2015, before and after the major coral bleaching event in 2010.

Coral Sampling

The study used data that stemmed from the Florida Reef Resilience Program (FRRP) (http://www.frrp.org), which was a two-stage stratified-random survey design to assess the condition of scleractinian corals along the Florida reef tract every summer from 2005 to 2015 (Wagner et al., 2010; Smith et al., 2011; Burman et al., 2012). The region was stratified into geographic sub-regions and habitats. To date the FRRP has surveyed 2,398 sites, using replicated 10 m by 1 m belt transects. Along each transect each coral colony was identified to species, measured for diameter, and examined for bleaching and disease. The database is available from The Nature Conservancy upon request.

Data Analysis

We used semivariograms to estimate the extent of autocorrelation of the coral and water-quality data, and plotted the semivariance of each variable expressed as a function of distance across the spatial field. The semivariogram value $\gamma(d)$, or estimated semivariance, for lag distance d was defined as:

$$\gamma\left(d\right) = \frac{1}{2N(d)} \sum_{i=1}^{N(d)} \left(z\left(x_i\right) - z(x_i + d)\right)^2, \qquad (1)$$

where $N(d)$ is the number of pairs of points separated by d, $z(x_i)$ are the data values for points x_i, and $z(x_i+d)$ are the data at cells separated from x_i by the lag distance d in the chosen direction. The semivariogram estimates assumed that: (i) the process that generated the data was random, (ii) the variance of the process was constant and independent across space, and (iii) the process was only dependent on the separation distance between points. We examined the semivariogram estimates for inherent changes through time (i.e., stationarity), and for directionality (i.e., isotrophy).

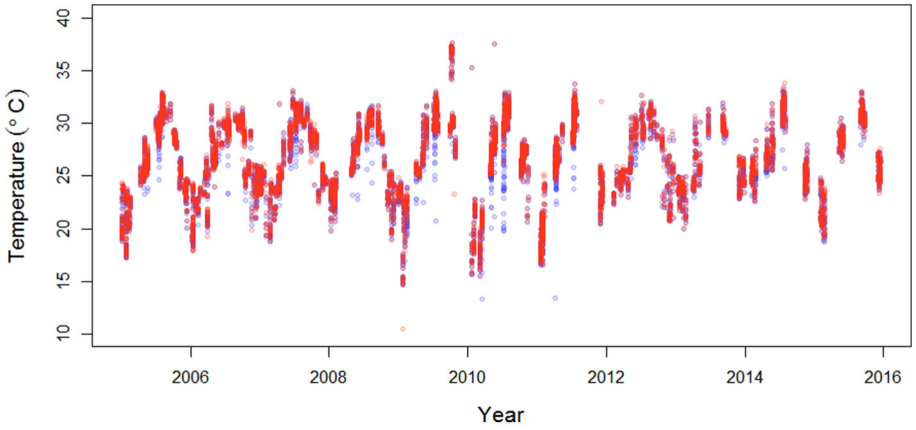

FIGURE 1 | Sea surface (red) and benthic (blue) temperatures (°C) along the Florida Keys (data from Southeast Environmental Research Center, http://serc.fiu.edu/wqmnetwork/) ($n = 6,849$).

We used generalized linear and non-linear models to examine relationships between coral bleaching and the water-quality parameters of interest, in particular water temperature and chlorophyll-a concentration. All linear and non-linear models showed spurious results, with significant negative slopes, suggesting that high-water temperature, for example, predicted low coral bleaching. We have long known that the opposite is true, because high-water temperatures cause coral bleaching. Therefore, the linear and non-linear models provided misleading predictions. We suspect that the negative slope is, in part, related to the high density of data, particularly around the 29.5°C, reducing the central tendency of the relationship. We instead considered using point pattern processes, which gain strength from high density data, because they utilize the intensity of spatially explicit geographic data as predictors. We therefore examined the coral responses as spatial point patterns and determined the dependence of those point patterns on environmental covariates (Baddeley et al., 2012), using the following:

$$\lambda(u) = \rho(X(u)), \tag{2}$$

where $\lambda(u)$ is an intensity function of a finite set of spatial data points of the coral localities (u), $X(u)$ is a spatial covariate (i.e., benthic temperature and chlorophyll-a in this study) at every locality. The data were modeled as a spatial point Poisson process, and ρ was determined using a nonparametric estimator with the R package "spatstat" (Baddeley et al., 2015). Although we analyzed the relationship between all stony corals present on the reefs and chlorophyll-a concentrations and temperature, we were also particularly interested in the corals *Acropora cervicornis*, which is a threatened species, and *Orbicella annularis*, which was common in the Florida reef tract in the past. We therefore further examined the relationship between these two species and chlorophyll-a concentrations and temperature. We also wanted to know whether the size of the coral colonies influenced the relationships with the environmental covariates, and therefore ran similar spatial point pattern analyzes after categorizing the coral colony diameters as either small (4–50 cm), medium (51–100 cm), or large (>100 cm). All analyses were run in R (R Core Team, 2016).

RESULTS

Water-Quality Data

Over the 11-year study period, within the study region, the benthic water temperature ranged from 13.4°C to 37.6°C, and chlorophyll-a concentrations ranged from 0.002 $\mu g\ l^{-1}$ to 12.29 $\mu g\ l^{-1}$. Sea surface temperatures (SSTs) were more variable than benthic temperatures (**Figure 1**), ranging from 10.5°C to 37.6°C. The highest temperatures were recorded in 2010, and the lowest temperatures were recorded in 2009 (**Figure 1**). The extent of homogeneous patches of benthic temperatures, evident from the range in the semivariograms, averaged approximately 15 km (SD ± 9.9 km) for the time period from 2005 to 2009, and approximately 17 km (SD ± 12 km) for the time period from 2010 to 2015. The semivariogram range of chlorophyll-*a* concentrations averaged approximately 23 km (SD ± 16 km) for the time period from 2005 to 2009, and approximately 33 km (SD ± 18 km) for the time period from 2010 to 2015 (see Supplementary document).

Coral Bleaching and Diseases

Coral bleaching was most prevalent in 2014 and 2015 (**Figure 2**), with average bleaching around 45 and 33% respectively. Coral bleaching was recorded at depths between 2 m and 28 m, although bleaching was most prevalent at depths between 6 and 8 m (**Figure 3**). The size of homogenous patches of bleached corals averaged at approximately 46 km (SD ± 47 km), although during extremely warm years the patch sizes were larger than in other years (see online Supplementary document). There was clear directionality (i.e., anisotropy) in the coral bleaching data, with most time periods showing east-west alignment along the

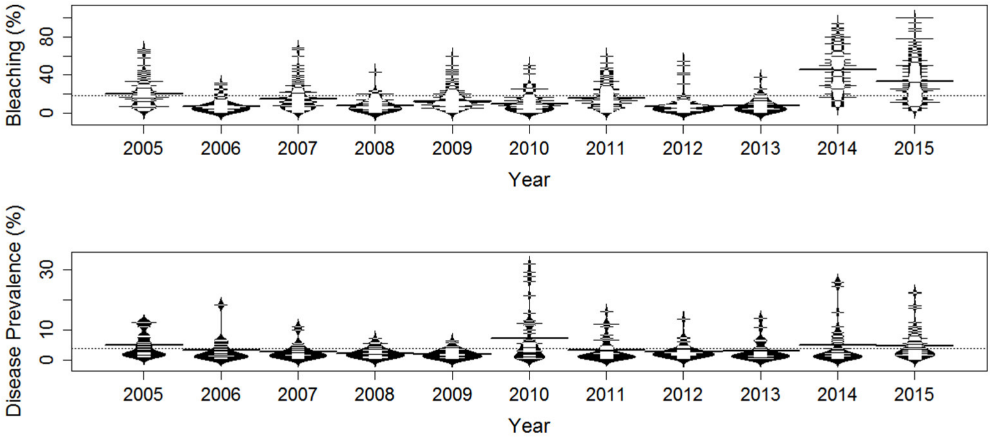

FIGURE 2 | Time series of the percentage of coral bleaching (upper panel), and the prevalence of coral disease (lower panel) at 2,398 sites along the Florida reef tract from 2005 to 2015. The longest horizontal line for each time period represents the yearly mean, and the dotted horizontal line displays the overall mean.

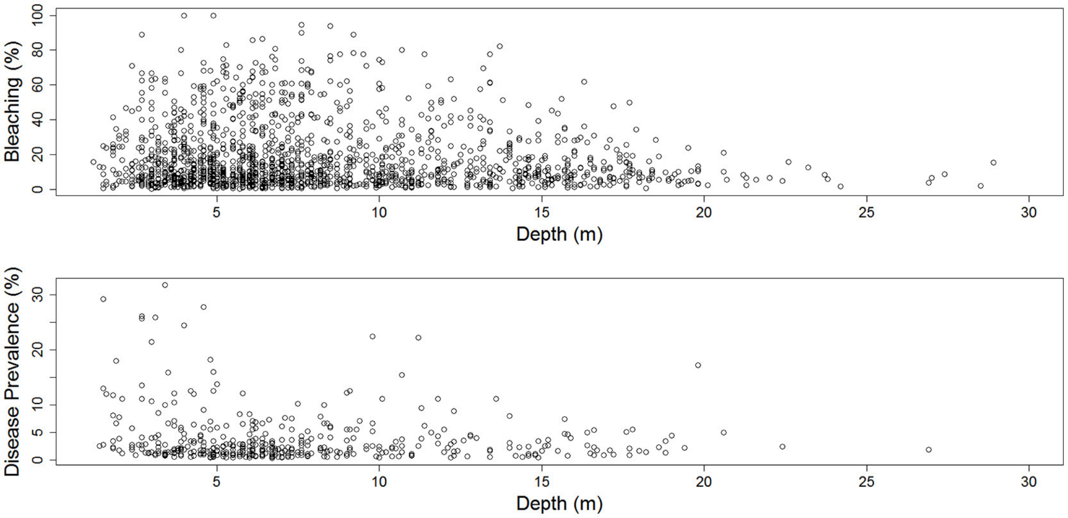

FIGURE 3 | The percentage of coral bleaching (upper panel), and the prevalence of disease (lower panel) across depth (m) at 2,398 sites along the Florida reef tract from 2005 to 2015.

geographic axis of the Florida Keys (see online Supplementary document).

Coral diseases were most prevalent in 2010, 2014, and 2015 (**Figure 2**), with average disease prevalence at 7, 5, and 4%, respectively. Diseases were most common at depths between 2 and 7 m (**Figure 3**). The average range of homogenous coral disease patches was typically 5 km or less, except in 2005 and 2014, when the sea surface and benthic temperatures were high, and when the range of homogeneous coral-disease patches averaged 14 km (SD ± 19 km). As occurred with the coral bleaching data, there was clear directionality (i.e., anisotropy) in the coral disease data, with most time periods showing east-west alignment along the geographic axis of the Florida Keys (see online Supplementary document).

Environmental Relationships

Most reef-building corals along the Florida reef tract were geographically located in habitats where the water temperatures were above 24°C during the winter season, and below 30°C in the summer season (**Figure 4**). Similarly, most corals favored habitats with low chlorophyll-a concentrations, yet these same oligotrophic conditions increased the prevalence of coral bleaching and disease (**Figure 5**). There was a considerable decline in coral bleaching and coral disease where chlorophyll-a concentrations were $>0.3\ \mu g\ l^{-1}$. The two main reef-building corals, *Acropora cervicornis* and *Orbicella annularis*, showed similar responses to chlorophyll-a concentrations and bleaching. Both coral species were most common in oligotrophic waters, with low chlorophyll-a concentrations, yet these same clear-water habitats were conducive to coral bleaching (**Figure 6**).

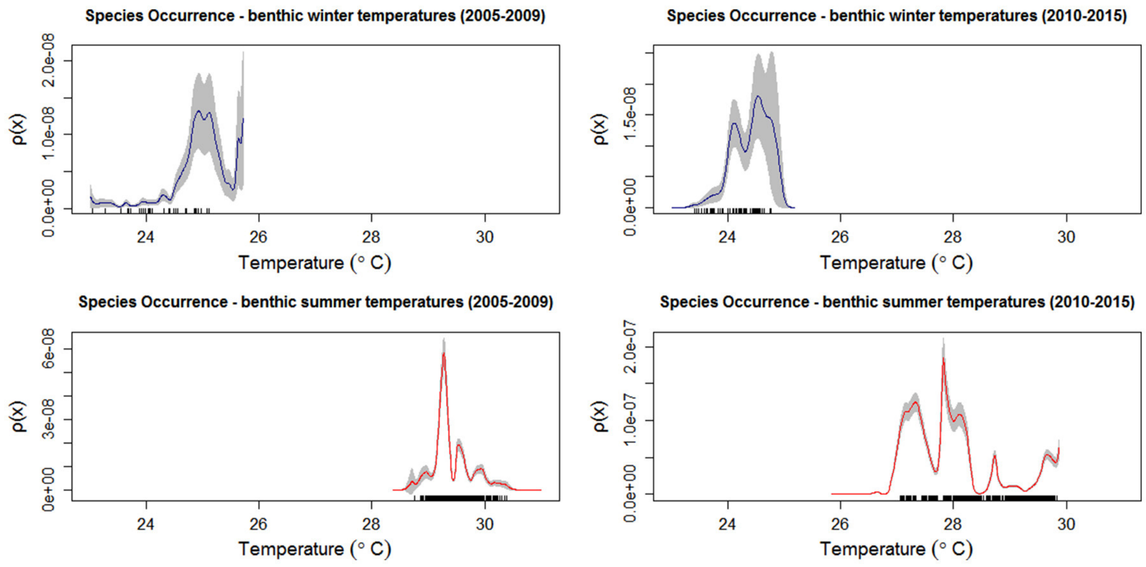

FIGURE 4 | Occurrence of all recorded coral species relative to winter and summer benthic temperatures (°C) in the Florida reef tract at 2,398 sites from 2005 to 2015. Kernel estimates of ρ (equation 2) (solid lines), and two-standard deviation confidence limits (gray shading) for winter (blue) and summer (red) temperatures. The rug plot indicates the number of sites that supported corals.

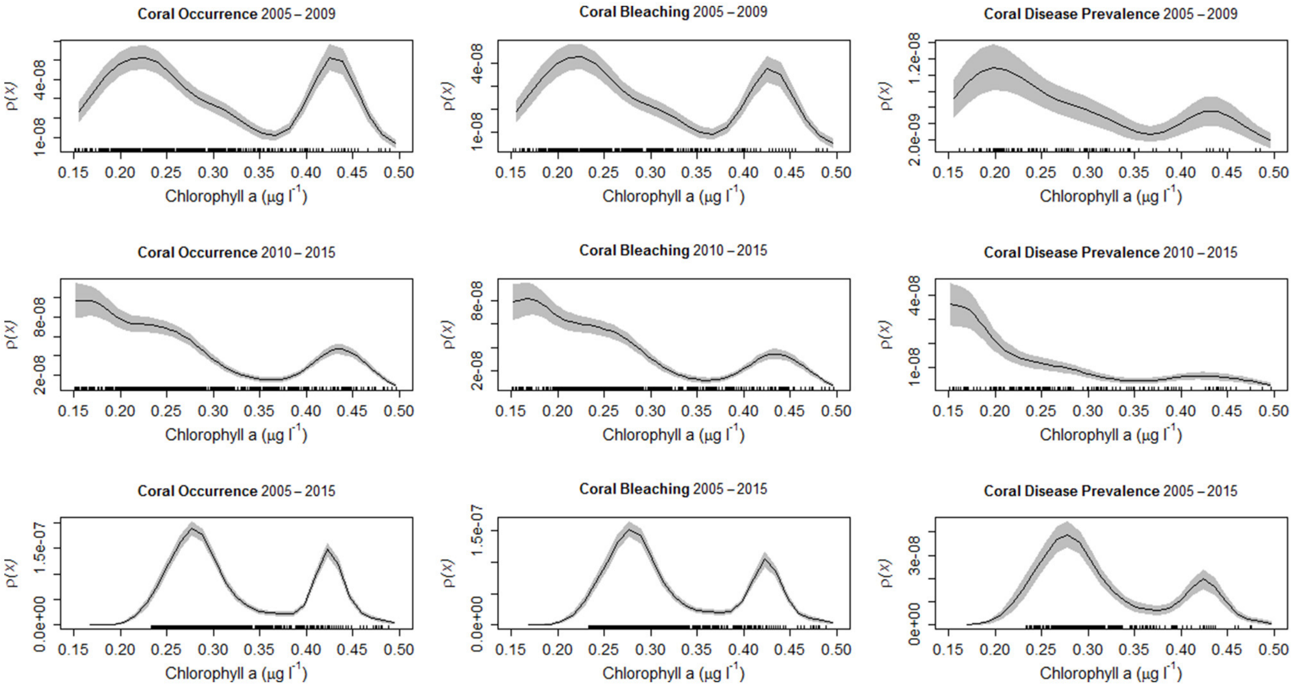

FIGURE 5 | All coral colonies in the Florida reef tract from 2005 to 2009 (upper row), from 2010 to 2015 (middle row), and throughout the entire study period (2005–2015) (lower row). Kernel estimates of ρ (equation 2) (solid black line), with two-standard deviation confidence limits (gray shading) for: (left column) the occurrence of all coral colonies as a function of chlorophyll-a concentrations (μg l^{-1}) in the water column, (central column) the prevalence of coral bleaching as a function of chlorophyll-a concentrations (μg l^{-1}), and (right column) the prevalence of coral disease as a function of chlorophyll-a concentrations (μg l^{-1}). The rug plots indicate the number of sites surveyed.

When we categorized the sizes of the coral colonies, and analyzed each size-class separately, both species showed a similar response, with most colonies occurring in waters with low chlorophyll-a concentrations independent of size class (**Figure 7**). By contrast, *Acropora cervicornis* colonies in localities with chlorophyll-a concentrations >0.3 μg l^{-1}

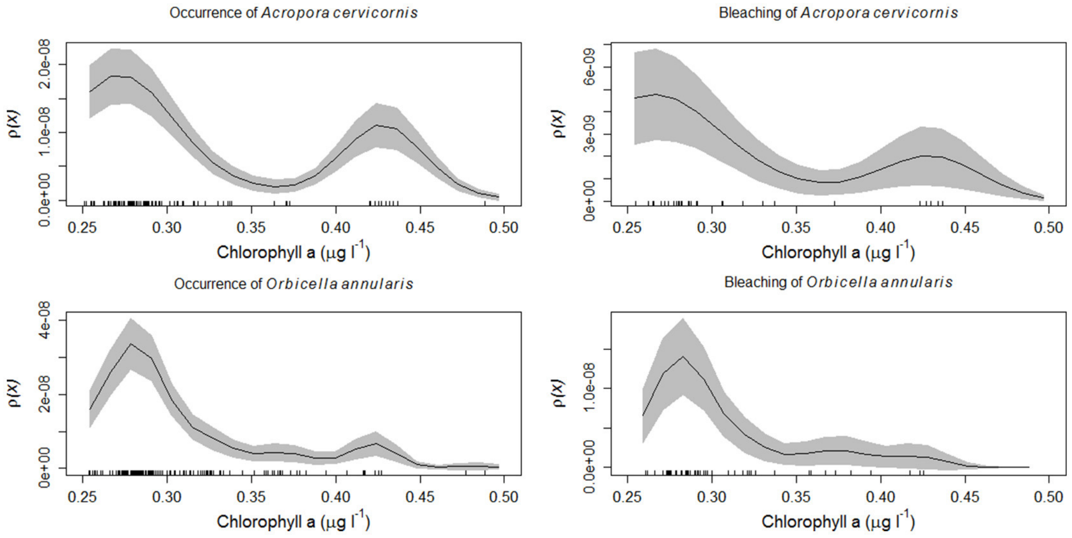

FIGURE 6 | *Acropora cervicornis and Orbicella annularis* from the Florida reef tract from 2005 to 2015. Kernel estimates of ρ (equation 2) (solid black line), with two-standard deviation confidence limits (gray shading) for: (top left panel) the occurrence of *Acropora cervicornis* as a function of chlorophyll-a concentrations (μg l^{-1}), (top right panel) the prevalence of coral bleaching of *Acropora cervicornis* as a function of chlorophyll-a concentrations (μg l^{-1}), (lower left panel) the occurrence of *Orbicella annularis* as a function of chlorophyll-a concentrations (μg l^{-1}), (lower right panel) the prevalence of coral bleaching of *Orbicella annularis* as a function of chlorophyll-a concentrations (μg l^{-1}). The rug plot indicates the number of sites surveyed that supported the coral species.

were less susceptible to bleaching, and *Orbicella annularis* in localities with chlorophyll-a concentrations > 0.4 μg l^{-1} were less susceptible to bleaching. Similarly, when summer temperatures and chlorophyll-a concentrations were considered together, as spatial covariates of the spatial-point-process-intensity estimates, the corals were most common at low chlorophyll-a concentrations and at 27.5°C. Bleached corals were most prevalent at low chlorophyll-a concentrations and at temperatures >29°C (**Figure 8**).

DISCUSSION

The analysis of this extensive dataset from the Florida reef tract suggests that thermal-stress events are responsible for coral bleaching and associated coral disease, but water clarity also plays an important role. We found that throughout the decade of observation, the clearer the water the more likely it was that corals bleached. Corals in general, and the two major reef-building corals, *Acropora cervicornis* and *Orbicella annularis*, in particular, occurred in greater numbers in habitats with low chlorophyll-a concentrations. Yet coral colonies in these low chlorophyll-a habitats showed more extensive bleaching during thermal stress events than coral colonies in high chlorophyll-a habitats. It is most likely that the high concentrations of chlorophyll-a acted as a thermal refuge for coral colonies because of the shading they provided to the corals.

Physiological studies have confirmed the benefits of reducing irradiance during temperature-stress events. Shading reduces stress on the symbiont's photosystem, which in turn reduces the likelihood of coral bleaching (Warner et al., 1999; Takahashi et al., 2004). Notwithstanding the obviously adverse effects that poor-water quality, with high levels of pollutants and high nutrient concentrations, has on corals (Wooldridge and Done, 2009; Wagner et al., 2010; Wiedenmann et al., 2013), some shading provided by high-primary productivity and high turbidity can benefit corals during thermal-stress events (Cacciapaglia and van Woesik, 2016). Indeed, since coral bleaching is essentially extreme photoinhibition, and high temperatures make that photoinhibition worse (Warner et al., 1999; Takahashi et al., 2004), high productivity and high turbidity during high temperature events should effectively reduce the probability of photoinhibition and coral bleaching.

Similarly, the results showed that corals in habitats with high water-column productivity had a lower prevalence of disease than elsewhere. Previously, Lesser et al. (2007) suggested that reducing chronic photoinhibition and bleaching reduces the likelihood of coral disease. Subsequent field studies have validated these observations. For example, Muller et al. (2008) showed that bleached *Acropora palmata* colonies were more likely to suffer disease than coral colonies that did not bleach.

Still, reducing irradiance can be detrimental to the calcification process, causing reductions in coral growth rates (Tomascik and Sander, 1987). Moreover, high sedimentation environments can deplete coral resources and increase their susceptibility to disease (Sheridan et al., 2014). Therefore, reducing irradiance, through primary productivity in the water column and high turbidity, can have beneficial effects up to a point, beyond which the costs may override the benefits for reef corals. Indeed, high and persistent productivity and extremely high turbidity can reduce the capacity of corals to build reefs entirely, because the photic zone becomes so narrow that there is insufficient irradiance for photosynthesis and

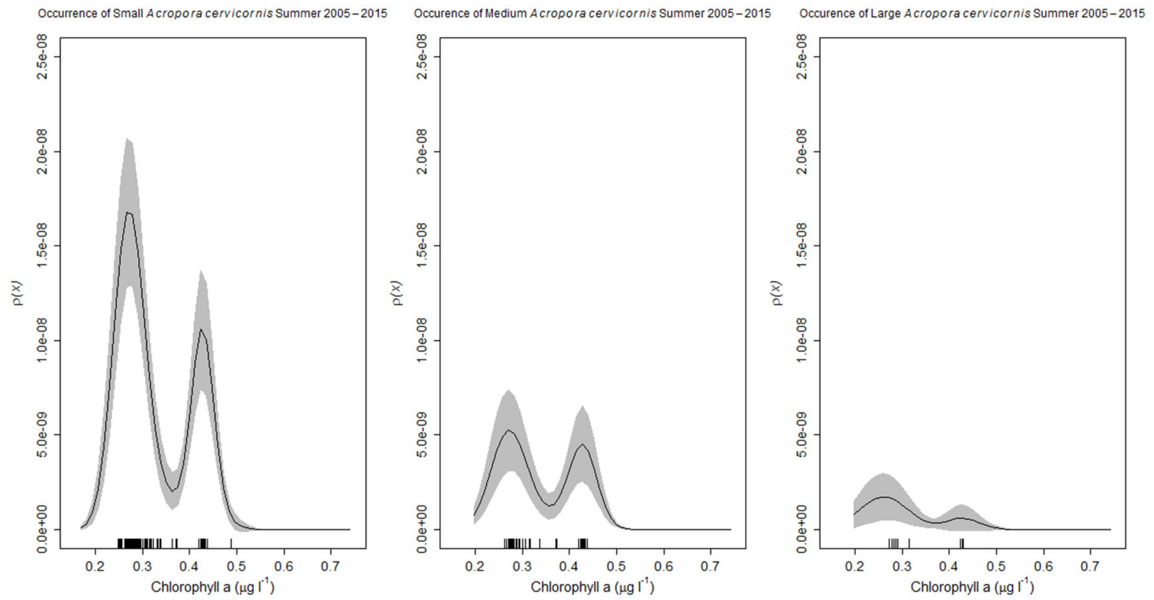

FIGURE 7 | *Acropora cervicornis* colonies of three size classes, small (4–50 cm), medium (51–100 cm), or large (> 100 cm), in the Florida reef tract from 2005 to 2015. Kernel estimates of ρ (equation 2) (solid black line), with two-standard deviation confidence limits (gray shading) for the occurrence of *Acropora cervicornis* as a function of chlorophyll-a concentrations (μg l^{-1}). The rug plot indicates the number of sites surveyed that supported the coral species of the specific size class.

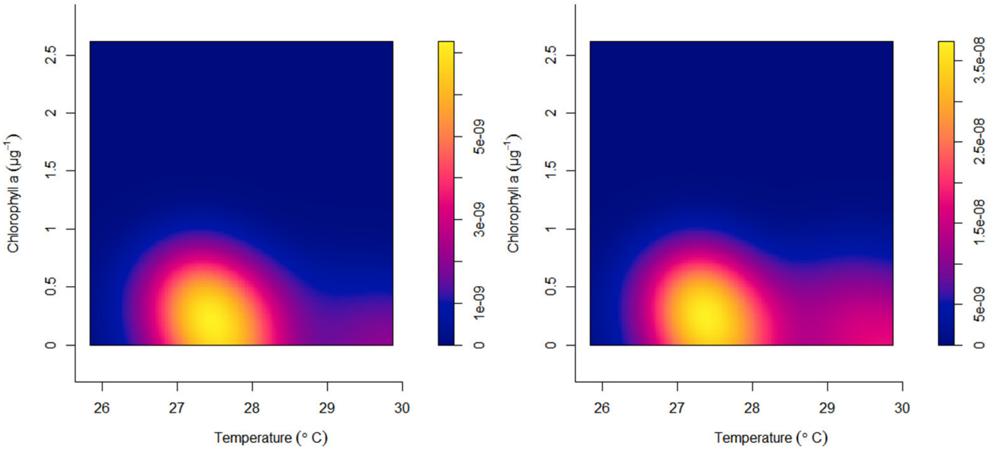

FIGURE 8 | *Acropora cervicornis* from 633 sites in the Florida reef tract from 2005 to 2015. Kernel intensity estimates of ρ (equation 2) for all colony occurrences (left panel) and all bleached corals (right panel) against chlorophyll-a concentrations (μg l^{-1}) and benthic temperatures (°C).

calcification (Tomascik et al., 1993; Kleypas, 1996; Toth et al., 2012). Previously, Kleypas et al. (1999) showed that reef building is unlikely in habitats with an average irradiance of <250 μE m^{-2} s^{-1} (at a depth of 3 m). Therefore, locating optimal niches, where corals can survive through thermal-stress events, should be a research priority, to not only detect natural refuges, but also for the rapidly burgeoning coral restoration endeavor that is expanding throughout Florida and the Caribbean.

Ocean temperatures are clearly increasing globally (Hansen et al., 2010; IPCC, 2013), and as the oceans continue to warm, thermal anomalies will most likely continue to cause coral bleaching and subsequent diseases (Hoegh-Guldberg, 1999; Harvell et al., 2002; Donner et al., 2005; Hoegh-Guldberg et al., 2007; Muller and van Woesik, 2012). Some researchers question the capacity of corals to adapt to rapid climate change (Hoegh-Guldberg, 2006; Frieler et al., 2013), whereas other researchers suggest that adaptive radiations and directional selection of thermally tolerant genotypes are likely (Thompson, 1998; Hoffmann and Sgro, 2011; Guest et al., 2012; Poloczanska et al., 2016). The present study suggests an additional, more nuanced, effect of ocean warming—causing geographical shifts of reef corals toward more turbid environments.

Adaptation, however, will occur only under persistent selective pressure. In the past, there may have been little selective pressure for corals to live in habitats with consistently high turbidity and high chlorophyll-a-concentrations, since reef-building corals grow best under moderate irradiance (Done, 1982). Most recently however that selective pressure may have increased. The almost annual reoccurrence of thermal-stress events and coral bleaching in the Florida reef tract, shown by this study, may be selecting for coral genotypes that can live in naturally shaded environments, with high primary productivity and turbidity. Corals in these shaded habitats are less likely to suffer thermal stress than elsewhere. Therefore, in a rapidly warming ocean, there is likely to be a fitness advantage for corals that can live in habitats with less than optimal irradiance, because those same environments shield corals from short-term temperature-stress events. This study suggests that directional selection in a warming ocean may favor corals that are able to tolerate inshore environments with high turbidity and productivity. Because of reduced thermal stress in those shaded environments, selection for colonies in these habitats may provide the genetic pool of corals needed to survive through climate change.

AUTHOR CONTRIBUTIONS

RvW designed the work, wrote the R code to conduct analysis, and wrote the manuscript. KM conducted the kriging analysis, wrote some of the R code, and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00182/full#supplementary-material

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Nearshore Turbid-Zone Corals Exhibit High Bleaching Tolerance on the Great Barrier Reef Following the 2016 Ocean Warming Event

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High sea surface temperatures (SSTs) on the Great Barrier Reef (GBR) during summer 2015/2016 caused extensive coral bleaching, with aerial and in-water surveys confirming high (but variable) bleaching-related coral mortality. In contrast, bleaching impacts on nearshore turbid-zone reefs, traditionally considered more "marginal" coral habitats, remain poorly documented. This is because rapid ecological surveys are difficult in these turbid water settings, and baseline coral community data from which to quantify disturbance are rare. However, models suggest that the extreme environmental conditions characteristic of nearshore settings (e.g., fluctuating turbidity, light, and temperature) may acclimate corals to the thermal anomalies associated with bleaching on offshore reefs, although validation by field evidence has to-date been sparse. Here we present a novel pre- (June 2013/2014) and post-warming (August 2016) assessment of turbid-zone coral communities and examine the response of corals to prolonged and acute heat stress within the Paluma Shoals reef complex, located on the central GBR. Our analysis of 2,288 still video frames (~1,200 m^2) which include 11,374 coral colonies (24 coral genera) suggest a high tolerance of turbid-zone corals to bleaching, with no significant changes in coral cover (pre: 48 ± 20%; post: 55 ± 26%) or coral community structure (e.g., *Acropora*, *Montipora*, *Turbinaria*, *Porites*) following the warming event. Indeed, only one coral colony (*Lobophyllia* sp.) exhibited full colony bleaching, and just 1.5% of colonies displayed partial pigmentation loss (<20% colony surface). Taxa-specific responses to this thermal stress event contrast with clear-water assessments, as *Acropora* corals which are normally reported as highly susceptible to bleaching on clear-water reefs were least impacted at Paluma Shoals, a phenomena that has been observed within other turbid settings. Importantly, field surveys confirm regional SSTs were sufficiently high to induce coral bleaching (i.e., comparable number of degree heating days in nearshore and offshore areas), but bleaching severity was much higher at central GBR offshore sites. A more optimistic outlook than is generally offered for nearshore reefs on the central GBR may be implied by our results, which highlights the importance of these resilient but often overlooked coral reef habitats as potential refugia during climate-related disturbances.

Keywords: turbid-zone, coral bleaching, Great Barrier Reef, refugia hypothesis, environmental change, turbidity

INTRODUCTION

Elevated global ocean temperatures since 2014 have caused widespread coral bleaching throughout all major reef-building regions, with temperatures peaking in 2015/2016. This temperature anomaly resulted in the onset of the "third global coral bleaching event" on record. The term "coral bleaching" refers to a loss of color in corals after they expel their endosymbionts (*Symbiodinium*) and occurs most often as a stress response to elevated sea surface temperatures (Brown, 1997; Baker et al., 2008). Resultant deleterious physiological effects include reduced coral growth and increased mortality (Douglas, 2003), and at a community level, reductions in coral cover and shifts in coral community structure to less diverse assemblages composed of the most resilient taxa only (Marshall and Baird, 2000; Hughes et al., 2007). This most recent warming event, which has been unprecedented in its magnitude and duration, has affected vast areas of coral-dominated habitat within the central Indian Ocean (Maldives), Western Australia, Pacific Ocean, the Red Sea, the Caribbean, and the Great Barrier Reef (GBR) (Lafratta et al., 2016; Hughes et al., 2017; Perry and Morgan, 2017; see DeCarlo et al., 2017). On the GBR, above-average sea surface temperatures (SSTs) occurred in the late austral summer (2015/2016). Aerial surveys of 911 mid- and outer-shelf reefs indicated high levels of bleaching (∼90% of surveyed reefs) within the northern and central GBR, with subsequent in-water assessments confirming highest mortality occurring within the northern GBR sector and reducing on the southern GBR (Great Barrier Reef Marine Park Authority, 2016; Hughes et al., 2017). Surveys of recently bleached reefs have focused on those that could be observed from the air and easily surveyed in the water. Thus the condition of nearshore turbid-zone reefs within the affected region was not investigated as; (1) both aerial and in-water surveys are difficult due to high turbidity; and (2) ecological baseline data against which to quantitatively assess bleaching impacts are available for very few of these reefs.

The response of nearshore turbid-zone coral assemblages to conditions responsible for the severe and widespread bleaching of clear-water reefs is, however, of major research interest as it has been hypothesized that they may represent potential refugia for corals from large-scale climatic disturbances (Potts and Jacobs, 2000; van Woesik et al., 2012; Cacciapaglia and van Woesik, 2015). Turbid-zone reefs have traditionally been perceived as unsuitable, or at best "marginal" for healthy coral growth because corals are exposed to high turbidity, low-light availability, large salinity and temperature fluctuations, high tidal ranges and prolonged aerial exposure (Kleypas, 1996; Kleypas et al., 1999). However, a growing number of field studies have documented the diversity and adaptive capacity of turbid-zone coral communities across a range of geographic locations and time-scales (Bull, 1982; Perry et al., 2009; Browne et al., 2010; Roche et al., 2011; Butler et al., 2013; Fellegara et al., 2013; Richards et al., 2015; Guest et al., 2016; Lafratta et al., 2016; Morgan et al., 2016a; Ryan et al., 2016). This collective body of research suggests that these reefs occupy far larger areas than previously thought and support high coral cover including taxa (e.g., *Acropora*) typically regarded as highly susceptible to thermal stress (Marshall and Baird, 2000; Browne et al., 2010; Morgan et al., 2016a; Hughes et al., 2017). Key to the success and ability of these corals to grow under light-limited conditions (often at rates similar to clear-water corals; Browne, 2012) appears to be their capacity to effectively utilize both phototropic/heterotrophic feeding and sediment sloughing mechanisms (Anthony and Fabricius, 2000; Anthony et al., 2005). Environmental factors (e.g., elevated suspended sediment concentrations) may also inhibit the harmful interaction between heat stress and high light intensity on corals within turbid settings by rapidly attenuating sunlight through the water column (Storlazzi et al., 2015). Combined, these factors form the basis of global-scale modeling efforts that have identified turbid reef areas (which include nearshore areas of the GBR) as potential coral refugia locations (Cacciapaglia and van Woesik, 2015). Critical to our understanding of whether turbid-zone corals may indeed have the capacity to withstand thermal extremes associated with major coral bleaching events is empirical field data documenting coral response during (or soon after) thermal stress has occurred, but such data are scarce.

Fortuitously, ecological surveys were conducted across the Paluma Shoals reef complex (PSRC), a series of nearshore turbid-zone reefs located in Halifax Bay on the central GBR, prior to the summer 2016 SST warming. These surveys revealed thriving coral communities that have displayed a remarkable resilience to the major factors which have contributed to the degradation of clear-water reefs further offshore (e.g., declining water quality, cyclone impacts, crown-of-thorns sea stars; De'ath et al., 2012). This existing dataset, collected using video during a period of exceptionally calm and clear water conditions captured substantial baseline information on coral community composition within these normally high turbidity settings close to the initial onset and subsequent progression of the mid-2016 warming event (data were collected in July 2013 and 2014). These data provide: (1) a unique opportunity to quantitatively assess the extent to which the 2016 ocean warming impacted turbid-zone coral communities at PSRC; and (2) to test the hypothesis that turbid-zone reefs may function as refugia from increased SSTs. Here we report data from repeat field surveys and subsequent bleaching assessments immediately following the warming event in the early austral winter (August 2016), and present pre- and post-warming coral community data to examine the response of turbid-zone reefs to prolonged thermal stress.

MATERIALS AND METHODS

Study Site

The Paluma Shoals reef complex (PSRC) covers an area of 15.5 km^2 (Latitude: −19.1145°, Longitude: 146.5497°) and is located within Halifax Bay on the central GBR (**Figure 1**). The area encompasses seven discrete reef structures, each of which presently exhibits different stages of geomorphic maturity (*sensu* Hopley et al., 2007) defined by the current depth relative to lowest astronomical tide (LAT; reef surfaces range from −0.6 to +0.5 m below LAT). The regional distribution and morphology of these reef structures has recently been described from acoustic surveys of seafloor bathymetry (see Morgan et al., 2016a for

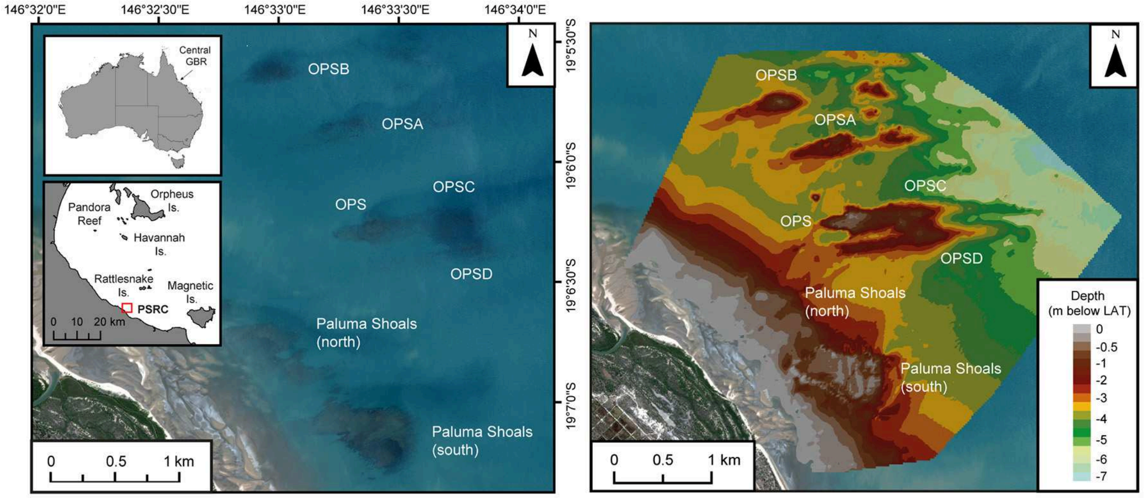

FIGURE 1 | Site map of the Paluma Shoals reef complex (PSRC) located within Halifax Bay on the central Great Barrier Reef, Australia. Satellite imagery and bathymetric seafloor model (m below lowest astronomical tide; LAT) show the position and morphology of the seven discrete nearshore turbid-zone coral reefs that comprise the complex. OPS [A, B, C, D], Offshore Paluma Shoals [A, B, C, D].

full physical and ecological descriptions) and shows coral reef growth to be concentrated above large submarine bedforms (1–1.7 km long and 200 m wide) orientated perpendicular to the coast (Larcombe and Carter, 2004; Morgan et al., 2016a). The topography of these bedforms provides elevation for corals above the muddy seafloor and into the shallower sediment resuspension zone (*sensu* Wolanski et al., 2005), as well as increasing access to light for coral photosynthesis. Under these conditions reef initiation in the area began on coarse lithic gravels between ∼2000 and 700 cal. y BP (calibrated years before present), and thus these reefs are geologically very young features with short growth histories as a consequence of their relatively recent initiation (Smithers and Larcombe, 2003; Morgan et al., 2016b). Since this time vertical reef growth has been driven by the carbonate production of established framework-building coral taxa (*Acropora*, *Montipora*, and *Turbinaria*) and interstitial terrigenous sediment inputs (Palmer et al., 2010; Perry et al., 2013; Morgan et al., 2016b; Johnson et al., 2017). The growth history and ecological communities (and the environmental conditions they inhabit) of these nearshore reefs are thus distinct from those inner-shelf (or "inshore") reefs on the central GBR further seaward which have recently experienced large-scale ecological disturbance (e.g., Pelorus Reef; Roff et al., 2013).

Coral cover on many nearshore turbid-zone reefs on the central GBR is high (up to 55%), and they support relatively diverse coral assemblages both within the contemporary communities and the palaeorecord (Perry et al., 2009; Browne et al., 2010; Roche et al., 2011; Morgan et al., 2016a; Ryan et al., 2016; Johnson et al., 2017). These coral communities provide important structural complexity in an otherwise flat soft sediment-dominated coastal zone. However, the abundance of fine clastic sediment, much of which is a legacy of material transported onshore during the last marine transgression and augmented by riverine inputs since sea level stabilized in the mid-Holocene (Larcombe and Woolfe, 1999), produces naturally high turbidity as seafloor sediment is continually resuspended by incident wave energy (Larcombe et al., 1995). The corals that occupy these turbid settings therefore tolerate large fluctuations in turbidity (Larcombe et al., 1995; Browne et al., 2013b; up to 385 mg l—1) and experience the low-light (or mesophotic) conditions typical of these nearshore settings. The term "mesophotic" was first used to describe muddy coastal reef settings in the fossil record (e.g., Rosen et al., 2000; Santodomingo et al., 2016), and whilst it has more recently been associated with coral reefs at depth (>30 m) (e.g., Bridge et al., 2011), it is a descriptor based on light (not depth) and should thus also be used for reefs occupying shallow-water turbid settings, such as those described here.

Sea Surface Temperature Anomalies (2015/2016) On the Great Barrier Reef

Mass coral bleaching occurred on the GBR in 2016 triggered by above normal SSTs (1–1.3°C higher than the 1961–1990 GBR average; Great Barrier Reef Marine Park Authority, 2016). A strong El Niño event across the Pacific indirectly intensified thermal stress on corals by reducing monsoon activity in the region that resulted in relaxed trade winds, long periods with no cloud cover, and clearer and calmer water conditions which warmed surface waters more than normal. During the late austral summer (February-June 2016) SSTs on the central and northern GBR (including coastal areas nearby to Paluma Shoals) were the highest on record, with 31% of reefs experiencing 8–16° Heating Weeks (DHWs) (Hughes et al., 2017; see Supplementary Figure S2). DHWs are an indicator of thermal stress calculated as the cumulative positive anomaly from mean SST and used to identify potential areas of coral bleaching (Liu et al., 2006). A latitudinal gradient in heat stress and coral bleaching was documented across the GBR, with the highest ocean temperature anomalies reported within the northern GBR sector, and "severe" to "minor" warming across the central and southern GBR, respectively. Satellite-derived sea surface temperature anomalies (SSTA) at a finer spatial scale (2 × 2 km grid size) indicate above-average SSTs (2–3°C) in the immediate region surrounding the PSRC between mid-February and early-August 2016 (**Figure 2**). SSTA are the difference between SST values and the long-term monthly mean SST and were used here to generate 14-day mosaic maps for Halifax Bay from 1-day night-only SST (data sourced from ReefTemp Next Generation; www.bom.gov.au/environment/activities/reeftemp/reeftemp.shtml; Garde et al., 2014). Given the magnitude and length of SSTA within nearshore areas of Halifax Bay and the documented relationship between heat exposure and coral bleaching reported following the 2016 event (see Hughes et al., 2017), it is reasonable to infer high thermal stress at PSRC over this period.

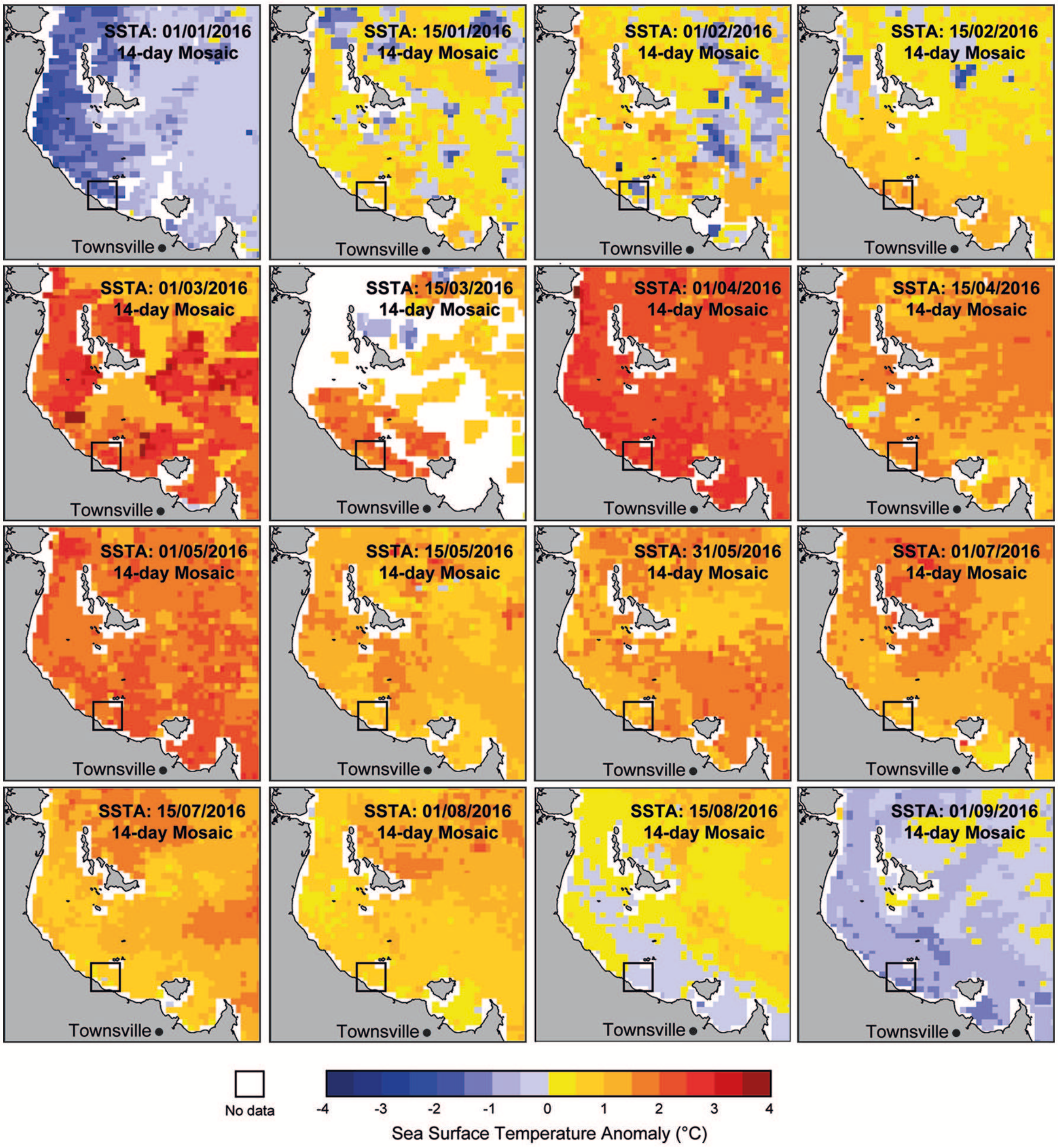

FIGURE 2 | Satellite-derived sea surface temperature anomalies (SSTA) for Halifax Bay (2 × 2 km grid size) showing the increase in SSTs since the start of 2016 in the region. SSTA are the difference between SST values and the long-term monthly mean SST. Maps were generated using 14-day mosaics for Halifax Bay from 1-day night-only SST (Garde et al., 2014). Note that temperatures in the vicinity of the proposed study area (black box) have been 2–3° above "normal" since February 2016. Data source: ReefTemp Next Generation (www.bom.gov.au/environment/activities/reeftemp/reeftemp.shtml).

Coral Community Surveys and Bleaching Assessments

Detailed surveys of coral cover and community assemblages were conducted across the PSRC during July 2013 and 2014 (see Morgan et al., 2016a), prior to the 2016 bleaching event. In early August 2016, at the beginning of the austral winter and immediately following the period of ocean warming, repeat ecological surveys were undertaken across the main PSRC structures to document coral cover and bleaching impacts. Towed video surveys using the same drop-down video system used in our 2013/14 surveys (SeaViewer with Sea-Track^{TM} GPS overlay) were carried out along the same 300 m transect lines (20–40 m spacings). A forward-facing GoPro camera was also attached to the frame to obtain oblique 4k resolution video of coral communities and of coral reef three-dimensionality (for rugosity classification scheme see Morgan et al., 2016a). Still frames ($\sim$0.5 m^2) were extracted from the drop-down video at automated 8 s intervals ($n =$ 2,288) and a digital 9-point grid overlay was added for coral taxonomic analysis (coral genera and growth morphology) by point-counting corals under each of the nine points. Each frame was assigned a specific depth value relative to LAT using a digital model of seafloor bathymetry for the area (**Figure 1**). Data were analyzed using a 10-frame moving average across consecutive frames to characterize the relative abundance (%) of coral taxonomic groups. Changes in coral cover and community structure pre- and post-warming were examined by comparing the two survey datasets (2013/2014 and 2016).

All coral colonies within the still images ($n =$ 2,288) were counted and assessed for signs of bleaching or recent mortality (dead *in situ* coral framework with no/little algal growth). Image analysis was undertaken by a single observer and then validated by two independent observers to ensure consistency. Coral colonies that exhibited bleaching were counted and categorized by the following bleaching states (modified from Beeden et al., 2008): (1) total bleaching = complete loss of symbiotic algae; (2) partial bleaching = small sections of the colony fully bleached; (3) non-focal bleaching = small diffuse patterns of bleaching on colony surfaces; (4) focal bleaching = small multifocal patterns of bleaching with discrete borders to healthy tissue; and (5) paling = lack of pigmentation/reduction in symbiont concentration (i.e., discoloration) (**Figure 3**). Each observed bleached colony was identified to the lowest taxonomic level possible and the intensity of bleaching across the colony surface estimated categorically (e.g., 0–10, 11–20, 21–30%).

Light attenuation through the water column at PSRC was measured at 0.5 m depth intervals (to 5 m below LAT) under low ($\sim$10 mg l^{-1}) and high ($\sim$80 mg l^{-1}) turbidity scenarios (based on values derived by Browne et al., 2013b). A light meter (LiCOR LI-192SA) was lowered through the water to each depth interval and average light intensity over a 15-second period recorded. Measurements were repeated 18 times over 3 days and then averaged to determine a mean value of light decay through the water column.

Data Analysis

Prior to analysis all data were tested for normality. Non-transformed data were then used to test for differences in coral cover (t-test) and reef rugosity (Kruskall-Wallis) between pre- (2013/2014) and post-warming (2016) surveys. Multivariate statistical analysis was used to test for differences in coral community composition, both in terms of the prevalence of different coral genera and growth morphologies using a one-way PERMANOVA based on a Bray-Curtis similarity matrix. Bleaching prevalence was calculated by dividing the pooled number of colonies that showed signs of bleaching by the total number of colonies recorded within the frames (11,374 colonies). A bleaching index (BI) was calculated for each taxon, and is a scaled index of coral thermal response (i.e., a single measure of susceptibility) which accounts for the relative proportion of the coral taxonomic group on the reef (modified from McClanahan et al., 2004). The BI of corals was estimated as follows:

$$BI = \frac{0c1 + 1c2 + 2c3 \ldots 9c10 + 10c11}{10} \tag{1}$$

Where $c1$ to $c11$ are the different categories of bleaching intensity (% surface area) observed on each of the coral taxa arranged from no bleaching ($c1$) to full colony bleaching ($c11$), and expressed as a proportion of the total number of colonies analyzed resulting in a normalized 0–100 scale (McClanahan et al., 2004; Guest et al., 2016).

RESULTS

Pre-and Post-warming Assessments of Coral Communities

A total of 2,288 still frames (covering $\sim$1,200 m^2 of reef) from PSRC reefs collected immediately following the warming event (August 2016) were analyzed for coral cover and coral community composition, and compared to existing pre-warming baseline data (2013/2014; $n =$ 4,420). A total of 11,374 coral colonies were analyzed in 2016, with 24 coral genera identified. Average (± s.d.) coral cover and reef structural complexity (R) in 2016 were both high (coral cover = 55 ± 26%; median R = 3; **Figure 4A**; see Supplementary Figure S1) and showed no statistical difference ($p > 0.05$ for both) when compared to pre-warming coral community data from comparable reef habitats in 2013/2014 (coral cover = 48 ± 20%; median $R = 3$). Furthermore, no significant difference in coral assemblages was found between the time-series [one-way PERMANOVA: $F_{(2,\,362)} = 22.8$, $p > 0.05$; **Figure 4B**], with communities dominated by *Montipora* spp. (pre: 50 ± 22%; post: 50 ± 23%), *Acropora* spp. (pre: 14 ± 15%; post: 15 ± 14%), *Turbinaria* spp. (pre: 13 ± 23%; post: 8 ± 17%), and to a lesser extent *Porites* spp. (pre: 1.7 ± 4.9%; post: 0.9 ± 2.4%). Other less abundant coral taxa collectively accounted for only 2.6 ± 0.16% of average post-warming coral cover (see **Figure 4B** for coral inventory). Similar proportional contributions in terms of coral growth morphologies were also observed pre- and post-warming [one-way PERMANOVA: $F_{(2,\,362)} = 62.3$, $p > 0.05$]; the morphological classes examined included encrusting (pre: 38 ± 27%; post: 34 ±

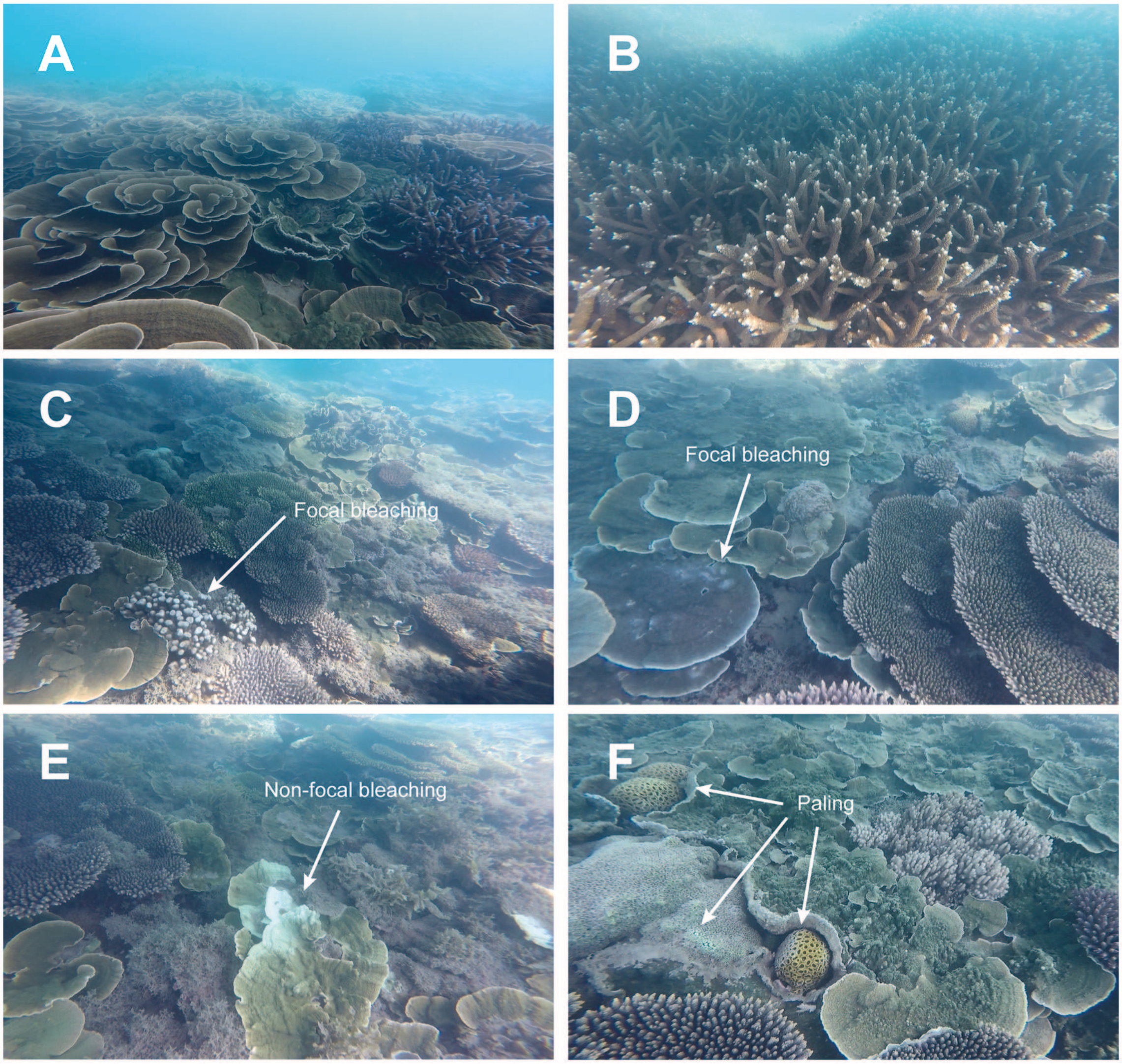

FIGURE 3 | Turbid-zone coral communities of the Paluma Shoals reef complex (PSRC) following the 2016 bleaching event (photos taken at 1–3 m water depth during a period of exceptional water clarity). **(A,B)** Corals exhibit high coral cover of taxa generally considered most susceptible to bleaching (e.g., branching *Acropora*). **(C,D)** Examples of focal bleaching (small multifocal patterns of bleaching with discrete borders to healthy tissue) typically observed on *Porites* sp. nubbins and *Montipora* sp. plates. **(E)** Non-focal bleaching (small diffuse patterns of bleaching on colony surface) affecting part of a *Montipora* sp. colony. **(F)** Coral paling (lack of pigmentation) associated with submassive coral colonies.

34%), foliose (pre: 25 ± 25%; post: 27 ± 19%) and branching (pre: 10 ± 16%; post: 11 ± 18%) corals (**Figure 4C**). Collectively, these observations indicate no change in the prevalence of any coral genera as a result of the thermal stress experienced, and that the 2016 repeat survey data sufficiently captured the full extent of reef habitat types and coral communities at PSRC, thus providing a reliable basis from which to assess coral bleaching susceptibility.

Prevalence of Coral Bleaching and Taxonomic Responses to Thermal Stress

Signs of bleaching were observed on only 173 coral colonies, or 1.5% of all colonies examined in our post-warming dataset. However, although evidence of thermal stress was observed on some colonies, the overall response by corals was very minor with only one individual colony (*Lobophyllia* sp.) exhibiting full bleaching (i.e., complete loss of zooxanthellae). This equates to only 0.008% of corals analyzed at PSRC. Therefore, any coral that showed visual signs of pigmentation loss (i.e., whitening) on the colony surface is referred to as "bleached" hereafter. On this basis, bleaching intensity (% of total tissue cover) on colonies was low, typically <20% (bleaching intensity: 0–10% = 64%; 11–20% = 21%), with only a small proportion of affected colonies (8.6%) exhibiting bleaching on >31% of their surface area (**Figure 5**). Although minor, the presence of bleaching clearly confirms that SSTs in the region of PSRC were above the thermal tolerance of some corals. Because of the timing of the surveys immediately following the period of high SSTs we were also able to assess recent coral death, and

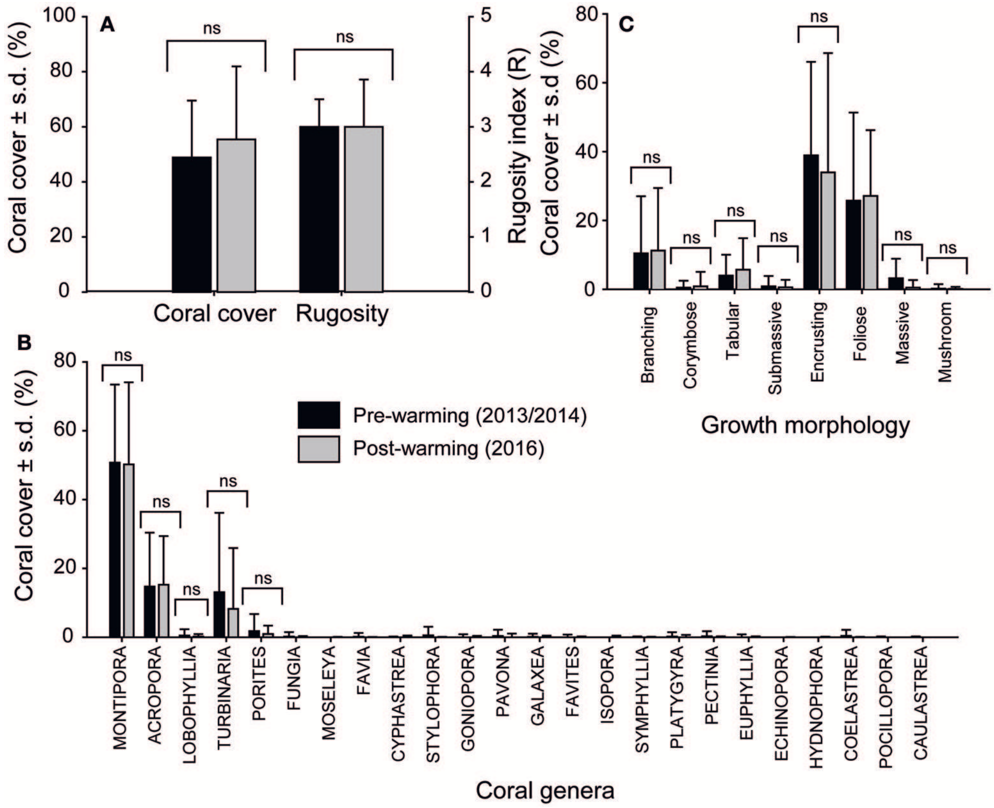

FIGURE 4 | Pre- (black) and post-warming (gray) comparisons of coral assemblages at Paluma Shoals reef complex. Plots show: **(A)** average (±s.d.) coral cover and rugosity, **(B)** the proportion of coral growth morphologies within communities, and **(C)** the prevalence of different coral genera (24 identified) observed in both survey time-series (July 2013/2014 and August 2016). ns, no significant difference between surveys.

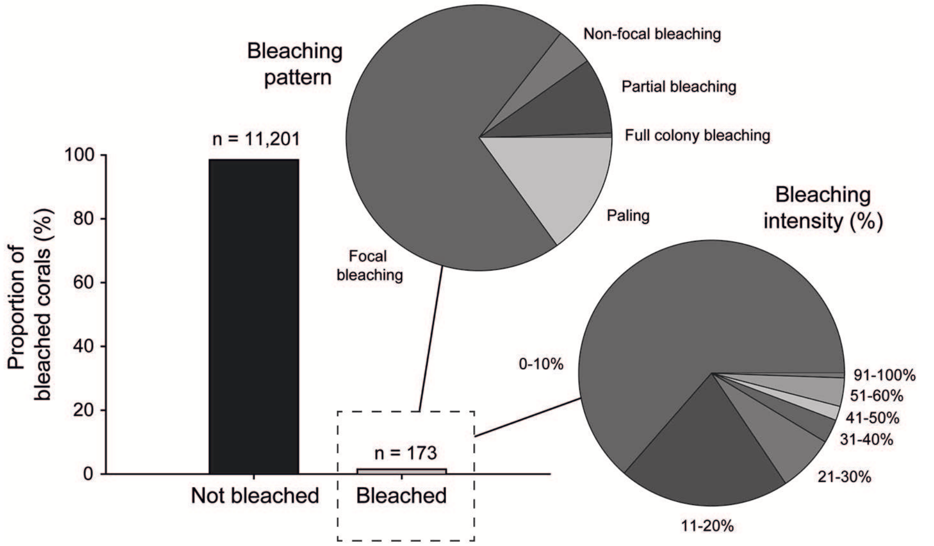

FIGURE 5 | Prevalence of non-bleached ($n = 11{,}201$) and bleached corals ($n = 173$) observed during the August 2016 surveys of the Paluma Shoals reef complex. Pie graphs illustrate the proportion of the bleached colonies that exhibit the different bleaching patterns and intensity (% of total colony surface area). Note that overall bleaching is very minor and mostly expressed as focal bleaching on <20% of the colony surface.

can report that no bleaching-related mortality occurred. Indeed, the most common bleaching response was focal bleaching, where multifocal patterns of bleaching occur scattered over the colony and with discrete borders adjacent to areas of healthy tissue being visible (**Figure 3**). This style of bleaching occurred on 70% of bleached colonies, and most commonly on foliose coral plates (e.g., *Montipora*) or massive colony ridges (**Figure 5**). Coral paling (15%) and partial colony bleaching (9%) was also observed but less commonly.

Of the 24 coral genera identified on PSRC, 12 taxa showed some signs of bleaching (**Table 1**). *Porites* (40%), *Montipora* (36%) and *Lobophyllia* (9%) colonies were most commonly bleached. However, these values can be standardized to reflect the relative abundance of taxa on PSRC to calculate its bleaching index. This index provides a more appropriate estimate of a given coral taxa's response to heat stress than raw count values (see **Table 1**). The bleaching response of *Montipora* was very low (BI: 0.1), because although signs of bleaching were observed on a relatively high number of *Montipora* colonies ($n = 64$), *Montipora* is the most abundant genera and thus the relative impact on the total assemblage is negligible. In comparison, the *Porites* BI was relatively high (BI: 5.9), suggesting *Porites* are more susceptible to bleaching at these sites (**Figure 3C**). *Acropora* corals are common at PSRC, contributing to a high proportion (15 ± 14%) of the coral assemblage (**Table 1**). Perhaps most interestingly, *Acropora* are typically very susceptible to thermal stress on clear-water reefs (Marshall and Baird, 2000) but exhibited very low bleaching ($n = 4$; BI: 0.01) at PSRC. Several less abundant taxa also had high BI values (*Coelastrea*: 36; *Favities*: 21; *Stylophora*: 9.1; *Lobophyllia*: 5.1), but this was mostly expressed as paling of surface tissue (**Figure 3F**). Depth-analysis indicates that all corals that exhibited signs of thermal stress inhabited waters <2 m (**Figure 6**), despite coral growth extending to >4 m depth. Highest bleaching prevalence occurred within the 1–1.5 m depth zone ($n = 96$).

DISCUSSION

The above-average SSTs that affected the GBR in 2015/2016 (see Supplementary Figure S2) caused widespread bleaching-related mortality on the remote northern GBR, and offshore reefs within the central GBR region (Hughes et al., 2017). Our findings suggest that nearshore coral communities on the central GBR experienced similar levels of heating, with water temperatures reaching up to 3°C above the mean monthly temperature, but were significantly more resilient to this heat stress with low incidences of minor bleaching observed (1.5% of corals). In the turbid nearshore setting of the PSRC, bleaching was mostly expressed as either partial/focal bleaching across <20% of the total colony surface area or as coral paling, and only one colony (*Lobophyllia* sp.) underwent complete pigmentation loss.

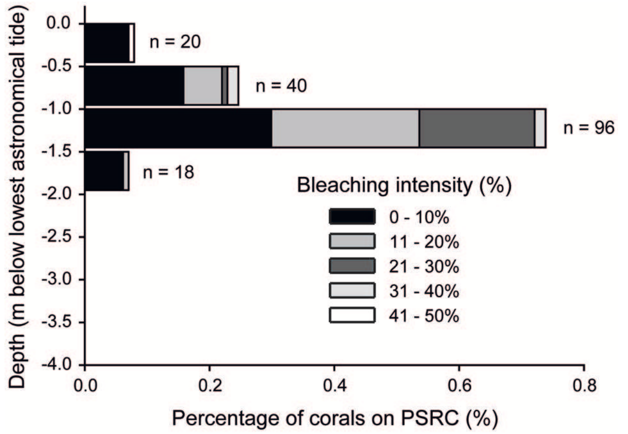

FIGURE 6 | Incidences of coral bleaching with depth (0.5 m depth intervals below lowest astronomical tide) at Paluma Shoals reef complex in August 2016. Bleaching intensity of corals (% of total colony surface) is also shown within each depth category.

TABLE 1 | Summary of taxa-specific responses to thermal stress of coral on Paluma Shoals reef complex following the 2016 ocean warming event.

Coral genera	Code	Mean ± s.d. cover (%)	Total corals (#)	Bleached corals (#)	Proportion of total bleached corals (%)	Bleaching index (BI)
Acropora	ACRO	15 ± 14	3,136	4	2	0.01
Favities	FAVIT	0.03 ± 0.2	7	5	3	21
Fungia	FUNG	0.1 ± 0.3	13	1	0.6	0.7
Coelastrea	COEL	0.01 ± 0.1	2	2	1.2	36
Hydnophora	HYDN	0.01 ± 0.2	3	1	0.6	6.1
Lobophyllia	LOBO	0.2 ± 0.7	43	15	9	5.1
Montipora	MONT	50 ± 24	6,204	64	37	0.1
Pavona	PAV	0.1 ± 1.0	23	5	3	2
Platygyra	PLATY	0.1 ± 0.6	17	1	0.6	1.6
Porites	PORI	0.9 ± 2.4	193	70	40	5.9
Stylophora	STYL	0.01 ± 0.1	2	1	0.6	9.1
Turbinaria	TURB	8 ± 18	1,692	4	2	0.02

The bleaching index (BI) for each genera is an adjusted value which accounts for the incidence of bleaching on colonies relative to the proportion of total coral cover for that genera.

Therefore, although signs of heat stress were visible on corals (**Figure 3**), confirming that water temperatures in the area did exceed the thermal tolerance of some coral taxa (Douglas, 2003), the overall stress responses exhibited by coral communities at this site were very minor. Importantly, similar high levels of heat stress occurred on both mid- and outer-shelf reefs within the central section of the GBR (compare nearshore and shelf-edge areas in the vicinity of Townsville in Supplementary Figure S2). However, coral bleaching and mortality in the central GBR varied markedly across the shelf, with bleaching-related mortality of up to 30% recorded at the clear-water shelf-edge sites (Great Barrier Reef Marine Park Authority, 2016; see Supplementary Figure S3), well above the very minor bleaching at the turbid-nearshore reefs we report here. Indeed, bleaching severity appears to have increased from inshore turbid-water sites to more optimal (clear-water) settings further offshore at the outer-shelf (Great Barrier Reef Marine Park Authority, 2016; see Supplementary Figure S3), despite thermal stress levels being at least as high (see Supplementary Figure S2) in the nearshore areas around PSRC. Furthermore, average coral cover on PSRC in 2016 remained high (55 ± 26%) with no significant change in cover observed between consecutive surveys indicating that no coral die-off occurred and that the 2016 thermal anomaly had no major impacts on the health of PSRC coral communities (see Supplementary Figure S1).

Arising from these observations is a simple question, why are incidences of coral bleaching so low within these high turbidity settings? Sedimentary processes associated within nearshore coastal settings play a critical role in not only determining the occurrence and extent of coral growth (Larcombe et al., 2001; Browne et al., 2010; Morgan et al., 2016a), but also in defining turbid-zone coral community structure and long-term rates and styles of vertical reef growth (Browne et al., 2013a; Perry et al., 2013; Morgan et al., 2016b; Johnson et al., 2017). High turbidity attenuates solar irradiance more rapidly than in clear-water settings resulting in light-limited growth conditions for corals (Larcombe et al., 1995; Storlazzi et al., 2015; Fabricius et al., 2016). Coral communities that inhabit low-light conditions have of late been increasingly discussed in the context of deep-water habitats along shelf edges (e.g., Bridge et al., 2011). However, they may also comprise a spatially important habitat type within shallow coastal areas on the GBR shelf. Although low light can be perceived as detrimental to coral growth, during lengthy periods of no cloud cover typical of El Niño events on the GBR, the buffering of UV by suspended sediment may have positively benefitted the coral assemblages by alleviating radiative stress (van Woesik et al., 2012). Comparable observations have been made with respect to cloud cover which have been demonstrated to reverse predictions of coral bleaching in statistical models throughout periods of large-scale basinal warming (Sheppard, 1999; Mumby et al., 2001). These same principles may apply to nearshore reefs on the GBR, in which the naturally turbid waters afford a similar degree of protection to corals (van Woesik et al., 2012; Cacciapaglia and van Woesik, 2015). Light measurements collected at PSRC under high (∼80 mg l^{-1}) and low turbidity (∼10 mg l^{-1}) scenarios (**Figure 7**) illustrate the rapid reduction in light that occurs over short depth intervals (<5 m). During high turbidity, 90% of light is attenuated by 2 m depth and

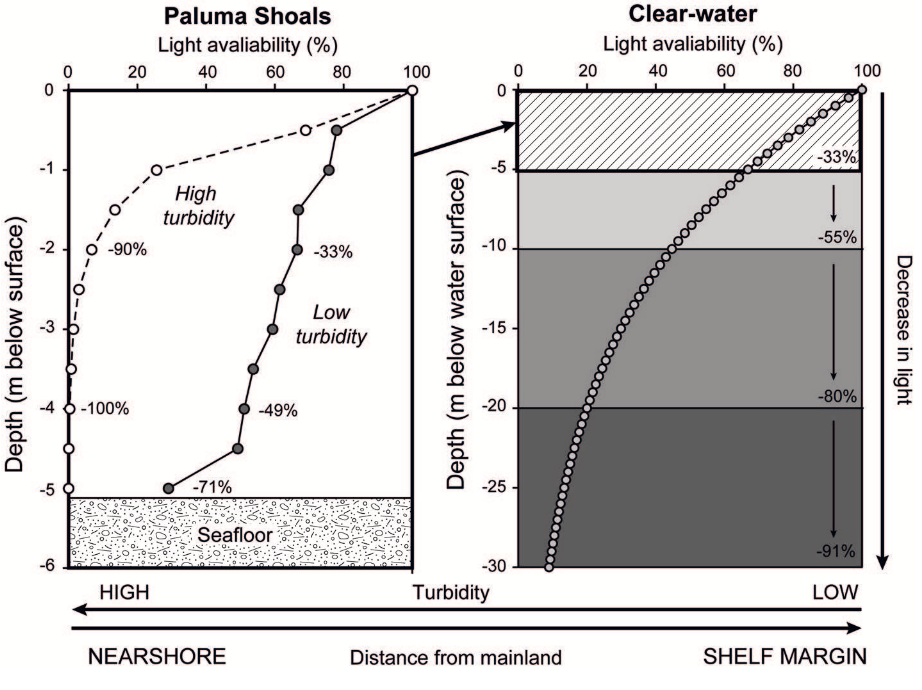

FIGURE 7 | Left-hand plot shows light attenuation data (% decay from the water surface) collected at Paluma Shoals reef complex at 0.5 m depth intervals during low and high turbidity scenarios. Note the rapid reduction in light availability at 2 m depth under high turbidity. Right-hand plot shows modeled light attenuation curve using equations generated for clear water (see Storlazzi et al., 2015).

100% of light has been attenuated by 4 m depth. These sharp declines in light coincide with the observed lower limits of coral growth at PSRC and maximum photic depths within wider coastal environments on the GBR shelf (Fabricius et al., 2016). Importantly, maximum light penetration also directly relates to the depth limits of coral bleaching observed at PSRC (no bleaching was observed below 2 m depth). Indeed, modeled light attenuation curves using equations generated for clear water settings (see Storlazzi et al., 2015) indicate only a 33% reduction in light over a similar 5 m depth range (**Figure 7**). Collectively, these data may imply that SST was not the sole driver of the (albeit limited) bleaching observed at PSRC, and that the penetration of UVB may significantly compound conditions of increased SST. However, the lighter wind conditions associated with the 2016 El Niño means that sediment resuspension can be assumed to have been lower throughout the warming event, and thus despite these "less turbid" conditions, corals still maintained a high thermal tolerance to heat stress.

In this context, it is also pertinent to consider that the PSRC has been shown to support higher than average coral cover compared to clear-water settings on the GBR (Browne et al., 2010; Morgan et al., 2016a). The PSRC also comprises high abundances of coral taxa (e.g., *Acropora*) that have reportedly suffered catastrophic collapse from declining water quality at inshore (as opposed to nearshore) sites within Halifax Bay (e.g., Pelorus reef; Roff et al., 2013), and which are regarded as being highly susceptible to thermal bleaching (Brown, 1997; Marshall and Baird, 2000; Baker et al., 2008). Underpinning this tolerance is the ability of corals to utilize heterotrophic (e.g., plankton predation, dissolved and particulate organic matter consumption) feeding mechanisms as an alternate food source to offset reduced autotrophy (Anthony and Fabricius, 2000; Anthony et al., 2005; Tremblay et al., 2016). This capability may increase a corals resistance to bleaching by increasing zooxanthellae density and chlorophyll content, as well as their survivorship potential if bleaching does occur by improving the corals ability to reactivate normal nutrient exchanges (Tremblay et al., 2016; Lim et al., 2017). However, experimental studies report that not all coral species can increase their heterotrophic capacity in this way. For example, *Montipora* corals could meet more than 100% of their daily metabolic energy requirements by increasing their feeding rates and CHAR (per cent contribution of heterotrophically acquired carbon to daily animal respiration) during bleaching, whereas *Porites* corals could not (Grottoli et al., 2006). This indicates that corals with a high-CHAR capability (such as *Montipora*) may be more resilient to temperature-induced stress, a fact that may help to explain their dominance on reefs in marginal settings (Grottoli et al., 2006; Done et al., 2007; Browne et al., 2010; Morgan et al., 2016a). Our field surveys support these findings, as *Montipora* colonies are the principal coral taxa at PSRC (55% of total corals) highlighting the likely importance of heterotrophy in the success and persistence of certain turbid-zone corals.

As discussed above, corals that inhabit turbid (and low-light) nearshore settings, which have abundant particulate organic matter, may become permanently or facultatively heterotrophic (Anthony and Fabricius, 2000). The efficiency of this feeding strategy can surpass the daily energy requirements of corals as they are no longer limited to the same diurnal feeding patterns as autotrophs, and may feed more readily as food supply is not as predictable as in clear-water settings (Anthony, 2000, 2006). Excess energy can be stored as lipids within coral tissues, and may be critical in sustaining turbid-zone corals during stress events, whilst zooxanthellae are expelled, or when normal nutrient exchanges are altered (Tremblay et al., 2016; Lim et al., 2017). Importantly, such energy reserves could lead to an increase in the response time of corals to bleaching events (i.e., the time it takes for corals to bleach under elevated SSTs). The implications of this are that although turbid-zone coral bleaching could be similarly linked to the length and frequency of SST anomalies (much in the same way as their clear-water counterparts), the time-scales over which corals respond may differ and could ultimately influence their long-term resilience if their energy reserves can outlast periods of acute heat stress. As global ocean warming events are predicted to increase under future modeled climate scenarios, consecutive periods of heat stress could be problematic. If accumulated energy reserves within coral tissues cannot sustain corals throughout the duration of the heat stress, then turbid environments may not provide long-term refuges against climate-related disturbance despite exhibiting high single-event bleaching resistance. Our findings, which report low and less severe bleaching at PSRC than on clear-water reefs, provide an important contribution to the ongoing understanding of the turbid-reef refugia hypothesis, and run contrary to recent regional-scale predictive models of coral bleaching sensitivity (e.g., Wooldridge et al., 2017). However, whether the disparity in the bleaching response of corals between shelf settings is driven directly by the naturally high turbidity, or indirectly through prior acclimation of corals to marginal conditions requires further examination.

Variability in the response of certain coral taxonomic groups to thermal stress both on and between reefs are established, with past clear-water bleaching impact assessments reporting a high susceptibility of branching *Acropora* and *Pocillopora* corals to bleaching-related mortality, and a greater tolerance within massive and encrusting *Porites* and *Faviids* corals (Marshall and Baird, 2000; McClanahan et al., 2004; Great Barrier Reef Marine Park Authority, 2016; Hughes et al., 2017). Our data, however, show no significant changes in coral community composition following the 2016 temperature anomaly, although we do note taxa-specific patterns in the type and intensity of coral bleaching observed. Normally stress tolerant massive and submassive corals (e.g., *Porites*, *Lobophyllia* and *Coelastrea*) had the highest incidences of focal bleaching (typically on colony ridges or nubbins), and had relatively high BI values overall (**Table 1**). In contrast, shallow-water branching and tabular *Acropora* corals (<1.5 m depth) exhibited very low levels of bleaching. Such reversals in coral taxonomic susceptibility to thermal stress run contrary to a wide body of data from existing studies from clear-water reef settings, although these findings are similar to bleaching patterns documented within turbid water settings in Singapore, Malaysia and Indonesia following the 2010 global bleaching event (Guest et al., 2012, 2016). On these turbid Southeast Asian reefs, *Porites* suffered highest incidences of bleaching and *Acropora* corals were relatively unaffected. This is likely attributed to the fact that "normal" susceptibility is usually determined for autotrophic clear-water corals, and neglects to include these "atypical" coral communities which inhabit different environmental conditions and have a distinct physiology from corals in offshore settings. More recently, reports of coral bleaching within the turbid waters of NW Australia (located 10–15 km off the coast of Pilbara, near Onslow) in 2016 indicated significant bleaching of *Turbinaria* corals, another genera usually considered tolerant to higher temperature ranges (Lafratta et al., 2016). Lafratta et al. (2016) report no evidence for adaptation or acclimation of corals in Pilbara but recognize that other factors may complicate patterns. However, these Western Australian reefs are located much further offshore than the PSRC (in a comparable setting to Pelorus Reef on the Queensland coast) and therefore likely experience different background environmental conditions which may drive differences in coral thermal response. Regardless, the high variability in coral bleaching response both between and within clear-water and turbid settings highlights the greater need for more field investigations of marginal reef habitats.

Our findings demonstrate a high level of bleaching resistance to the 2016 warming episode, however, the impacts of consecutive warming events are less certain. For an unprecedented second time in 12 months, severe coral bleaching occurred on the GBR and was, this time, focused on the central third of the GBR (see Supplementary Figure S4). Increased efforts have been made to examine a number of inshore reefs, but these sites are still >18 km further offshore PSRC, and experience different environmental conditions from those very nearshore reefs (within <5 km of the mainland coast) that we present here. Therefore, the ongoing fate of turbid-zone coral communities in the region remains unknown and requires further long-term monitoring.

CONCLUSION

The magnitude and extent of the 2016 mass coral bleaching event that has affected large areas of the GBR demands that steps be taken to learn from it. The sporadic nature and difficulty associated with predicting these climate anomalies means that scientific assessments both during and following these events are critical to furthering our understanding of the response of coral reefs to global environmental change. Our assessment of nearshore reefs that incorporates substantial baseline information and extensive post-bleaching surveys of turbid-zone coral communities adds to the ongoing efforts to better understand these marginal reef types on the GBR. During the 2016 bleaching event, satellite-derived analysis of SST showed above-average temperatures across the wider central GBR. However, bleaching impacts varied from relatively "minor" at inshore sites to "severe" at outer-shelf reefs (Great Barrier Reef Marine Park Authority, 2016). Our results suggest even lower incidence of bleaching (0.008%) occurred on the most nearshore reefs, highlighting large cross-shelf gradients in bleaching prevalence which match well-documented changes in water quality and average coral cover for the region (Fabricius et al., 2016; Morgan et al., 2016a). Lowest incidences of bleaching were observed in shelf areas with poorest water clarity, but increased in more favorable clear-water settings. Therefore, prior acclimation of corals (both phenotypic and morphotypic) to acute thermal fluctuations may help them cope with episodic ocean warming. However, the mechanisms that influence coral bleaching thresholds are complex and remain poorly understood. Although turbid-zone corals at PSRC show high tolerance to single-event climate-related disturbance (2016), it is uncertain whether the resilience of corals will be long-lasting as an unprecedented consecutive bleaching event in 2017 has occurred.

AUTHOR CONTRIBUTIONS

Project funding was secured by CP, KM, and SS. Field work and logistical support was carried out by KM, JJ, and SS. Data analysis was undertaken by KM and JJ. The manuscript was prepared by KM, CP, SS, and JJ. All authors gave their final approval for publication.

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SUPPLEMENTARY MATERIAL

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Environmental Drivers of Variation in Bleaching Severity of *Acropora* Species during an Extreme Thermal Anomaly

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High sea surface temperatures caused global coral bleaching during 2015–2016. During this thermal stress event, we quantified within- and among-species variability in bleaching severity for critical habitat-forming *Acropora* corals. The objective of this study was to understand the drivers of spatial and species-specific variation in the bleaching susceptibility of these corals, and to evaluate whether bleaching susceptibility under extreme thermal stress was consistent with that observed during less severe bleaching events. We surveyed and mapped *Acropora* corals at 10 sites ($N = 596$) around the Lizard Island group on the northern Great Barrier Reef. For each colony, bleaching severity was quantified using a new image analysis technique, and we assessed whether small-scale environmental variables (depth, microhabitat, competition intensity) and species traits (colony morphology, colony size, known symbiont clade association) explained variation in bleaching. Results showed that during severe thermal stress, bleaching of branching corals was linked to microhabitat features, and was more severe at reef edge compared with lagoonal sites. Bleaching severity worsened over a very short time-frame (∼1 week), but did not differ systematically with water depth, competition intensity, or colony size. At our study location, within- and among-species variation in bleaching severity was relatively low compared to the level of variation reported in the literature. More broadly, our results indicate that variability in bleaching susceptibility during extreme thermal stress is not consistent with that observed during previous bleaching events that have ranged in severity among globally dispersed sites, with fewer species escaping bleaching during severe thermal stress. In addition, shaded microhabitats can provide a refuge from bleaching which provides further evidence of the importance of topographic complexity for maintaining the biodiversity and ecosystem functioning of coral reefs.

Keywords: spatial refugia, environmental gradients, *Symbiodinium*, niche construction, thermal performance

INTRODUCTION

Mass coral bleaching in response to increased sea surface temperature is a major threat to the persistence of coral reefs. Analyses of sea surface temperature data indicate that ocean warming has accelerated in recent decades, and that coral reefs are increasingly being exposed to thermal stress (Heron et al., 2016). Since the 1980s, global mass bleaching events have caused large-scale and significant coral loss. For example, in 1998, increased seawater temperatures caused widespread bleaching and coral mortality in most of the world's coral reef regions, with mortality in excess of 90% on some reefs in the central and western Indian Ocean (Spalding and Brown, 2015). Moreover, between June 2014 and April 2016, bleaching was observed throughout the global oceans during what is now considered to be the longest bleaching event on record (Eakin et al., 2016). In the context of bleaching, temperature stress is often measured in "degree heating weeks" (DHW, °C-weeks), a metric which summarizes the duration of time over which temperatures have been above the average temperature of the warmest summer month at each location (e.g., Eakin et al., 2010). The recent thermal stress event caused severe bleaching on the northern section of the Great Barrier Reef in 2016, where approximately one third of reefs experienced levels of heat stress that were up to two-fold higher than those experienced in the 1998 bleaching event in the same region (Hughes et al., 2017). We here investigate whether species susceptibility to bleaching under extreme heat stress is consistent with species susceptibility reported during previous bleaching events.

Different coral species respond differently to environmental stressors, leading to substantial among-species variability in bleaching susceptibility. In general, the literature documents relatively high bleaching severity for branching corals from the genera *Stylophora*, *Acropora,* and *Pocillopora*, and lower bleaching severity for mound-shaped *Porites* and *Diploastrea* (e.g., Marshall and Baird, 2000; Loya et al., 2001; van Woesik et al., 2011; Swain et al., 2016). However, bleaching severity is spatially patchy (e.g., Wooldridge and Done, 2004; Penin et al., 2007). For instance, bleaching severity varies between habitats with some studies reporting bleaching to be less severe in shallow compared with deep lagoons (Grimsdich et al., 2010), while others report the opposite trend (Fisk and Done, 1985; Muhando, 1999). Bleaching severity can also vary with depth (e.g., Penin et al., 2007), although some studies have reported no significant variation in bleaching with depth when values were pooled across genera (Bruno et al., 2001). While temperature stress is recognized to be the primary driver of mass-bleaching (Berkelmans et al., 2004; Hughes et al., 2017), there is no strong consensus about additional environmental drivers of spatial variation in bleaching severity. It is likely that a combination of environmental factors (e.g., local light intensity and water flow) and biological factors (including species-specific responses, and local abundances of susceptible vs. tolerant species) influence spatial patterns of bleaching severity.

In addition to among-species variation in bleaching susceptibility, there is often high variation in the bleaching responses of individuals of the same species. For instance, during the 1998 bleaching event, massive *Porites* were more susceptible to bleaching in the Palm Islands on the central GBR than they were at nearby Magnetic Island (Marshall and Baird, 2000). Similarly, during a bleaching event in the central Pacific, bleaching was observed at some sites but not others for each of several monitored species (Fagerstrom and Rougerie, 1994). Indeed, numerous studies report within-species variation in bleaching severity across different habitats (e.g., Bruno et al., 2001; Aronson et al., 2002; Hardman et al., 2004). There are numerous potential biotic drivers of this within-species variability. First, different types of *Symbiodium* are more resistant to increased ocean temperature than others (e.g., Thornhill et al., 2006; Jones et al., 2008; Lesser et al., 2010; Howells et al., 2013), and many coral species can associate with more than one type of *Symbiodinium* (Baker, 2003; Sampayo et al., 2008). Therefore, we assessed whether species that have the capacity to associate with more than one symbiont type show lower bleaching severity, on average, than other species. Second, bleaching severity is influenced by coral colony size. For example, larger colonies experienced more extensive bleaching than smaller colonies of several species during a major Caribbean bleaching event in 2005 (Brandt, 2009). However, other studies have found contrary results with higher bleaching for smaller colonies for some species (Pratchett et al., 2013), or that colony size only influences bleaching prevalence for certain colony morphologies in certain locations (Wagner et al., 2010). Finally, other benthic organisms that compete for space with corals, such as soft corals and macroalgae, contain secondary metabolites that can lead to the expulsion of *Symbiodinium* (i.e., bleaching, Aceret et al., 1995). Moreover, competition can influence coral fitness more generally (e.g., by growth suppression, see Horwitz et al., 2017), and such effects might act as an additional stressor that increases bleaching severity. To the best of our knowledge, effects of competition on bleaching severity have not previously been investigated *in situ*.

The topographic complexity of reefs results in high variability in environmental conditions over small spatial scales. For instance, stable and biologically significant temperature variation occurs at small scales (1–2 m, e.g., Gorospe and Karl, 2011), and also at larger between-habitat scales (hundreds of meters, e.g., Lundgren and Hillis-Starr, 2008). Water flow also varies within- and among-habitats (e.g., Fulton and Bellwood, 2005; Hoogenboom and Connolly, 2009). Therefore, spatial variation in abiotic drivers, such as light intensity, water flow, temperature, and turbidity, influences which corals bleach and where (e.g., West and Salm, 2003). Previous studies report different effects of water flow on bleaching severity, with evidence of increased bleaching severity at exposed sites with high wave activity (McClanahan et al., 2007), as well as evidence of reduced bleaching, along with higher survival of bleached corals, under high water flow conditions (Nakamura and van Woesik, 2001; Nakamura and Yamasaki, 2005). Variability in bleaching among different reef habitats is also associated with site-specific turbidity levels (e.g., Williams et al., 2010). However, observed responses range from a negative effect of turbidity whereby suspended particulates are thought to act as an additional stressor that lowers temperature tolerance (Williams et al., 2010; Hongo and Yamano, 2013), to predictions that turbidity may lessen the severity of bleaching in some shallow habitats by reducing light penetration (West and Salm, 2003; Cacciapaglia and van Woesik, 2016).

Methodological issues associated with quantifying bleaching severity in the field might also lead to variation between studies. While observer differences are unlikely to explain variation in bleaching severity between habitats reported in a single study, observers can differ in color sensitivity or in training (e.g., Siebeck et al., 2006). Many observer methods measure bleaching in simple categories (e.g., "pale," "partially bleached," and "bleached"), and this categorization can obscure color gradation. To overcome issues associated with categorization of bleaching, some studies estimate the proportion of each coral colony that is healthy vs. bleached (e.g., Obura, 2001), providing a finer resolution of bleaching severity. Despite these advances, however, a recent review highlighted the relatively high measurement uncertainty for bleaching severity, and noted that standardizing measuring protocols would help to increase the precision of bleaching estimates (Swain et al., 2016). To help standardize bleaching measurements, we developed a new quantification of bleaching severity by measuring coral "whiteness" in individually white-balanced images of healthy, pale and bleached corals.

The objective of this study was to understand the drivers of small-scale variation in the bleaching susceptibility of branching corals, and to evaluate whether bleaching susceptibility under extreme thermal stress is consistent with that observed during previous (less severe) bleaching events. We focused on corals from the genus *Acropora* due to their high abundance on Indo-Pacific reefs, their importance for the structural complexity of reefs, and their variable bleaching severity within- and among-species (e.g., Marshall and Baird, 2000; Loya et al., 2001; Swain et al., 2016). Specifically, we aimed to understand whether and how variation in bleaching severity was associated with depth, spatial location of colonies relative to the reef edge (a measure of exposure to wave energy and general reef habitat), microhabitat, colony size, colony morphology, and the level of competition and the identity of competitors. We also evaluated whether association with multiple symbiont types could explain among-species variation in bleaching severity using data from the Geosymbio database (Franklin et al., 2012). Finally, we compiled literature data on the response of *Acropora* species during previous thermal stress events, and assessed whether those species that have been consistently reported to be severely bleached in previous studies were also the most severely bleached during the extreme thermal anomaly which occurred on the Great Barrier Reef during the austral summer of 2016.

MATERIALS AND METHODS

Field Data Collection

Surveys of coral bleaching were conducted at predominantly shallow, lagoonal sites, and at one additional mid-shelf location, within and around the Lizard Island group (northern Great Barrier Reef, 14°40.140S, 145°27.649E) during early March 2016 ∼2 weeks after bleaching was first reported at the location. Thermal stress at this location reached ∼10 DHW during this bleaching event (Hughes et al., 2017) and *in situ* temperature loggers (Onset Hobo) measured an average temperature of 30.3°C (range 27.7–33.2°C) at two reef crest sites during February and March 2016. At the time of the surveys, significant bleaching of susceptible coral species had been observed, but mortality was still negligible (widespread bleaching-related mortality was observed on reefs in the region 1 month later, Hoogenboom unpubl. data). Over a period of 8 days, divers conducted in-water surveys at 10 sites where the bleaching status of ∼60 *Acropora* colonies was monitored per site. Colonies were selected haphazardly as divers swam along a depth contour from a randomly selected starting place, making a conscious effort to observe colonies from different reef microhabitats as far as practicable given the topography of each site. The spatial position of each colony was taken using a towed GPS (Garmin eTRex) that was time-synchronized with a dive watch, and the depth of each colony was recorded using a dive computer (Suunto, D4 and Zoop). Each colony was photographed from directly above (as described below), and additional photographs of colony morphology, local reef topography and colony microhabitat, neighboring competitors, and corallite shape were taken to enable measurement of colony size and competition intensity, and to assist species-level identification. We also kept track of the time and date of observations because ongoing heat stress suggested that bleaching severity would continue to increase during and after the observation period. The full dataset, including coral images and spatial positions, is available in Critchell and Hoogenboom (2017).

Measurement of Bleaching Severity (Response Variable)

Individual coral colonies were photographed from directly overhead, without flash, and from as close as practicable, with a Canon G16 digital camera in an underwater housing. Each photograph contained a color reference chart and scale bar. As differing light conditions of each colony did not allow for identical camera settings to be used in each photograph, individual settings based on the highest image quality (pixel count) and lowest sensitivity (ISO) settings were used. Post-processing was conducted using Adobe Photoshop Creative Cloud (2015) software with images transformed into the device-independent CIEL*a*b* color space which measures color based on lightness (L), along a green-red gradient (a), and along a blue-yellow gradient (b). All images were individually white balanced by identifying true black, true white, and 50% gray thresholds in each photograph. Subsequently, four regions of the colony were selected haphazardly from across the surface area of each coral colony, using the color sample tool. Each sampled region was a constant distance from the branch tip (1–2 cm), and avoided the outer margins of the colonies where branches are often oriented in slightly different directions, and can be shaded by upper branches. The color sample tool in the software was set to capture an 11 × 11 pixel sample for each region of the coral surface, and calculated the average color across each 121 pixels region. The four L*a*b* color samples were averaged for each colony, in order to gain a single numerical measurement of color, the divergence of each L*a*b* average value from black was calculated as ΔE (after Riggs, 1997). This method generated a value for each colony within a range of 0–100, with increasing values representing increasingly bleached (nearest to white) colonies. To determine a reference point for the color of healthy (unbleached) corals, the same technique was used to calculate "whiteness" values for *Acropora* colonies ($n = 12$) that showed normal colouration, and that were surveyed and photographed during March 2016 at sites around Orpheus Island. These additional colonies included the same species and colony morphologies as observed at Lizard Island.

Drivers of Bleaching Severity (Explanatory Variables)

Image Analysis

Images of each coral colony ($N = 596$) were analyzed to determine coral colony morphology after Wallace (1999) as either digitate, corymbose, arborescent, tabular, arborescent table, or hispidose/caespitose. Each coral colony was identified to species level based on Wallace et al. (2012) and Wallace (1999) except for 7 colonies for which species identification could not be reliably determined from the photographs (referred to in our dataset as *Acropora* spp.). We note that many coral species display morphological plasticity and certain pairs of species have overlapping variation in morphology which poses a challenge for species identification. In our study, some colonies within the following species pairs were difficult to distinguish from each other from photos alone and, therefore, species-level differences between these pairs should be interpreted with caution: *A. loripes* and *A. longicyathus*, *A. nasuta* and *A. valida*, *A. humilis* and *A. gemmifera*.

Colony planar surface area was measured for each colony using image analysis in Image J (version 1.51 h, US National Institute for Health). For each colony we measured the longest diameter and the diameter perpendicular to that and calculated planar area based on the geometric formula for the area of an ellipse. The microhabitat of each colony was also assessed from images of the localized reef topography, and was categorized as; "elevated" (where the topography of the reef meant the coral was $> \sim 40$ cm above the surrounding corals) "open" (where the colony was on flat reef substratum without any obvious shading by competitors), "crevice" (where the colony grew within a crack in the reef matrix), "overhang" (where the colony was shaded by the reef matrix or other colonies), or "sand" (where the colony grew above a sand patch). Competition intensity was measured by dividing each coral into 8 equal segments centered over the mid-point of the colony, and counting the number of these "octants" in which a benthic competitor was within ~ 5 cm of the focal colony, after Hoogenboom et al. (2011). These data were subsequently categorized as either: "no competitors," "low" (competitors present in 1–2 of octants), "medium" (competitors present in 3–4 octants), and "high" (competitors present in >4 octants). In addition, we noted whether competitors included soft corals (categorical variable with soft corals present or absent) and macroalgae (categorical variable with macroalgae present or absent). Only 8 of 596 colonies were in competition with macroalgae so this variable was excluded from subsequent analysis.

Spatial Data

For each colony, depth data measured in the field were converted to depth below lowest astronomical tide based on the known tidal height at the time of sampling. The spatial position data for each colony was used to calculate the position of each colony relative to the open ocean. To do this, the position of the reef edge was defined from reef polygons extracted from Google Earth images (Lizard Island, −14.666777S 145.462971E, image date 10/10/2011 accessed 06/02/2017 with eye altitude of 6.9 km; No Name Reef, −14.641968S 145.653061E, image date 15/09/2016 accessed 07/02/2017 with eye altitude of 4.36 km), and were imported into ArcGIS (ESRI, version 10.2). The spatial position of each coral colony and the reef polygons were transformed to GDA 1994 MGA Zone 55 projection to enable measurement of distances in meters with conversion from decimal degrees. The "near" function was used in ArcGIS to calculate the distance (m) of each point (i.e., each coral colony) from the nearest reef edge.

Coral-Symbiodinium Associations

Given the influence of different *Symbiodinium* on the thermal tolerance of *Acropora* corals (e.g., Howells et al., 2013), we determined the total number of *Symbiodinium* clades reported in the GeoSymbio database for the surveyed *Acropora* species (Franklin et al., 2012). Only records that identified *Symbiodinium* using denaturing gradient gel electrophoresis profiles of the internal transcribed spacer 2 region of rDNA were included to avoid confounding effects due to the use of different methods of identifying *Symbiodinium*. Furthermore, only *Acropora* species for which there were more than three records in the database were included in this analysis.

Reported Bleaching Severity of *Acropora* during Previous Bleaching Events

To compare the results from our in-water surveys with observations of *Acropora* bleaching in previous events, we conducted a comprehensive literature search using Web of Science to conduct cited reference searches for Marshall and Baird (2000) and Loya et al. (2001), and an additional keywords search for "*Acropora*" and "bleaching." To capture the gray literature we also scanned all papers listed in the online bleaching database ReefBase (1631 records, as of March 2016, ReefBase, 2017) and extracted data from publications that were publically available. Among this set of publications, data were only used if the study reported field observations during a thermal bleaching event (not laboratory experiments), if corals were identified to species level, and if bleaching was quantified in a way that captured gradation in bleaching severity. We excluded papers where bleaching effects were measured as a change in coral cover between different observation periods due to difficultly ascribing changes in abundances solely to bleaching. In total, 57 publications matched our criteria, yielding 527 records of bleaching for 86 *Acropora* species. We retained species names as reported in the original publications despite some subsequent synonymization of names (e.g., *A. wallaceae* was synonymized with *A. samoensis* by Wallace, 1999), and we recorded colony morphologies of species based on Wallace (1999) and Veron (2000).

To standardize bleaching metrics between studies, data extracted from each publication were re-categorized as follows: "none" means no bleaching of that species was reported in that study; "low" means that the study recorded the species to be partially bleached or with <25% of colonies affected; "moderate" means that 26–50% of colonies were bleached or there was partial bleaching with low levels of recorded mortality; "high" means 50–80% of colonies were bleached and/or mortality was observed; "severe" means that more than 80% of colonies of that species were bleached and/or high levels of bleaching-related mortality were recorded. Data are presented as the percentages of records for each species that fell within each of these categories. In both the data from Lizard Island, and the literature data, the measurement of bleaching severity reflects the short- and long-term thermal history of each colony because measurements were made under natural field conditions. The database we have compiled is accessible in the Supplementary Material.

Data Analysis

To identify the strongest predictors of bleaching severity during the extreme thermal anomaly, we used a linear mixed-effects model that included all main effects (day of observation, colony morphology, depth, microhabitat, competition intensity, presence of soft corals, colony size, and distance to open ocean, where the latter captures variation in environmental conditions between reef-edge and lagoon habitats), and a set of specific interaction terms that were established *a-priori* based on evidence in the literature. Water flow potentially modulates bleaching severity through effects on gas exchange which are, in turn, affected by both colony morphology and colony size (Hoogenboom and Connolly, 2009). Consequently, we included interaction terms between distance from ocean (a proxy for wave exposure and general reef habitat) and colony morphology, and between distance from ocean and colony size. Colony morphology determines how much light impinges on the coral tissue surface, and light intensity also changes with depth (Hoogenboom et al., 2008). Therefore, we considered that different morphologies might bleach differently at different depths and included a depth by morphology interaction. Different coral morphologies use different competition strategies and the outcome of competition can depend on colony size (Jackson, 1979). Therefore, we included competition by colony size and competition by morphology interaction terms. Finally, we considered that different coral morphologies might bleach at different rates and included the interaction between day of observation and morphology. We had no *a priori* reason to expect that effects on bleaching severity from the day of observation (duration of exposure to thermal stress), or that effects of the presence of soft corals, should depend on any other environmental factor and therefore omitted those interactions. The dataset includes two random effects; "site" (because corals were observed at a random selection of sites at the location) and "species" (because we observed a random subset of the pool of species based on which species were present at each site rather than observing species selected *a priori*). We used model selection based on a likelihood ratio test to assess whether the mixed-effects model should include random effects for both "site" and "species within site." All statistical analyses were performed using the R statistical software (R Development Core Team, 2017).

Our assessment of the *Acropora* community naturally present at each site meant that we were likely to have different numbers of observations of bleaching severity for different species, and a different composition of species at different sites. To determine whether differences in species composition between sites contributed to among-site variation in bleaching severity we categorized sites as either "exposed" (<420 m from reef edge, 4 sites) or "lagoon" (>510 m from reef edge, 6 sites), and calculated community similarity between pairs of sites using the Bray–Curtis index of dissimilarity. The categorization of "exposed" vs. "lagoon" was based on a natural distance division in our data which yielded approximately equal numbers of sites in each category. This community similarity approach was chosen in place of a multivariate species-by-site ordination because the latter technique is not recommended when there are many more variables (species) than samples (sites). A similar approach was used to assess whether the relative frequency of microhabitats differed between exposed and lagoon sites using a χ^2 goodness of fit test.

Data describing *Symbiodinium* association of *Acropora* were only available for a subset of the species we observed. These sparse data did not permit quantitative analysis and, therefore, we used graphical analysis to assess whether the capacity to host different symbiont types was related to bleaching severity. Finally, hierarchical cluster analysis was used to group coral species based on their bleaching severity during previous bleaching events as reported in the literature. Subsequently, we applied the same species groupings to the species observed at Lizard Island, and assessed whether mean bleaching severity observed at our study site differed systematically among these predetermined species groups.

RESULTS

Bleaching severity values measured using our new method ranged from 42 (least "white") to 99 (very close to pure white) across the 10 Lizard Island study sites. In contrast, "whiteness" values for unbleached corals at Orpheus Island (photographed at the same time of year, and including the same coral species and morphologies as at Lizard Island) averaged 43 (±s.e. 3.2, range 21–61). Overall, 97% of coral colonies observed at Lizard Island ($N = 596$) showed whiteness values outside of the range observed for unbleached corals at Orpheus Island, and 71% of colonies had whiteness values >80 (**Figure 1**).

Among the set of hypothesized correlates of bleaching severity, only day of observation, microhabitat, distance of colonies from the open ocean, and colony morphology explained a significant amount of the variation in bleaching severity. We observed a clear signal of increased bleaching severity over time, despite the relatively short observation period (8 days, **Table 1**). This temporal variation was equivalent in magnitude to the variation in bleaching severity among microhabitats (average bleaching values were ∼79 on day 1 and ∼88 on day 8, **Figures 2A,C**). In addition, hispidose, digitate, and

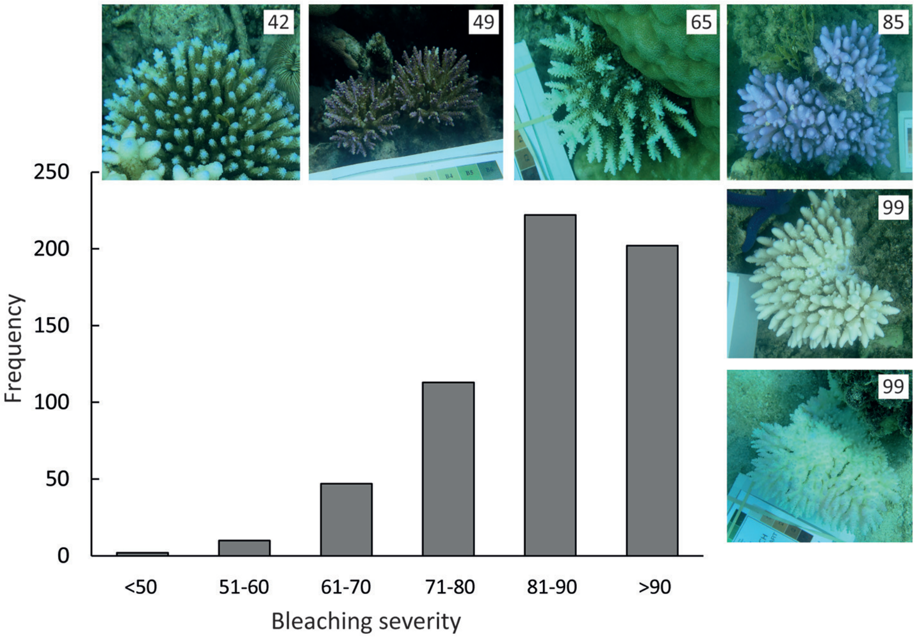

FIGURE 1 | Frequency distribution of bleaching severity measurements for *Acropora* corals ($N = 596$) at Lizard Island in March 2016, as measured from white-balanced images of corals *in situ*. Photos show representatives of coral colonies with different bleaching severity, and numbers in the upper right hand corner of each image show the bleaching severity for each coral.

TABLE 1 | Results of general linear mixed effects model of bleaching severity, with site and species included as random effects in the model.

Factor	*Df*	*F*	*p*
Day of observation	1, 8	13.3	<0.01
Colony morphology	5, 381	3.5	<0.01
Microhabitat	4, 381	20.6	<0.001
Distance from open ocean	1, 381	5.5	<0.02

All other main effects and interaction terms were not significant ($p > 0.08$) and were excluded from the final model based on a backwards-deletion approach.

arborescent morphologies were the most severely bleached, whereas tabular morphologies were the least severely bleached (**Table 1**, **Figure 2B**). Finally, bleaching severity decreased with distance away from the open ocean, with corals at sites in the lagoon generally showing lower bleaching severity than those at sites close to the reef edge (**Table 1**, **Figure 2D**).

Corals growing in crevice and overhang environments showed significantly less severe bleaching than corals in open, elevated, and sand microhabitats (**Figure 2**, **Table 1**), supporting the general consensus that bleaching is more severe under conditions of high irradiance. In contrast, depth (range −0.5 to 5 m below LAT) was not significantly associated with bleaching [GLMM, "depth" effect, $F_{(1,\,570)} = 0.08$, $p = 0.78$]. The relative frequency of different microhabitats occupied by the coral colonies we observed differed between sites that were close to the reef edge and sites that were close to the center of the lagoon (**Figure 3**). Overall, *Acropora* colonies were more frequently found in open microhabitats at reef edge sites compared with a higher frequency of elevated and crevice microhabitats at lagoonal sites (Goodness of fit test, $\chi^2 = 19.3$, $df = 4$, $p < 0.001$). Despite these differences in microhabitat availability, Bray–Curtis similarity of species composition between pairs of sites was approximately equal when reef edge sites were compared with each other (mean dissimilarity 0.54 between 6 pairs of sites), to when lagoonal sites were compared with each other (mean dissimilarity 0.53 between 15 pairs of sites), and to when lagoonal sites were compared with reef edge sites (mean dissimilarity 0.51 between 24 pairs of sites).

Corymbose coral species, including *A. secale*, *A. selago,* and *A. nasuta* were among the least severely bleached whereas arborescent species, including *A. listeri*, *A. grandis* and *A. aspera*, were among the most severely bleached (**Figures 2B, 4A**). Species' mean bleaching severity values ranged from 74 (for *A. aculeus*) to 95 (for *A. carduus*) and we observed relatively small within-species variation in bleaching severity with the coefficient of variation of bleaching severity for each species ranging from 1 to 21% (average 10%). However, clear interpretation of among-species variation is hindered by differences in sample sizes; our assessment of the *in situ Acropora* community meant that we observed only single colonies of some species but >40 colonies of other species (**Figure 4A**). In addition, formal model selection did not support the inclusion of "species within site" as a random effect in the GLME (likelihood ratio test, model with "species within site" was not superior to a model with only "site" as a random effect, likelihood ratio 0.49, $p = 0.48$). This result indicates that differences in bleaching intensity among species were generally consistent among sites. Finally, although data

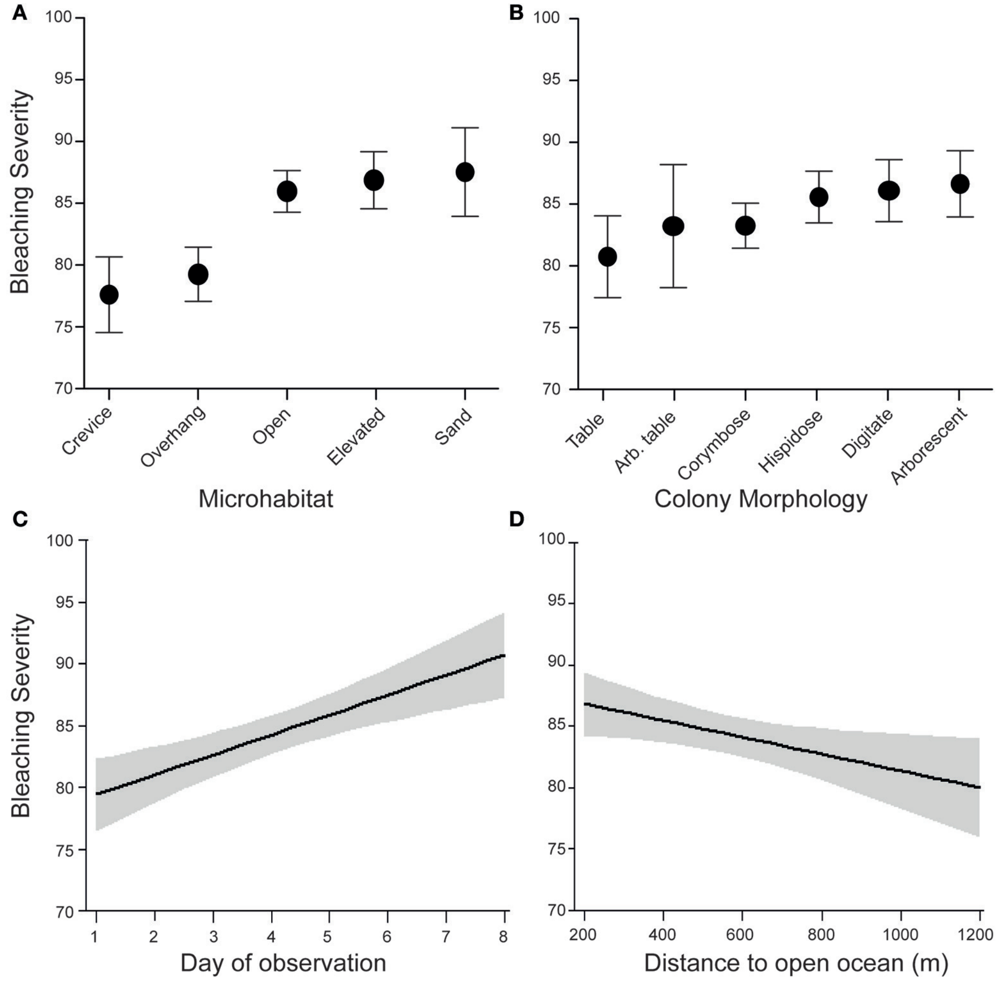

FIGURE 2 | Environmental and morphological correlates of bleaching severity for corals at sites around Lizard Island in March 2016. Data show effects of **(A)** microhabitat, **(B)** colony morphology, **(C)** day of observation and **(D)** distance to open ocean from linear mixed effects model with $N = 596$ coral colonies, site included as a random effect, and main effects of the minimal model obtained from backwards deletion of non-significant terms.

documenting symbiont clade diversity for the coral species we observed were too sparse to permit formal analysis, we found no clear indication that species which associated with more than one symbiont clade bleached less severely (**Figure 4B**).

Competition intensity had no effect on bleaching severity [GLME, "competition" effect, $F_{(3,\,570)} = 2.2$, $p = 0.09$], nor did the presence of soft corals [GLME, "soft corals" effect, $F_{(1,\,570)} = 0.31$, $p = 0.58$], or the size of the coral colony [GLME, "colony area" effect, $F_{(1,\,570)} = 0.02$, $p = 0.90$]. We found no evidence that distance from the open ocean, depth, or competition intensity affected bleaching severity differently for different colony morphologies [GLME, "morphology by distance," $F_{(5,\,535)} = 1.8$, $p = 0.12$; "morphology by depth," $F_{(5,\,535)} = 1.0$, $p = 0.39$; "morphology by competition," $F_{(15,\,535)} = 0.9$, $p = 0.57$]. Similarly, the effect of competition intensity on bleaching severity did not depend on colony size [GLME, "competition by colony area," $F_{(3,\,535)} = 0.57$, $p = 0.63$], nor did the effect of distance from the open ocean depend on colony size [GLME, "colony area by distance," $F_{(1,\,535)} = 1.9$, $p = 0.16$]. Finally, our analysis did not support the hypothesis that different morphologies bleached at different rates [GLME, "day by morphology," $F_{(5,\,535)} = 0.63$, $p = 0.68$].

Published records of bleaching severity of *Acropora* species from previous bleaching events indicate high variability between morphologies (**Figure 5**), as well as high variability within and among species (**Figure 6**). Consistent with our observations of *Acropora* at Lizard Island, the literature demonstrates that arborescent and hispidose *Acropora* are more frequently observed to be severely bleached, while arborescent tables are among the least severely bleached in both datasets (**Figures 2B**, **5**). However, digitate and tabular morphologies showed contrasting bleaching severity at Lizard Island compared with the literature. When the responses of different coral species are considered, the literature indicates a greater degree of within- and among-species variability in bleaching severity than we observed at Lizard Island, despite having similar number of

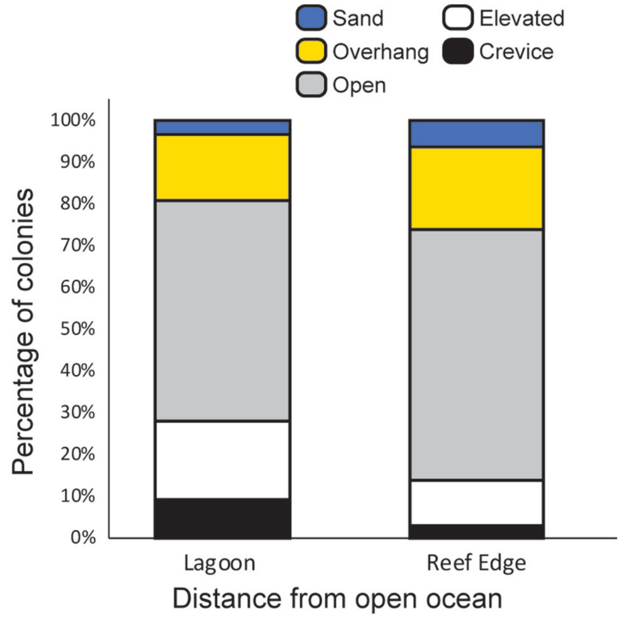

FIGURE 3 | Relative frequency of different microhabitats for *Acropora* colonies ($N = 596$) observed at lagoonal sites (>510 m from reef edge, 6 sites) and reef edge sites (<410 m from reef crest, 4 sites).

observations in both cases ($N = 596$ colonies measured at Lizard Island, $N = 532$ literature records), and data for a large number of species in both cases (40 species at Lizard Island, 87 species in the literature). In the literature, for the 48 species with at least 5 records of bleaching severity, 27% (13 species) showed high fidelity to a single bleaching category despite inevitable variation in the intensity of thermal stress among locations and bleaching events. In addition, 63% of species had records of bleaching within at least 3 categories, and 23% of species showed the full range of bleaching severity scores (from none to severe, **Figure 6**). Only one species (*A. desalwii*) was never recorded to show above "moderate" bleaching, likely due to its restricted geographic distribution and occurrence below 15 m depth (Wallace, 1999). Cluster analysis of the literature data for the subset of *Acropora* species we observed at Lizard Island revealed 7 clusters based on the bleaching severity categories most often recorded for those species during previous bleaching events (**Figure 7**). However, we found no evidence of systematic variation in average bleaching scores measured at Lizard Island for these clusters of species (**Figure 8**).

DISCUSSION

The results of this study show that during severe thermal stress, small-scale spatial variation in the bleaching susceptibility of branching corals is linked to microhabitat availability, and the proximity of sites to the open ocean, and that bleaching severity worsens over a very short time-frame (∼1 week). We found no evidence that water depth (range −0.5 to 5 m below LAT), competition intensity (range no competition to competitors surrounding entire colony circumference), or colony size (range 5–90 cm diameter) systematically influenced bleaching severity. At our study location, different colony morphologies differed in their bleaching severity under temperature stress, but within- and among-species variation in bleaching severity was low compared with the variation reported in the literature.

Environmental Drivers of Bleaching Severity

Our results generally support the hypothesis that coral bleaching is caused by a combination of high water temperature and high solar radiation (Jokiel and Coles, 1990; Lesser et al., 1990; Brown et al., 1994). Colonies in shaded microhabitats (crevices and overhangs) were less severely bleached than those in microhabitats with higher light exposure (open, elevated, and sand). The structural complexity of reefs causes high variation in irradiance among microhabitats (Brakel, 1979), whereby overhangs and crevices receive ≤40% of the irradiance that reaches open habitats at a similar depth (3–5 m, Anthony and Hoegh-Guldberg, 2003). Consistent with previous studies (e.g., Williams et al., 2010), colonies in sandy patches were the most severely bleached, likely because carbonate sand is highly reflective and amplifies light intensity (Ortiz et al., 2009). While colonies in microhabitats with low irradiance can have low survival (Baird and Hughes, 2000) and growth (Anthony and Hoegh-Guldberg, 2003) under normal conditions, our results support that crevice and overhang habitats may serve as refuges from thermal stress (see also West and Salm, 2003). Consequently, reefs' structural complexity supports ecosystem functioning and biodiversity not only by providing habitat and shelter for mobile reef organisms (Syms and Jones, 2000; Pratchett et al., 2008), but also by providing microhabitats that can increase coral survival during periods of thermal stress. In contrast to the strong effect of microhabitat, competition intensity had no effect on bleaching severity. One explanation for this is that some corals retract their polyps when exposed to high water temperatures (Jones et al., 2000) which might lower the incidence of contact between competitors and/or prevent the release of secondary metabolites. However, other species increase their feeding rates in response to bleaching (Grottoli et al., 2006), which is likely to increase the incidence of tissue contact between adjacent colonies. Further research into species-specific tissue retraction behaviors during thermal stress is required to explain this result.

In our study, water depth did not influence bleaching severity for corals that occur within the upper ∼6 m depths of the reef. A likely explanation for this finding is that water temperatures are often similar across this depth range, as the thermocline occurs at depths that are usually well below 20 m on coral reefs (e.g., Grigg, 2006). Moreover, the generally high water clarity at the study sites means there would have been limited attenuation of light over this depth range. Both still water conditions and water clarity increase the penetration depth of solar radiation into seawater, consequently increasing radiant heating throughout the water column and reducing variability in temperature with depth (Glynn, 1993; Brown, 1997). In our dataset, 90% of the surveyed

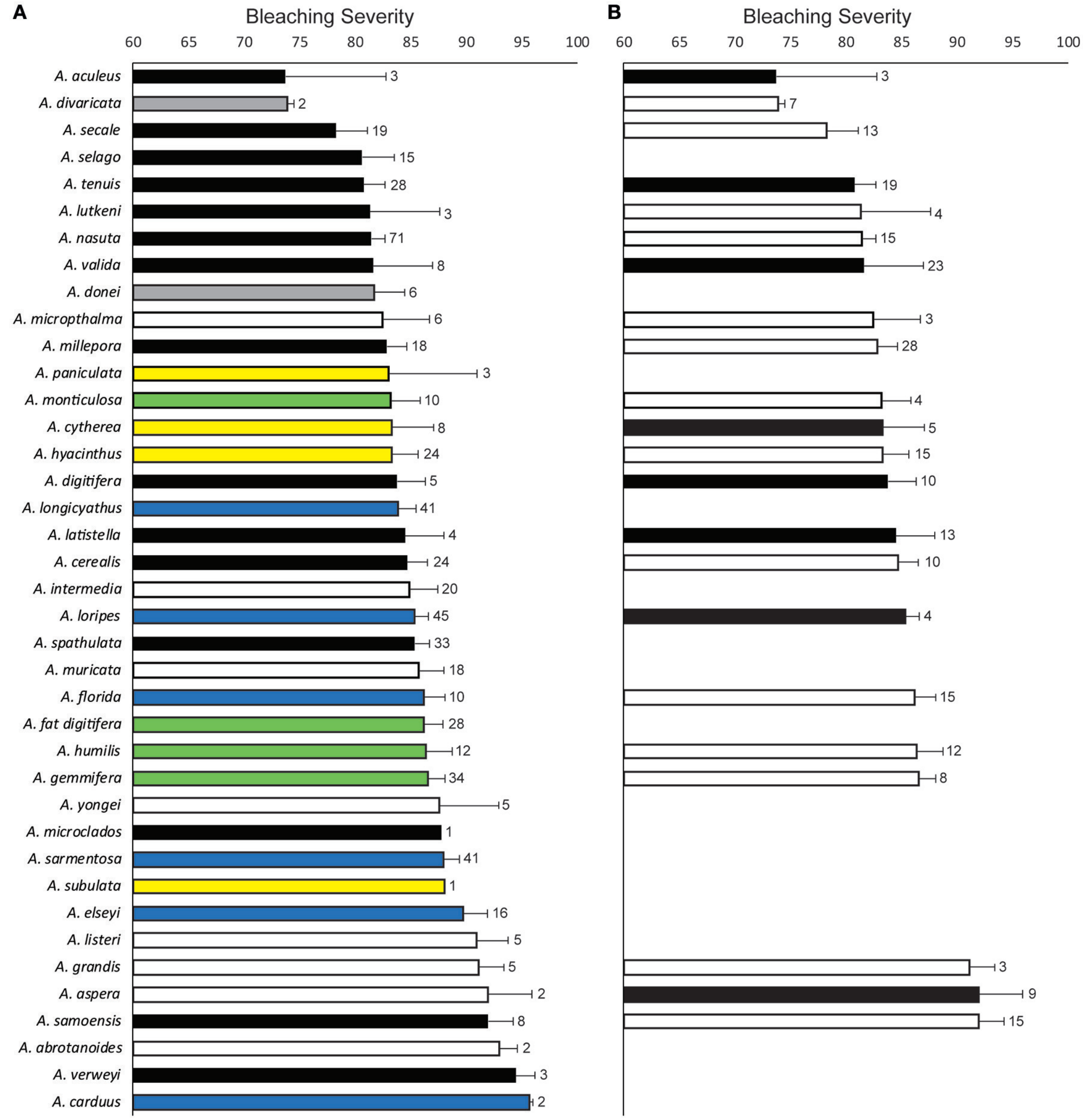

FIGURE 4 | Variation in bleaching severity within- and between-species in the genus *Acropora* observed at sites around Lizard Island in March 2016. Bars show the mean bleaching severity (colony "whiteness") measured from white-balanced images of colonies of each species. Error bars show standard error and numbers adjacent to error bars indicate sample sizes. In **(A)** bars are colored by colony morphology as: black (corymbose), gray (arborescent table), white (arborescent), yellow (table), blue (hispidose), and green (digitate) and numbers indicate colonies observed in the field. In **(B)** bars are colored by symbiont association as: black (species has been recorded to associate with multiple symbiont types) and white (species has been recorded to only associate with a single symbiont type) and numbers indicate records of *Symbiodinium* type in the Geosymbio database.

colonies were located at a depth of <2.5 m below LAT (~3–4 m water depth given the tidal range at the location). Based on estimates of light attenuation from other offshore reefs with high water clarity (Cooper et al., 2007), light intensity at this depth would be ~70% of subsurface light intensity. Collectively these results indicate that crevice and overhang microhabitats provide a greater shading effect than light attenuation with depth in clear waters across the surveyed depth range. The absence of a depth effect also demonstrates that abnormally low sea levels were not the cause of coral bleaching at our study location. Although low sea levels due to El Niño Southern Oscillation have been associated with a local coral mortality event in Indonesia (Ampou et al., 2017), a strong depth-dependent pattern of bleaching severity, with higher severity in the shallowest depths (i.e., <1 m depth), would be expected in areas where coral bleaching was caused by tidal emersion.

We used distance from the open ocean as a metric to capture potential spatial variation in wave energy and other environmental conditions between reef-edge and lagoonal sites. Previous studies reveal contrasting effects of water flow on bleaching severity. Thermal bleaching is linked to photoinhibition of photosynthesis (e.g., Jones et al., 2000) and

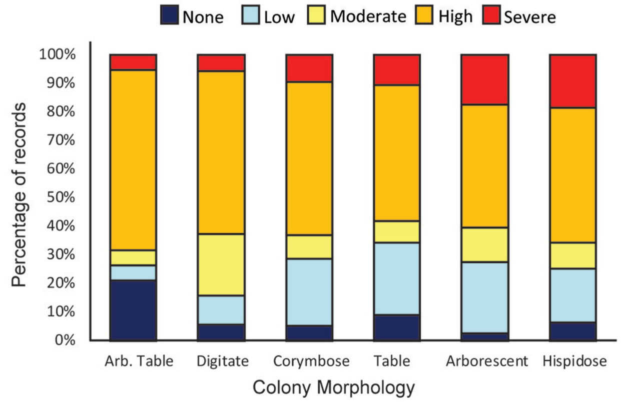

FIGURE 5 | Records of bleaching severity for different *Acropora* colony morphologies compiled from the literature. Bars show the percentage of records in the literature for each colony morphology in each bleaching severity category ($N = 429$). Data for elkhorn and encrusting colony morphologies have been excluded to facilitate comparison with data from Lizard Island plotted in **Figure 2B**. Numbers of records for each morphology are 19 (Arb. Table), 70 (digitate), 95 (corymbose), 64 (table), 149 (Arborescent) and 32 (hispidose/caespitose).

this inhibition can be mitigated by higher water flow (Nakamura et al., 2005). However, contrary to such effects, we found lower bleaching severity in lagoon sites which generally have low wave energy and low flow compared with reef edge locations (Fulton and Bellwood, 2005). This result is consistent with a field study in the Indian Ocean which also found a positive correlation between bleaching intensity and water flow speed (McClanahan et al., 2007). Coral reef lagoons are characterized by shallow water with limited mixing, which facilitates heating until surface waves force cooler waters over the reef crest (Monismith, 2007). Consequently, corals in lagoon environments experience greater variability in their local temperature. Heat stress experiments indicate that corals from habitats with high variability in temperature have lower mortality rates than corals from habitats with moderate thermal variability (Oliver and Palumbi, 2011). While we do not have site-specific temperature data at our survey sites, temperature loggers deployed at the study location indicate that the lagoon had slightly higher and more variable temperatures than the reef edge during December through to March 2016 (reef edge site: average 29.7°C range 27.9–31.7°C; lagoon site: average 30.0°C range 25.6–33.2°C). Overall, our results support the hypothesis that prior exposure to variable temperature regimes can promote thermal tolerance of coral colonies. Nevertheless, the declining bleaching severity with distance from the open ocean might also be related to differences in microhabitat availability across this gradient as we observed a higher frequency of crevice microhabitats, and a lower frequency of open microhabitats, at lagoonal sites.

Among-Species Variation in Bleaching Severity

Bleaching severity differed among the various branching morphologies of *Acropora* observed at Lizard Island. Previous studies have reported disparate results regarding the effect of colony morphology on bleaching, including: no clear effect of morphology (Williams et al., 2010); higher bleaching susceptibility for branching and tabular corals compared with massive and encrusting colonies (Marshall and Baird, 2000; Loya et al., 2001); and higher bleaching severity of massive corals compared with branching corals (Ortiz et al., 2009). These disparate results might be partially explained by variation in growth rates, both among-species and among-locations due to changes in environmental conditions. Fast-growing branching morphologies are more susceptible to bleaching than morphologies with slower growth rates (e.g., massive corals, Hoegh-Guldberg and Salvat, 1995; Marshall and Baird, 2000; Brandt, 2009). This pattern is thought to be related to metabolic rates: fast-growing colonies have higher metabolic rates and, thus, accumulate more harmful oxygen free radicals which results in oxidative stress that is linked to bleaching susceptibility (e.g., Jokiel and Coles, 1974; Hoegh-Guldberg and Salvat, 1995; Baird and Marshall, 2002). Among *Acropora* corals specifically, a recent study by Dornelas et al. (2017) showed that digitate and corymbose growth forms have slower growth rates than arborescent and tabular growth forms. These results are broadly consistent with the bleaching severity of these species reported in the literature. However, in our surveys, tabular corals were the least severely bleached despite having rapid growth rates (Dornelas et al., 2017). At present, we do not have a clear explanation for these contrasting results and further studies are required to disentangle the influence of growth rate compared with other environmental variables on coral bleaching susceptibility.

The type of *Symbiodinium* present within coral tissues can have a significant influence on the bleaching susceptibility of corals (e.g., Glynn, 1993; Baker, 2003; Berkelmans and Van Oppen, 2006; Abrego et al., 2008). In particular, some corals can increase their thermal tolerance if they can change the dominant symbiont clade in their tissues to a more thermally tolerant one (Berkelmans and Van Oppen, 2006). This implies that corals harboring multiple symbiont types potentially have an ecological advantage if they can shuffle their symbionts to "match" their ambient environmental conditions. However, under times of stress, this advantage can only manifest if the symbiont community includes symbionts that are tolerant to a given stressor. Our data showed no clear relation between bleaching severity and the capacity of *Acropora* species to harbor multiple *Symbiodinium* types. This result suggests that it is the presence of a specific heat-tolerant symbiont, rather than the ability to host multiple symbiont types, that confers thermal tolerance. We note, however, that while there is an increasing research emphasis on the functional differences between *Symbiodinium* clades (e.g., Suggett et al., 2015, 2017), the coral species coverage of these data remains relatively sparse and this constrained our analyses. We limited our analysis to the level of *Symbiodinium* clades, but differences in thermal tolerance exist among *Symbiodinium* belonging to the same clade (Tchernov et al., 2004; Sampayo et al., 2008; Correa and Baker, 2009; LaJeunesse et al., 2014). Thus, while our results suggest that *Acropora* species known to associate with one or multiple *Symbiodinium* clades did not

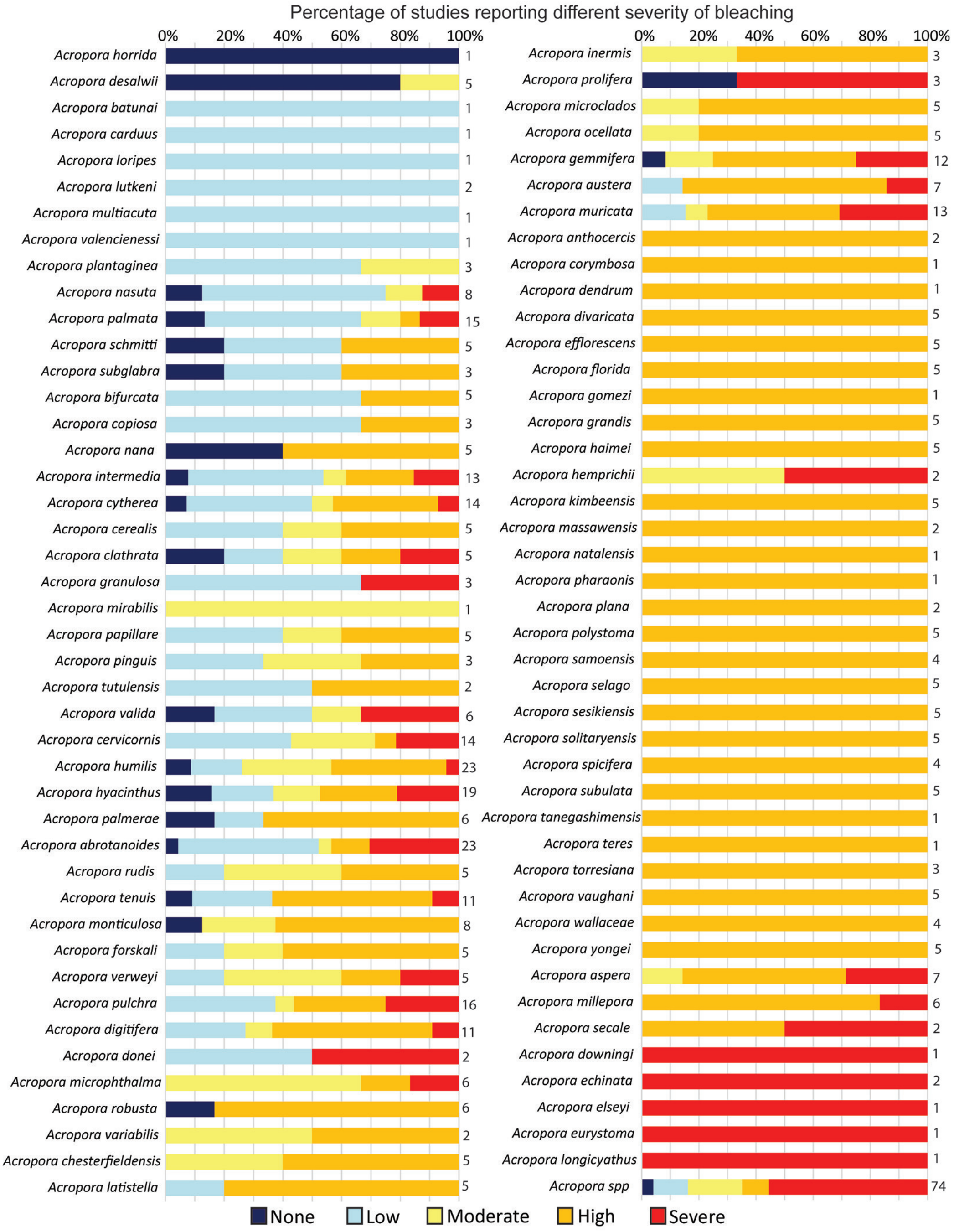

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FIGURE 6 | Records of bleaching severity for different *Acropora* species compiled from the literature. Bars show the percentage of records in the literature for each species in each bleaching severity category (*N* = 527) and numbers adjacent to bars indicate number of records per species.

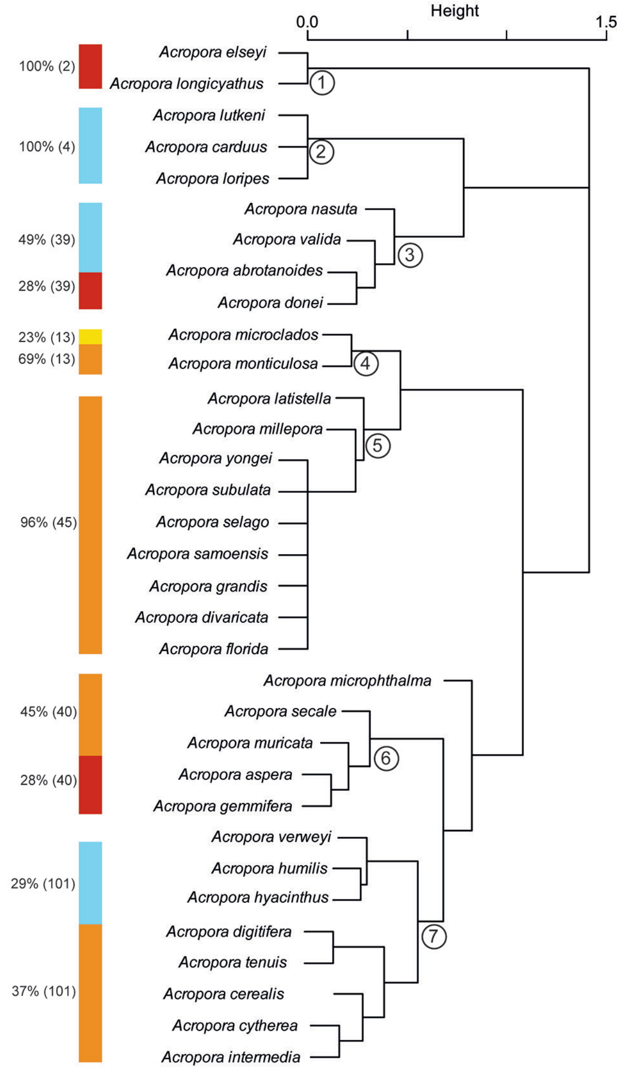

FIGURE 7 | Cluster analysis of *Acropora* species observed at Lizard Island based on records of occurrence of different bleaching severity in the literature. Color bars adjacent to each cluster show the bleaching severity observed in at least 20% of records for the species (dark blue, no bleaching; pale blue, low bleaching; yellow, moderate bleaching; orange, high bleaching; red, severe bleaching). Percentage values adjacent to color bars show percentage of records in each bleaching category and values in parentheses show number of records.

exhibit differences in bleaching resistance, finer-scale resolution of symbiont identities may have explained additional variation in bleaching intensity (Sampayo et al., 2008).

A Standardized Method for Measuring Bleaching Severity

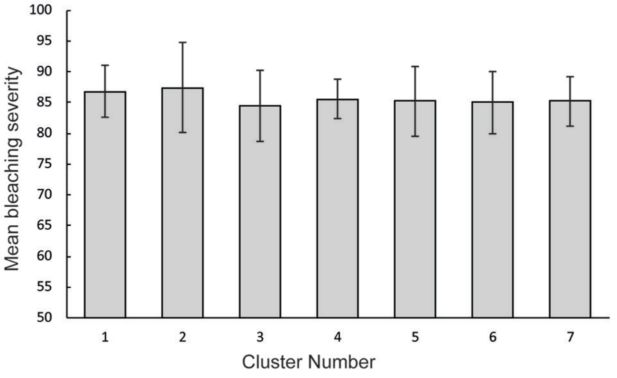

FIGURE 8 | Mean bleaching severity for different groups of *Acropora* species observed at Lizard Island. Groups were identified using hierarchical cluster analysis and error bars show standard error.

The image analysis technique developed here provides a sensitive measure of bleaching severity that captures gradation within and between species, and that overcomes some of the limitations of survey observation methods (e.g., Siebeck et al., 2006). First, our technique eliminates *in situ* observer bias and corrects for color variation due to differences in the *in situ* light environment. Second, the data are continuous which allows a more precise measure of bleaching severity by avoiding the loss of information that occurs with categorical data. Third, photographs provide a permanent photographic record of the state of each individual colony which may be useful for future comparisons. Finally, this technique can be developed further, and extended to other coral groups, by quantifying the "whiteness" of healthy corals to provide a species-specific baseline for coral colony health in the absence of environmental stressors. Despite these advantages, this new technique is more time consuming than *in situ* observer based techniques. White-balancing and color analysis took ∼3–5 min per image, with approximately half of this time spent on white-balancing. In addition, many corals contain fluorescent proteins in their tissues which give colonies a blue or pink colouration that overlays the golden brown color of the *Symbiodinium* within the coral cells (e.g., Alieva et al., 2008). Our technique likely underestimates bleaching severity of heavily pigmented colonies because these host-pigments make them appear to be less white than a non-pigmented colony with the same level of bleaching (i.e., symbiont loss). However, this issue makes our results conservative as to the differences between morphologies, microhabitats and sampling days because it introduces additional variability in the dataset. We also note that, when colonies are only partially bleached (e.g., where the upper surface of the colony is whiter than the lower surfaces, Harriott, 1985), more than four measurement points may be needed to accurately represent the color distribution of each colony.

CONCLUSIONS

During the extreme heat stress that affected the northern GBR in 2016, 97% of *Acropora* colonies observed at our study location were pale or bleached, and ∼70% of colonies had whiteness values consistent with a categorization of "severe" bleaching. In contrast, in previous bleaching events nearly a quarter of *Acropora* species were reported to show high within-species variability in bleaching severity, with scores ranging from "none" to "severe." Overall, we consistently observed severe bleaching during the extreme thermal anomaly experienced at our study location, in comparison to more variable bleaching severity reported during a broad range of bleaching events described in the literature. These comparisons highlight the importance of measuring and reporting the magnitude of thermal stress experienced at different sites during bleaching so that species- and/or location-specific temperature thresholds for different levels of bleaching can be quantified. Our results also highlight the importance of monitoring and reporting the timing of bleaching surveys relative to the onset of thermal stress, as our new image analysis technique detected a 10% increase in bleaching severity over a period of 1 week. Microhabitat structure, but not competition intensity, water depth or colony size, also contributed to variation in bleaching severity of *Acropora* corals. Crevices and overhang microhabitats, which can mitigate bleaching severity, are more prevalent in structurally complex reefs. Such complexity is a product of the successful recruitment and growth of morphologically complex species, such as *Acropora* species that are important contributors to spatial complexity in Indo-Pacific reefs (Pratchett et al., 2008). Collectively, these results suggest a negative feedback loop whereby bleaching reduces the abundance of branching species, which lowers the occurrence of shaded microhabitats, which then leads to more severe bleaching.

AUTHOR CONTRIBUTIONS

All authors contributed to the initial conceptualization of this project. Field data were collected by GF, TC, and SJ (at Lizard Island) and by KP, BR, KB, and MH (at Orpheus Island). Color analyses were conducted by GF and AP, and colony size measurements were conducted by MÁ-N and SJ. Coral identification, microhabitat and competition data were compiled by MH, KN, AP, TC, and GF. Spatial analyses were conducted by KC. MH analyzed the data and wrote the first draft of the paper with all authors making a substantial contribution to subsequent drafts (particularly SJ, KP, and MÁ-N).

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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.2017.00376/full#supplementary-material

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High Latitude Corals Tolerate Severe Cold Spell

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Climatically extreme weather events often drive long-term ecological responses of ecosystems. By disrupting the important symbiosis with zooxanthellae, Marine Cold Spells (MCS) can cause bleaching and mortality in tropical and subtropical scleractinian corals. Here we report on the effects of a severe MCS on high latitude corals, where we expected to find bleaching and mortality. The MCS took place off the coast of Perth (32°S), Western Australia in 2016. Bleaching was assessed before (2014) and after (2017) the MCS from surveys of permanent plots, and with timed bleaching searches. Temperature data was recorded with in situ loggers. During the MCS temperatures dipped to the coldest recorded in ten years (15.3°C) and periods of <17°C lasted for up to 19 days. Only 4.3% of the surveyed coral colonies showed signs of bleaching. Bleaching was observed in 8 species where those most affected were *Plesiastrea versipora* and *Montipora mollis*. These findings suggest that high latitude corals in this area are tolerant of cold stress and are not persisting near a lethal temperature minimum. It has not been established whether other environmental conditions are limiting these species, and if so, what the implications are for coral performance on these reefs in a warmer future.

Keywords: Marine cold spell (MCS), coral bleaching, *Plesiastrea versipora*, *Montipora mollis*, stress-tolerant species

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INTRODUCTION

Extreme weather events can cause long term ecological changes by impacting species across multiple scales from physiological performance to biogeographic distributions (e.g., Gaines and Denny, 1993; Hawkins et al., 2009). In the marine environment, extreme temperature events can be particularly detrimental with potentially wide ranging and catastrophic impacts (e.g., Southward and Burrows, 1995; Garrabou et al., 2009; Lirman et al., 2011; Wernberg et al., 2016). Both marine heatwaves (MHW's) and cold spells (MCS's) have only recently been defined in the literature (MHW's; Hobday et al., 2016, MCS; Schlegel et al., 2017). However, in contrast to many recent examples of impacts of MHWs, MCS's have received much less attention (Schlegel et al., 2017).

Marine Cold Spells often result from upwelling and/or atmospheric forcing (Schlegel et al., 2017) causing temperature declines, resulting in reduced metabolic capacity and stress in warm-adapted organisms (e.g., invertebrate mortality; Gunter, 1951; Firth et al., 2011, fish kills; Gunter, 1941, 1951; Holt and Holt, 1983; Rehage et al., 2016, coral bleaching; Roberts et al., 1982; Paz-García et al., 2012).

Temperature is a key factor determining the distribution of scleractinian corals, as they are generally warm water species confined to tropical and subtropical latitudes (Wells, 1957; Stehli and Wells, 1971; Veron, 1995). As seasonally cool isotherms limits the performance and distribution of many corals, this group of species can be expected to be sensitive to severely cooler conditions such as Marine Cold Spells (MCS). For tropical and subtropical scleractinian corals cold stress has been shown to impact the symbiotic relationship with zooxanthellae (Krause, 1992; Saxby et al., 2003; Hoegh-Guldberg et al., 2005). Under cold stress the onset of Photosystem II quenching in the zooxanthellae slows, which causes an excess of oxygen to build up in the tissue (Krause, 1992). Similar to warm water stress the excess oxygen can cause the formation of oxygen radicals, leading to tissue damage and the expulsion of the zooxanthellae (coral bleaching) (Saxby et al., 2003; Hoegh-Guldberg et al., 2005; Pontasch et al., 2017). Extreme cold stress, such as MCS, has thus been shown to be limiting for lower latitude corals and symbionts, and induce coral bleaching.

In addition to causing photosynthetic declines and disruptions to the coral–zooxanthellae symbiosis, cold stress can be lethal. Exposure to cold stress (3 −11°C below ambient) for as little as 9–12 h initially induces reduced photosynthesis and coral bleaching but beyond 12 h at severe cold stress (11°C below ambient) coral mortality can occur (Saxby et al., 2003). Cold spells have resulted in large scale coral bleaching on low latitude reefs such as the Great Barrier Reef (Australia, 23°S), where living coral cover plummeted from >80 to <12% (Hoegh-Guldberg et al., 2005). Similarly in Florida (USA, 24–27°N) coral mortality averaged 90% in some areas following cooler temperatures of 15°C (Voss, 1973; Davis, 1982; Roberts et al., 1982). MCS's thus have the potential to be significant drivers of stress and mortality in coral communities.

Modern coral communities in high latitude areas of Western Australia are typified by coral species with wide geographical ranges, or subtropical or temperate affinity (Greenstein and Pandolfi, 2008). These species are largely generalists with broad niche requirements (Sommer et al., 2014; Keith et al., 2015; Mizerek et al., 2016), and they regularly experience temperatures that are considered "cold" (<18°C), for these inherently tropical taxa (Veron, 1995). Although resilient, these corals are not impervious to the stressful conditions at high latitudes. For example high latitude conditions suppress reef building processes and limit corals to distinct communities (Kleypas et al., 1999). Furthermore, these populations are locally adapted, reproductively isolated and have low genetic diversity (Ayre and Hughes, 2004; Miller and Ayre, 2008; Noreen et al., 2009; Thomas et al., 2017). Similar to what has been observed in low latitude corals, cold stress, such as can be expected during unusually cold MCS, could be limiting for corals and symbionts and induce bleaching in high latitude corals.

In this study, we documented responses of high latitude corals to a severe MCS off the coast of Perth (32°S), Western Australia, where the coolest water temperatures in more than a decade, were recorded in the austral winter of 2016. As cold stress impairs metabolic processes and survival for low latitude coral reefs we expected the MCS to have caused stress in corals around Perth. As a result, we hypothesized that the high latitude coral communities would have undergone widespread bleaching and mortality from cold stress experienced during the 2016 MCS.

METHODS

This study took place in Marmion Marine Park off the coast of Perth, Western Australia (**Figure 1**).

In June 2014, five permanent plots of one meter diameter (3.14 m^2), were established at three offshore sites of comparable habitat and environmental conditions. The center of each plot was marked with a labeled stake for later identification. Plots were established haphazardly across the limestone reef, separated by a minimum of 10 meters at a depth of 8–12 m in areas dominated by corals, turf and fleshy seaweeds. Each plot was mapped for coral colonies, and each colony was photographed with a scale (Three Mile Reef North and South), or the whole plot was photographed as visual reference (Centaur Reef). Photographs were used for subsequent measurements of size and colony health, by comparing against a coral health chart (www.coralwatch.org) to quantify levels of bleaching. For this study, only colonies with color codes B1, C1, D1, or E1 were considered to be bleached (www.coralwatch.org). This avoided potentially assigning bleaching status to colonies with perpetual lighter pigmentation or seasonal pigment variation. Plots were surveyed in September–October 2014 prior to the marine cold spell of 2016. Survey sites were visited regularly (every ∼2–3 months between 2014 and 2015, monthly 2015–2016, and ∼3–4 months 2016–2017) and bleaching in >1 colony was not noted. Coral bleaching was noted anecdotally in plots in December 2016, prompting a resurvey in January 2017 (austral summer). Summer temperatures prior to the surveys were comparable to regularly recorded high temperatures (December average 2006-15 = 21.4°C (max 24.0°C) vs. December average 2016 = 21.7°C (max 24.0°C); Wernberg unpublished data) and unlikely to have been the source of bleaching. Overgrowth by turf algae on all bleached colonies further indicated that the bleaching had not occurred more recently in December 2016, immediately prior to the re-surveys. Due to loss of labeled stakes three plots were surveyed from Three Mile Reef North, four from Three Mile Reef South and four from Centaur Reef in 2017. In addition to the permanent plots, timed searches for additional coral bleaching was also undertaken in January and February 2017, at all three sites as well as at an additional three inshore sites (**Figure 1**). All colonies encountered in the 30 min searches were photographed for subsequent measurements of size and colony health (as above).

Chi-square goodness of fit tests were used to determine if the proportion of bleached colonies was significantly different between species, and between inshore and offshore reefs.

Temperature was recorded *in situ* every hour by an Onset Tidbit logger attached to a stake ∼5 cm above the reef surface at Centaur Reef (**Figure 1**). See Smale and Wernberg (2009) for additional information.

RESULTS

During 2016 temperatures in Marmion dipped to 15.3°C, the coldest temperature recorded in >10 years. Anomalously cold temperatures occurred in nine months of the year, based on ten year average monthly temperatures, and a continuous period of

<17°C (below any long term monthly average) occurred for ~19 days during August–September (**Figure 2**). In the months prior to bleaching being noted in December 2016, other temperature anomalies (e.g., heat spikes) were not seen (**Figure 2**).

A total of 244 coral colonies were found and re-surveyed in the nine permanent plots after the marine cold spell (**Figure 3**) and the number of colonies increased in total due to an increased number of small corals (<1 cm) (**Table 1**). The number of bleached colonies increased from zero before to ten (4.3%) after the MCS, and of the ten bleached corals four were > 50% bleached and six <50% bleached (**Figure 4A**). The bleached colonies occurred at all sites and were found in six of the nine plots. Bleaching was found in two of the ten species recorded within the plots. *Montipora mollis* had slightly more bleached colonies than *Plesiastrea versipora* (**Figure 4B**). Of the 234 healthy colonies the majority were *P. versipora* and *Paragoniastrea australensis* (**Figure 4C**). A large majority of the healthy colonies were also recruits so the highest taxonomic identification they could be assigned was family (*Merulinidae*).

Timed searches revealed an additional eight species had undergone bleaching than was found in the permanent plots. In addition to more *P. versipora* and *M. mollis*, we found bleached colonies of *P. australensis*, *Turbinaria reniformis*, *Coelastrea aspera*, *Dipastrea favus*, *Turbinaria mesenterina*, and *Pocillopora damicornis* (**Table 2**). The frequency of bleaching was significantly different between species (Chi-square test $p < 0.05$) and the frequency of bleaching in the eight effected species was not independent of shelf position (inshore vs. offshore, Chi-square test $p < 0.05$). This was likely the result of the large proportion of bleached *M. mollis* on offshore reefs and only bleached *M. mollis* and *P. versipora* being common to both inshore and offshore reefs (**Table 2**).

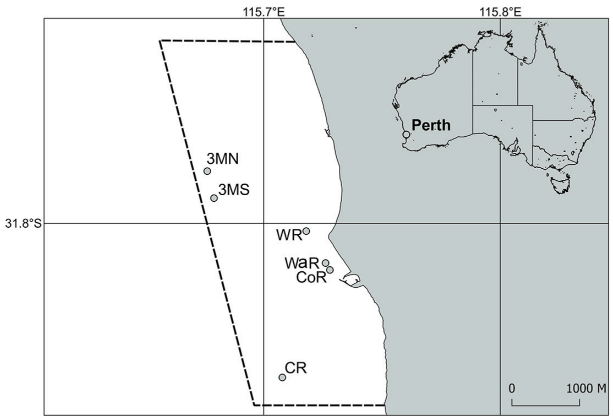

FIGURE 1 | Sample region and sites within Marmion Marine Park off of Perth, Western Australia. The dashed lines indicate the boundary of the marine park. 3MN, Three Mile Reef North; 3MS, Three Mile Reef South; WR, Wreck Rock; WaR, Wanneroo Reef; CoR, Cow Rocks; CR, Centaur Reef.

DISCUSSION

In this study we found corals in Marmion Marine Park (32°S) to be largely unaffected by a severe marine cold spell. Our hypothesis, that corals would undergo bleaching and mortality was documented but not extensively. We had expected the unusually low temperature anomalies and duration of the MCS would have induced physiological stress, leading to a disruption in the coral-zooxanthellae symbiosis and to coral bleaching. However, this only occurred for a small number of corals and was not widespread across the coral community. The coastal area adjacent to Marmion Marine Park did not receive unusually high solar exposure between October–December 2016 compared to previous years (www.bom.gov.au) nor were other temperature anomalies seen in late 2016, ruling out warm water or light induced bleaching. This suggests that the symbiotic relationship

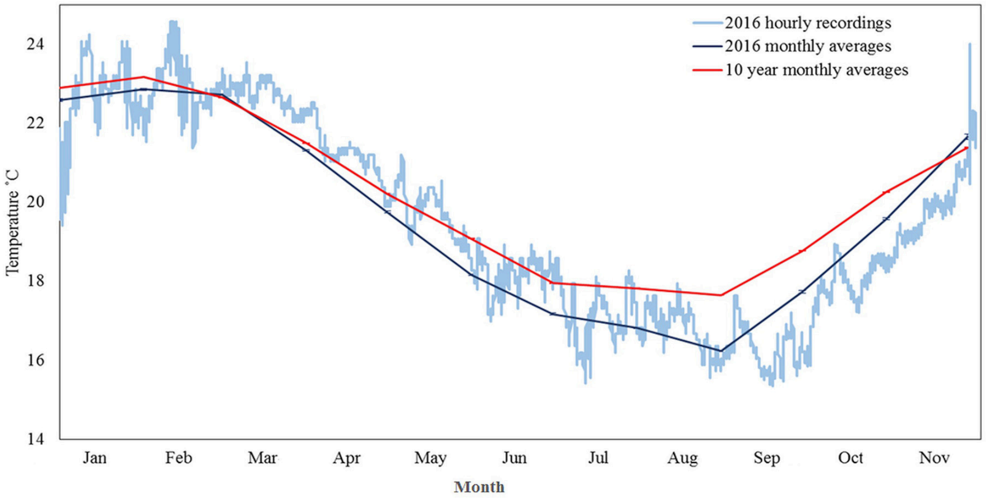

FIGURE 2 | *In situ* (± se) temperatures logged by an Onset Tidbit logger attached to a stake ~5 cm above the reef surface at Centaur Reef. Light blue line denotes hourly temperature records for 2016, dark blue line monthly temperature averages for 2016 and red line 10 year monthly (2006–2016) temperature averages.

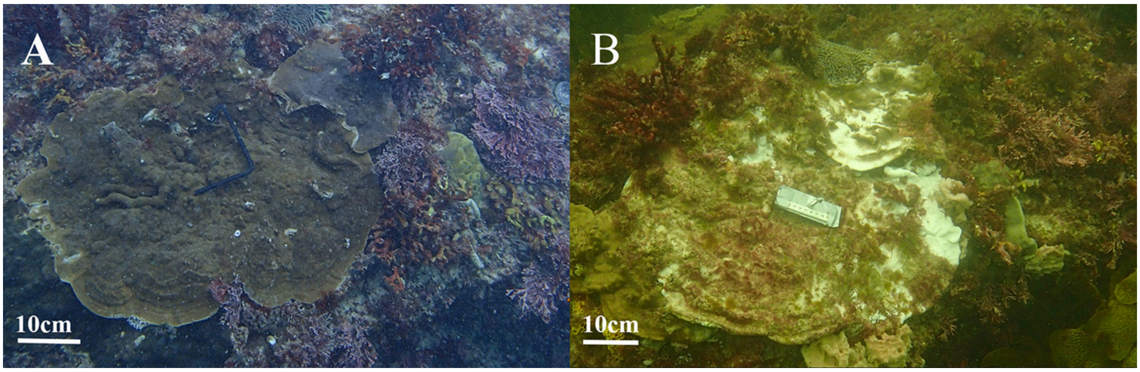

FIGURE 3 | Underwater photographs of coral colonies from Three Mile Reef South in Marmion Marine Park showing **(A)** healthy coral colonies in 2014 before the 2016 Marine Cold Spell and **(B)** bleached *Montipora mollis* colonies with turf algae overgrowth after, in January, 2017. Photo credits: C. Tuckett.

TABLE 1 | Relative abundances of species at different life stages before (2014) and after (2016) the Marine Cold Spell in permanent plots within Marmion Marine Park.

Species	Life Stage	2014	2016
Turbinaria reniformis	Adult	2	2
Montipora mollis	Adult	5	5
Favites abdita	Adult	1	1
Dipastrea favus	Adult	2	2
Coscinaraea mcneilli	Adult	1	1
Pocillopora damicornis	Adult	1	1
Turbinaria mesenterina	Adult	1	1
Plesiastrea versipora	Adult	9	11
	Recruit	19	24
Coelastrea aspera	Adult	7	11
	Recruit	0	3
Paragoniastrea australensis	Adult	8	21
	Recruit	0	1
Total		56	84

Abundances are from Three Mile Reef North and South only where plots where mapped for individual colonies, and recruits refer to colonies with a diameter ≤ 1 cm.

TABLE 2 | Species found with coral bleaching after the Marine Cold Spell on inshore and offshore reefs of Marmion Marine Park, Perth, Western Australia in timed searches.

Species	Offshore		Inshore		
	N	Percent (%)	*N*	Percent (%)	Total
Montipora mollis	17	42.5	6	15.0	23
Paragoniastrea australensis	2	5.0	0	0.0	2
Plesiastrea versipora	2	5.0	2	5.0	4
Turbinaria reniformis	1	2.5	0	0.0	1
Coelastrea aspera	0	0.0	2	5.0	2
Dipastrea favus	0	0.0	1	2.5	1
Pocillopora damicornis	0	0.0	3	7.5	3
Turbinaria mesenterina	0	0.0	4	10.0	4
Total	22	55.0	18	45.0	40

N = total count of bleached colonies per species, percent = percentage each species contributed to the total bleaching pool.

between zooxanthellae and high latitude corals is not particularly stressed by anomalously cold temperatures, and that these corals are not persisting near their lethal temperature minima.

High latitude areas are challenging environments for inherently tropical taxa such as scleractinian corals. Low temperatures, low light availability and high attenuation in winter, low aragonite saturation and high competition with seaweeds are pervasive stressors for corals in these environments (Miller, 1995; Miller and Hay, 1996; Kleypas et al., 1999; Sommer et al., 2017). These stressors filter species so that high latitude coral communities are largely dominated by corals which are generalists with broad niche requirements (Sommer et al., 2014; Keith et al., 2015; Mizerek et al., 2016). The stress tolerant nature of most high latitude species could thus explain the low impact of the 2016 MCS.

It has been shown that low temperatures do not necessarily have detrimental impacts for corals and symbionts. Prolonged exposure to cold stress (−5°C below ambient) in aquaria has shown corals to acclimate and recover after initial declines in health and mild bleaching (Roth et al., 2012; Roth and Deheyn, 2013). One mechanisms enabling tolerance to cold stress, particularly when energy transfer from zooxanthellae to coral is absent or drastically reduced, is supplementing with heterotrophic feeding (Miller, 1995; Leletkin, 2000; Howe and Marshall, 2001; Anthony and Connolly, 2004; Grottoli et al., 2006; Houlbrèque and Ferrier-Pagès, 2009; Levas et al., 2013). Corals also maintain energy reserves (as lipids), which are utilized by some species to aid recovery after bleaching (Rodrigues and Grottoli, 2007). Thus mechanisms for energy acquisition may play an important role in managing stress to low temperatures such as those experienced during the 2016 MCS.

Although high latitude corals tolerate low temperatures these conditions often have sub lethal impacts. In broad terms, temperatures which regularly drop below 18°C for extended periods of time (weeks to months; Veron, 1995) are considered cold for corals as they limit reef building processes. In some areas of southern Australia, for example, temperatures can dip to 12°C (Petrusevics, 1993), however this is at the cost of

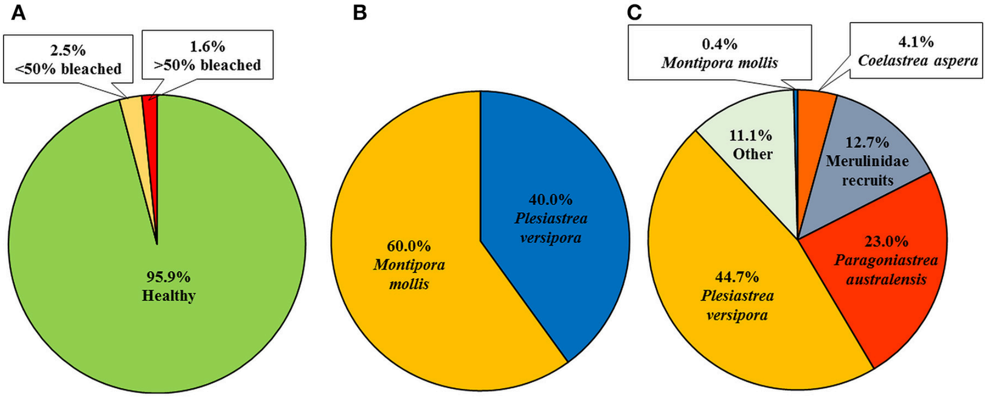

FIGURE 4 | Summary of coral colonies within long term growth plots in Marmion Marine Park as surveyed in January, 2017. **(A)** Proportion of coral colonies healthy, <50% bleached and >50% bleached, **(B)** species breakdown of the bleached corals, and **(C)** healthy corals.

growth which ranges from 1.5–7.8 mm year^{-1} (Burgess et al., 2009). The 2016 MCS likely had similar sub lethal impacts and we expect that these corals would have depressed growth and possibly additional trade-offs such as reduced reproductive fitness.

It is clear that the 2016 MCS had little impact on high latitude corals in this study. This suggests that high latitude corals are not particularly limited by low temperatures, and other factors (potentially light, aragonite saturation and competition with seaweeds; Miller, 1995; Miller and Hay, 1996; Kleypas et al., 1999; Sommer et al., 2017) play a significant role. Therefore under a warmer future, temperature increase alone, may not make high latitudes any more suitable for coral performance than current conditions. However temperature increases have already indirectly alleviated competition with seaweeds at high latitude (Vergés et al., 2014; Tuckett et al., 2017), and its role in mitigating other limiting factors (e.g., light) has been proposed (Sommer et al., 2017). It has not been established if other environmental conditions are limiting these species, and if so, what the implications are for coral performance on these reefs in a warmer future.

AUTHOR CONTRIBUTIONS

CT and TW designed the study; CT and TW collected data; CT identified corals, performed data analysis and led the writing; both authors contributed to the final version.

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Demographic Mechanisms of Reef Coral Species Winnowing from Communities under Increased Environmental Stress

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Winnowing of poorly-adapted species from local communities causes shifts/declines in species richness, making ecosystems increasingly ecologically depauperate. Low diversity can be associated with marginality of environments, which is increasing as climate change impacts ecosystems globally. This paper demonstrates the demographic mechanisms (size-specific mortality, growth, fertility; and metapopulation connectivity) associated with population-level changes due to thermal stress extremes for five zooxanthellate reef-coral species. Effects vary among species, leading to predictable changes in population size and, consequently, community structure. The Persian/Arabian Gulf (PAG) is an ecologically marginal reef environment with a subset of Indo-Pacific species, plus endemics. Local heating correlates with changes in coral population dynamics and community structure. Recent population dynamics of PAG corals were quantified in two phases (medium disturbed MD 1998–2010 and 2013–2017, severely disturbed SD 1996/8, 2010/11/12) with two stable states of declining coral frequency and cover. The strongest changes in life-dynamics, as expressed by transition matrices solved for MD and SD periods were in *Acropora downingi* and *Porites harrisoni*, which showed significant partial and whole-colony mortality (termed "shrinkers"). But in *Dipsastrea pallida, Platygyra daedalea*, *Cyphastraea microphthalma* the changes to life dynamics were more subtle, with only partial tissue mortality (termed "persisters"). Metapopulation models suggested recovery predominantly in species experiencing partial rather than whole-colony mortality. Increased frequency of disturbance caused progressive reduction in coral size, cover, and population fecundity. Also, the greater the frequency of disturbance, the more larval connectivity is required to maintain the metapopulation. An oceanographic model revealed important local larval retention and connectivity primarily between adjacent populations, suggesting that correlated disturbances across populations will lead to winnowing of species due to colony, tissue, and fertility losses, with resultant insufficient dispersal potential to make up for losses—especially if disturbances increase under climate change. Variable extinction thresholds exist based on the susceptibility of species to disturbance ("shrinkers" vs. "persisters"), determining which species will be winnowed from the community. Besides projected changes in coral community and population structure, no species are projected to increase in cover. Increased marginality due to climate change will lead to a net loss of coral cover and novel communities in PAG.

Keywords: coral reefs, climate change, Persian/Arabian gulf, population dynamics, matrix model, oceanographic model, metapopulation, connectivity

INTRODUCTION

Gradients in latitude, habitat, and anthropogenic disturbance characterize the distribution of biodiversity in general, and also of zooxanthellate reef-building shallow-water corals (Reaka et al., 2001; Schluter and Pennell, 2017). Reef-coral diversity declines from a presumed center toward the edges (Rosen, 1971; Coudray and Montaggioni, 1982; Jokiel and Martinelli, 1992; Veron, 1995; Glynn, 1997; Veron et al., 2009). This pattern is usually ascribed to physiological limitations of zooxanthellate reef corals in marginal environments of the tropical belt. Increased excursions from a typical tropical environmental envelope seems to determine the limits of adaptation (Veron, 1995; but see discussion concerning the Mid Domain Effect; Colwell et al., 2004; Connolly, 2005; Hawkins et al., 2005; Currie and Kerr, 2008). These mechanisms are not only evident along latitudinal gradients but increasingly also along temporal and anthropogenic gradients (vanHooidonk et al., 2013; Riegl and Purkis, 2015; Hughes et al., 2017a,b; Schluter and Pennell, 2017). Although species may evolve and adapt to new conditions (Jones et al., 2008; Atweberhan et al., 2013; Makino et al., 2014; Palumbi et al., 2014), generally fewer reef-coral species persist within suboptimal environments. Peripheral endemism can counter-act at least some diversity-loss, with some peripheral seas species-poorer than the distributional center but rich in local endemics, and some marginal environments of the tropical belt appear to be centers of evolutionary innovation (Jokiel and Martinelli, 1992; Reaka et al., 2001; Budd and Pandolfi, 2010). Even within highest-diversity zones, gradients in environmental quality cause gradients of species richness, with species winnowed from zones beyond their physiological or ecological optima (Veron, 1995).

Climate change increases variability of diversity-controlling parameters. Temperature and photosynthetically active irradiation are key determinants of coral distribution and many future climate projections suggest physiologically unsustainable changes (Sheppard, 2003; Donner et al., 2005; vanHooidonk et al., 2013; Cacciapaglia and vanWoesik, 2015). This may alter geographic distributions of many coral species through increased frequency and severity of mortality (Jackson, 2001; Sheppard, 2003; Donner et al., 2005; Cacciapaglia and vanWoesik, 2015; Hughes et al., 2017a,b), retarded regeneration (Osborne et al., 2017), or range extension (Precht and Aronson, 2004; Yamano et al., 2011). Dramatic changes in community patterns have already been observed (Harii et al., 2014; Hughes et al., 2017a). In the Caribbean, marginal reef areas like Florida suffered severe reduction of their most important frame builders *Acropora* and *Orbicella* (Jaap et al., 2008). The Persian/Arabian Gulf (PAG) is another marginal sea where coral cover has precipitously declined concomitant with increased disturbances (Riegl, 1999; Purkis and Riegl, 2005; Burt et al., 2011; Bauman et al., 2013; Riegl and Purkis, 2015; Bento et al., 2016) that changed population and community dynamics (Riegl and Purkis, 2015). Due to its shallow nature (maximum depth 90 m) and high-latitude position (24–30°N) within an area of rapid temperature increase (Hoegh-Guldberg et al., 2014), PAG is well-suited to explore effects of climate change and other human impacts on the demographics, and thus future persistence, of corals (Sheppard et al., 2010; Burt et al., 2011; Purkis et al., 2011; Riegl and Purkis, 2012; Bauman et al., 2013).

Coral community dynamics related to disturbance has changed in southeastern PAG. Pre-1996, disturbances due to unusual heat or cold recurred ∼15–20 years (Riegl, 1999; Riegl and Purkis, 2009, 2012) with coral mortality ∼50 but >90% of all *Acropora* dying. This disturbance frequency and severity was apparently typical for most of the Holocene until the closely-spaced events of 1996 and 1998 (Riegl and Purkis, 2009, 2012). From 1998–2010 and from 2012–2017, moderate disturbances recurred every 5 years, again preferentially killing *Acropora*, with ∼10% overall coral mortality. Closely-spaced disturbances, such as, in 1996/8, 2010/11/12, caused annual or biennial severe mortality with no intermittent regeneration possible due to short spacing of successive events. Coral mortality of ∼20–50% and *Acropora* mortality of ∼90% were typical (Riegl, 1999; Burt et al., 2008, 2011; Riegl and Purkis, 2012, 2015).

These phases of disturbance-spacing are reflected in coral communities, due to species-specific differences in mortality. Coral cover declined across PAG since 1996/1998 (**Figures 1A,B**) and a progression in dominance from *Acropora* to *Porites* to merulinids (where summed merulinid cover exceeded that of *Porites*, **Figure 1C**) with increased disturbance-frequency has been recorded (Riegl and Purkis, 2015).

The disturbance-mediated change in community composition along the time-axis (Riegl and Purkis, 2015) resembles the partitioning of coral communities along a geographical gradient of increasing environmental stress across southern PAG (Sheppard, 1988). With more heat and salinity, branching genera (*Stylophora* and *Acropora*) are generally replaced by columnar massives (*Porites harrisoni*) and, in the more extreme habitats primarily merulinids. Since climate warming may cause an expansion of high salinity and high temperature regimes in PAG, more habitat may become marginal and therefore become characterized by higher cover of stress-adapted corals. In turn, less-tolerant species from the assemblages may eventually disappear from the entire region.

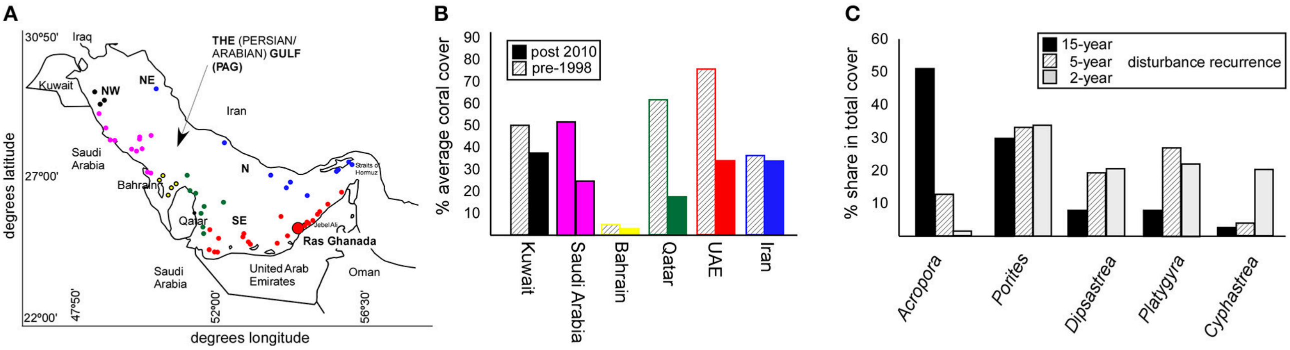


FIGURE 1 | Effects of temperature-related disturbances (bleaching events) on coral cover and coral community structure across PAG. **(A)** Map of the Persian/Arabian Gulf (PAG). Colored dots show reef locations that were used to derive coral cover trends shown in **(B)** Coral cover changes from the period with the least known disturbances preceding the 1996/8 first double-bleaching event, to after the severe 2010/11/12 disturbances. Color of bars corresponds to color code of reef locations in panel **A**. **(C)** Each disturbance phase (15-year disturbance spacing; 1–2 year disturbance spacing, 5-year disturbance spacing) is reflected in community structure at a monitoring site at Ras Ghanada, Abu Dhabi.

While patterns of species attenuation with increased environmental stress have been described (Kayanne et al., 2002; Harii et al., 2014), more details of associated processes, physiological and especially demographic, are needed (Pratchett et al., 2017). To examine the amount of plasticity among species, and the local or global loss of species that cannot persist in changing environments, it is important to understand which coral life-history stage may be most susceptible to changes in survival probability. The present study explores changes in demographics of the most common reef corals in PAG (Sheppard and Sheppard, 1993; Riegl, 1999) over the last decade. The five most common reef-coral species in southeastern PAG (*Acropora downingi*, *P. harrisoni*, *Dipsastrea pallida*, *Platygyra lamellina*, *Cyphastrea microphthalma*) were selected for a 10-year monitoring time-series, in which size-class specific survival, growth, shrinkage due to partial tissue loss, as well as estimated fertility and connectivity were quantified. With thus parameterized transition matrices, population trajectories were forecast. The connectivity across the region was quantified with an oceanographic model that allowed tracking of theoretical coral larvae release from the region. Subsequently a metapopulation matrix model was developed to evaluate changes in connectivity and meta-population persistence caused by changes in demographic parameters of the corals caused by environmental (here: temperature) stress. Overall, the study seeks to demonstrate whether temperature-driven modifications in survival and growth probabilities of individual species (Riegl and Purkis, 2015) will be sufficient to cause shifts in population structure (colony size distribution), resulting in altered fertility, connectivity, and changed species composition in communities.

METHODS

Environmental Conditions and Coral Condition

To understand the distribution of coral communities under different PAG environmental regimes, coral assemblages were assessed by photo-transects at various reefs in Qatar (Fasht el Hurabi, Khor al Odaid, Ras Rakan, Halul) and the United Arab Emirates (UAE) (Ras Ghanada, Makasseb, Yasat Islands, Delma, Arzanah, Das). These data, along with data from published literature (Purser, 1973; Sheppard, 1988; Fatemi and Shokri, 2001; Rezai et al., 2004, 2010; Purkis and Riegl, 2005; Aramco, 2007; Burt et al., 2011, 2013; Kavousi et al., 2011; Foster et al., 2012; Riegl and Purkis, 2012; Bauman et al., 2013, 2014; Mohammadizadeh et al., 2013; Grizzle et al., 2016; Shuail et al., 2016), were used to produce **Figure 1**.

Temperature is among the most obvious drivers in latitudinal patterns of zooxanthellate reef-coral species (Veron, 1995) and a key driver of coral bleaching, which causes variable coral mortality among species (Loya et al., 2001; vanWoesik et al., 2011). Water temperatures were continuously recorded from 2014 to 2017 at Ras Ghanada at 6 m water depth (high-tide) in Abu Dhabi, UAE using *in-situ* loggers (VEMCO Minilog II and HOBO Temp II). A longer-term air-temperature dataset of daily means, maxima and minima from Sharjah airport (since 1944, continuous data since 1978), situated 98 km away from the coral monitoring site was also obtained (klimexp.kmnl.nl). For the 4 years of continuous data recording on the reef, daily means, maxima and minima were regressed against the Sharjah air-temperature dataset. Since the coral monitoring site was shallow and Gulf water temperatures are notoriously responsive to air temperatures (review in Riegl and Purkis, 2012; Riegl et al., 2015), close coincidence was expected. Analyses of relationships between temperature and mortality concentrated on mean conditions, rather than extremes in the dataset, since *in-situ* water-temperature recordings only recorded a recovery period and the last disturbance. While means (monthly, seasonally, annually) of air and water temperature can be expected to be robustly correlated, this is not necessarily the case with extremes and variance. Since several hours are required for even a shallow marine water body to equilibrate with air temperatures, we decided that inclusion

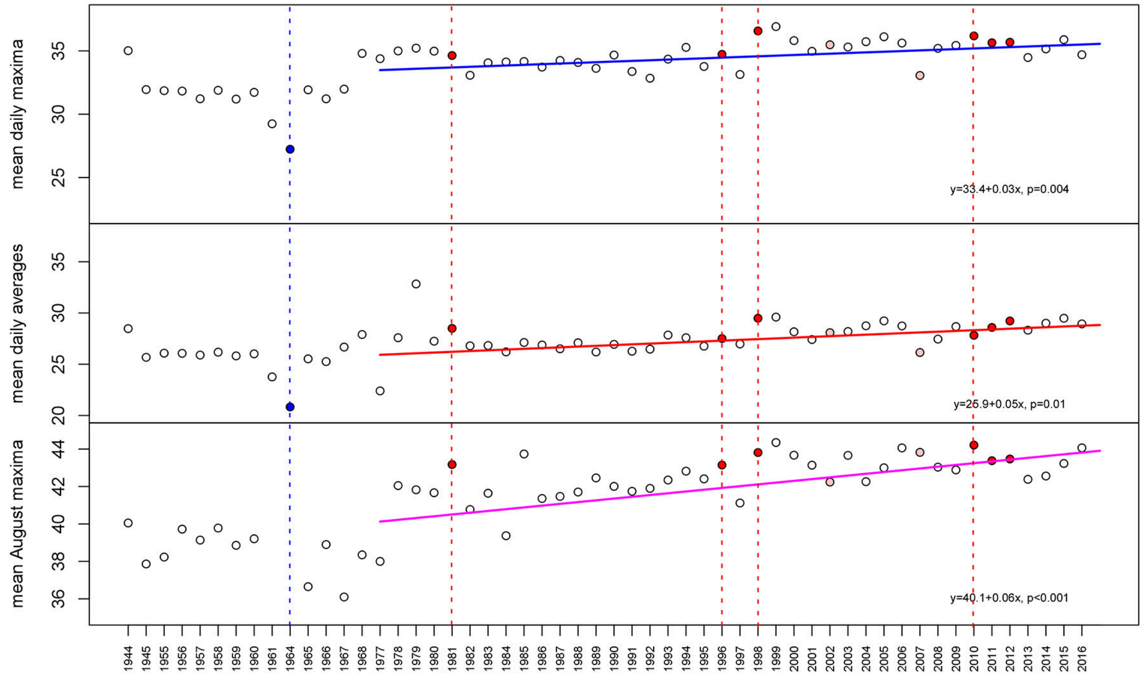


FIGURE 2 | Air temperatures at Sharjah airport, 97 km from the monitoring site (correlation of air temperatures and water temperatures at the monitoring site $R^2 = 0.88$). It is clearly visible that over the measured period (complete data since 1977, therefore regressions begin in 1977) temperature stress indicators, especially mean daily maxima in August, the bleaching month, have steadily increased. Known local bleaching and mass coral mortality events shown by vertical red broken line and red dot if unusual heat was implicated, blue if unusual cold was implicated (only 1964) in coral mortality events. The high temperatures in 1985 and 1999 were not identified as significant bleaching events primarily because they had been preceded by mass coral mortality that had left few corals to be impacted.

of extremes and variance of air temperature as proxy for the corals' environment might have introduced spurious results (**Figure 2**).

The preferential distribution of PAG corals with regards to environmental conditions such as preferred depth, salinity, and average temperature ranges was determined from our own samples and information in the literature (Sheppard, 1988; Sheppard and Sheppard, 1993; Riegl, 1999; Riegl and Purkis, 2012). The naturally occurring gradients in these conditions roughly follow from most benign conditions on offshore reefs, to more stressful conditions on inshore reefs, to the most stressful conditions in embayments and lagoons such as, in the Gulf of Salwah or the Abu Dhabi lagoons (Purser, 1973; Sheppard and Sheppard, 1993) and are generalized in **Figure 3**.

Matrix-Based Derivation of Coral Population Dynamics

Coral population dynamics were monitored continuously at the same reef sites in southern PAG at Ras Ghanada (Abu Dhabi, UAE) over the last 10 years. Data exist from 1996 onward, but between 2007 and 2017, at two sites, 40 phototransects consisting of overlapping 0.75 × 5 m photos, were placed haphazardly within 50 m of GPS-defined points three times per year. Merged images were re-gridded to unit pixel-size (1 pixel = 1 mm^2), corals were identified, outlines were digitized and assigned a unique color. For the purpose of colony counts, any freestanding coral colonies or parts thereof with living tissue were considered individuals (Bauman et al., 2013), a definition allowing to include partial tissue mortality as mechanism of fission and asexual reproduction. Coral areas were measured as horizontally projected surface area within five size bins defined by radius: size class 1 (=SC1, recruits and very young corals), SC2 (young corals), SC3 (corals entering sexual maturity above a given puberty size, however, variability can exist in minimum size at puberty; Soong, 1993), SC4 (large corals), and SC5 (very large corals = relatively rare). Size-classes are justified by life-history traits from literature (citations in Riegl et al., 2012b). The five most common species (*A. downingi*, *P. harrisoni*, *D. pallida*, *P. lamellina*, *C. microphthalma*) with the highest proportional cover in the community were chosen for detailed investigation. Diameters defining SCs differed among species (*A. downingi*: <10, 10.1–50, 50.1–90, 90.1–120, >120 m; *P. harrisoni*: <5, 5.1–25, 25.1–45, 45.1–65, >65 cm; *D. pallida*: <2, 2.1–6, 6.1–10, 10.1–14, >14 m; *P. lamellina*: <3, 3.1–6, 6.1–12, 12.1–24, >24 m; *C. microphthalma*: <3, 3.1–6, 6.1–12, 12.1–24, >24 cm). To avoid excluding the largest corals, those that were truncated at edges of the transect image were included if their diameter or projected area within transects were sufficient to placed them in SC3 or SC4. SC5 corals were rare and were counted by 30 min roving diver surveys. Small truncated corals (i.e., that only partially fell within the phototransect) were ignored since inclusion might have artificially bolstered smaller size-classes than the truncated corals actually belonged to. Since numbers of recruits varied and showed a clumped distribution (see also

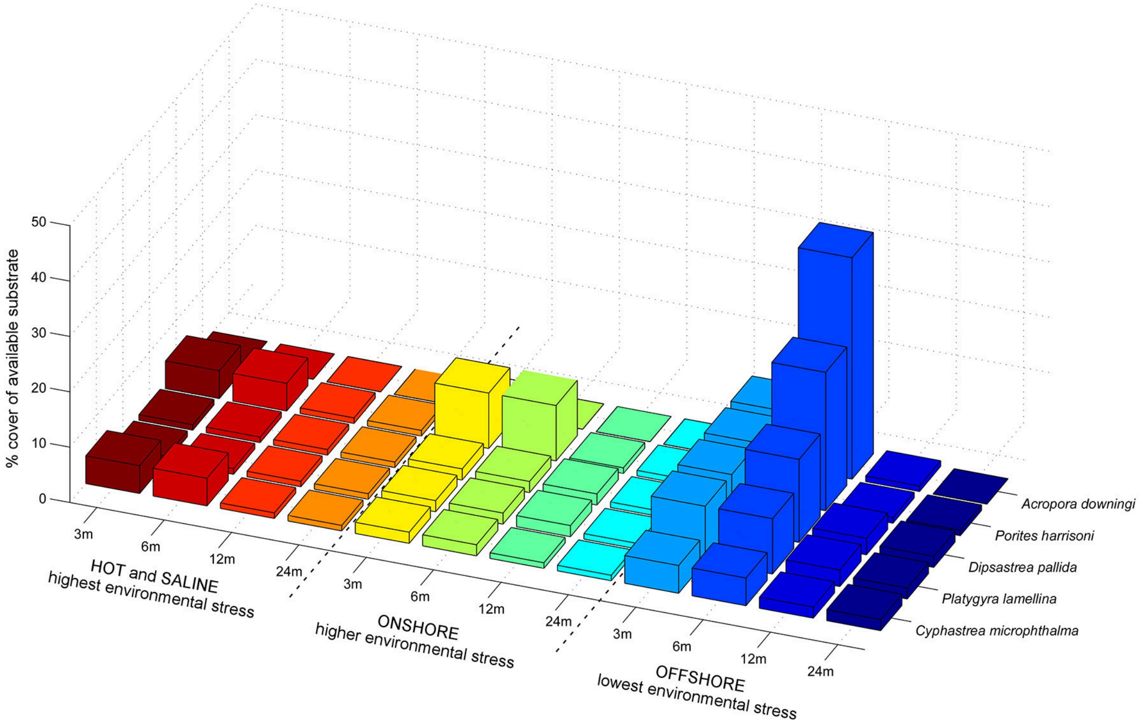


FIGURE 3 | Preferential habitat distribution of the evaluated species in PAG. The gradient of environmental quality from coral-friendly to harsh, goes from right to left. Temperatures are lowest and most equitable on offshore reefs (Riegl and Purkis, 2012). Marked changes are observed in the occurrence and dominance of species, which suggests that similar changes may be expected if environments change over time. "Offshore" environments are typical of the numerous offshore islands in the Gulf and coral communities situated several km from the mainland shoreline in well-flushed areas (such as, the monitoring site at Ras Ghanada). "Onshore" environments are found near the mainland shore, for example in tidal passes in Abu Dhabi or Qatar, "Hot and saline" environments are found for example within the lagoons behind the Abu Dhabi barrier islands, entrances to Qatar's Khor al Odaid or the Gulf of Salwah.

Bauman et al., 2011, 2014) and recruits were often found close to larger corals, potential confusion existed with asexual propagules. Due to the difficulty of obtaining consistent and defensible counts of sexual recruits, this size-class was included in a larger SC1 (of, depending on species, 2–10 cm diameter), which also included many asexual recruits (i.e., coral fragments).

Two distinct periods existed with regards to disturbances during the 10-year monitoring period. A sequence of strong disturbances occurred in 2010/11/12 with coral bleaching and disease outbreaks. This period was a discrete pulse of heat-related stress that had clearly visible effects on coral populations. Thus, a transition matrix (the severe disturbance = SD model) was created for this period. The period from 2007–2010 and from 2013–2017 was characterized by the absence of severe stress with only moderate bleaching in 2007, but no mortality. Thus, a transition matrix (the moderate disturbance = MD model) was created for this period. This was done using Wood's method (Caswell, 2001), essentially a linear optimization approach, on the sequence of size-class distributions in population vectors that contained primarily survival, growth, and shrinkage probabilities. These size-class transition models were verified by back-testing in model runs that began by multiplying the transition matrices by the first (oldest) monitoring population vector that had not been used when solving for the matrix, running for as many time-steps as available from the monitoring effort (max. $N = 19$), and comparing results (Riegl and Purkis, 2015; Zhao et al., 2016). Several possible transition models could be solved, as defined by constraint matrices that define matrix positions into which values are optimized. The one with lowest RMS (root-mean-squared) error of hindcast vs. the observed vectors was chosen. Matrices are shown in this paper as life-cycle graphs with bubble-sizes in each SC scaled to proportional contribution to the right eigenvector corresponding to the dominant eigenvalue (**Figure 4**). In matrix models, a theoretical stable size-class distribution is expressed by the right eigenvector and the corresponding eigenvalue is akin to a population's asymptotic growth rate (if >1 the population will grow; Caswell, 2001). Note must be taken that stable size-class distribution can best be reached in a closed population (recruits are exclusively derived from within the modeled population) and only then is the dominant eigenvalue an adequate approximation of population growth rate.

The matrices solved from the undisturbed period could be compared to those of the disturbed period as a Life Table Response Experiment (LTRE; Caswell, 2001) which allowed exploration of the influences of changes in life-stages (i.e., survival/growth/shrinkage probabilities of individual SCs) on the eigenvalues (**Figure 5**).

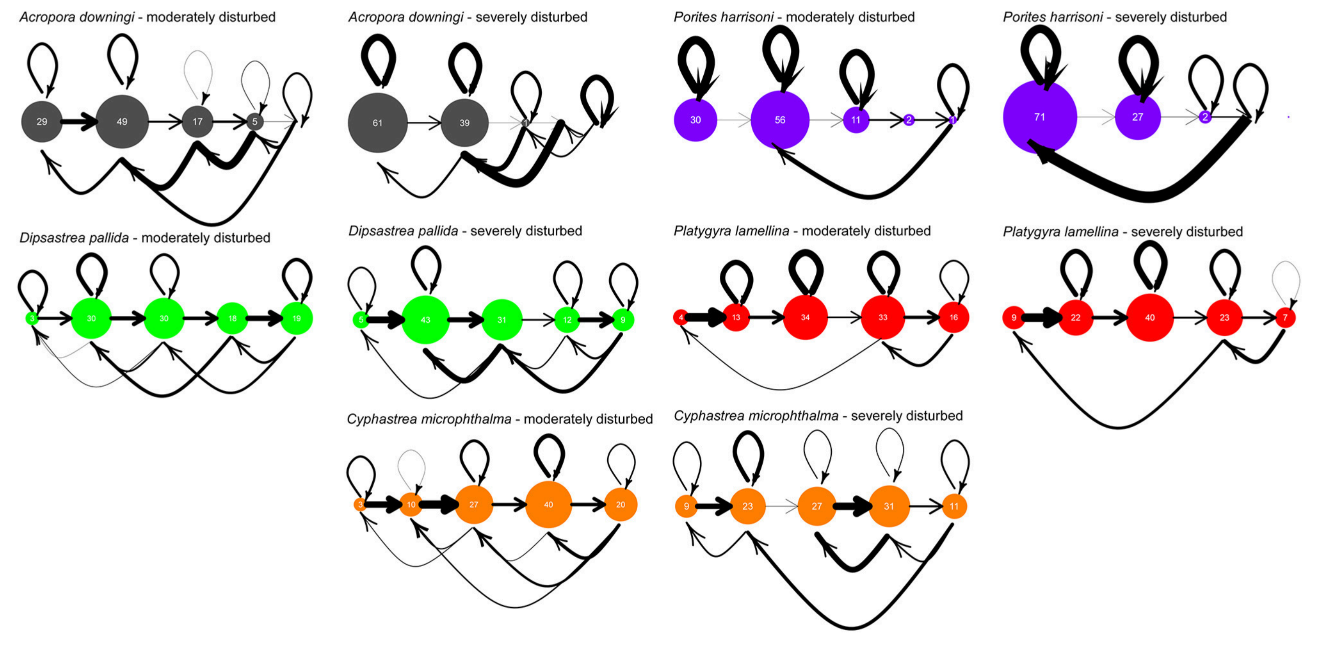


FIGURE 4 | Life-cycle graphs of the evaluated species, based on 10 years of monitoring at Ras Ghanada, Abu Dhabi. Bubble size is relative to proportional frequency of size class in the eigenvector corresponding to the dominant eigenvalue of the matrix, i.e., the theoretical expected size distribution. Closed populations will tend to converge onto this distribution and it is therefore of theoretical interest. The thickness of arrows is related to the value of transition likelihood—bold arrows are values close to 1, the thinner the arrow, the closer to 0 (life-stage transitions range 0–1, i.e., the proportion of individuals transiting between stages).

To estimate fertility (i.e., production of gametes), data from Bauman et al. (2011), Howells et al. (2016), both from PAG reefs, and Shlesinger et al. (1998) from the Red Sea, were used for estimation of number of oocytes per polyp or mesentery. The following values.cm^{-2} were assigned: 12 polyps * 14 oocytes.cm^{-2} in *A. downingi*, 60 polyps (30 female) * 10 oocytes.cm^{-2} in *P. harrisoni* (this species is gonochoric with unknown sex ratio in the examined population, thus a ratio of 1:1 was assumed), 1 polyp * 700 oocytes.cm^{-2} in *D. pallida*, 15 polyps * 78 oocytes.cm^{-2} in *C. microphthalma*, and 20 mesenteries * 14 oocytes.cm^{-2} in *Platygyra daedalea*. Fecundity calculated as number of polyps/mesentaries.cm^{-2} * number of oocytes per polyp/mesentery * projected surface area of colony, expressed as "standard fecundity," which was the summed oocyte output of 100 colonies apportioned into observed fertile size classes (SC3 through SC5). This process accounted for size-dependency of life-processes, especially fecundity (Hughes et al., 2000). A space cover of "1" was assigned to 100 colonies (see above). Disturbances reduce space cover and to obtain per-spatial-unit reproductive output, "per unit" fecundity was reduced by multiplication of "standard fecundity" by decline in space cover. A given fecundity value (for example, 1,000 oocytes in 100 corals with a cover-value 1) decreased with availability of fewer individuals and thus less reproductive surface-area (example: 1,000 oocytes in 100 corals * 0.5 * 0.5, if overall cover was halved and cover of the fertile SCs was also halved). See also Riegl and Purkis (2015). These values were used for **Figure 6**. All corals treated in this paper are broadcast spawners (Shlesinger et al., 1998; Kongjandtre et al., 2010; Bauman et al., 2011).

Theoretical (Matrix-Based) Connectivity Considerations

Metapopulation models allowed quantification of the effects of connectivity and disturbance (the parameters to which the model had highest sensitivity) into a single index called "connectivity requirement," which refers to the required recruit flow among sub-populations to maintain a growing trajectory of the meta-population. Models were created separately for all five species, and consisted of a combined matrix of several sub-matrices (variably MD, SD) with a connectivity component and added local recruitment (values >1 in SC4 and SC5) in the most upstream population (**Figure 7**). Using a variable combination of the known matrices (LD-matrix upstream, MD-matrix downstream) uncorrelated fates across metapopulation, and correlated fates across the metapopulation (exclusively MD- or SD matrices up- and downstream) and climate change effects (reduced connectivity; Figueiredo et al., 2014), were examined.

The metapopulation matrix consisted of four connected subpopulations (transition matrices, inset **Figure 7**) with either one-way (P1➔P2➔P3➔P4) or two-way connectivity in populations 3 and 4 (P1➔P2➔P3⟷P4). This metapopulation structure was suggested by the oceanographic connectivity model (see below). Step-wise, 10-fold decrease of local recruitment (added as a fractional multiplier) in subpopulation 1 and in connectivity between the remaining subpopulations, were examined. Outcome of the models was a quantification of "connectivity requirement," which is a multiplier of the reproducing SC4-5, determining how many successful recruits each individual of an upstream subpopulation must establish in

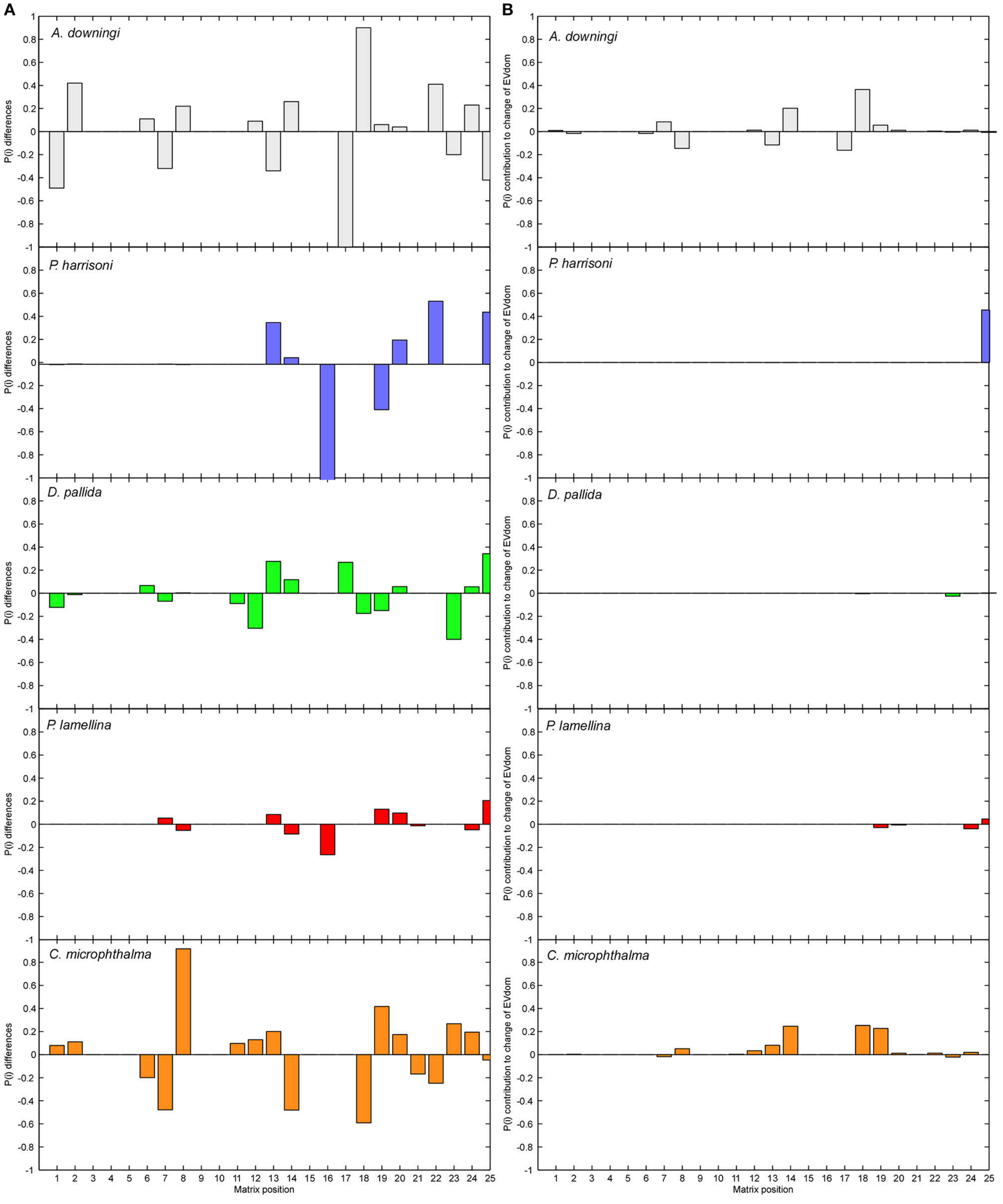


FIGURE 5 | Treatment of disturbances as LTRE (Life Table Response Experiment). Column **(A)** shows the difference in matrix positions between the MD and SD matrices Column **(B)** shows the influence of each of these changes on the dominant eigenvalue. Matrices were expressed in vector form (matrix column 1 is vector positions 1–5, matrix column 2 is vector positions 6–10, and so on until vector position 25). In **(A)** the contribution of vector position 16 (transition from SC4 into SC1, largely shrinkage into small tissue fragments) is truncated in *P. harrisoni* (true value −5).

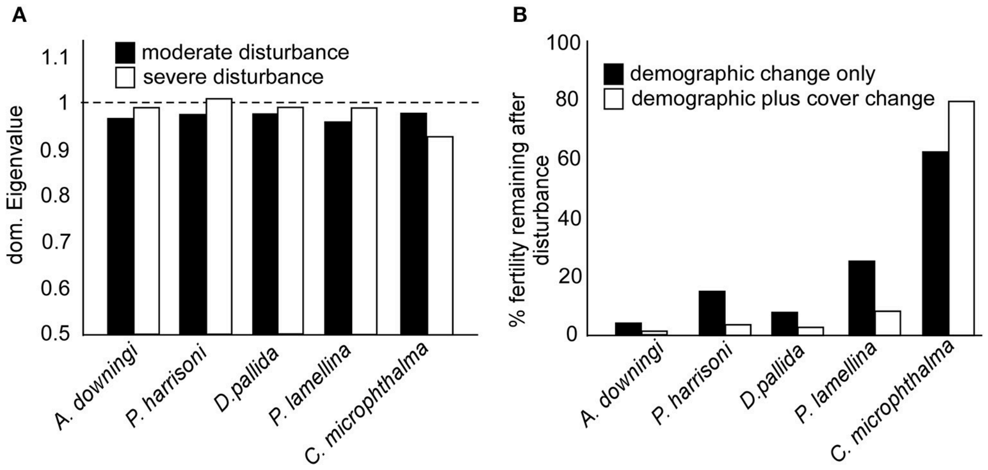


FIGURE 6 | **(A)** Asymptotic rates of population increase (dominant eigenvalues) of moderate disturbance (black bars) and severe disturbance (white bars) size-transition models. A value of 1 (broken line) is needed for population stability, smaller values indicate a shrinking population. **(B)** Changes in Standard fecundity (expressed as oocytes per 100 colonies) prior to, and after, the significant coral cover reduction of 2011–2013. Changed size distributions reduce fecundity (black bars), which is exacerbated by reduced overall coral cover (white bars). "standard fecundity" is relative to 100 fertile (SC3-5) colonies, standard fecundity was multiplied by the proportion of space-cover (planar coral area) remaining after the disturbances and the proportion of corals in SC3-5 (see section Materials and Methods).

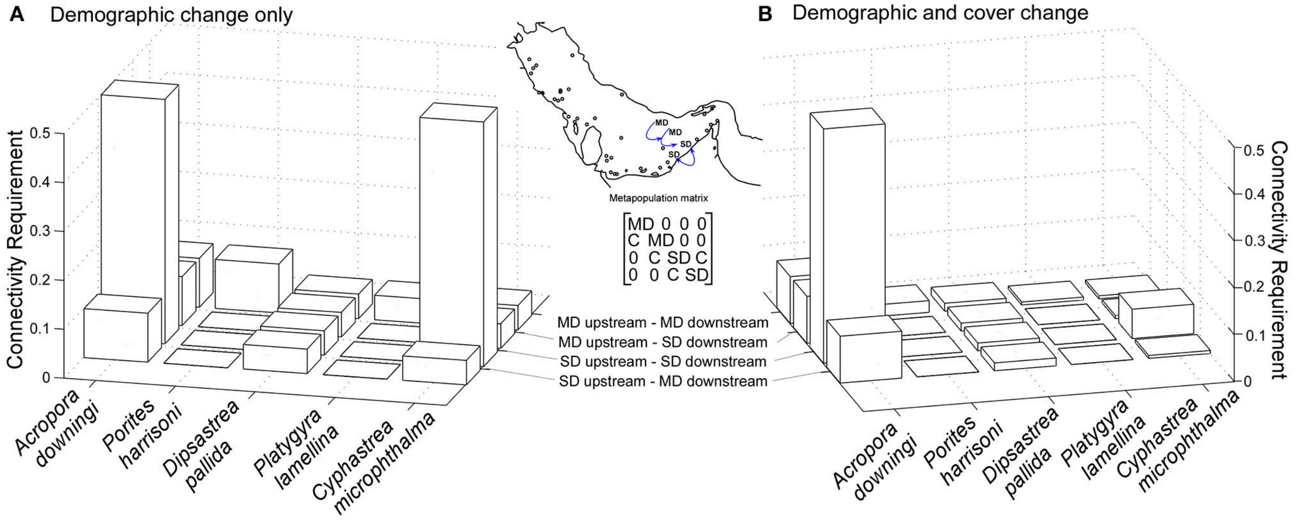


FIGURE 7 | Minimum recruitment requirement is a multiplier of the existing recruitment by number of propagules acquired per colony in connected population. Connectivity factor of 0.5 = one offspring acquired from 50% of all SC4 and SC5 in a connected sub-population. Inter-specific plasticity exists in the reaction to disturbance in general, and the correlation of disturbance over the metapopulation. Note that this requirement will be more easily fulfilled in *C. microphthalma*, since its relative cover increases in the disturbed community, while that of *A. downingi* is drastically reduced. **(A)** is calculated as gamete production times proportional frequency of corals in fertile size class **(B)** as gamete production times proportional frequency of corals in fertile size class times remaining cover after disturbance. Inset: structure of metapopulation matrix illustrated with two medium disturbance (MD) populations upstream and two severe disturbance (SD) downstream. C = connectivity.

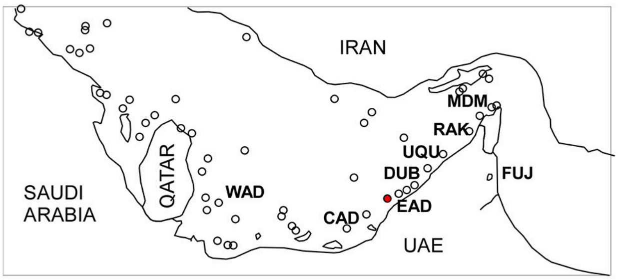
the downstream subpopulation for the entire metapopulation to maintain a positive asymptotic population growth rate (= dominant eigenvalue of metapopulation matrix > 1). The correlation of disturbance across the metapopulation could be controlled by whether only few, or all connected populations switched from MD to SD matrices (see four scenarios in **Figure 7**).

Oceanographic Model of Connectivity

To model larvae transport and to validate estimates of connectivity and recruitment, an oceanographic model for the area 47°E to 59°E longitude and 21°N to 31.5°N latitude was developed (Cavalcante et al., 2016). Bathymetry used a 2 km Cartesian grid offshore and 50 m in the nearshore region. Bathymetry data were from RDA (http://dss.ucar.edu) based at

CISL Research Data Archive; datum value of MSL+1 m was selected. MIKE 21, a two-dimensional depth-averaged Eulerian time integration scheme was then utilized to compute current velocities in the model domain (DHI Water and Environment, 2001; Cox, 2003; Kankara et al., 2007; Zhao et al., 2014). A time step of 60 s was selected during the calibration and validation period (March 2010). The forward model (27 April to 19 June 2010) was run based on the output produced from the velocity field during the warm up period (12–27 April 2010), meaning that the initial velocity field and initial boundary forcing were not initiated in "cold-start" mode. Zonal and meridional wind components, pressure, and tidal elevations along the offshore boundary at the 59°E longitude were introduced. Model runs used following coefficients: wind friction factor (0.001255), Manning's number (38 $m^{1/3}$ s^{-1}) and Eddy viscosity coefficient (Smagorinsky formulation) (0.28). Wind components were 1-h averages of effective neutral wind at a height of 10 m and within grid spacing of 0.25° in both zonal and meridional wind directions. The offshore boundary location at the 59°E longitude of the model domain was forced by tidal elevations. Predicted tidal elevations were linearly interpolated to each grid at the east boundary of the model and applied. The large-scale current patterns observed in this model corresponded well with those from published models (Thoppil and Hogan, 2010; Yao and Johns, 2010; Cavalcante et al., 2016) but showed higher resolution in the nearshore areas, which is important for modeling larval trajectories on the many inshore reefs.

To simulate larval transport and retention, the particle tracking module of MIKE 21 was used (DHI Water and Environment, 2001), simulating transport and fate of suspended particles using a Lagrangian random-walk technique. Larval traits important for dispersal (larval weight, spawn number, and pelagic larval duration) as well as spawning period and spawning date were averaged from literature (Connolly and Baird, 2010). Larval size was taken as 0.04 mg, with one modeled particle deemed equivalent to 100 larvae. The simulation period for particle tracking (i.e., pelagic larval dispersal) was taken as 45 days; after this period the majority of coral larvae are considered to have settled or to no longer be competent. Larvae were defined as passive (no swimming), neutrally buoyant, particles that followed the prevailing flow. 24 release sites across eight source areas were modeled (**Figure 8**). Release was started at peak high tide at full moon on 27 April (8 a.m.) and continued for 8 days, finishing on 4 May 2010 (23.00), as was observed to be peak spawning period in the study area (Bauman et al., 2011; Howells et al., 2014). Release periods occurred twice a day following the 2 high tides, covering 16 tidal cycles, again comparable to field observations. Within each release period 1,000 particles were released from each site, resulting in 1.6 million larvae being released across the time period. Modeling of larval dispersal was then tracked for 45 days, from 4 May to 18 June. Dispersal and settlement across sites was plotted at 10 day time steps, with larvae tracked hourly. The number of larvae settling into each site was assessed at day 1, day 15, day 30, and day 45. Data were expressed as a connectivity matrix showing the percentage of larval flow among sites.



larvae settle in

larvae originate in	FUJ	MDM	RAK	UQU	DUB	EAD	CAD	WAD
FUJ	4.9	2.4						
MDM	7.6	10.3						
RAK			35.6	1.4				
UQU			6.61	35.9	1.9			
DUB				4.3	17.1			
EAD						21.3	2.3	
CAD						3.2	13.4	
WAD								36.1

FIGURE 8 | Percentage of larvae particles recruiting in source areas (the remainder to 100% died) and larval contribution from surrounding regions in eight source areas of PAG. Western Abu Dhabi (WAD), Central Abu Dhabi (CAD), Eastern Abu Dhabi (EAD), Dubai (Dub), Umm Al Quwain (UQu), Ras Al Khaimah (RAK), Musandam (Mdm), Fujairah (Fuj). Number in brackets is number of particles retained in source area. 1,600,000 particles released at each site. Small circles represent reef areas.

RESULTS

Environmental and Coral Condition

Due to the shallow depth (6 m), water temperatures at Ras Ghanada correlated highly with air temperatures at Sharjah, 96 km distant (mean daily maxima from 2013 to 2016: Pearson's Product-Moment Correlation 0.88, CI: 0.86–0.89, $t = 48.25$, df $= 654$, $p < 0.001$). Therefore, air temperatures could be used as proxy for shallow marine temperature conditions. Since 1944, annual mean daily maxima and annual mean daily averages increased (linear models, **Figure 1**). PAG bleaching events coincide with high temperatures in August (Riegl and Purkis, 2015) and the mean August maxima increased more than annual means (**Figure 2**). Mean August maximum air temperatures rose from 1977–2017 (the period with a continuous record) by 2.34°C. PAG bleaching thresholds were at 35.7°C water temperature for 1 day and 3 weeks of daily mean temperatures at 35°C (Riegl et al., 2011) suggesting a steady increase of hot days at Sharjah (45°C daily max. air temperature correlates with ∼35°C daily max. water temperature at Ras Ghanada) will increase the likelihood of bleaching and result in a shorter temporal spacing between bleaching events on the Ras Ghanada reef.

Based on temperature and monitoring records, two distinct phases exist in coral population monitoring data. A severely disturbed period (SD) included the triple bleaching and mortality events of 2010/11/12, that were sandwiched between a prior

(2008–2010) and subsequent (2013–2017) moderately disturbed (MD) period. During the latter only some disease and low-level bleaching (paling) without drastic mortality occurred and not all species were affected. In August 2017, another bleaching event was recorded.

Matrix-Based Derivation of Coral Population Dynamics

For the five most common species at Ras Ghanada (*A. downingi*, *P. harrisoni*, *D. pallida*, *P. lamellina*, *C. microphthalma*) transition matrices for five life-stages during SD and MD periods were solved from observed size distributions. These five species showed clear distributional peaks with regards to certain environments, being the characteristic species of stress-specific communities. While they can co-occur, dominance patterns differed among environments (**Figure 3**).

Correspondingly, parameters of the matrix models, as well as model structure, differed among species and among the two periods with different disturbance frequency (SD, MD; **Figure 4**).

Impacts of severe disturbances on life-dynamics, when comparing SD and MD matrices, were most marked in *A. downingi* and *P. harrisoni*. In both species, growth into the largest SC5 ceased, leading to eventual loss of this size class (no growth into SC5, no loop within, no shrinkage from SC5; **Figure 4**). In *A. downingi*, loops (i.e., retention within size-class = absence of growth) became much more important in the SD period and in *A. downingi* and *P. harrisoni* shrinkage strongly increased. This resulted in SC1 replacing SC2 as the most common SC at theoretical stable-SC distribution in both species (expressed by bubble-sizes in **Figure 4**). In the other species, no SC were lost, but growth transitions also decreased and shrinkages increased with the effect of stronger contribution to the smaller SC. In *D. pallida*, population size-distribution was expected to change so that smaller SC (SC3➔SC2) would predominate at the theoretical stable SC distribution. *P. lamellina* and *C. microphthalma* only exhibited some shrinkage with increases in SC1 and 2 with SC3 (*P. lamellina*) and SC4 (*C. microphthalma*) remaining predominant.

Matrices from moderately and severely disturbed periods were compared as a Life Table Response Experiment (LTRE, Caswell, 2001). The results highlight the differences between the MD and SD matrices (**Figure 5A**) and the effects of changes on the dominant eigenvalue (**Figure 5B**), which is equivalent to the population's asymptotic growth rate. The biggest changes in transition probabilities were in *A. downingi* and *P. harrisoni*. The strongest overall changes in any species were the very strong shrinkage of large colonies (SC4) into small fragments (SC1) in *P. harrisoni*. In *D. pallida* and *P. daedalea*, the smallest changes in transition probabilities of all species were observed, with small but equitable contributions to eigenvalue change across the SCs. In *C. microphthalma* relatively larger changes in transition probabilities were seen, and changes in the growth probabilities of the largest size classes had the strongest influence on the eigenvalue. In all species, except *A. downingi*, changes in survival and shrinkage in SC5 most influenced the eigenvalue. In *A. downingi* and *C. microphthalma*, it was changes in SC4.

Transition matrices of all species had been solved without explicit assumption of local recruitment, and dominant eigenvalues were mostly <1 (**Figure 6A**). This suggested shrinking local populations and a need for connectivity to other populations for larvae import (and export). The slight increase in asymptotic growth rate in the SD matrices of four species can be traced to shrinkage. Shrinkage due to partial tissue loss will increase the smallest SC (i.e., the "recruits"), because many small tissue fragments remain after partial colony mortality. This is a form of asexual reproduction that can provide a transient boost to population numbers, but comes at the cost of reduction of the large SC and therefore overall population (sexual) fecundity (**Figure 6**).

Severe disturbances (SD matrices) resulted in more of the populations being in small SC due to partial or total mortality of colonies, with concomitant loss of large SC and decline of total tissue-covered area. Since population fecundity declines exponentially with coral size, the combination of loss in large corals (demographic change in **Figure 6B**) and overall tissue covered area (demographic plus cover change in **Figure 6B**) translated into significant fertility loss (**Figure 6B**).

Theoretical (Matrix-Based) Connectivity Considerations

Connectivity requirement to keep the dominant eigenvalue of the metapopulation matrix >1 depended heavily on correlation of disturbance across the metapopulation. In the extreme cases where there were either no severe disturbances across the entire metapopulation, or severe disturbances everywhere, the connectivity requirements are shown in **Figure 7**. *P. harrisoni* and, to a lesser degree, *D. pallida* and *P. lamellina* had a higher theoretical connectivity requirement in moderately disturbed conditions, because during severe disturbance, the abundant shrinkage into the smallest size-classes boosted asexual recruitment. This suggests that these three species should be resilient to severe disturbances. Both *C. microphthalma* and *A. downingi* required more connectivity-derived recruitment in severe disturbances, especially when correlated across the metapopulation (SD upstream, SD downstream), *A. downingi* requiring a five-fold increase. In *C. microphthalma,* the lower whole-colony mortality and tissue loss resulted in a lower connectivity requirement when demographic change and cover change were taken into account (**Figure 7B**).

The key demographic effects that could influence the persistence vs. winnowing of species from the community were:

- Severe reduction of large size classes and total populations size due to whole colony mortality (*A. downingi*)
- Reduction of large size classes without reduction of population size due to partial mortality (*P. harrisoni*)
- Reduction of relative cover in community due to loss of colonies and slow regeneration (*A. downingi*)
- Loss of relative population fertility due to loss of most fertile large size classes (all species, least in *C. microphthalma*)

- Severely increased need for connectivity due to loss of local fecundity (*A. downingi*)
- Steep decline in cover causing lower local fertility and thus also connectivity declines (*A. downingi*).

Oceanographic Model of Connectivity

Declining fecundity and increased requirements for connectivity were central issues that could, besides levels of mortality, determine which species would be winnowed from the local fauna. In the oceanographic model, southern PAG showed clear indications of local retention of larvae (**Figure 8**) where between 5 and 36% of all larvae were locally retained in their region of origin. Connectivity between sources was apparent between (i) Dubai, Umm al Quwain and Ras al Khaimah, and (ii) central and eastern Abu Dhabi (**Figure 8**). Connectivity was primarily associated with larvae moving between neighboring subpopulations. Dubai, Umm al Quwain, and Ras al Khaimah sites showed low larval connectivity. From Dubai, 4.6% of larvae moved to Umm al Quwain, 6.61% of larvae released there reached Ras al Khaimah sites. Larval connectivity from west to east was lower. 1.37% of Ras al Khaimah larvae appeared in Umm al Quwain, 1.87% of Umm al Quwain larvae appeared in Dubai. 3.15% of larvae from central Abu Dhabi were apparent in eastern Abu Dhabi, while 2.28% of larvae released in eastern Abu Dhabi moved the opposite way. Western Abu Dhabi seemed isolated from all other sites. There was no larval connection between the adjacent areas of eastern Abu Dhabi and Dubai or Ras Al Khaimah and Hormuz Straits. Most larvae from the Hormuz Straits dispersed into northern Gulf of Oman or Iran.

DISCUSSION

Environmental and Coral Condition

The environmental variable immediately responsible for most coral death in the southeastern PAG is the average August daily maximum temperature, which increased over the past half century. The primary environmental disturbance used in this paper to measure species-specific variance in demographic effects was the first-ever recorded triple bleaching event that occurred in PAG during 2010/11/12 (Riegl and Purkis, 2015). Such bleaching disturbances are predicted to be common from about 2050 onward (Donner et al., 2005; vanHooidonk et al., 2013) and in 2016/17, a double bleaching event has compromised reef health on the hitherto relatively unaffected Great Barrier Reef (Hughes et al., 2017a).

The principle of species winnowing by environmental disturbances is compatible with concepts like "winners and losers" in response to bleaching (Loya et al., 2001; vanWoesik et al., 2011). Concomitant changes in community structure are not merely theoretical expectations but have already been observed in PAG and elsewhere (Kayanne et al., 2002; Purkis and Riegl, 2005; McClanahan et al., 2011; Edmunds et al., 2014; Harii et al., 2014; McClanahan, 2014, among many others) and it has been shown that coral recovery is delayed in a warming ocean (Osborne et al., 2017). Our study demonstrates the primary mechanisms causing delayed recovery, namely reduced population fertility due to tissue death resulting in fewer, and smaller coral colonies (**Figure 6B**). This, in turn, requires more recruitment and more connectivity. The former is difficult to achieve in degraded populations (**Figure 7**), the latter is limited by oceanography (**Figure 8**).

The disappearance of three previously common species, through much of their former distribution in southeastern PAG, supports the results of our study. All were highly susceptible to bleaching (Loya et al., 2001; McClanahan et al., 2011; vanWoesik et al., 2012). *Stylophora pistillata* was zone-forming in Tarut Bay (Coles et al., 1995) and quite common in Abu Dhabi until 2010 (pers.comm.). It has disappeared from most of Saudi Arabia and Abu Dhabi (Coles, pers. comm.), but is present in cooler waters at Iranian islands near Hormuz Straits (Samimi-Namin pers.obs. in Riegl et al., 2012a). *Pocillopora damicornis* was zone-forming at Jana, Saudi Arabia (Vogt, 1995) and present throughout Abu Dhabi. No records exist from Saudi Arabia since 1998 or Abu Dhabi since 2010 but it also still occurs in Iran (Samimi-Namin pers.obs. in Riegl et al., 2012a). *Montipora* spp. (*M. aequituberculata* and *M. circumvallata* listed by Vogt (1993); *M. aequituberculata*, *M. informis,* and *M. spongiosa* listed by F. Benzoni in Riegl et al., 2012a) were common around Qatar until the 1980s (Emara et al., 1985) but are no longer present (Sheppard et al., 2010). The most recent record of this genus comprises three colonies from Kuwait (F. Benzoni in Riegl et al., 2012a). Elsewhere it is only recorded from Iran near Hormuz Straits (Samimi-Namin et al., 2009; and Samimi-Namin in Riegl et al., 2012a).

Matrix-Based Derivation of Coral Population Dynamics

While differential resilience to environmental stresses has been documented, exact demographic mechanisms of persistence or extinction are less clear (but see Edmunds and Elahi, 2007; Edmunds, 2010; Roth et al., 2010; Doropoulos et al., 2015). Dynamics of PAG species, with respect to potential winnowing from the community, fell into two categories. Firstly, those that were immediately affected by environmental disturbance in its first year (2010), and suffered either predominantly whole-colony mortality and some partial mortality (*A. downingi*) or predominantly partial mortality and only little whole-colony mortality (*P. harrisoni*). In both species, populations consisted of markedly smaller corals after disturbance and had changed survival probabilities (**Figure 4**). In *A. downingi*, both average coral size as well as population size shrank, in *P. harrisoni* population size increased due to abundant colony fission, but average colony size shrank. These corals are referred-to as the "shrinkers." The second group consisted of those species that were not affected in the first, but only the second and/or third disturbance, and while affected by partial mortality, it was less dramatic than in the "shrinkers." This group consisted of *D. pallida, P. daedalea, C. microphthalma* (**Figure 4**) and is referred to as the "persisters." Interestingly, temperate corals seem to show different reactions to heating. Populations of temperate, shallow water azooxanthellate corals skewed increasingly toward the larger sizes with heating (Goffredo et al., 2008) or showed no effects at all (Caroselli et al., 2012).

Shrinkage by partial mortality is problematic for reef corals, since smaller colonies tend to have a higher mortality rate (Edmunds, 2010). Since fecundity tends to scale with size (Hughes et al., 2000), it necessarily declines in a population of smaller corals. Consequently, significant losses in fecundity were observed (**Figure 6**). However, while sexual fecundity (fertility) was lost, asexual fecundity increased due to abundant fission into surviving tissue remnants. This survival was most marked in the columnar *P. harrisoni*. Tips of columns tended to survive as isolated ramets, while the areas between columns frequently died (hence the very strong change in the matrix value signifying transition from SC4➔SC1, **Figures 4**, **5**). In *A. downingi*, there was no clear pattern where tissues survived preferentially but regeneration of several ramets, originating from a single parent colony, was frequent. Also the "persisters" formed many new ramets from tissue remnants.

The abundant production of ramets consisting of variably-sized tissue fragments was important in the modeling of population dynamics. Due to the difficulty of correctly identifying small recruits, the smallest size class (SC1) integrated young-of-the-year as well as smaller ramets. This had the effect of raising the population's apparent rate of increase (dominant eigenvalue of the transition matrix; Caswell, 2001; **Figure 6A**) after the disturbances. While at first sight counterintuitive, the large number of ramets can indeed increase the numerical frequency of larger colonies as they grow (unless ramets fuse again into bigger colonies), but at the cost of genetic diversity.

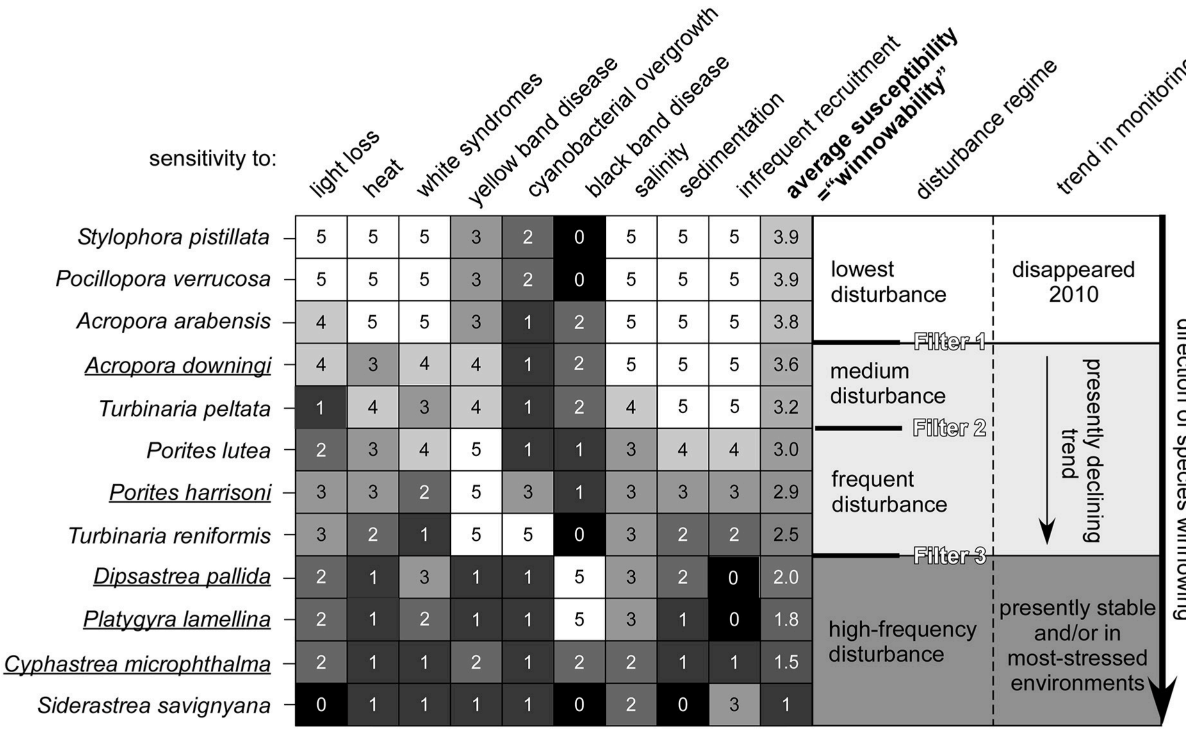
Even if population growth rate was boosted temporarily by the ramets, declined fertility of smaller colonies may have the opposite effect in the long term. Smaller colonies tend to be less fertile (sexually), and metapopulations of shrinking corals may find recruit flow among subpopulations increasingly compromised. Primarily asexually reproducing populations would be, at least temporarily, lost to the metapopulation with the consequence of breaking connectivity ratchets and endangering the persistence of downstream populations, if these depended on imported recruitment. The metapopulation model suggested potentially negative effects on *A. downingi*, a species requiring good connectivity. Shrinking (both numerically and in colony size) populations required help from connected populations and the need for connectivity increased with correlation of disturbance across the metapopulation. Graham and vanWoesik (2013) showed that ramets of some corals (in the family Merulinidae, formerly Faviidae, related to the PAG "persisters"), can remain fertile even if shrunk below puberty-size. If that was also the case in PAG corals, a strong regeneration mechanism would exist, even in the "shrinkers" (especially *P. harrisoni*) since fertility and connectivity might decline less than in model calculations. Also, vanWoesik et al. (2011) found that small (<5 cm, so SC1) *Acropora* fared better than many other corals, at least in the short term, and that fragmentation and survival from remnants was a long-term winning strategy. Thus, shrinking may not be all problematic and might include some defense mechanisms. This suggests that hope may exist for the "shrinkers" but most certainly for the "persisters," even if they should experience partial mortality in bad periods.

Connectivity Considerations

The problems created to PAG corals by declining fecundity would be compounded by a dispersal pattern with strong local retention and connectivity primarily among neighboring sub-populations. Further, if the dominant reproductive mode of the population were to shift, impacts of declining overall fertility could be compounded since brooding corals release fewer larvae into the water column than broadcasting species. In the case of the investigated PAG corals, all were broadcast spawners (Bauman et al., 2011), thus changes in the overall number of larvae available for connectivity here would be a simple function of changes in the fertile coral tissue area. The metapopulation suggests highest connectivity requirement under correlated disturbances, i.e., when neighboring populations are stressed. Tissue mortality in neighboring populations would reduce fertility and thus larvae flow, causing disadvantages especially to populations that are highly self-seeding and the connected downstream populations. The most isolated populations would be winnowed first due to the absence of larval rescue. Highly isolated western Abu Dhabi (**Figure 8**), with higher temperature extremes than eastern Abu Dhabi (Riegl and Purkis, 2012) is home to dense coral growth devoid of *Acropora*, *Monipora*, *Stylophora,* and *Pocillopora* (Foster et al., 2012; Bauman et al., 2013)—the most heat-sensitive coral genera showing whole-colony mortality and, as demonstrated for *A. downingi*, a high connectivity requirement. Species winnowing as envisaged in this paper seems to have already occurred in PAG, certainly helped by its apparent reproductive isolation.

The observed and modeled population dynamics of PAG corals suggested a hierarchy of negative demographic effects by environmental stress from the "shrinkers," where *A. downingi* was worse affected than *P. harrisoni*, to the "persisters." Within the latter, the hierarchy was less clear, but *C. microphthalma* appeared as a particularly robust species with the least fertility loss and least changes in demographic parameters. Based on the knowledge of environmental disturbances and demographic responses, a generalized scheme of the winnowing response in PAG coral communities was developed (**Figure 9**). The differentially strong reaction among species to environmental stressors seems to generate disturbance filters related to the thresholds of resistance of individual species. In the discussion regarding changed coral communities in future seas, a better anticipation of which species are likely to get winnowed at specific environmental filters may be a valuable management tool. Many predictions as to impact severity and positioning of potential refuges exist (Riegl and Piller, 2003; vanHooidonk et al., 2013; Cacciapaglia and vanWoesik, 2015) which will be supported and strengthened by an understanding of the demographic realities (such as, shrinking, persisting, and connectivity) that can make or break a refuge.

Since many environmental stressors are ultimately driven by human societal behavior (Hughes et al., 2017b), demonstration of the filters and the reality of species winnowing that cause loss of diversity in reefs can help to predict the evolutionary price tag that will be associated with the absence of effective conservation or climate action or misguided management approaches. PAG



sensitivity to:	light loss	heat	white syndromes	yellow band disease	cyanobacterial overgrowth	black band disease	salinity	sedimentation	infrequent recruitment	**average susceptibility ="winnowability"**	disturbance regime	trend in monitoring site
Stylophora pistillata	5	5	5	3	2	0	5	5	5	3.9	lowest disturbance	disappeared 2010
Pocillopora verrucosa	5	5	5	3	2	0	5	5	5	3.9		
Acropora arabensis	4	5	5	3	1	2	5	5	5	3.8		
Acropora downingi	4	3	4	4	1	2	5	5	5	3.6	medium disturbance	presently declining trend
Turbinaria peltata	1	4	3	4	1	2	4	5	5	3.2		
Porites lutea	2	3	4	5	1	1	3	4	4	3.0	frequent disturbance	
Porites harrisoni	3	3	2	5	3	1	3	3	3	2.9		
Turbinaria reniformis	3	2	1	5	5	0	3	2	2	2.5		
Dipsastrea pallida	2	1	3	1	1	5	3	2	0	2.0	high-frequency disturbance	presently stable and/or in most-stressed environments
Platygyra lamellina	2	1	2	1	1	5	3	1	0	1.8		
Cyphastrea microphthalma	2	1	1	2	1	2	2	1	1	1.5		
Siderastrea savignyana	0	1	1	1	1	0	2	0	3	1		

FIGURE 9 | Conceptual environmental filters leading to loss of species from PAG coral communities. Dynamics of underlined species was quantified. Values identify strength of mortality response to environmental parameter 5 = strongest, 1 = weakest. These values were derived semi-quantitatively from monitoring and impact observations and literature (Sheppard, 1988; Sheppard and Sheppard, 1993; Riegl, 1999; Foster et al., 2012; Bauman et al., 2013; Riegl and Purkis, 2015).

has witnessed severe loss of coral reefs (Sheppard et al., 2010; Sale et al., 2011). Only swift and decisive management action utilizing information as presented within this paper can help to stabilize the continuously declining quality of the region's coral reefs—its most biodiverse but most imperiled ecosystem.

AUTHOR CONTRIBUTIONS

BR conceptualized the paper and wrote matrix models, GC wrote oceanographic model, SP and AB collected coral data, AB, DF, and SS did meta-analyses. All authors wrote and corrected the manuscript.

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Settlement Patterns of Corals and other Benthos on Reefs with Divergent Environments and Disturbances Histories around the Northeastern Arabian Peninsula

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Larval supply is a principal factor determining the establishment, structure, and diversity of sessile benthic assemblages on coral reefs. Benthic reef communities in north-eastern Arabia have been subject to recurrent disturbances in recent years, and subsequent recovery will be, in part, driven by variation in the supply of available colonists. Using settlement tiles deployed seasonally over 1 year at eight sites encompassing three environmentally divergent regions (southern Arabian Gulf, the Musandam Peninsula in the Strait of Hormuz, and the Sea of Oman) we assessed spatial and seasonal variability in settlement of benthic reef organisms. There was strong spatial variation in composition of new colonists among regions, mainly driven by the high abundance of coralline algae in the Arabian Gulf, colonial ascidians on the Musandam Peninsula and barnacles in the Sea of Oman. Seasonal differences in composition of new colonists were less important than regional differences, with seasonal variation in settlement not consistent among regions. The number of corals settling to the tiles was low compared to those reported for other regions, with mean densities ranging from 0 corals m^{-2} $year^{-1}$ in the Sea of Oman to 30 (± 0.6 SE) and 38 (± 0.5 SE) in Musandam and the Arabian Gulf, respectively. Peak coral settlement abundance in the Gulf occurred in summer and autumn and in Musandam in spring (averaging 82 and 70 settlers m^{-2} $year^{-1}$, respectively, during the peak settlement season). This work provides the first record of large-scale spatial and seasonal patterns of settlement in north-eastern Arabia and provides valuable information on the supply of settlers available to recolonize heavily disturbed reefs in this region. The extremely low rates of coral settlement suggest that these marginal reefs are likely to be extremely slow to recover from on-going and future disturbances.

Keywords: Arabian Peninsula, benthic communities, coral recruits, settlement tiles, seasonality, sessile invertebrates

INTRODUCTION

Coral reefs provide a variety of significant socio-economic benefits to coastal communities (Ferrario et al., 2014; Guannel et al., 2016), however, climate change and increasing local pressures are jeopardizing the future of reefs (Ateweberhan et al., 2013; Bruno, 2013; Spalding and Brown, 2015). Over the past several decades, reefs have been increasingly degraded by overfishing, pollution, sedimentation, disease and coral predator outbreaks (Maina et al., 2013; Riegl et al., 2013; Pollock et al., 2014; Wear and Thurber, 2015; Mumby, 2016). These stressors have resulted in an estimated loss of up to 50% of coral cover from many reefs in the past several decades (De'ath et al., 2012; Hughes et al., 2017), with a third of reef-building coral species now considered at risk of extinction (Carpenter et al., 2008).

Disturbances such as bleaching, cyclones and crown of thorns outbreaks that cause large-scale coral mortality are becoming increasingly common (Spalding and Brown, 2015). Whether reefs can recover from these disturbances will depend, in part, on the supply of colonists available to settle to newly opened space that appears on reefs following a disturbance (Gilmour et al., 2013). Both stochastic processes which affect the supply of potential colonists and deterministic processes such as habitat availability, larval preferences, and interactions with existing community members, can influence settlement patterns (Lillis et al., 2016). Post-settlement processes then further shape subsequent community development (Caley et al., 1996). As a result, the trajectory of community recovery following disturbance is highly dynamic, with some studies reporting a relatively rapid return to pre-disturbance assemblage structure (Halford et al., 2004; Adjeroud et al., 2009), while others have observed dramatic and long-term shifts (Roff et al., 2015; Guest et al., 2016).

Historically, studies of the role of supply in recovery dynamics have focused on coral recruitment, and have largely overlooked settlement by other members of the benthic community (Zhang et al., 2014). However, algae, sponges, ascidians, and various other sessile members of the benthos are also abundant and integral members of reef communities that support diverse functional roles (Mallela, 2007; Bell, 2008; Glynn and Enochs, 2011; De Goeij et al., 2013; Enochs and Glynn, 2017), although the role that these organisms play in recovery dynamics is not well understood. Non-coral benthos are typically far more abundant than coral spat in early settlement communities (Dunstan and Johnson, 1998; Díaz-Castañeda and Almeda-Jauregui, 1999; Glassom et al., 2004; Mangubhai et al., 2007; Stubler et al., 2016), and initial colonization patterns by these organisms can strongly influence the trajectory of subsequent community development (Stubler et al., 2016). Non-coral settlement patterns may translate into long-term shifts in reef community structure, as variation in the early recruitment rates of non-coral benthos can considerably influence adult abundance of these organisms (Jackson, 1984; Caley et al., 1996; Cowen and Sponaugle, 2009; Zabin, 2015). Further, many non-coral settlers can alternately inhibit or facilitate subsequent colonization by corals (Dunstan and Johnson, 1998; Mangubhai et al., 2007; Birrell et al., 2008; Arnold et al., 2010; Diaz-Pulido et al., 2010). Thus, developing an understanding of the settlement of non-coral benthos can provide valuable insights into the role that recruitment across the wider benthic community may play in affecting the trajectory of initial community development on reefs following disturbance.

Coral reefs in north-eastern Arabia have been subject to widespread and substantial disturbances in recent years. Recurrent bleaching events and disease outbreaks have heavily affected reefs in the southern Persian/Arabian Gulf (hereafter 'the Gulf') while reefs in the adjacent Sea of Oman have been impacted by a super-cyclone and a large-scale harmful algal bloom (Bauman et al., 2010; Riegl and Purkis, 2015; Burt et al., 2016). All of these disturbances have caused substantial declines in coral cover and shifts in the composition of the wider benthic community (Bento et al., 2016). Recovery of reef communities in subsequent years has been variable, with a return toward pre-disturbance assemblages observed in some locations but not others (Burt et al., 2008, 2011; Bento et al., 2016). Several studies have suggested that this divergence in recovery patterns can largely be attributed to variation in the abundance and composition of juvenile corals that have recruited to these reefs (Burt et al., 2008; Pratchett et al., 2017). However, it is unclear whether these patterns in juvenile corals (up to 5 cm diameter) were primarily shaped by larval supply or post-settlement processes.

The purpose of this study was to investigate spatial and seasonal variability in settlement of benthic organisms on reefs spanning > 750 km of coastline in the north-eastern Arabian Peninsula. Terra-cotta settlement tiles were deployed seasonally over 1 year on reefs in the highly disturbed Gulf and Sea of Oman, and on relatively undisturbed reefs in the Musandam Peninsula. Comparison of seasonal dynamics provides insights into peak settlement periods for sessile benthic invertebrates, while large-scale spatial comparisons provide insights into regional scale disturbance and recovery dynamics.

MATERIALS AND METHODS

This study was performed across eight sites in three regions spanning >750 km of coastline in the north-eastern Arabian Peninsula: three sites in the southern Arabian Gulf (Saadiyat, Dhabiya, and Ras Ghanada), three sites along the Musandam Peninsula (Al Harf, Falcon Rock, and Coral Garden) and two sites in the Sea of Oman (Dibba and Al Aqa) (**Figure 1**). All sites were fringing reefs at comparable depths (2–8 m) with coral cover varying between ca. 20–60% among reefs. Communities were generally dominated by faviids and poritids in all regions, with other subdominant families differing in relative abundance among sites. A full description of the benthos in each region is provided in Bento et al. (2016).

Settlement of benthic organisms was quantified at all sites using unglazed terracotta settlement tiles (10 × 10 × 1.5 cm) following methods adapted from Mundy (2000). At each site, 30 tiles were attached to the substratum at ca. 5 m depth and spaced 1–3 m apart. Each tile was secured to the reef using a stainless steel stud that was epoxied into the substratum and

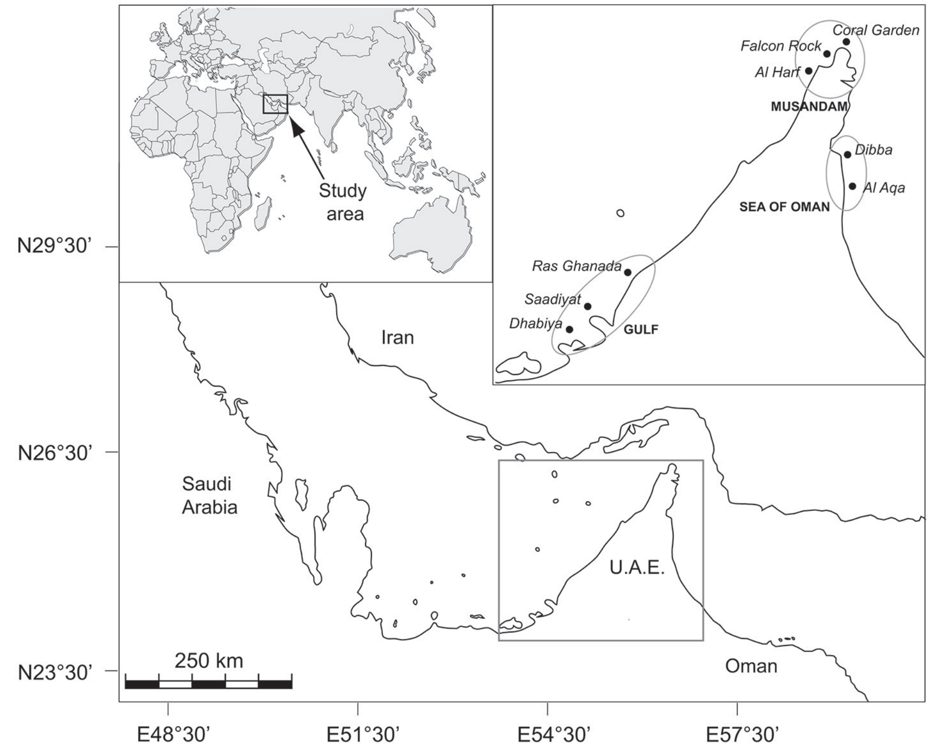

FIGURE 1 | Map of northeastern Arabian Peninsula indicating the location of study sites within each of the three regions.

passed through a 1 cm hole in the center of each tile. A 2 cm plastic washer was placed over each stud to position the tile 2 cm above the reef substratum. The textured (i.e., corrugated) surface of each tile was always positioned facing the substratum, as previous studies have shown that settlement primarily occurs on the underside of tiles and that textured materials generally have higher settlement than smooth surfaces (Burt et al., 2009). To assess seasonal variation in settlement, tiles were deployed and replaced every 3 months over 1 year. Each deployment represented a specific season: (summer: July–September 2012, autumn: October–December 2012, winter: January–March 2013, and spring: April–June 2013), with all tiles deployed/collected across all sites within ca. 7–10 days at the beginning/end of each season. These four seasons were selected based on the periods of highest (summer) and lowest (winter) sea surface temperatures, as well as the transitional spring and autumn periods that are known to be important discrete spawning and/or settlement seasons for a variety of marine fauna in this region (e.g., Bauman et al., 2011; John, 2012; Howells et al., 2014).

Upon retrieval, the bottom of each tile was photographed with a 10 megapixel Nikon D-80 digital camera fitted with a macro lens. Only the bottom surfaces of tiles were analyzed as virtually all settlement in this region occurs on the bottoms of tiles (Burt et al., 2009; Bauman et al., 2014). Percent cover of various benthos on each tile was calculated by image analyses using the software CPC with Excel extension (Kohler and Gill, 2006), with coverage tabulated from 50 random point intercepts per tile. Substratum and benthic community type was categorized into 15 broad groups and several sub-groups: bare tile, coralline algae, coral, ascidiacea (subgroups: colonial ascidian, solitary ascidian), sponge, cnidaria (subgroups: anemone, hydrozoa, zoanthid), arthropoda (subgroup: barnacle), mollusca (subgroups: bivalve, chiton, gastropoda), annelid (subgroup: polychaeta), bryozoa, other live (subgroups: mobile invertebrate, urchin, other), algae (subgroups: algae, turf algae), sand/silt, non-benthos (subgroups: gap, tape, shadow), and unknown taxa. Due to the small size of coral recruits (age: $\leq$3 mo) and their relatively limited coverage, density of coral juveniles was tabulated separately. Following photography for community analysis, tiles were cleaned of living tissue in bleach for 24 h, rinsed and air dried before tabulating the number of coral recruits on each tile using an Olympus DP-70 stereo-microscope (40X magnification).

Data Analyses

Before statistical analyses, percent cover for the various benthic groups was standardized as a proportion of the total living benthos (i.e., relative abundance), and an arcsine-square root transformation was applied to normalize the data, as recommended by Zar (2010). Coral densities were $\log(x + 1)$ transformed. Prior to multivariate analyses, benthic categories occurring in $<5\%$ of samples were excluded from analyses to avoid the influence of outliers (McCune et al., 2002).

To explore the overall spatial and seasonal structure of settlement assemblages, and to identify which components of the benthos were driving any settlement differences, multivariate analyses were performed using Primer, v6 (Clarke and Gorley, 2006). Non-metric multi-dimensional scaling (nMDS) analyses based on Bray-Curtis distance matrices were used to illustrate the influence of regions and seasons on benthic community composition, with taxa strongly driving divergence along nMDS axes identified using Pearson rank-correlations ($r \geq \pm 0.5$ for either axis). To ease interpretation, each season was manually shaded in the resulting nMDS and the vector plot overlaid. Spatial and seasonal differences in settlement community structure were tested with a partially-nested permutational multivariate analysis of variance (PERMANOVA) on the main effects of seasons and regions with sites nested within regions. A similarity percentages analysis (SIMPER) was used to assess which benthic components contributed most to the observed variation in settlement community structure (Clarke and Gorley, 2006). Spatial and seasonal differences in settlement community structure were tested with a partially-nested permutational multivariate analysis of variance (PERMANOVA) on the main effects of seasons and regions with sites nested within regions based on our a priori hypotheses. Key benthic groups and sub-groups identified by our multivariate analyses and coral settlement densities were then then tested with univariate PERMANOVAs to identify significant settlement differences.

A multiple regression was also employed to determine whether the density of coral spat was associated with percent cover of any other components of the settlement community (including each live benthos category plus bare tile). Before regression analyses, the normality of the residuals and homogeneity of variances were confirmed by plotting residuals against fitted values and using QQ plots (Zuur et al., 2007).

RESULTS

Multivariate ordination of the overall settlement community observed in this study indicated strong differences in community structure between regions, with individual sites clustering as region-specific groups across all seasons with no overlap among regions (**Figure 2**). Vector plots indicated regional differences were primarily driven by variation in the relative abundance of three benthic groups: coralline algae, colonial ascidians, and barnacles (**Figure 2**), although other benthos also made strong contributions (Supplementary Table 1). SIMPER analyses showed that settlement communities in the Gulf were primarily characterized by the presence of coralline algae, polychaetes, and bryozoans, which together contributed >80% to similarity in tile assemblage structure in this region (**Table 1**). In the Musandam region, over half of the similarity in settlement communities was driven by strong contributions from both colonial ascidians and bryozoans, with polychaetes and turf algae making more modest contributions (**Table 1**). Bryozoans were also the most common component of Sea of Oman settlement communities, where they contributed over a third of the similarity in community structure, followed by barnacles and turf algae also playing important roles. The SIMPER analysis showed higher abundances of coralline algae in the Gulf was the main driver of differences between both Musandam and Sea of Oman communities, where colonial ascidians, bryozoans, and turf algae were more abundant (**Table 1**). Differences between Musandam and the Sea of Oman settlement communities were largely driven by higher cover of colonial ascidians in the Musandam vs. cover of bryozoans, barnacles, polychaetes and turf algae in Sea of Oman sites (**Table 1**).

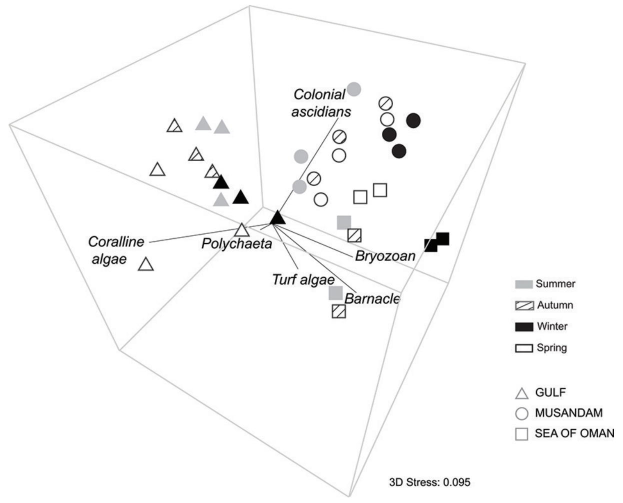

FIGURE 2 | Three-dimensional plot of non-metric multidimensional scaling ordination (nMDS) illustrating the spatial and seasonal variation in benthic community structure across three Arabian water bodies. The vector overlay shows the strength and direction of individual benthos' Pearson rank correlations (restricted to those with $r > 0.5$ for any axis).

While assemblage structure primarily grouped regionally, there were also modest seasonal changes in the settlement community within each region (**Figure 2**), although these changes were not consistent within regions as shown by a significant interaction between seasons and regions in PERMANOVA (**Table 2**). In the Gulf the settlement community showed considerable overlap in structure across summer, autumn, and winter, indicating a good degree of similarity across these seasons, with divergence in the remaining season (spring) being primarily due to higher abundances of coralline algae settling into a single site (Ras Ghanada; **Figure 2**) within this season. In the Musandam the settlement community composition was more similar to Gulf communities during the warm summer season but diverged in the cooler autumn and spring seasons, with the greatest divergence from the Gulf occurring in the cold winter season, when all three Musandam sites had highly convergent community structure, with higher settlement of colonial ascidians (**Figure 2**). The settlement community in the Sea of Oman varied spatio-temporally. The community at Dibba was fairly consistent across summer, autumn, and spring, while the community at Al Aqa was comparable to that found within Dibba in spring, but diverged markedly in the summer and autumn (**Figure 2**). In the winter there were dramatic shifts in the settlement community at both of the Sea of Oman sites, with the assemblages at the two sites

TABLE 1 | Benthic groups responsible for >90% of within-regions similarities and >70% of among-regions dissimilarities based on SIMPER analysis.

Gulf			Gulf vs. Musandam				
Within group similarity: 46.3%	**Cont. (%)**	**Cum. (%)**	***Between-group dissimilarity: 62.2%***	**Gulf % cover**	**Musandam % cover**	**Cont. (%)**	**Cum. (%)**
Coralline algae	33.7	33.7	Coralline algae	28.2	1.2	18.1	18.1
Polychaeta	25.2	58.9	Colonial ascidian	12.5	30.7	17.4	35.5
Bryozoan	24.5	83.4	Bryozoan	20.7	25.3	13.5	49.0
Colonial ascidian	7.1	90.5	Polychaeta	19.2	15.4	11.8	60.9
			Turf algae	5.6	9.5	10.0	70.9
Musandam			**Gulf vs. Sea of Oman**				
Within group similarity: 50.9%			***Between-group dissimilarity: 67.5%***	**Gulf % cover**	**Sea of Oman % cover**		
Bryozoan	27.6	27.6	Coralline algae	28.2	3.3	16.2	16.2
Colonial ascidian	27.4	55.0	Bryozoan	20.7	32.2	14.6	30.8
Polychaeta	19.1	74.0	Barnacle	0.2	22.2	14.4	45.3
Turf algae	12.3	86.3	Polychaeta	19.2	7.8	12.4	57.6
Barnacle	5.4	91.7	Turf algae	5.6	14.3	11.2	68.8
			Colonial ascidian	12.5	8.6	10.7	79.5
Oman			**Musandam vs. Sea of Oman**				
Within group similarity: 42.7%			***Between-group dissimilarity: 59.3%***	**Musandam % cover**	**Sea of Oman % cover**		
Bryozoan	36.2	36.2	Colonial ascidian	30.7	8.6	18.8	18.8
Barnacle	23.0	59.2	Bryozoan	25.3	32.2	15.7	34.4
Turf algae	18.2	77.4	Barnacle	5.1	22.2	14.5	48.9
Polychaeta	9.0	86.4	Polychaeta	15.4	7.8	12.2	61.1
Colonial ascidian	4.4	90.9	Turf algae	9.5	14.3	11.5	72.5

Mean relative abundance (as % of live cover) in each region and individual (Cont.) and cumulative (Cum.) contribution to dissimilarity are shown.

TABLE 2 | Results of the three factor partially nested PERMANOVA analyses assessing differences between regions, seasons and sites (within regions) in benthic community composition.

Source	Df	SS	MS	Pseudo-F	P(perm)
Region	2	3.09E5	1.54E5	7.83	0.0035
Season	3	84334	28111	4.70	0.0001
Site (Region)	5	99698	19940	17.97	0.0001
Region × Season	6	1.5E5	25599	4.26	0.0001
Site (Region) × Season	15	90840	6056	5.46	0.0001

converging with each other but diverging from the communities observed in all other seasons in this region, due to the settlement of barnacles in both sites. SIMPER analyses (**Table 3**) showed that the major taxa driving seasonal changes largely reflected the same groups that were associated with regional differences (above; **Figure 2**), indicating that fluctuations in the relative abundance of these key regional taxa was the primary driver of seasonal shifts in settlement communities.

SIMPER analyses were further used to examine the main benthos driving seasonal differences within regional settlement communities (**Table 3**). The only benthic group that showed wide seasonal variation in all three regions were the bryozoans; all other benthos that were key drivers of seasonal change were important in just one or two regions. In addition to bryozoans, seasonal differences in the Gulf were mainly attributable to variation in the amount of coralline algae, colonial ascidians, and polychaetes, in the Musandam to colonial ascidians, and in the Sea of Oman to barnacles. These seasonal drivers largely reflected the same benthos associated with regional community differences (above; **Figure 2**).

There was a significant interaction between the main effects of season, region and sites (within region) in structuring settlement of each major benthos (**Figure 3**), indicating that patterns of change were not consistent among the main effects for any of these benthic groups (PERMANOVA Pseudo- $F_{(15,\ 824)}$: bryozoans = 11.0, polychaetes = 7.2, turf algae = 5.0, coralline algae = 3.9, barnacles = 7.4, colonial ascidian = 2.7; $p < 0.001$ for each]. Bryozoans showed strong but inconsistent seasonal fluctuations in all regions, with highest cover in the winter in the Gulf and Musandam (**Figures 3A,B**), while densities peaked in the autumn in the Sea of Oman when cover was nearly 50% higher than peak densities in the other regions (**Figure 3C**). While coralline algae cover was negligible in other regions, it

TABLE 3 | Benthic taxa identified as important seasonal drivers of divergence in community structure in SIMPER.

Region	Season comparison	δ	Percent contribution to dissimilarity					
			Coralline algae	Colonial ascidian	Bryozoan	Polychaetes	Turf algae	Barnacle
Gulf	Spring vs. Summer	51.1	15.1	17.0				
	Spring vs. Autumn	53.1	16.2	14.8	15.2	16.8		
	Summer vs. Autumn	51.9		17.0		15.0		
	Spring vs. Winter	56.6	20.9		17.6	15.5		
	Summer vs. Winter	59.8	16.7	15.2	16.8			
	Autumn vs. Winter	56.4	16.9		18.8	16.2		
Musandam	Spring vs. Summer	46.9		19.4				
	Spring vs. Autumn	49.1		19.1	15.6			
	Summer vs. Autumn	50.3		18.6				
	Spring vs. Winter	47.6		21.2	17.7			
	Summer vs. Winter	50.5		19.2	19.1			
	Autumn vs. Winter	55.4		18.5	19.0	15.2		
Sea of Oman	Spring vs. Summer	56.2			15.4			15.1
	Spring vs. Autumn	65.4			22.0		19.1	
	Summer vs. Autumn	59.7			20.4			15.8
	Spring vs. Winter	61.2					18.3	24.7
	Summer vs. Winter	54.8			16.6			20.0
	Autumn vs. Winter	69.2			23.4			26.3

Only benthic groups strongly contributing to the dissimilarity (δ >15%) in each pairwise comparison are shown.

was the most abundant benthic component on tiles in the Gulf, and it doubled in cover from winter to summer (mean cover: 16.3% ± 2.2 SE to 31.6% ± 2.7 SE respectively; **Figure 3A**). Colonial ascidians were considerably more abundant in the Musandam than other regions, explaining its identification as a major distinguishing taxa for tiles in this region in earlier SIMPER analyses, and cover was generally comparable across seasons for this group (**Figure 3B**). In the Sea of Oman barnacles heavily dominated settlement in winter, when they comprised over half of the benthos at each site and were substantially more widespread than in other seasons; barnacles were uncommon in Musandam and nearly non-existent in the Gulf.

Coral Recruits

In total, 216 coral recruits were observed on the 845 tiles deployed across the 8 sites throughout the study. No coral settlers were observed across the entire study in the Gulf of Oman, and there was inconsistent and high variation in coral settlement among sites and seasons within the Gulf and Musandam (**Figure 4**; **Table 4**). In the Gulf, mean settlement was highest in autumn but this was mainly due to a large pulse at Saadiyat reef (90% of spat this season); a second peak in settlement also occurred in summer, with a small number of spat recorded in spring as well. In the Musandam, coral settlement mainly occurred in the spring, although spat were observed in low densities in all seasons in at least one site.

Multiple regression revealed that coral density was unrelated to cover of other benthic components [including bare tile space; $R^2 = 0.27$; $F_{(10,\ 96)} = 0.736$, $p = 0.69$], reflecting the considerable variability and low incidence of coral settlement observed in this study.

DISCUSSION

Coral reef communities in north-eastern Arabia have been subject to various large-scale disturbances in recent years. To date, there had been limited knowledge of the spatial and seasonal patterns of settlement of coral and non-coral benthos, limiting our understanding of the important role that supply may play following disturbance. The results of this study show that settlement of corals was extremely low and that non-coral benthic settlement was highly variable between regions and across sites within regions.

The most striking result of this study was the strong regionally structured patterns of non-coral settlement, with regional differences persisting across seasons throughout the study. These large-scale differences in non-coral settlement mirror the divergence of benthic community structure on reefs across these regions (Bauman et al., 2013; Bento et al., 2016), and is likely driven by the highly divergent environmental conditions among these seas, which have also been subject to varying degrees of disturbance.

The southern Gulf represents one of the most extreme coral reef environments on earth, with sea surface temperatures ranging >25°C annually, daily mean maxima >34°C for several months during summer, and salinities that consistently exceed 44 PSU (Sheppard et al., 1992; Coles, 2003; Foster et al., 2012). In addition, these reefs have experienced numerous large-scale

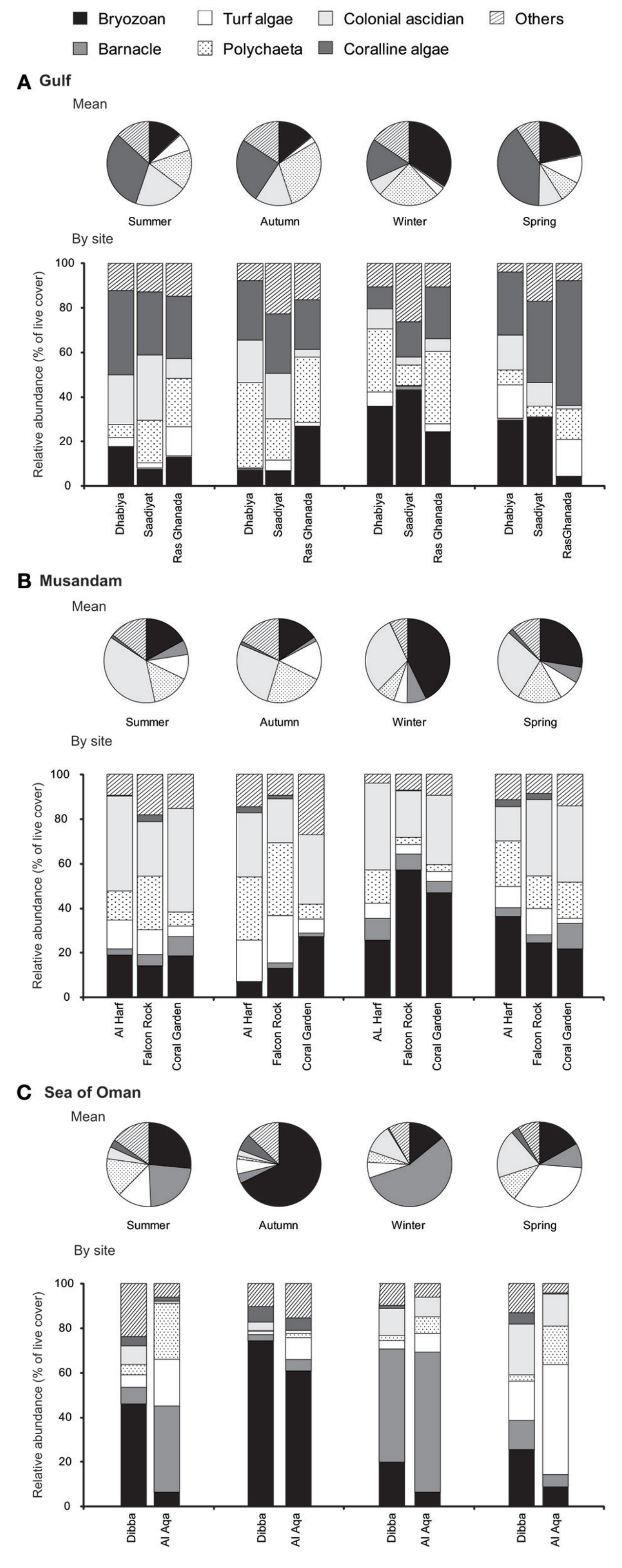

FIGURE 3 | Seasonal changes in benthic community structure: **(A)** across the Gulf and within each Gulf site, **(B)** across Musandam and within each Musandam site, **(C)**, across the Sea of Oman and within each Sea of Oman site. Values are shown as relative abundance (percentage of benthic cover).

bleaching events over the past two decades (Riegl and Purkis, 2015), resulting in widespread shifts in benthic community structure from which there has been only limited recovery (George and John, 2000; Sheppard and Loughland, 2002; Burt et al., 2008, 2011). In the wake of earlier mass bleaching events, coralline algae dramatically increased in abundance on southern Gulf reefs (George and John, 2000, 2002). In the current study, coralline algae dominated the settlement community on southern Gulf reefs (covering 28% of tile surfaces, on average), and it was the primary differentiator in settlement community structure from the other regions (where it covered <3.5% of tile surfaces in both areas). Thus, the presence of coralline algae as a major component of the settlement community in the southern Gulf appears to be a persistent, long-term characteristic of this highly disturbed, extreme environment.

In contrast to the Gulf, the Sea of Oman has environmental conditions that are more benign. Due to its greater depth and exchange with the wider Indian Ocean, SSTs in the Gulf of Oman are less extreme (mean summer maxima <32°C, range 10°C annually) and salinity is comparable to oceanic conditions (37 PSU) (Foster et al., 2012; Howells et al., 2014). Its waters are also highly productive compared with the Gulf and Musandam as a result of monsoon-induced upwelling (Sheppard et al., 1992). Although reefs in the Sea of Oman have experienced widespread disturbance in the past decade as a result of cyclone storm damage and a hypoxic event associated with an algal bloom (Bauman et al., 2010; Burt et al., 2016), the frequency of impacts to coral reefs here has not been as severe as in the Gulf and there are indications that recovery of reef communities is underway (Bento et al., 2016; Pratchett et al., 2017). Barnacles were one of the primary drivers of the divergence of Sea of Oman reefs from the other regions, with barnacles here covering nearly a quarter of settlement tiles (22%) on average, compared with low abundance in the Musandam (5% cover) and a near absence in the Gulf (0.2% cover). Barnacles are reported to be among the most abundant members of settlement communities in Oman (Wallström et al., 2011; Dobretsov et al., 2013; Polman et al., 2013; Dobretsov, 2015), likely a reflection of their success as filter-feeders in this high-productivity environment (Sheppard et al., 1992), suggesting that the high barnacle abundance we observed is a result of long-term supply dominance in the Sea of Oman.

The Musandam Peninsula sits at the interface between the Arabian Gulf and the Sea of Oman at the Strait of Hormuz. Environmental conditions in the Musandam are generally comparable to the Sea of Oman, although productivity is lower due to a lack of monsoonal upwelling in this area (Sheppard and Salm, 1988; Sheppard et al., 1992; Reynolds, 1993). In addition to having relatively benign environmental conditions, Musandam reefs have also escaped the various large-scale disturbances that affected reefs in the adjacent seas, and reef communities here have among the highest coral cover and diversity in northeastern Arabia and are considered among the most pristine in the region (Sheppard et al., 2010; Bento et al., 2016; Burt et al., 2016). Colonial ascidians were the primary driver of divergence of Musandam reefs from those in the other regions, with these organisms covering nearly a third of Musandam tiles (30.7% cover), nearly triple the coverage in the other regions

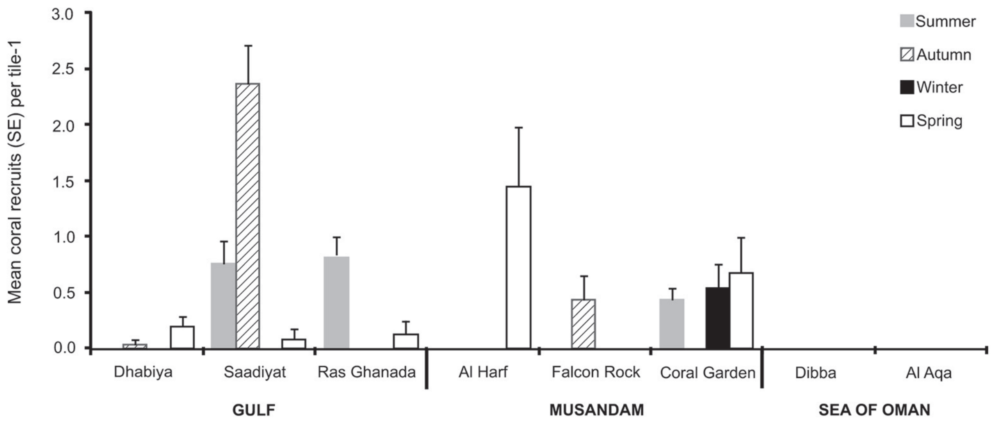

FIGURE 4 | Spatio-temporal variability in the density of coral spat (mean ±SE) on settlement tiles.

TABLE 4 | Results from PERMANOVA tests comparing mean coral recruits densities among regions, sites and seasons.

Source	df	MS	Pseudo-F	*p*-value
Region	2	2.0454	0.68978	0.5171
Season	3	0.54429	0.20592	0.8917
Site (Region)	4	3.0654	24.549	**0.0001**
Region * Season	6	1.4905	0.55661	0.7421
Site (Region) * Season	12	2.7596	22.1	**0.0001**
Total	747			

Values in bold are significant (p < 0.05).

(8.6–12.5% cover). Ascidians are relatively common members of the benthic community on reefs in the Musandam (R. Bento, unpubl. data), particularly compared to reefs in the southern Gulf or Sea of Oman where they are virtually undetected in benthic surveys (Burt et al., 2011; Grizzle et al., 2016). Given their short pelagic duration and limited larval swimming ability, ascidians generally have a relatively localized dispersal (Shanks et al., 2003; Weersing and Toonen, 2009), suggesting that the high abundance of colonial ascidians observed on Musandam settlement plates likely relates to their high abundance in the wider reef community.

While regional differences primarily structured settlement communities, there were also modest within-region shifts in settlement communities over the course of the year. Much of these within-region shifts were related to fluctuations in the abundance of bryozoans, a dominant member of the community across all regions, as well as to fluctuations in the relative abundance of those same key benthic categories that drove between-region differences. In all three regions the period of peak bryozoan settlement coincided with a reciprocal decline in the abundance of the region-specific key taxa; peak bryozoan abundance in the winter coincided with the lowest annual mean cover of coralline algae in the Gulf and colonial ascidians in the Musandam, while peak bryozoan settlement in the autumn in the Sea of Oman and coincided with a decline of barnacle cover on tiles. In all cases, peak coverage of bryozoans occurred in the season with maximum chlorophyll-*a* concentrations for every region (Nezlin et al., 2010; Piontkovski et al., 2011; Moradi and Kabiri, 2015), suggesting that while bryozoans settle year round, their success in these particular seasons may be related to enhanced post-settlement growth due to higher planktonic food availability. Together, these observations suggest that while there are distinct regional settlement signatures, seasonality in bryozoan settlement is largely responsible for modulating within-region temporal dynamics. It should be noted, however, that these results represent seasonal settlement data from a single year. While this is useful information given the lack of data available previously, benthic recruitment is highly variable from year to year and it is unknown whether the results of this study are representative of longer-term patterns. A multi-year year settlement study to assess the role of recruitment in sessile benthic population dynamics is warranted.

Coral Settlement Patterns

Coral settlement was low across all three regions in this study. Across the full year of study, coral densities were minimal in the Gulf and Musandam (mean: 38 and 30 coral settlers m^{-2} $year^{-1}$, respectively, across the year, and averaging 82 and 70 settlers m^{-2} $year^{-1}$ even when considering only the peak settlement season), and corals were entirely absent from settlement tiles in the Sea of Oman throughout the study. The observed densities were substantially lower than has commonly been reported in tropical reef environments (Seychelles: 595 spat m^{-2} $year^{-1}$, Chong-Seng et al., 2014; Indonesia: 286–705 m^{-2} $year^{-1}$, Sawall et al., 2013; Kenya: 101–908 m^{-2} $year^{-1}$, Mangubhai et al., 2007), and less than half of densities reported for comparable high latitude marginal reefs (Eilat: 190 m^2 $year^{-1}$, Glassom and Chadwick, 2006; Solitary Islands: 132 spat m^{-2} $year^{-1}$, Harriott and Banks, 1995; Taiwan: 111 spat m^{-2} $year^{-1}$, Soong et al., 2003). The observed densities are also low compared with a recent study of coral settlement in Dubai in the southern Gulf where densities of 121 coral settlers m^{-2} $year^{-1}$ were reported (Bauman et al., 2014), although those data were mainly collected on breakwaters that have been suggested to entrain eggs, potentially enhancing settlement compared with what would occur on natural reefs (Burt et al., 2009). Overall, the low densities noted in this region are similar to that seen in heavily degraded, highly disturbed reef environments (Singapore: 55 m^{-2} $year^{-1}$, Bauman et al., 2015; Florida: 38 m^{-2} $year^{-1}$, Van Woesik et al., 2014). Together, the low densities observed in the Gulf and Musandam and the complete absence of coral settlement in the Sea of Oman suggest that there is cause for concern for the regeneration of degraded coral reef communities within the Arabian Peninsula.

The low abundance of coral spat observed here is unlikely to be due to interactions with other members of the settlement community. The abundance of coral recruits was unrelated to cover of any other benthos in our analyses, and bare space was relatively common (ranging from 55% in the Gulf to 20% in the Sea of Oman), suggesting ample availability of habitat for coral settlement. Instead, the low coral settlement likely reflects a limited supply of coral larvae. Low coral settlement has been reported earlier in the southern Gulf (Bauman et al., 2014), and is likely the result of depressed fecundity of corals being exposed to recurrent bleaching events and extreme environmental conditions (Riegl and Purkis, 2015; Howells et al., 2016). Although coral cover is high in the Musandam (Bento et al., 2016; Burt et al., 2016), we observed low levels of coral settlement. This suggests that low coral recruitment is characteristic of reefs in northeastern Arabia, and the high coral cover in the Musandam is likely the result of the relatively low levels of disturbance in this area rather than high larval supply. The implication is that the relatively pristine reefs in the Musandam may be highly vulnerable to any future disturbances that may occur, as any recovery would be potentially limited by low recruitment levels. The absence of coral settlement to tiles in the Sea of Oman was surprising. Reproductive studies occurring near these sites have shown that common coral species were spawning during this study in April 2013 (Howells et al., 2014), and fecundity was substantially higher than conspecifics in the southern Gulf (Howells et al., 2016). Additionally, juvenile surveys on these sites in 2012 showed that corals were recruiting to these reefs, although densities were half of that observed in the southern Gulf (Pratchett et al., 2017), suggesting that recruitment is impaired here. Reefs in the Sea of Oman sites have low coral cover (18%) relative to the southern Gulf and the Musandam (56 and 58%, respectively, Bento et al., 2016), mainly as a result of a algal bloom in 2009 when 50–90% of corals were lost from reefs (Bauman et al., 2010; Foster et al., 2011). As a result, while individual corals here are fecund, reef-wide reproductive output for a variety of dominant coral species is low as a consequence of the limited number of fecund adults in the community (Howells et al., 2016), potentially explaining the absence of coral settlers on tiles and the relatively low overall juvenile recruitment rates observed by Pratchett et al. (2017). It should be noted, however, that recovery on highly disturbed reefs typically takes 10–15 years (Purkis and Riegl, 2005; Burt et al., 2008; Ateweberhan et al., 2011), even in areas where larval supply remains depressed for up to 6 years (Gilmour et al., 2013). As the current study was performed 8 years after the catastrophic HAB event, this suggests that there is hope that recovery may occur in the near future. It is unclear whether the absence of coral settlement observed here extends to other parts of the Sea of Oman. A recent survey of coral reefs 400 km southwest around Muscat, Oman, suggested that many coral reefs there continue to have high coral cover despite showing indications of localized decline in some areas over the past two decades, with available evidence suggesting that declines were primarily due to a recent cyclone rather than the dramic HAB induced loss that impacted the coral communities on reefs studied here (Coles et al., 2015). An assessment of the reproductive capacity and settlement patterns of corals on reefs elsewhere in the Sea of Oman is highly warranted.

Coral reefs around the world are becoming increasingly degraded as a result of climate change and localized anthropogenic impacts (Hughes et al., 2010; Pandolfi et al., 2011) with widespread shifts toward a dominance of non-coral benthos (Colvard and Edmunds, 2011; Kelmo et al., 2013, 2014). While many studies have focused efforts on understanding the dynamics of coral settlement following disturbance (Glassom et al., 2004; Abelson et al., 2005; Green and Edmunds, 2011; Sawall et al., 2013; Bauman et al., 2014), few studies have explored the role that non-coral benthos may play in affecting early recovery dynamics on reefs (Colvard and Edmunds, 2011; Luter et al., 2016). Non-coral benthos are among the first colonists to settle on substrates opened by disturbance, and typically reach an abundance and coverage that greatly exceeds that of coral spat (Dunstan and Johnson, 1998; Díaz-Castañeda and Almeda-Jauregui, 1999; Glassom et al., 2004; Mangubhai et al., 2007; Stubler et al., 2016). Given that many of these non-coral benthos can alternatively facilitate or inhibit subsequent coral recruitment in the space opened by disturbance, their presence could dramatically impact the trajectory of subsequent recovery on disturbed reefs. Our results showed that the initial settlement community was highly region-specific, with non-coral benthos being the primary members of the settlement community in all areas. In some regions, these initial communities were dominated by taxa known to facilitate settlement of coral larvae (for example, over a quarter of Gulf tile space was covered by crustose coralline algae, a well-known inducer of larval coral settlement (Ritson-Williams et al., 2014; Tebben et al., 2015), suggesting conditions favorable to coral colonization following disturbance. In others, however, early settlement communities were dominated by fauna known to inhibit coral larval settlement (e.g., ascidians covered a third of tiles in the Musandam, and various ascidians are known to produce allelochemicals that can inhibit coral settlement (Chadwick and Morrow, 2011). Our knowledge of the types of benthic organisms and the mechanisms that they use to interact with coral larvae is relatively under-developed (Ritson-Williams et al., 2009), but our results here suggest that such information is essential if we are to understand how the initial settlement community may affect the trajectory of early community development. Initial settlement communities will, of course, be shaped by post-settlement processes that will likely lead to mature assemblages that are markedly different in their structure. But because this first stage of development provides the foundation open which all post-settlement processes can act, it represents a critical bottleneck that has important implications for whether or not a disturbed reef has the capacity to recover.

AUTHOR CONTRIBUTIONS

RB: Responsible for data collection, analysis and writing process. DF and AH: Responsible for reviewing the data analysis and writing. JB: Responsible for data analysis and writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00305/full#supplementary-material

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Coral Community Structure and Recruitment in Seagrass Meadows

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Coral communities are increasingly found to populate non-reef habitats prone to high environmental variability. Such sites include seagrass meadows, which are generally not considered optimal habitats for corals as a result of limited suitable substrate for settlement and substantial diel and seasonal fluctuations in physicochemical conditions relative to neighboring reefs. Interest in understanding the ability of corals to persist in non-reef habitats has grown, however little baseline data exists on community structure and recruitment of scleractinian corals in seagrass meadows. To determine how corals populate seagrass meadows, we surveyed the established and recruited coral community over 25 months within seagrass meadows at Little Cayman, Cayman Islands. Simultaneous surveys of established and recruited coral communities at neighboring back-reef sites were conducted for comparison. To fully understand the amount of environmental variability to which corals in each habitat were exposed, we conducted complementary surveys of physicochemical conditions in both seagrass meadows and back-reefs. Despite overall higher variability in physicochemical conditions, particularly pH, compared to the back-reef, 14 coral taxa were capable of inhabiting seagrass meadows, and multiple coral families were also found to recruit to these sites. However, coral cover and species diversity, richness, and evenness were lower at sites within seagrass meadows compared to back-reef sites. Although questions remain regarding the processes governing recruitment, these results provide evidence that seagrass beds can serve as functional habitats for corals despite high levels of environmental variability and suboptimal conditions compared to neighboring reefs.

Keywords: seagrass, coral, recruitment, environmental variability, marginal habitats, benthic ecology, climate change, marine chemistry

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INTRODUCTION

Scleractinian corals occupy a range of habitat types and form the architectural framework within different reef zones (e.g., Goreau, 1959; Logan, 2013). However, corals also colonize non-reef habitats, such as mangrove systems and seagrass beds that can exhibit high levels of variability in abiotic conditions relative to neighboring reefs (e.g., Riegl, 1999; Perry and Larcombe, 2003; Yates et al., 2014; Camp et al., 2016a). Despite the presence of corals in these non-reef habitats, many assessments of coral communities focus only on fore-reef zones (e.g., Mumby et al., 2007; Castillo et al., 2012). Few studies exist to characterize coral populations outside such classical reef systems.

To understand the importance of non-reef habitats for corals, it is critical to establish baseline data on the structure of coral assemblages in such habitats. Habitat monitoring and assessment data is widely acknowledged as a critical factor in the success of conservation initiatives and adaptive management (e.g., Jackson et al., 2014). However, prioritizing indicators for monitoring ecosystem health can be challenging (Borja et al., 2014). Live coral cover alone is increasingly acknowledged as an insufficient metric for characterizing the ability of a coral-bearing habitat to persist over time (Hughes et al., 2010). For example, recruitment is recognized as a valuable metric for evaluating coral community function, as it can provide insight into a system's capacity for replenishment, a critical component of resilience (Nyström et al., 2008; Hughes et al., 2010). A holistic examination of a coral community should therefore characterize both established and recruited coral assemblages.

Here we focus on seagrass beds that, to-date, have been understudied with respect to their suitability as a non-reef coral habitat. Typically, seagrass beds have not been considered important coral habitats due to a lack of solid substrate (Jackson, 1986; Manzello et al., 2012). Coral communities inhabiting seagrass meadows have been reported from both the Caribbean (Rützler and Macintyre, 1982; Johnson, 1992) and Indo-Pacific (Higuchi et al., 2014; Camp et al., 2016a). These studies have focused on the ecology of free-living coral species (Johnson, 1992) and physiology of corals (Higuchi et al., 2014; Camp et al., 2016a,b) in such habitats, or have described coral colonies in seagrass meadows as part of larger reef systems (Rützler and Macintyre, 1982). Johnson (1992) investigated coral recruitment within a seagrass habitat, however this study focused on a single coral species rather than the coral community as a whole. Others have briefly noted the presence of corals living among seagrass during unrelated experiments (e.g., Wulff, 2008).

For coral communities in seagrass beds, measurements of physicochemical conditions are important given the characteristic variability in ocean chemistry associated with these sites (Higuchi et al., 2014; Camp et al., 2016a). Seagrass systems routinely experience highly variable environmental conditions relative to coral reefs, such as reduced pH and increased temperature (Semesi et al., 2009; Challener et al., 2016), which could be critical in shaping resident coral communities. Studies of corals living among these high-variability systems can therefore also provide insight into which coral species are able to successfully acclimatize or adapt to survive under such conditions (Barshis, 2015). We are unaware of any study that has comprehensively characterized coral community structure within a seagrass meadow, particularly in the context of adjacent reef communities and the physicochemical variability within the system. A lack of baseline data on the composition and condition of coral communities in seagrass meadows inhibits our ability to understand how these systems may change over time.

We conducted a 25-month study to characterize the coral community at understudied seagrass sites in a location with minimal direct anthropogenic impact (Little Cayman, Cayman Islands). To fully understand how coral communities in seagrass meadows differ from those of local reefs, adjacent back-reefs were also surveyed for comparison. We assessed key attributes to provide a robust characterization of each site, specifically: (i) physicochemical conditions, (ii) benthic structure, and (iii) coral recruitment, including the relationship between the established and recruited coral community. Our study thus provides detailed insight into an important but poorly understood coral habitat, as well as a comprehensive comparison to an adjacent but very different shallow reef habitat. In doing so, we provide novel information on how environmentally-variable seagrass beds can function as a coral habitat.

METHODS

Study Site

This study was conducted off the north coast of Little Cayman, Cayman Islands (19.6897°N, 80.0367°W), at three shallow (≤ 2 m) sites with adjacent back-reefs and seagrass meadows (**Figure 1**). The first site was located in Grape Tree Bay, (GTB), a lagoon approximately 0.10 km wide and 1.50 km long, situated within the Bloody Bay Marine Park. The two remaining sites were located at either end of the larger Mary's Bay, approximately 0.15 km wide and 4.00 km long. The two sites within Mary's Bay were designated as Mary's Bay West (MBW) and Mary's Bay East (MBE). At each site, three sampling replicates, spaced 50 m apart, were selected within each habitat type [i.e., seaward back-reef ($n = 3$) and inshore seagrass meadow ($n = 3$); **Figure 1**]. Across sites, seagrass was comprised of $88.0 \pm 1.5\%$ *Thalassia testudinum* and $12 \pm 0.6\%$ *Syringodium filiforme*.

Physicochemical Conditions

To characterize the physicochemistry of each site, discrete seawater samples were collected over two 6-week periods, one in the wet season (July-August) and one in the dry season (February–March) of 2012. Within each sampling period, three 24 h sampling sessions were conducted during both neap and spring tidal phases. Samples were collected every 3 h over the 24 h period at each site and replicate ($n = 48$ total samples per site, per sampling session). In addition, diurnal (1 h before sunrise and 1 h after sunset) open-ocean water samples were collected ($n = 6$ samples per site) to act as an off-shore reference for the ocean chemistry. Discrete water samples were collected from a depth of *ca.* 0.5 m following Carbon Dioxide Information Analysis Center (CDIAC) standards. Samples were collected in borosilicate bottles and fixed with $HgCl_2$ [0.05 ml of saturated (aq) solution] (Dickson et al., 2007). Stoppers were inserted to ensure a gas tight seal and samples were stored in the dark until they were returned to the laboratory (within 30 min) for analysis.

An additional seawater sample was collected at each replicate during every sampling period to allow immediate measurements of pH, temperature, oxygen, and salinity to obtain the *in situ* conditions used for calculation of carbonate parameters. An Orion^{TM} 5 Star meter (Thermo Scientific^{TM}) fitted with a pH/temperature probe and DO probe (Thermo Scientific^{TM}) and a handheld refractometer to measure salinity (ExTech®) were used throughout. The pH probe was calibrated with TRIS buffer using the potentiometric technique and the total scale (pH_T). Water flow was also measured at each replicate following every sample collection using a mechanical flow meter (General

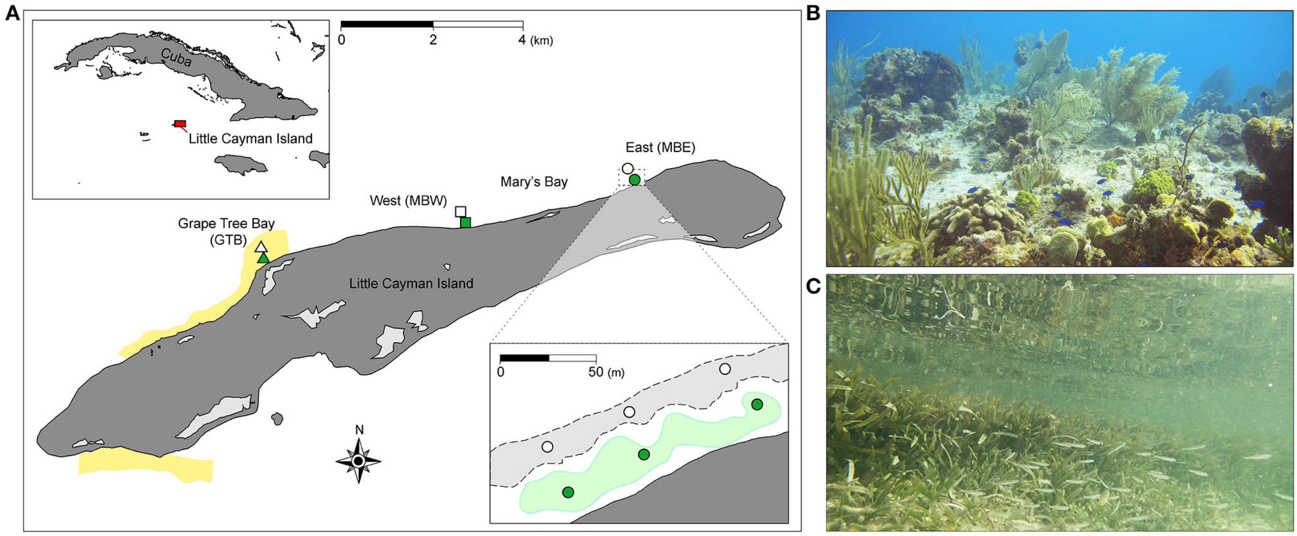

FIGURE 1 | Study sites on Little Cayman Island. Map of Little Cayman Island **(A)** located within the Caribbean Sea (upper inset), yellow highlighting denotes the location of marine parks. Three locations, Mary's Bay East (**MBE, circles**) and West (**MBW, squares**), and Grape Tree Bay (**GTB, triangles**) were chosen as study sites. Back-reef (light gray areas with dashed lines, lower inset) and seagrass (green areas, lower inset) sites were selected within each study location ($n = 3$ per site spaced 50 m apart, **lower inset**). Typical benthic scenes are indicated for back-reef and seagrass sites in **(B,C)**, respectively. The base data for the map **(A)** were collected from www.openstreetmap.org (© OpenStreetMap contributors) under the Open Database License and customized in Adobe Illustrator (version 16).

Oceanics). All laboratory and field equipment were calibrated as recommended by their instruction manuals and/or CDIAC protocols (Dickson et al., 2007).

Samples were returned to a climate-controlled laboratory where pH was re-measured to check for pH drift using a pH electrode (Thermo Scientific™) calibrated with TRIS buffer using the potentiometric technique and the total scale (pH_T). An open-cell potentiometric titration procedure was used to measure total alkalinity (A_T) using the Gran method to determine the second end point of the carbonate system. A_T of all samples was determined using a titrator (Metrohm) with an accuracy and precision of *ca.* $\leq 2\ \mu\text{mol kg}^{-1}$ as verified with certified reference materials distributed by A. Dickson (Scripps Institution of Oceanography). All carbonate parameters [$p\text{CO}_2$, TCO_2 and aragonite saturation (Ω_{arg})] were calculated with CO2SYS from A_T and pH_T (Riebesell et al., 2000), and *in situ* temperature, salinity, and sampling depth (m) as a proxy for pressure (Lewis and Wallace, 1998). For CO2SYS the dissociation constants provided by Mehrbach et al. (1973) were used for carbonic acid (as refined by Dickson and Millero, 1987), and those provided by Dickson (1990) were used for boric acid. In addition, HOBO® data loggers (Onset® Computer Corporation) were used to measure light (in lux subsequently converted to PAR, see Long et al., 2012) in the back-reefs and seagrass meadows for a period of 25-months beginning in January 2012. Loggers were screwed onto a PVC mount installed at each site using a galvanized nail and marine epoxy. Loggers were cleaned and data was downloaded monthly *in situ* using a HOBO® Waterproof Shuttle (Onset® Computer Corporation). Fouling on the loggers was found to alter light quality after the first 10 days following cleaning, therefore only light data collected within these 10 day periods were analyzed ($n = 250$ days of light data for the full 25-month experiment).

Benthic Surveys

Benthic surveys were conducted in February 2012 and February 2013. To characterize the benthos of the back-reef and seagrass meadow, continuous-line intercept video transects were conducted using a high-definition video camera with an underwater housing (Canon®). At each site and habitat type, three 50 m transects were laid parallel to shore. The start and end points of each transect were recorded using a handheld GPS (Garmin®) and marked *in situ* using semi-permanent metal pickets. Benthic composition was quantified using categories defined by Atlantic and Gulf Rapid Reef Assessment protocol version 5.4 (Lang et al., 2010), and scleractinian corals were identified to species level.

The size-frequency, density, and health of established scleractinian coral populations were also assessed within each habitat. Established coral populations refer to all coral colonies identified on natural substratum within each habitat (e.g., not recruited on to settlement tiles, see proceeding section). A 20 m^2 (5 × 4 m) quadrat was placed at the start point of each transect, and species, size, and condition of each coral (≥1 cm) was recorded. Colonies were measured using calipers or measuring tape. Colony condition characteristics recorded included depigmentation and evidence of new, transitional, or old mortality (as defined by Lang et al., 2010).

Recruitment

Within this study, recruited coral populations refer to corals recruited onto settlement arrays. Settlement arrays were deployed in January 2012 to assess scleractinian coral recruitment patterns within each habitat type. Pre-conditioned limestone settlement tiles were used, as they have demonstrated coral recruitment rates comparable to natural substrate (e.g., Salinas de León et al., 2011). Arrays consisted of six unglazed limestone tiles (10 × 10 × 1 cm) with 0.8 cm holes drilled in the center (modified from Mundy, 2000; Salinas de León et al., 2011). Each tile was labeled for identification and attached to a PVC base with a plastic cable tie. Tiles were conditioned for 1 month in their respective target habitats in Grape Tree Bay prior to installation. Arrays were installed using galvanized nails through either end of the PVC base. The PVC base created a 2.5 cm gap between the tiles and the substrate, which has been shown to facilitate coral settlement (Harriott and Fisk, 1987). Three settlement arrays were deployed at every sampling replicate at each of the three study sites ($n =$ 18 tile arrays per site, $n = 54$ arrays (324 tiles) total). Arrays were spaced a minimum of 5 m apart (Salinas de León et al., 2011).

Tiles two, three, and six (selected at random prior to deployment) were removed and replaced with new, conditioned tiles 1 month following installation and monthly thereafter. Tile removal allowed for the timing and frequency of recruitment to be assessed. Removed tiles were examined microscopically (20x) in the laboratory under blue light (Leica Microsystems). Tiles with coral recruits present were laid in a single layer in a bath treated with 10% aq chlorine solution for 48 h to remove organic matter and examined with the microscope (per Schmidt-Roach et al., 2008). Recruits belonging to the families Acroporidae, Agariciidae, Faviidae (now part of family Mussidae, see Budd et al., 2012), Poritidae, and Siderastreidae were identified using photomicrographs published previously (English et al., 1994; Babcock et al., 2003; de Putron, 2005, 2007). Recruits belonging to other families (for which photomicrographs were unavailable), or those that could not be identified, were recorded as other (per Schmidt-Roach et al., 2008). All tile arrays were removed after 25 months and analyzed following the same protocol as the monthly assessments.

Statistical Analysis

Mean and coefficient of variation (C_V) of each abiotic factor (i.e. pH_T, temperature, A_T, Ω_{arg}, salinity, and water velocity) were compared between back-reefs and seagrass meadows and relative to the open-ocean sites using ANOVA and *post hoc* Tukey tests. Benthic structure of each habitat was compared between years using a Principal Component Analysis (PCA), with unpaired *t*-tests on the first and second principal components extracted for each site. Data were square-root transformed and clusters (80 and 90% similarity) were generated from a Bray-Curtis similarity matrix of all benthic data. The PCA vectors were generated by Pearson's Correlations exceeding $R > 0.6$, between plot ordinations and benthic categories. To characterize the established coral populations of each habitat, coral abundance, disease prevalence, species richness, diversity (Shannon-Wiener Index) and evenness (Shannon's Evenness) were calculated. The abundance of established corals per year, for each site, were compared by a 2 × 2 contingency table and a Pearson's Chi-squared test. Size-frequency of the established coral communities of each habitat was binned into size categories; larger categories were pooled together to avoid the problems associated with low expected counts (Starnes et al., 2012). The maximum diameter for each colony was used for comparison to ensure standardization among colonies with different growth forms (per Suggett et al., 2012). Fits of exponential decay across the counts in each bin were performed for both 2012 and 2013 to assess the population size-classes (Santangelo et al., 2004). The log count in each bin was plotted against the middle size category, with fits only done on categories until the first zero bin was reached; thus, avoiding issues with non-defined logarithms. Population sizes between years, for each habitat, were also assessed initially by a 2 × 2 × 5 contingency table and then with Pearson's chi-squared test.

To analyze recruitment, all tile data was pooled and considered as a mean per site (see Hurlbert, 1984). The density of recruits was determined per family. For both the recruited coral population (determined from settlement tiles) and established coral populations (determined from the quadrat surveys), the proportional abundance of each species was determined for the back-reef and seagrass meadow habitats. Differences between the established and recruited coral populations were assessed through the z-test. Data was pooled from the two communities to obtain a pooled sample abundance of:

$$p_{diff} = \frac{p_{rec}N_{rec} + p_{est}N_{est}}{N_{rec} + N_{est}}$$

where p_{rec} is the sample proportion for the recruited population, N_{rec} is the sample size for the recruited population, p_{est} is the sample proportion for the established population, and N_{est} is the sample size for the established population.

With a pooled standard error of:

$$SE_{diff} = \sqrt{p_{diff}(1 - p_{diff})\left(\frac{1}{N_{rec}} + \frac{1}{N_{est}}\right)}$$

Using test statistic $z = \frac{p_{est} - p_{rec}}{SE_{diff}}$, *p*-values were calculated for each family for the null hypothesis that the recruited and established coral population proportions were equal. At the end of the study, the recruited benthic taxa were determined by the CPCe analysis and compared between habitat types ($n = 9$ replicates per habitat type) using MANOVA with *post-hoc* Tukey tests. Statistical analysis was performed using R (R Core Team, 2014) and Graphpad Prism (version 7.01). Data were assessed and found to meet the assumptions of linearity, independence, homogeneity of variance, and normality.

RESULTS

Physicochemical Conditions

Both the back-reef and seagrass meadow sites had significantly greater variability (C_V) in abiotic conditions compared to the open-ocean sites (**Tables 1**, **2**). With the exception of salinity, all mean abiotic variables were also different between the seagrass meadows and back-reefs compared to the open-ocean reference (**Tables 1**, **2**). Specifically, mean pH_T was elevated at both of the inshore habitats (back-reef = 8.17 ± 0.01 and seagrass meadow = 8.16 ± 0.01) relative to the open-ocean (8.12 ± 0.01),

TABLE 1 | Physicochemical data for the seagrass and back-reef habitats on Little Cayman, Cayman Islands, British West Indies.

			Habitat					
			Back-reef		**Seagrass**		**Open-ocean**	
Abiotic Variable	**Season**	**Lunar Cycle**	**Mean (± SE)**	**Range**	**Mean (± SE)**	**Range**	**Mean (± SE)**	**Range**
pH_T	Summer	Spring	8.12 (0.01)	0.31	8.13 (0.02)	0.61	8.12 (0.01)	0.02
		Neap	8.16 (0.01)	0.27	8.17 (0.02)	0.58	8.11 (0.01)	0.02
	Winter	Spring	8.19 (0.01)	0.23	8.15 (0.02)	0.51	8.12 (0.01)	0.01
		Neap	8.20 (0.01)	0.22	8.19 (0.02)	0.50	8.12 (0.01)	0.01
$p\text{CO}_2$ (atm)	Summer	Spring	309 (9.97)	274	285 (20.08)	608	321 (0.67)	35
		Neap	281 (6.71)	219	279 (17.74)	570	320 (0.89)	61
	Winter	Spring	246 (6.11)	187	276 (12.62)	433	317 (0.74)	57
		Neap	206 (3.60)	139	243 (11.97)	459	320 (0.45)	81
Total Alkalinity (μmol/kg^{-1})	Summer	Spring	2,239 (7.03)	248	2,264 (8.14)	351	2,357 (6.70)	110
		Neap	2,279 (9.36)	302	2,250 (10.64)	302	2,365 (5.60)	100
	Winter	Spring	2,232 (1.66)	201	2,251 (6.30)	277	2,420 (2.50)	50
		Neap	2,244 (3.86)	138	2,242 (4.86)	176	2,350 (6.10)	99
Aragonite Ω	Summer	Spring	4.2 (0.08)	2.5	4.4 (0.15)	4.7	3.5 (0.01)	0.21
		Neap	4.2 (0.07)	2.3	4.5 (0.15)	4.6	3.5 (0.01)	0.22
	Winter	Spring	4.9 (0.06)	2.0	4.9 (0.13)	4.3	3.6 (0.01)	0.15
		Neap	5.4 (0.06)	2.5	5.1 (0.13)	4.1	3.5 (0.01)	0.16
Temperature (°C)	Summer	Spring	29.6 (0.05)	2.1	29.8 (0.07)	2.8	28.6 (0.01)	0.2
		Neap	29.2 (0.11)	3.8	29.2 (0.12)	4.1	28.5 (0.01)	0.3
	Winter	Spring	27.4 (0.12)	3.2	28.1 (0.20)	6.7	27.5 (0.01)	0.2
		Neap	26.4 (0.09)	2.8	26.9 (0.10)	4.3	27.5 (0.02)	0.3
Salinity	Summer	Spring	35.2 (0.03)	0.5	35.2 (0.06)	2.0	35.5 (~0.00)	~0.00
		Neap	35.2 (0.03)	0.5	35.0 (0.07)	2.0	35.5 (~0.00)	~0.00
	Winter	Spring	35.2 (0.03)	0.5	35.3 (0.04)	0.5	35.5 (~0.00)	~0.00
		Neap	35.2 (0.03)	0.5	35.2 (0.03)	1.0	35.5 (~0.00)	~0.00
Water Movement (cm^{-1} s^{-1})	Summer	Spring	18 (0.54)	19	16 (0.65)	19	21 (0.88)	19
		Neap	18 (0.46)	13	16 (0.64)	21	23 (0.74)	18
	Winter	Spring	13 (0.39)	12	12 (0.41)	14	19 (0.66)	17
		Neap	12 (0.35)	11	10 (0.36)	12	21 (0.47)	17
Light (μmol m^{-2} s^{-1})	Summer	Spring	304.1 (54.48)	1735	327.5 (54.43)	1225		
		Neap	350.8 (57.19)	1480	308.4 (53.08)	1276		
	Winter	Spring	319.1 (55.19)	1429	265.8 (43.53)	970		
		Neap	324.8 (53.89)	1531	252.0 (40.53)	919		

Data from the open-ocean reference sites is also provided for comparison. The carbonate chemistry data shown is the mean (± SE) and range of $n = 3$ days per season and lunar cycle (discrete water samples: $n = 432$ for the back-reef and seagrass and $n = 54$ for the open-ocean). Light data was obtained from in situ HOBO® data loggers that were set to log at 1 min intervals over the study duration. Data shown is for the first ten days of each month (due to fouling, see Methods, with $n = 24$-33 days per season and lunar cycle).

irrespective of season or phase of the lunar cycle (**Tables 1**, **2**). The elevation in mean pH_T and corresponding depletion in $p\text{CO}_2$ was significant enough to elevate mean Ω_{arg} in the seagrass meadow and back-reef habitats relative to the open-ocean sites [$F_{(2,\,105)} = 166.45, p < 0.001$, **Tables 1**, **2**].

The seagrass meadows had greater variability in environmental conditions across the measured parameters than the back-reefs (see **Table 1**), with pH_T the most variable condition measured. Specifically, the pH_T range in the seagrass meadows over diurnal (0.51 ± 0.07), seasonal (0.62 ± 0.03) and lunar cycle (0.58 ± 0.04) time scales was *ca.* double that of the back-reefs (diurnal 0.22 ± 0.02, seasonal 0.29 ± 0.04, lunar 0.24 ± 0.05). Both habitats experienced a greater range of pH_T conditions during the summer season and on spring tides (**Table 1**), with the seagrass meadows reaching a maximum pH_T of 8.28 ± 0.02 around mid-day and a low of 7.80 ± 0.01 at night

TABLE 2 | Statistical results for comparisons of abiotic variables among the back-reef and seagrass habitat types and relative to the open-ocean reference sites.

Abiotic variable	*F*-value (D.F)	*P*-value	Site type	*Post-hoc* Grouping
(A)				
pH_T	$104.87_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	C
Temperature	$4.21_{(2, 105)}$	<0.05	Open-ocean	A
			Back-reef	AB
			Seagrass	B
Total Alkalinity	$417.27_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	B
Aragonite Ω	$166.45_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	C
Salinity	$0.32_{(2, 105)}$	N/S		
Water Velocity	$69.56_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	B
(B)				
pH_T	$371.97_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	C
Temperature	$173.56_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	B
Total Alkalinity	$12.46_{(2, 105)}$	<0.01	Open-ocean	A
			Back-reef	B
			Seagrass	B
Aragonite Ω	$325.90_{(2, 105)}$	<0.001	Open-ocean	A
			Back-reef	B
			Seagrass	C
Salinity	$12.39_{(2, 105)}$	<0.01	Open-ocean	A
			Back-reef	B
			Seagrass	B
Water Velocity	$8.43_{(2, 105)}$	<0.01	Open-ocean	A
			Back-reef	B
			Seagrass	B

__(A)__ Results from analysis of variance (ANOVA) comparing daily mean values of abiotic variables among habitat types. Seasonal and lunar data were grouped by site to generate n = 36 daily means per habitat type. Post-hoc grouping letters denote differences among habitat types identified using Tukey's post-hoc test. __(B)__ Results from ANOVA comparing the coefficient of variation (Cv) for abiotic variables among habitat types. Seasonal and lunar data were grouped by site to generate n = 36 values per habitat type. Post-hoc grouping letters denote differences among habitat types identified using Tukey's post-hoc test.

(**Figure 2**). Oxygen co-varied with pH, with maximum levels experienced in the day (7.11 ± 0.2) and lowest levels occurring at night (4.6 ± 0.1). Mean values of temperature, light, A_T, salinity, and water velocity did not differ between the back-reefs and seagrass meadows (**Table 1**).

Benthic Structure

In the seagrass meadows, benthic cover was primarily photoautotrophs (seagrass and non-calcifying algae), with the back-reefs predominantly comprised of abiotic-hard and abiotic-soft ground (**Figure 3**). Across years there was little variation in the benthic composition of each site (see Supplementary Figure 1). Only the GTB back-reef site was different between 2012 and 2013 [two-tailed *t*-test, $t_{(4)} = 3.79$, $p < 0.05$], resulting from changes in the composition of photoautotrophs and a 1.7 fold increase in scleractinian coral cover in 2013.

The back-reefs had *ca*. twice the mean coral cover of the seagrass meadows (back-reef: 6.5 ± 1.2%, seagrass: 2.7 ± 0.4%) and coral community composition within each habitat did not differ between years (**Table 3**). Coral species richness, diversity, and evenness were also higher in the back-reefs compared to the seagrass meadows in both years (**Table 3**). Although coral cover was higher in the back-reefs, there was a greater density of corals in the seagrass meadows than in the back-reefs (back-reef 119.5 ± 12.8, seagrass 236 ± 95.6 per 20 m^2). No dependence between year and habitat type was detected for absolute counts of corals. Coral colonies were relatively small in both habitats, however faster exponential decay rates suggests that seagrass communities were dominated by higher numbers of small coral colonies, while counts were more even across size classes in the back-reefs (**Figure 4**). Size profile of colonies did not differ significantly across the two years of study. Coral disease prevalence was low across habitats for both years (<1%). However, the prevalence of old mortality was higher on the back-reefs compared to the seagrass meadows [back-reef: 14 ± 0.07%, seagrass: 2 ± 0.02%; $F_{(2, 36)} = 253.46$, $p < 0.001$].

Seagrass coral communities were comprised almost entirely of Poritidae (49.0 ± 0.02%) and Siderastreidae (49.8 ± 0.04%), while these families comprised 65.0 ± 0.03% of total coral cover on the back-reefs (followed by Faviidae which contributed 11.4 ± 0.01%). The dominant coral species in the back-reefs for both years was *Porites astreoides* (2012: 32 ± 0.7%, 2013: 36 ± 0.4%), while *Siderastrea radians* was the dominant species in the seagrass meadows both years (2012: 49 ± 0.3%, 2013: 52 ± 0.5%). Supplementary Table 1 provides a full list of coral species observed in each habitat across both years of study.

Recruitment

Coral recruitment onto settlement tiles was only observed during the months of August and September (in both 2012 and 2013). More coral spats recruited to the tile arrays in the back-reefs compared to the seagrass meadows [**Figure 5A**; $t_{(17)} = 8.84$, $p < 0.001$]. A greater diversity of corals also recruited to the back-reef compared to the seagrass meadows (**Figure 5**). Poritidae and Siderastreidae were the most common families observed on the tiles from both habitat types (**Figure 5**). In general, the proportional density of coral species in the

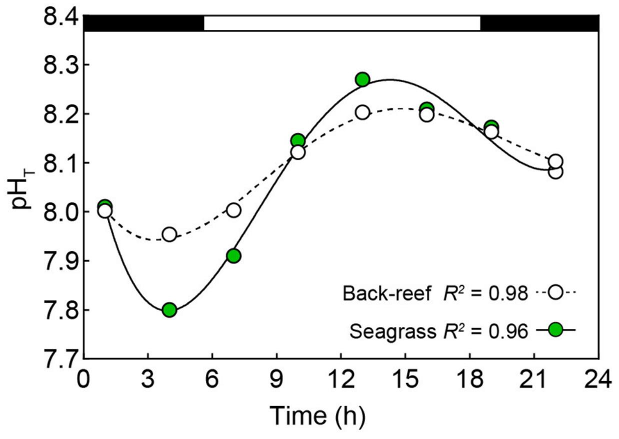

FIGURE 2 | Mean (±SE, note: not visible below symbols) pH_T (total scale) values for the back-reef (open symbols) and seagrass habitats (green symbols) obtained at eight-time points over a full night (black horizontal bar) and day (white horizontal bar) cycle (discrete water samples: $n = 432$). R^2 produced by fitting the data to a fourth order polynomial function ($Y = a + bx + cx^2 + dx^3 + ex^4$).

recruited populations mirrored the proportional density in the established populations (**Figure 5**). Acroporidae and Agariciidae were absent from both the recruited and established population in the seagrass. However, Faviidae was absent from only the established population in the seagrass (**Figure 5C**). In the back-reefs, the proportional density of Acroporidae, Agariciidae and "other" recruits were significantly higher compared to that of the established population ($p < 0.01$). Also, on the back-reef the proportional density of Faviidae recruits was significantly lower compared to that of the established population ($p < 0.01$). Both the back-reefs and seagrass meadows had more corals that belonged to families other than Acroporidae, Agariciidae, Poritidae, Siderastreidae and Faviidae (and thus fell into the "other" category) in the recruited population compared to the established population ($p < 0.001$).

Analysis of the composition of all benthic taxa on the experimental tiles following the full 25-month study revealed significant differences between the back-reefs and seagrass meadows [$F_{(4,\,13)} = 200.73$, $p < 0.01$; Supplementary Figure 2]. Notably, the percent cover of recruited corals was less than 1% in both habitats. Also, cover of calcareous Rhodophyta (i.e., crustose coralline algae) was significantly higher on tiles in the back-reefs compared to the seagrass meadows (*post-hoc* Tukey test: $p < 0.05$).

DISCUSSION

Seagrasses are recognized as important primary producers (Duarte and Chiscano, 1999) and for their roles in sediment stabilization and carbon sequestration (Duarte et al., 2013), but the role of seagrass meadows as a habitat in which scleractinian corals can recruit, grow, and reproduce has not been well-studied. We observed up to 14 established scleractinian taxa living within seagrass meadows, despite considerable physicochemical variability. Our data also demonstrate that the larvae of multiple coral families are able to recruit into seagrass meadows. These findings are consistent with previous reports of established coral communities among seagrasses (Rützler and Macintyre, 1982; Johnson, 1992; Higuchi et al., 2014).

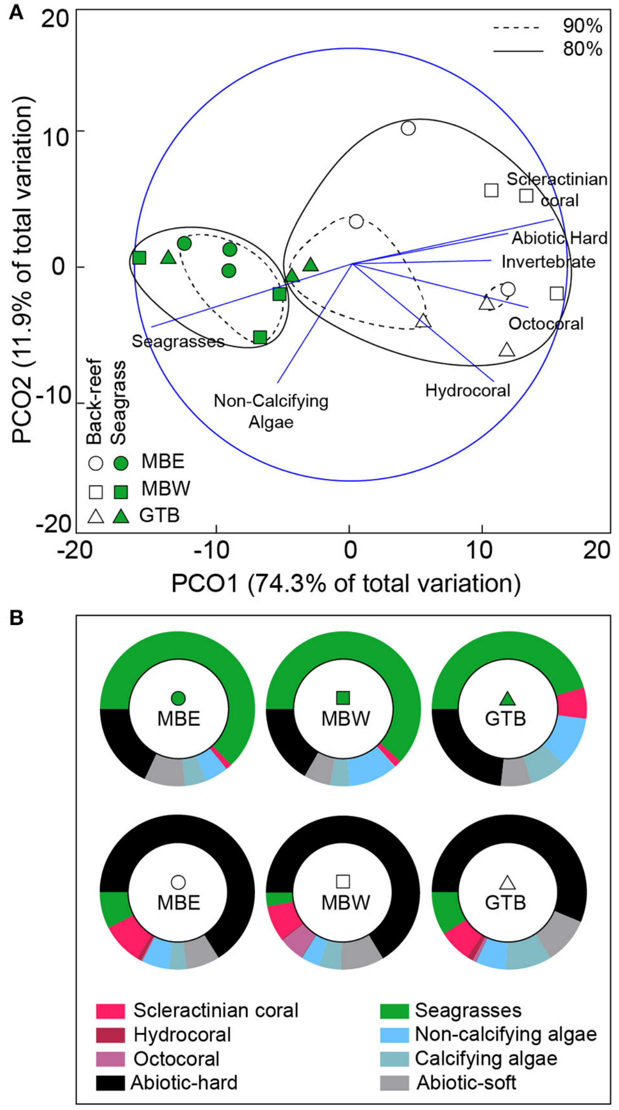

FIGURE 3 | Benthic composition of back-reef and seagrass sites. Principal co-ordinate analysis (PCA) plot **(A)** of the benthic categories pooled across both 2012 and 2013 (using all species and abiotic categories) per sites with 80% (solid) and 90% (hashed) similarities shown. Pearson's correlations that exceed $R > 0.6$ are represented as vectors in blue. The proportional composition of each benthic category pooled across years is shown in **(B)**. Note: invertebrates other than the Cnidarians are not visible due to their low density.

Physicochemical Conditions

Seagrass beds were characterized by higher variability in both temperature and pH compared to the adjacent back-reef. This is

TABLE 3 | Summary of established coral community characteristics in the back-reef and seagrass habitats of Little Cayman, Cayman Islands.

Year	Habitat	Average density (per $20m^2$)	Mean (± SE) colony size (cm)	Species richness	Shannon- wiener index	Shannon- wiener evenness
2012	Back-reef	107 ± 12.4	12.0 ± 0.75	18	1.18	0.48
2013	Back-reef	132 ± 10.2	10.0 ± 0.34	21	1.45	0.58
2012	Seagrass	209 ± 112.5	4.3 ± 0.08	13	0.78	0.35
2013	Seagrass	262 ± 98.3	6.0 ± 0.22	14	0.84	0.37

consistent with previous studies of physicochemical conditions at this study site (Barry et al., 2013; Camp et al., 2016a,b). High physicochemical variability has also been reported for shallow seagrass beds globally; a diel temperature range of as much as 6°C has been reported for shallow seagrass beds (Semesi et al., 2009), consistent with the range of up to 6.7°C recorded in the present study. Similarly, mean diel fluctuations of 0.34 (Saderne et al., 2013) to 0.35 pH units (Challener et al., 2016) have been reported previously from studies of macrophyte beds. One study reported diel fluctuations in excess of 1 pH unit (Semesi et al., 2009). The pH range recorded in Little Cayman seagrass beds (0.51–0.62 pH units) is therefore consistent with previous reports, and is similar to the pH range reported from a study of Grape Tree Bay in 2011 (0.47 pH units, Barry et al., 2013). These substantial fluctuations in pH result from changes in pCO_2 driven by seagrass photosynthesis and respiration (Semesi et al., 2009; Saderne et al., 2013; Challener et al., 2016). Covariance of DO with pH is also consistent with previous reports (Barry et al., 2013), and supports the idea that seawater chemistry is altered by seagrasses (Challener et al., 2016). Although physicochemical conditions fluctuated less on the back-reef, variability was still high compared to the open ocean reference site. This is likely due to the effects of the adjacent seagrass meadow; seagrasses have been shown to alter carbonate chemistry of seawater on adjacent reefs (Manzello et al., 2012).

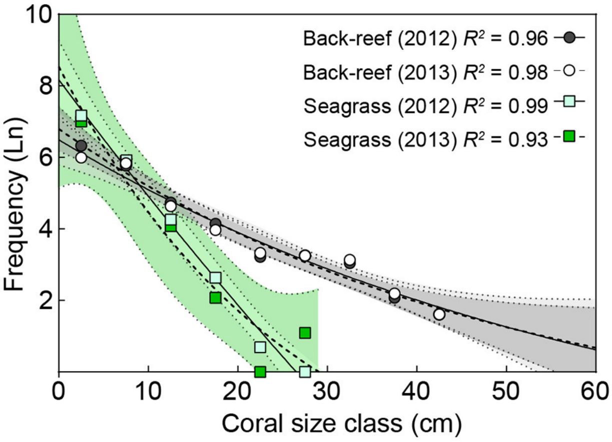

FIGURE 4 | A comparison of coral colony sizes in back-reef and seagrass habitats. Exponential decay model of coral colony size vs. the natural log (Ln) of the frequency of corals within each size class for 2012 (solid lines) and 2013 (hashed lines) in back-reef (circles) and seagrass (squares) habitats. Data are pooled across study sites ($n = 3$) and 95% confidence bands of each model are shown by areas colored corresponding to symbol colors.

Living under more variable physicochemical conditions can place an enhanced energetic burden on physiological maintenance (Hofmann and Todgham, 2010). Although extreme temperatures are known to be detrimental to coral populations (Eakin et al., 2009), some populations have shown capability for adapting or acclimating to temperature extremes (Craig et al., 2001; Palumbi et al., 2014; Schoepf et al., 2015). Thermal tolerance is also known to vary among coral taxa (Darling et al., 2012), and this variability could therefore explain why some taxa were only observed in the less-variable back-reef in the present study. Similarly, although some sites have been shown to maintain high coral cover and diversity in low-pH conditions (e.g. Golbuu et al., 2016), reduced pH has been shown to limit the abundance (Price et al., 2012) and diversity (Fabricius et al., 2011; Crook et al., 2012) of calcifying organisms at other locations. In the present study, pH at the seagrass sites routinely dropped to values considered unfavorable for most corals (e.g., <7.8, **Figure 2**; see also Camp et al., 2016a), and therefore may have resulted in environmental filtering against some coral species (Sommer et al., 2014). The ability to tolerate reduced pH varies among coral species (McCulloch et al., 2012), and importantly, low pH appears to inhibit settlement of *Acropora palmata*, potentially through alteration of larval settlement processes or chemical settlement cues from crustose coralline algae (Albright et al., 2010). Together these factors governing sensitivity provide one possible explanation for the lack of Acroporidae spats either on settlement tiles or in the established coral community at the seagrass sites despite the presence of established and recruited *Acropora* spp. in the adjacent back-reef. It is however critical to note that the ability of seagrasses to alter seawater carbonate chemistry is dependent on the seagrass species present, water depth, water residence time, and a variety of other local conditions (Unsworth et al., 2012). It is therefore possible that seagrass meadows in other locations could harbor a higher diversity of coral species.

Benthic Structure

Previously published data on coral community composition within seagrass meadows is limited, however our observations of *Manicina areolata* (Johnson, 1992), *Porites furcata* (Wulff, 2008), and *S. radians* (Rützler and Macintyre, 1982) populating seagrass meadows are consistent with previous Caribbean studies. In contrast to our observations, Rützler and Macintyre (1982) report occasional *Acropora cervicornis* colonies within seagrass patches in Belize; however this data was published prior to the widespread

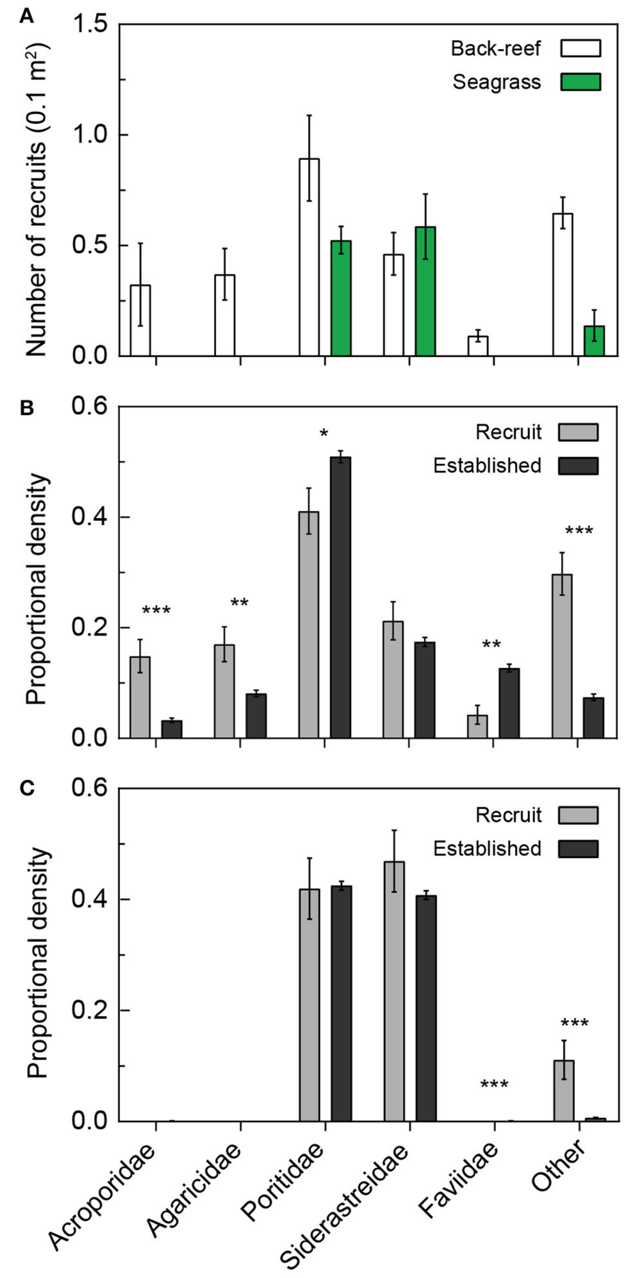

FIGURE 5 | Recruitment of corals into back-reef and seagrass habitats relative to the established population. Number of coral recruits (0.1 m^2) on settlement tiles **(A)** located in back-reef (white bars) and seagrass (green bars) habitats pooled across 2012 and 2013. Coral recruits (gray bars) are compared to the respective proportions of established corals (dark gray bars) within the same families in back-reef and seagrass habitats in **(B,C)**, respectively. Significant differences between the proportions of established and recruited corals are denoted by asterisks, specifically $p < 0.05$ (*), < 0.01(**), and < 0.001 (***).

regional decline of Caribbean acroporids (Aronson and Precht, 2001), which could partially explain its absence within seagrass meadows in our study. Low mean coral cover within seagrass meadows in the present study (2.7 ± 0.4%) is also generally consistent with, although somewhat lower compared to, reported coral cover in Indian Ocean (4.20% coral cover) and Pacific Ocean (5.40% coral cover) seagrass meadows (Camp et al., 2016a).

Although size data for corals in seagrass meadows are also rare, previous studies suggest that coral colonies within seagrass in the Caribbean are generally small (Johnson, 1992; Wulff, 2008), consistent with our findings of relatively small colonies in Little Cayman seagrass meadows. Small colony size is characteristic of species that are better able to survive poor conditions (Darling et al., 2012) that may occur frequently in shallow seagrass meadows, including sedimentation, thermal stress, and reduced pH. Small size is also characteristic of the dominant coral species in the seagrass meadow, *S. radians* (Lirman and Manzello, 2009). Decreased colony size has also been directly associated with low pH conditions (Crook et al., 2012), which regularly occurred in the seagrass meadows studied.

Although the seagrass meadows and back-reefs assessed in this study were in close proximity to one another, species richness and diversity of the established coral community were lower in seagrass meadows. Given that availability of hard substrate is fundamental in structuring benthic communities (Jackson, 1977; Taylor and Wilson, 2003), higher availability of hard substrate in the back-reef is likely a significant factor in the observed higher cover and diversity of corals. Hard substrate is characteristic of reefs, as reef structure is formed by deposition of calcium carbonate skeleton by living corals (Hallock, 2015). In contrast, seagrasses generally require soft sediment, and therefore seagrass meadows typically lack abundant hard substrate (Hemminga and Duarte, 2000). Many of the common coral species in the seagrass meadows studied (i.e., *S. radians*, *Porites divaricata*, *P. porites*) are capable of recruiting to suboptimal habitats (Darling et al., 2012). *S. radians* in particular has been shown to be highly tolerant of sediment burial (Lirman and Manzello, 2009), which is likely frequent in the soft-sediment seagrass meadow.

Recruitment

Recruitment onto experimental tiles during the 25-month study was only observed during the months of August and September, which is consistent with observations of multiple species spawning in the Cayman Islands during these months in 2012 and 2013 (C. McCoy, Cayman Islands Department of Environment, personal communication), and with published reports for spawning times among Caribbean broadcast-spawning corals (e.g., Jul-Sept, Szmant, 1986). However, our results contrast with previous studies that have documented year-round planulation in Caribbean brooding species with varying species-specific annual peaks in larval release (Szmant, 1986; Chornesky and Peters, 1987; Soong, 1991; Schlöder and Guzman, 2008). Recently reported coral recruit densities vary among sites within both the Caribbean [e.g., 0.14–1.17 spat m^{-2} (Edmunds et al., 2014), 30 ± 46 – 236 ± 143 spat m^{-2} (Humanes and Bastidas, 2015)] and the Indo-Pacific [e.g., 1.42 ± 0.33 – 1.72 ± 0.64 spat m^{-2} (Salinas de León et al., 2011), 54.74 spat m^{-2} (Bauman et al., 2015)]. Johnson (1992) reported recruitment ranging from <1 to 5 spat m^{-2} for *M. areolata* in a seagrass meadow. Recruit densities in our study (i.e., back-reef 1.2 ± 0.05

spat m^{-2}, seagrass: 0.5 ± 0.03 spat m^{-2}) fall within the range reported from Caribbean sites in the published literature.

Factors governing coral recruitment are complex, and recruitment success can be temporally and spatially variable due to factors such as temporal variability in fecundity and physical disturbances (Fitzhardinge, 1985; Williams et al., 2008). The presence or absence of other species can also influence recruitment. For example, crustose coralline algae and microbial biofilms are known to provide cues that induce coral settlement (Heyward and Negri, 1999; Webster et al., 2004). Though our current data set provides new information regarding coral recruitment into seagrass meadows and adjacent back-reefs, it precludes fully understanding the complex nature of differences in recruitment between habitats.

Comparison of Established and Recruited Communities

Although the diversity and density of coral recruits differed between the seagrass and back-reef, community composition of recruited corals largely mirrored that of established corals within sites. This contrasts with multiple studies of coral reefs, which have reported variability in the composition of established and recruited coral communities (e.g., Dunstan and Johnson, 1998; Bramanti and Edmunds, 2016). However, our findings are consistent with those of Johnson (1992), who found that recruitment rates for *M. areolata* in a seagrass bed related to local density of reproductive adult colonies. The established and recruited coral communities in seagrass meadows were comprised almost entirely of brooding species (**Figure 5**), which are believed to have a relatively short dispersal distance as a result of rapid settlement following release of planulae (Szmant, 1986; Harriott, 1992; Johnson, 1992; Carlon and Olson, 1993; Kenkel et al., 2013). Brooded planulae also typically receive zooxanthellae from their parent colonies in Caribbean species (Szmant, 1986; Thornhill et al., 2006), and planulae may therefore have a physiological advantage to settle locally, as symbionts and hosts are both adapted to local abiotic conditions (Kenkel et al., 2013). Short dispersal distance combined with local adaptation may therefore explain why the recruited population was highly similar to the established population in each habitat, and also why brooding Agariciidae were not found to disperse from the back-reef to the seagrass.

Despite overall similarity between the recruited and established community within habitats, differences were apparent for some coral families. These intra-habitat differences may also be explained by differences in reproductive strategy. Broadcast spawning corals are particularly susceptible to "Allee effects" and subsequent sexual recruitment failure, especially when densities of mature colonies are low (Knowlton, 2001). For example, Acroporidae are known to have low sexual reproductive success and recruitment in the Caribbean, and thus rely heavily on asexual fragmentation as a reproductive mechanism (Tunnicliffe, 1981; Richmond and Hunter, 1990; Williams et al., 2008). Reliance on asexual fragmentation could explain why relatively high cover of established Acroporidae was observed in the back-reef despite low levels of recruitment across both years of study. Asexual fragmentation is also used as a reproductive mechanism in some poritids, such as *P. furcata* (Highsmith, 1982). This could potentially explain the abundance of Poritidae in the established population in both the back-reefs and seagrass meadows, as fragmentation can play a role in establishing local dominance by certain species (Highsmith, 1982). Local abundance of Poritidae achieved through fragmentation could ultimately lead to higher rates of sexual reproduction and subsequent recruitment, which was also observed in both habitats. In contrast, lower relative cover of established Faviidae compared to the recruited population could suggest post-settlement mortality, which was found to be common for *Orbicella faveolata* (Szmant and Miller, 2006; Miller, 2014). Dispersal of coral larvae from distant reefs could also explain observed differences in community composition between established and recruited corals (Harriott and Fisk, 1988). We currently lack data to determine whether outer reef sites may have served as a larval source for recruits in either habitat, however recent work has demonstrated high levels of connectivity between reefs (Schill et al., 2015); it is therefore conceivable that larval exchange between the outer reef, back-reef, and seagrass meadow is possible.

CONCLUSIONS AND FUTURE CONSIDERATIONS

Our study demonstrates that multiple coral species are able to live within and recruit to seagrass meadows, suggesting that corals are capable of using such systems as a habitat regardless of naturally high variability in environmental conditions relative to neighboring reefs. Fluctuating physicochemical conditions in seagrass meadows can expose corals to both periods of high temperature and periods of low pH, which could enhance tolerance to thermal and chemical stress, respectively (Camp et al., 2016a). Evidence suggests that transgenerational acclimatization is possible following exposure to extreme temperature and pH conditions (Putnam and Gates, 2015); however, exposure of the corals *P. astreoides* and *A. palmata* to environmental variance found within seagrass meadows resulted in no enhanced resistance to subsequent temperature and pH stress (Camp et al., 2016b). Furthermore, some seagrass meadows have been shown to buffer against ocean acidification by elevating mean pH in their vicinity, potentially improving the ability of downstream corals to calcify (Manzello et al., 2012). The potential biogeochemical-services seagrass meadows can provide under climate change remains unresolved. Given that seagrasses will be potentially selected for under future climates (Garrard and Beaumont, 2014), they may continue to provide habitat for some coral species. Clearly large gaps still remain in understanding the nature of coral populations in these habitats and the extent to which they can persist in a changing climate. Further studies are needed across other geographic locations to fully understand the extent to which seagrass beds may serve as coral habitats. Importantly however, the added role of seagrass systems in providing coral habitat emphasizes the critical importance in managing and conserving these sites.

AUTHOR CONTRIBUTIONS

All authors have agreed to be listed on and approve this manuscript. EC, DJSu, and DJSm conceived and designed the study; KL and EC collected the data; EC, AD, MN, and SW analyzed the data; MN prepared all figures; KL, EC, and DJSu wrote the manuscript; all authors discussed and critically 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.2017.00388/full#supplementary-material

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Physiological and Biogeochemical Responses of Super-Corals to Thermal Stress from the Northern Gulf of Aqaba, Red Sea

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Mass coral bleaching is increasing in frequency and severity, leading to the loss of coral abundance and diversity. However, some corals are less susceptible to bleaching than others and can provide a model for identifying the physiological and biogeochemical traits that underlie coral resilience to thermal stress. Corals from Eilat in the Gulf of Aqaba in the northern Red Sea do not bleach unless seawater temperatures are sustained at +6°C or higher above their average summer maximum. This extreme thermal tolerance qualifies these as super-corals, as most corals bleach when exposed to temperatures that are only +1–2°C above their thermal maximum. Here, we conducted a controlled bleaching experiment (+6°C) for 37 days (equivalent to 32° heating weeks) on three species of corals from Eilat: *Stylophora pistillata, Pocillopora damicornis,* and *Favia favus*. To assess the response of the holobiont to thermal stress, the following variables were measured on each coral: endosymbiotic algal cell density, Chlorophyll *a*, endosymbiotic mitotic cell division, total lipids, protein, carbohydrate, and the stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopic composition of the skeleton and the $\delta^{13}C$ of the animal host tissue and endosymbiotic algae. While all three species appeared visibly bleached, their physiological and biogeochemical responses were species-specific. *S. pistillata* catabolized lipids but still maintained total energy reserves and biomass. Increases in both skeletal $\delta^{13}C$ and $\delta^{18}O$ indicates that calcification declined in this species. *P. damicornis* was the least affected by bleaching. It maintained its total energy reserves and biomass, and isotopic evidence suggests that it maintained calcification and was not dependent on heterotrophy for meeting metabolic demand when bleached. Finally, *F. favus* catabolized protein and carbohydrates, and suffered losses in total energy reserves and biomass. Nevertheless, isotopic evidence suggest that photosynthesis and calcification were maintained, and that this species has a high baseline heterotrophic capacity. Thus, just like their non-super-coral conspecific counterparts, maintaining energy reserves and biomass, and heterotrophic capacity appear to be traits that underlie the thermal tolerance of these super-corals from Eilat. Given the high thermal tolerance of these super-corals, these populations could provide viable seed stock for repopulating coral losses on other reefs.

Keywords: coral bleaching, heterotrophy, energy reserves, isotopes, resilience, physiology, biogeochemistry, Red Sea

INTRODUCTION

Increased atmospheric carbon dioxide (CO_2) is causing the oceans to warm and to become more acidic. Over the course of this century, tropical seawater temperatures are expected to rise by 1–3°C coupled with a drop in pH of 0.2–0.4 (IPCC, 2013). At this rate, tropical reefs are expected to experience significant declines in coral abundance, coral diversity, and reef growth during the second half of this century (e.g., Hoegh-Guldberg et al., 2007; Eakin et al., 2009; Veron et al., 2009; Hoegh-Guldberg, 2011). While coral calcification is projected to decline by 5% by 2034, severe bleaching will be annual by 2030 in some regions and globally by 2055 (van Hooidonk et al., 2014). Recent studies have shown that the warming of tropical oceans is a much more immediate threat to the survival of coral reefs than is ocean acidification (e.g., Cantin et al., 2010; Frieler et al., 2012; Chua et al., 2013). Corals can survive slight decreases in calcification, but it is not likely that they can physiologically survive severe bleaching on an annual basis.

Elevated temperatures can cause corals to bleach: a physiological response to sustained elevated temperatures that results in a breakdown of the coral symbiosis, the loss of the coral's algal endosymbiont partners, which results in a white appearance. The consequences of bleaching to the coral are reduced coral growth, disease, reduced fertility, and death (e.g., Brown, 1997; Hoegh-Guldberg, 1999; Omori et al., 1999; Buddemeier et al., 2004; Tchernov et al., 2011). The frequency of bleaching events appears to be increasing (Eakin et al., 2009; Heron et al., 2016) and back-to-back bleaching years have been observed on basin-wide scales (coralreefwatch.noaa.gov). Annual bleaching is predicted to occur by 2030 in some regions (van Hooidonk et al., 2013, 2014), resulting in large coral losses.

Interestingly, there are corals that are less susceptible to and/or recover more quickly from bleaching (e.g., Loya et al., 2001; Grottoli et al., 2006, 2014; Fine et al., 2013). Resilience to bleaching has been associated with high energy reserves, heterotrophic plasticity, and endosymbiont type (Rowan et al., 1997; Baker et al., 2004; Tchernov et al., 2004; Berkelmans and van Oppen, 2006; Grottoli et al., 2006, 2014; Rodrigues and Grottoli, 2007; Anthony et al., 2009; Guest et al., 2012). Corals with elevated levels of energy reserves (i.e., lipids, protein, carbohydrates) either take longer to bleach, bleach less severely, and/or recover more quickly from bleaching than corals with lower energy reserves because they have an energy source to buffer them against losses in photosynthetically derived fixed carbon (e.g., Rodrigues and Grottoli, 2007; Anthony et al., 2009; Grottoli et al., 2014; Schoepf et al., 2015). Corals that increase their intake of heterotrophic carbon (i.e., zooplankton, dissolved and particulate organic carbon) or increase the proportionate contribution of heterotrophic vs. photoautotrophic carbon in their tissues when bleached, are able to partially or fully supplement the deficit in their carbon budgets due to declines in photosynthesis when bleached, and are able to recover more quickly from bleaching (Grottoli et al., 2006, 2014; Rodrigues and Grottoli, 2006; Palardy et al., 2008; Levas et al., 2013, 2016). Corals that are able to shuffle or switch their dominant endosymbiont type for a thermally tolerant one are less sensitive to repeat exposures to thermal stress (e.g., Rowan et al., 1997; Baker et al., 2004; Berkelmans and van Oppen, 2006; Grottoli et al., 2014). In addition, there are regions such as the northern region of the Gulf of Aqaba, where entire communities of corals can already tolerate extreme warming conditions, thought the underlying traits that produce that extreme tolerance is poorly understood. These corals may provide seed stock for restoring dying reefs as well as be a model system for identifying the physiological and biogeochemical traits that underlie coral resilience to thermal stress.

Corals in the northern tip of the Gulf of Aqaba in the Red Sea do not bleach when exposed to temperatures that are ≥6°C above their average summer time maximum temperatures for 3–4 weeks (Fine et al., 2013) coupled with extreme salinities of 41ppt (Paldor and Anati, 1979). This is remarkable resilience to extreme increases in seawater temperature given that most corals bleach when seawater temperatures exceed summertime maximum temperature by as little as 1–2°C for as little as 2–4 weeks (e.g., Hoegh-Guldberg, 2011). Fine et al. (2013) proposed that this extreme thermal tolerance in these northern Red Sea corals is due to natural selection processes on the larvae transported to the northern section of the Gulf of Aqaba through the very hot straights of Bab el Mandeb in the southern Red Sea. However, the underlying physiological traits responsible for the resilience of these corals is not fully understood. We hypothesized that like their less thermally tolerant counterparts, maintenance of energy reserves and biomass, as well as heterotrophic plasticity, are all traits responsible for extreme temperature tolerance in super-corals of the northern Gulf of Aqaba. To test this hypothesis, bleaching was induced by thermal stress in an experiment conducted on three species of corals (*Stylophora pistillata, Pocillopora damicornis,* and *Favia favus*) from the Gulf of Aqaba near Eilat, Israel and the physiological and biogeochemical responses of the host and algal endosymbiont were assessed.

MATERIALS AND METHODS

Two fragments from five healthy colonies of *S. pistillata* and *P. damicornis* (5–7 cm tall), and two fragments for seven healthy colonies of *F. favus* (6–8 cm in diameter) were collected between 2 m and 4 m depth in the Gulf of Eilat (northern Gulf of Aqaba), Israel (29° 30′ 5.55″ N, 34° 55′ 2.49″ E) in mid-February 2005 and glued to labeled gray PVC tiles using underwater epoxy putty. All three species are common in this region. *S. pistillata* is a branching coral, a reproductive brooder, and is dominated by the endosymbiont *Symbiodinium* clade A (Shlesinger and Loya, 1985; Karako-Lampert et al., 2004; Winters et al., 2009; Byler et al., 2013; Ziegler et al., 2017). *P. damicornis* is also a branching coral, is a member of a genus that reproduces by both broadcasting and brooding (though spawning has never been documented for this species in the Red Sea), and is dominated by the endosymbiont *Symbiodinium* clade C (Shlesinger and Loya, 1985; Karako-Lampert et al., 2004; Fine et al., 2013; Sawall et al., 2015; Ziegler et al., 2017). *F. favus* is a mounding coral, a broadcast spawner, and dominated by the endosymbiont *Symbiodinium* clade C (Shlesinger and Loya, 1985; Karako-Lampert et al., 2004; Fine et al., 2013). *Symbiodinium* clade D has never been reported for healthy or bleached corals in this region (Fine et al., 2013).

One fragment from each colony was placed in each of two 95-liter outdoor flow-through seawater tanks at the Interuniversity Institute for Marine Science of Eilat, Israel at the northern tip of the Gulf of Aqaba, Red Sea, and allowed to acclimate to the tanks and recover for 2 weeks. The tanks were shaded with black shading nets to simulate photosynthetically active radiation levels at collection depth, and the seawater was filtered through a small coarse gravel filter (70–200 μm pore size), allowing only small organic particulates and dissolved organics into the tanks. Thus, heterotrophic food sources available to the corals were limited to dissolved and particulate organic matter that came through the tank system. Coral were not supplemented with zooplankton. Flow rates were maintained in each tank at 2 l/min allowing each tank to fully flush every 47 min. On 28 February 2005, the seawater temperature was gradually increased over 3days using three 300W ATMAN aquarium heaters per tank yielding an average daily temperature of 32°C, while the second tank remained at ambient seawater temperature as controls with an average temperature of 26°C. The rate of temperature increase in the 32°C tank was chosen to minimize heat shock and also get the tank up to temperature relatively quickly. Since these corals are very tolerant of elevated temperatures, the rate of increase was not detrimental to these corals. The original temperature logger data has been lost, but the typical standard deviation of average daily temperatures in experimental tanks at the institute are ± 0.5°C. On 6 April 2005 (37 days later), the fragments were collected, frozen at −80°C, and shipped frozen to the Grottoli laboratory for analyses. In the lab, a quarter of each fragment was used for the following analyses: (1) chlorophyll *a* (Chl *a*) concentration, (2) total lipid, soluble animal protein, and soluble animal carbohydrate concentrations, (3) endosymbiotic algae concentrations and mitotic indexes, and (4) stable isotopic analyses of the host tissue, endosymbiotic algae, and underlying skeleton.

Algal Endosymbiont Analyses and Coral Energy Reserves

Chl *a* was extracted from ground samples in 100% acetone and the absorbance measured at 663 and 630 nm wavelengths using a Spectronic 20 Genesis visible spectrophotometer. The Chl *a* concentration was calculated using equations from Jeffrey and Humphrey (1975) corrected for turbidity with the absorbance value measured at 750 nm. Algal endosymbionts were separated from the animal tissue by centrifugation and three subsamples were counted with a hemocytometer and light microscope. The total number of algal cells and the number of mitotically dividing algal cells were recorded.

Total lipids were extracted in a 2:1 chloroform/methanol solution, washed in 0.88% KCl, and then dried to a constant weight (method modified from Grottoli et al., 2004). Soluble animal protein was extracted using the bicinchoninic acid method (Smith et al., 1985) with bovine serum albumin as a standard (Pierce BCA Protein Assay Kit). Soluble animal carbohydrate was extracted using the phenol-sulfuric acid method (Dubois et al., 1956) with glucose as a standard. All analyses were made from whole ground coral samples, converted into Joules (Gnaiger and Bitterlich, 1984), and standardized to both grams of ash free dry weight (gdw) and to surface area as measured using the aluminum foil technique (Marsh, 1970). However, normalization to ash free dry weight is more robust when comparing species with different tissue depths, morphology, and polyp structure than the same data normalized to surface area (Edmunds and Gates, 2002). Therefore, only results of data standardized to ash free dry weight are reported here (However, note that all statistics were also performed on the area normalized data and yielded almost identical patterns). Total energy reserves were calculated as the sum of total lipids, proteins, and carbohydrates. Total dry biomass was standardized to surface area. These analytical methods have been successfully used in corals before (e.g., Rodrigues and Grottoli, 2007).

Stable Isotopic Analyses

Coral tissue was completely removed from the skeleton using a Water-pik (Johannes and Wiebe, 1970). The tissue slurry was separated into animal host and algal endosymbiont fractions by centrifugation using established methods (Rodrigues and Grottoli, 2006). Briefly, coral slurry was homogenized to break open the animal cells, then centrifuged at 4,000 rpm for 5 min to separate the animal host and endosymbiotic algal fraction. The supernatant (i.e., animal host) was decanted and the algal pellet resuspended in deionized water and centrifuged again to remove any remaining animal host particles. The supernatants from both centrifugations were combined. Each organic fraction was isolated onto a pre-burned glass fiber filter under vacuum, and individually combusted in a Costech Elemental Analyzer. The resulting CO_2 gas was analyzed for $\delta^{13}C$ [$\delta^{13}C$ = permil deviation of $^{13}C{:}^{12}C$ relative to Vienna Peedee Belemnite Limestone standard (VPDB)] with a Thermo Delta Advantage IV via a Thermo ConFlow III open split in the Grottoli lab. At least 10% of all samples were run in duplicate. The standard deviation of repeated measurements of the USGS24 standard for $\delta^{13}C$ was ±0.08 ‰. The host tissue isotope values were reported as $\delta^{13}C_h$ while the algal endosymbiont isotope data were reported as $\delta^{13}C_e$. In general, as the incorporation of isotopically depleted zooplankton and other heterotrophic carbon sources (i.e., dissolved and particulate organic carbon) into coral tissues increases, the $\delta^{13}C_h$ decreases (Rodrigues and Grottoli, 2006; Levas et al., 2013; Schoepf et al., 2015). As the rate of photosynthesis increases, isotopic fractionation decreases, and endosymbiotic algae incorporate relatively less ^{12}C than ^{13}C into their tissues, resulting in increased $\delta^{13}C_e$ (Muscatine et al., 1989; Rodrigues and Grottoli, 2006). The difference between the $\delta^{13}C_h$ and $\delta^{13}C_e$ were also calculated to assess the proportionate contribution of heterotrophy and photoautotrophy in the carbon budget (*sensu* Muscatine et al., 1989). Specifically, decreases in $\delta^{13}C_h$–$\delta^{13}C_e$ are interpreted to mean that the proportionate contribution of heterotrophic carbon to coral tissues has increased.

The skeleton was prepared for $\delta^{13}C$ ($\delta^{13}C_s$) and $\delta^{18}O$ ($\delta^{18}O_s$)[$\delta^{18}O$ = permil deviation of ^{18}O:^{16}O relative to VPDB] analysis by shaving the top 100–200 μm of skeletal material off the tip of each coral fragment using a Dremel tool with a diamond-tipped drill bit. Approximately ~80 μg of skeletal material was acidified with 100% ortho-phosphoric acid in an automated Kiel III carbonate device, and the $\delta^{13}C$ and $\delta^{18}O$ values of the resulting CO_2 were measured using a Finnigan MAT 252 mass spectrophotometer at Stanford University. At least 10% of all samples were run in duplicate. The standard deviation of repeated measurements of an internal standard was ±0.03 ‰ for $\delta^{13}C$ and ± 0.05 ‰ for $\delta^{18}O$. Skeletal values were reported as $\delta^{13}C_s$ and $\delta^{18}O_s$. In general, as the rate of photosynthesis increases or as the incorporation of heterotrophic carbon into coral tissues decreases, the pool of inorganic C available for calcification through animal respiration becomes enriched resulting in increased $\delta^{13}C_s$ (Grottoli and Wellington, 1999; Grottoli, 2002). In addition, variability in $\delta^{18}O_s$ results from temperature-induced kinetic fractionation and seawater $\delta^{18}O$ (Epstein et al., 1953). As temperature increases, $\delta^{18}O_s$ decreases (Weber and Woodhead, 1972; Kim and O'Neil, 1997). Since seawater $\delta^{18}O_s$is constant in this study because the source seawater was the same in all tanks, it did not influence the $\delta^{18}O_s$ values.

Statistical Analysis

Univariate two-way analysis of variance (ANOVA) was used to test the effects of species and temperature on Chl *a*, algal endosymbiont, mitotic index, lipid, protein, carbohydrate, total energy reserves, and tissue biomass concentrations as well as $\delta^{13}C_s$, $\delta^{18}O_s$, $\delta^{13}C_h$, $\delta^{13}C_e$, and $\delta^{13}C_h$–$\delta^{13}C_e$. Prior to statistical analysis, all data was tested for normality using a Shapiro-Wilk's test and homogeneity of variance was assessed with plots of expected vs. residual values. Any data failing to meet this assumption was log transformed and then met the assumptions of normal distribution. A posteriori slice tests (i.e., tests of simple effects, Winer, 1971) determined if bleached and control averages significantly differed within species. Bonferroni corrections were not used due to increased likelihood of false negatives (Quinn and Keough, 2002). With only one tank for treatment and one tank for controls, we were unable to assess tank effects independent of treatment effects. However, every aspect of both tanks that were measured were the same (i.e., seawater source, flow, light, position relative to the sun's arc) except for temperature. In addition, one bleached *P. damicornis* and two control *F. favus* fragments were lost during shipping or storage, yielding an unbalanced number of samples in the treatment and controls for these two species. Statistical analyses were generated using SAS software, Version 8.02 of the SAS System for Windows. Values of $p < 0.05$ were considered significant.

To get an overall assessment of the effect of treatment across all variables, non-parametric multi-variate statistics were employed. The non-parametric analyses were conducted on three sub-sets of the data: (1) all of the physiology data, (2) all of the isotopic data, and (3) all of the physiology and isotopic data combined. Since two samples did not have isotopic data, the multi-variate analyses that included the isotopes were comprised of 29 corals whereas the analyses of the physiological variables alone included 31 corals. Euclidean-distance based resemblance matrix was constructed using normalized data of all of the measured variables. Non-parametric multidimensional scaling (NMDS) plots were generated to graphically represent relationships between each coral sample across all treatments and species. Analysis of similarities (ANOSIM) was then used to test for the effect of species and treatment. ANOSIM simultaneously uses all variables measured, and tests whether all data (i.e., all physiological and/or isotopic) from one coral group differs from another coral group. The ANOSIM pairwise test statistic R ranges from 0 (no difference and complete overlap between groups) to 1 (maximum difference and no overlap between groups) and is a strong indicator of separation between groups, especially at low sample sizes such as in this study, as long as the overall ANOSIM test statistic R is significant (Clarke and Gorley, 2006). Multi-variate analyses were conducted using the software package Primer V6, and for the ANOSIMs a $p < 0.05$ was considered significant. Finally, since fragments pairs of each colony were included in both treatments, differences between treatment and control for any variable were due to treatment alone, independent of genotype.

RESULTS

The temperature exposure of the treatment corals was equivalent to 32° heating weeks (DHW) (coralreefwatch.noaa.gov) relative to the controls. All three species in the elevated temperature treatment (i.e., 32°C) appeared pale or white and as such were bleached, whereas all of the corals in the control treatment (i.e., 26°C) were brown in color and appeared non-bleached.

Endosymbiotic Algae

Average endosymbiotic algal concentrations dropped to 5, 49, and 19% of control concentrations in *S. pistillata, P. damicornis,* and *F. favus*, respectively (**Table 1**, **Figure 1A**). At the same time, Chl *a* concentrations in bleached *S. pistillata* and *P. damicornis* decreased to 37 and 33% of control values, respectively (**Table 1**, **Figure 1B**), and mitotic divisions were 26-fold lower in bleached *S. pistillata* and 9-fold lower in bleached *F. favus* corals relative to

TABLE 1 | Results of three two-way ANOVAs testing for the effect of species (S), and temperature (T) on average chlorophyll *a* concentration, endosymbiotic algal density and mitotic index.

Species	Effect	*df*	SS	*F*	*p*
Endosymbiontic	Model	5	5.8798	18.86	**0.0001**
Algal density	S	2	0.4347	3.49	**0.0462**
	T	1	4.4111	70.76	**<0.0001**
	S × T	2	0.8797	7.06	**0.0037**
Chlorophyll *a*	Model	5	14932873	18.13	**0.0001**
	S	2	7111311	21.59	**0.0001**
	T	1	5460974	33.16	**<0.0001**
	S × T	2	2169097	6.59	**0.0050**
Mitotic Index	Model	5	7.8572	12.78	**0.0001**
	S	2	0.0875	3.28	0.0541
	T	1	5.3524	43.54	**<0.0001**
	S × T	2	1.1424	4.65	**0.0192**

Effects of species (S) and temperature (T) were fixed and fully crossed. Endosymbiontic algal concentration and mitotic index values were log transformed to meet assumptions of normal distribution before ANOVA analysis. df, degrees of freedom; SS, type III sum of squares of the main effects. Significant effects are in bold.

their controls (**Table 1**, **Figure 1C**). While endolithic algae were not present in noticeable quantities in either *P. damicornis* or *S. pistillata*, *F. favus* showed evidence of harboring endolithic algae. Because all samples of *F. favus* showed approximately the same quantity of endolithic algae irrespective of treatment, it was assumed that their contribution to Chl *a* was relatively constant and that any differences in Chl *a* between the bleached and control fragments was due to the bleaching effect alone.

Energy Reserves

While lipids and protein were unaffected by bleaching overall, a posteriori slice tests revealed that lipid concentrations in bleached *S. pistillata* and protein concentrations in bleached *F. favus* were 49 and 48% lower, respectively, than in their controls (**Table 2**, **Figures 2A,B**). Carbohydrate concentrations dropped to 40 and 41% of control values in bleached *P. damicornis* and *F. favus*, respectively (**Table 2**, **Figure 2C**). Despite losses of at least one component of energy reserves in each species, only bleached *F. favus* had significantly lower total energy reserves (43% decrease) and experienced a 27% decrease in biomass compared to controls at the species level (**Table 2**, **Figures 2D,E**).

Stable Isotopes

Average $\delta^{13}C_s$ values were significantly higher in bleached than in control corals overall (**Table 3**), but this difference was only significant at the species level for *S. pistillata* where bleached $\delta^{13}C_s$ was 1.7 ‰ higher than control corals (**Table 3**, **Figure 3A**). Average $\delta^{18}O_s$ was 0.9 ‰ higher in the bleached than in control *S. pistillata* (**Table 3**, **Figure 3B**). At the same time, average $\delta^{13}C_h$ values were 2.2 ‰ and 1.8 ‰ higher in bleached than in control *S. pistillata* and *F. favus* (**Table 3**, **Figure 3C**), respectively, while average $\delta^{13}C_e$ values were 1.0 ‰ higher in bleached than in control *F. favus,* and at least 2.4 ‰ higher in *F. favus* overall compared to the other two species (**Table 3**, **Figure 3D**). Finally, average $\delta^{13}C_h$–$\delta^{13}C_e$ values were 0.8 ‰ higher in bleached than in control corals overall (**Table 3**), but this difference was only significant at the species level for *S. pistillata* where the average $\delta^{13}C_h$–$\delta^{13}C_e$ was 1.5 ‰ higher in bleached than in control corals (**Figure 4**).

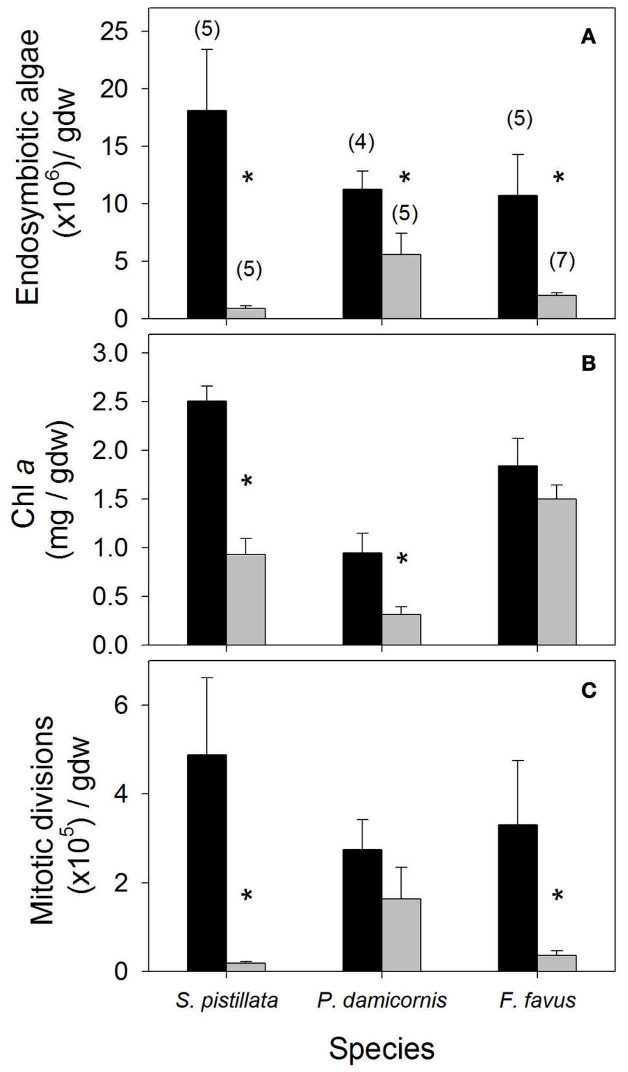

FIGURE 1 | Average **(A)** endosymbiotic algal density, **(B)** chlorophyll *a* (Chl *a*), and **(C)** mitotic division density in control (black bars) and bleached (gray bars) *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia favus* corals. Averages are plotted ± 1 standard error, sample sizes for all panels indicated in brackets in **(A)**, and significant differences between average control and bleached values within each species are indicated with a *. Corresponding ANOVA results are given in **Table 1**. gdw, grams of ash free dry weight.

Multi-Variate Assessments

Overall, both bleached *S. pistillata* and *F. favus* corals significantly differed from their controls, whereas bleached and control *P. damicornis* corals did not differ from each other (**Table 4**, **Figure 5**). This was true for all combinations of the data (i.e., physiological variables alone, isotopic variables alone, of both physiological and isotopic data combined). The degree of

TABLE 2 | Results of five two-way ANOVAs testing for the effect of species (S), and temperature (T) on average lipid, protein, carbohydrate, total energy reserves, and total biomass.

Species	Effect	*df*	SS	*F*	*p*
Lipid	Model	5	101.51×10^6	2.09	0.1008
	S	2	16.42×10^6	0.84	0.4420
	T	1	16.99×10^6	1.75	0.1983
	S × T	2	66.51×10^6	3.42	**0.0488**
Protein	Model	5	0.5714	2.40	0.0660
	S	2	0.4106	4.31	**0.0247**
	T	1	0.1199	2.52	0.1253
	S × T	2	0.0796	0.84	0.4456
Carbohydrate	Model	5	1.8037	11.14	**<0.0001**
	S	2	0.9926	15.33	**<0.0001**
	T	1	0.6349	19.61	**0.0002**
	S × T	2	0.1912	2.95	0.0706
Total En Res	Model	5	61.83×10^7	3.14	**0.0246**
	S	2	22.46×10^7	2.85	0.0765
	T	1	18.33×10^7	4.66	**0.0407**
	S × T	2	22.93×10^7	2.91	0.0730
Biomass	Model	5	0.0069	8.02	**0.0001**
	S	2	0.0058	16.85	**<0.0001**
	T	1	0.0000	0.23	0.6329
	S × T	2	0.0018	5.10	**0.0139**

Effects of species (S) and temperature (T) were fixed and fully crossed. Carbohydrate and protein values were log transformed to meet assumptions of normal distribution before ANOVA analysis. df, degrees of freedom; SS, type III sum of squares of the main effects; Total En Res, total energy reserves. Significant effects are in bold.

separation between the bleached and control corals of both *S. pistillata* and *F. favus* was similar with R values produced from the physiological and isotopic data combined of 0.66 and 0.64, respectively. In addition, all species significantly differed from each other, though *F. favus* differed the most from the other two species as indicated by $R > 0.7$ when compared to either of the other two species when both the physiological and isotopic data were considered (**Table 5**, **Figure 5**).

DISCUSSION

Overall, all treatment corals bleached (**Figure 1**), but the degree to which they were physiologically affected by the temperature stress varied among species (**Figures 1–5**). Here, we discuss the physiological and isotopic responses of each coral species, and explore the implications of those responses to the persistence of corals in the future.

Stylophora pistillata

S. pistillata bleached the most severely of all three species studied with the greatest percentage drop in endosymbiotic algal density (**Figure 1A**). Large drops in endosymbiotic algal density are associated with dramatic decreases in photosynthesis, resulting in corals that are unable to meet their total metabolic demand (Grottoli et al., 2006, 2014; Tremblay et al., 2012). Here, *S. pistillata* catabolized its lipid reserves (**Figure 2A**), presumably

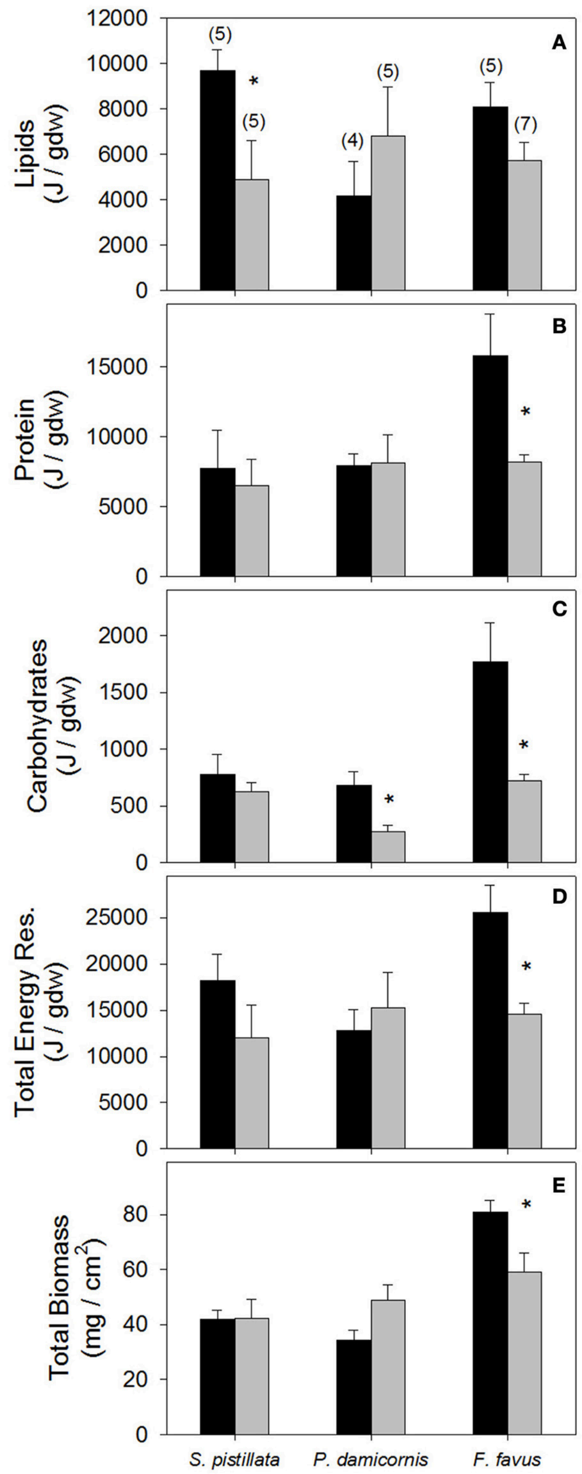

FIGURE 2 | Average **(A)** Lipid, **(B)** protein, **(C)** carbohydrate, **(D)** total energy reserves, and **(E)** total biomass in control (black bars) and bleached (gray bars) *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia favus* corals. Averages are plotted ± 1 standard error, sample sizes for all panels indicated in brackets in **(A)**, and significant differences between average control and bleached values within each species are indicated with a *. Corresponding ANOVA results are given in **Table 2**. J, Joules; Total Energy Res, total energy reserves which is the sum of lipids, protein, and carbohydrate values.

TABLE 3 | Results of five two-way ANOVAs testing for the effect of species (S), and temperature (T) on coral skeletal $\delta^{13}C$, skeletal $\delta^{18}O$, host tissue $\delta^{13}C$, endosymbiontic algal $\delta^{13}C$, and the difference between host and endosymbiontic algal $\delta^{13}C$ ($\delta^{13}C_h$–$\delta^{13}C_z$).

Species	Effect	*df*	SS	*F*	*p*
Skeletal $\delta^{13}C$	Model	5	14.3713	4.37	**0.0060**
	S	2	4.5647	3.47	**0.0475**
	T	1	7.1402	10.86	**0.0030**
	S × T	2	2.6548	2.02	0.1548
Skeletal $\delta^{18}O$	Model	5	16.4869	27.37	**<0.0001**
	S	2	13.2130	54.83	**<0.0001**
	T	1	0.5164	4.29	**0.0494**
	S × T	2	2.0703	8.59	**0.0015**
Host tissue $\delta^{13}C$	Model	5	46.6370	12.61	**0.0001**
	S	2	21.9482	14.83	**<0.0001**
	T	1	10.7377	14.51	**0.0009**
	S × T	2	8.5440	5.77	**0.0090**
Endosymb. $\delta^{13}C$	Model	5	55.8993	14.63	**<0.0001**
	S	2	45.4508	29.74	**<0.0001**
	T	1	0.3171	0.42	0.5253
	S × T	2	4.5973	3.01	0.0675
$\delta^{13}C_h$–$\delta^{13}C_z$	Model	5	14.4986	4.33	**0.0060**
	S	2	8.6119	6.43	**0.0058**
	T	1	6.3445	9.48	**0.0051**
	S × T	2	1.3528	1.01	0.3790

Effects of species (S) and temperature (T) were fixed and fully crossed. df, degrees of freedom; SS, type III sum of squares of the effect; Endosymb., endosymbiotic algae. Significant effects are in bold.

to compensate for losses in photosynthetically fixed carbon. The decline in lipids could have been further exacerbated by the absence of supplemental feeding, since heterotrophic carbon is critical to lipid synthesis in bleached corals (Baumann et al., 2014). Increases in $\delta^{13}C_h$ (**Figure 3C**) suggest that the lipids catabolized during bleaching (**Figure 2A**) were isotopically depleted and/or that in the absence of isotopically depleted zooplankton in the diet, coral tissues became progressively enriched. Given that bleached Hawaiian corals were found to catabolize isotopically enriched lipids (Grottoli and Rodrigues, 2011), it is most likely that the enriched $\delta^{13}C_h$ observed here in bleached corals is a result of a lack of zooplankton. In addition, increases in $\delta^{13}C_{h-e}$ (**Figure 4**) suggests that *S. pistillata* incorporated less heterotrophic C into its tissues when bleached [i.e., increases (decreases) in $\delta^{13}C_{h-e}$ are indicative of dramatic decreases (increases) in the incorporation of heterotrophic carbon in tissues (Rodrigues and Grottoli, 2006)]. This is consistent with the fact that corals in this study were not fed zooplankton during the experiment. However, even if they had been fed, this species is known to decrease feeding rates on zooplankton, pico-, and nano-plankton, as well as suffer increases in total organic carbon losses when bleached (Ferrier-Pages et al., 2010; Tremblay et al., 2012), and that it has limited heterotrophic plasticity capacity in response to a changing environment (Alamaru et al., 2009). Despite the loss of lipids and isotopic evidence of reduced heterotrophic carbon input, bleached *S. pistillata* only showed a trend of declining total energy reserves ($p < 0.13$) and maintained its biomass (**Figures 2D,E**). This may be because this species is able to rapidly curb apoptosis and acclimate to sustained thermal stress when exposed to elevated temperatures (Kvitt et al., 2014, 2016).

The increase in $\delta^{13}C_s$ and $\delta^{18}O_s$ when bleached (**Figures 3A,B**) is consistent with decreases in calcification during bleaching (Rodrigues and Grottoli, 2006) due to greater equilibration with seawater DIC when calcification rates drop (McConnaughey, 1989). Increases in $\delta^{13}C_s$ could also indicate an increase in photosynthesis rates (Grottoli and Wellington, 1999; Grottoli, 2002). However, this is not likely since this species typically experiences significant declines in photochemical efficiency (Fv/Fm) and photosynthesis rates at elevated temperatures (Tremblay et al., 2012; Fine et al., 2013), and because it is not physiologically possible to increase photosynthesis rates when bleached. In addition, the increase in $\delta^{18}O_s$ deceptively suggests that seawaters were cooler, not hotter, in the bleached coral tank (**Figure 3B**). Increases in $\delta^{18}O_s$ in bleached corals are caused by isotopic equilibration with seawater as calcification dramatically slows (Rodrigues and Grottoli, 2006). Thus, the skeletal isotopic signature here indicates a decline in calcification in bleached *S. pistillata.* Decreasing calcification rates is one mechanism by which *S. pistillata* may reduce its energetic demand and maintain total energy reserves and biomass. In principle, maintenance of energy reserves and biomass should confer an advantage to *S. pistillata* and facilitate recovery from bleaching, as has been found for the branching Caribbean coral *Porites divaricata* (Grottoli et al., 2014).

Pocillopora damicornis

Of all three species studied here, *P. damicornis* was the least affected by bleaching with the smallest decline in endosymbiont cell density and the only species to maintain mitotic cell division (**Figure 1**). Fine et al. (2013) showed that photochemical efficiency of PSII in this species is among the least affected by 34°C temperatures compared to other corals from this site, despite hosting the typically thermally sensitive clade C *Symbiodinium* (Karako-Lampert et al., 2004). At the same time, *P. damicornis* preserved its energy reserves and biomass (**Figure 2**), showed no metabolic shifts in its isotopic signatures (**Figures 3**, **4**), and overall was unchanged when bleached (**Figure 5**). The maintenance of its skeletal isotopic values when bleached (**Figures 3A,B**) suggests that calcification was maintained when bleached (Rodrigues and Grottoli, 2006). This is not an unreasonable interpretation as some populations of Pacific *P. damicornis* corals have optimal calcification rates at 31°C (Clausen and Roth, 1975)—only 1° cooler than the experimental temperatures. The lack of any shifts in $\delta^{13}C_h$, $\delta^{13}C_e$, and $\delta^{13}C_{h-e}$ indicate that the proportionate contribution of photoautotrophic and heterotrophic C to tissues did not change with bleaching. Given that these corals were not fed zooplankton during the experiment, these results further suggest that *P. damicornis* may not be very dependent on heterotrophic C for meeting metabolic demand or may not be able to change

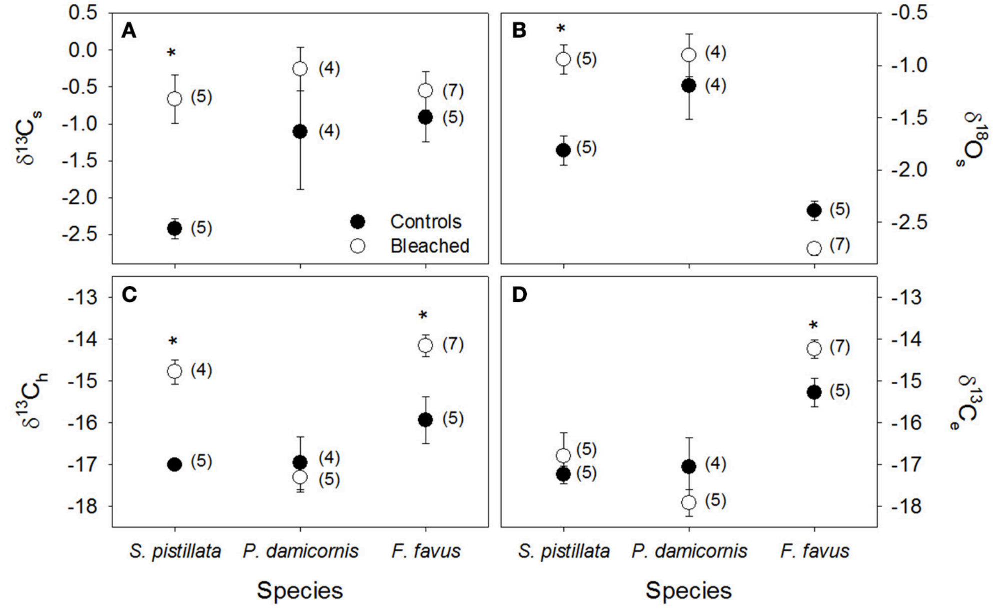

FIGURE 3 | Average stable isotopes in control (black circles) and bleached (white circles) coral skeleton (s), host tissue (h) and algal endosymbiont (e) fractions. **(A)** $\delta^{13}C_S$, **(B)** $\delta^{18}O_S$, **(C)** $\delta^{13}C_h$, and **(D)** $\delta^{13}C_e$ in *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia favus* corals. All data are reported in permil (‰) relative to V-PDB. Averages are plotted ± 1 standard error, sample sizes for each average are indicated in brackets, and significant differences between average control and bleached values within each species are indicated with a *. Corresponding ANOVA results are given in **Table 3**.

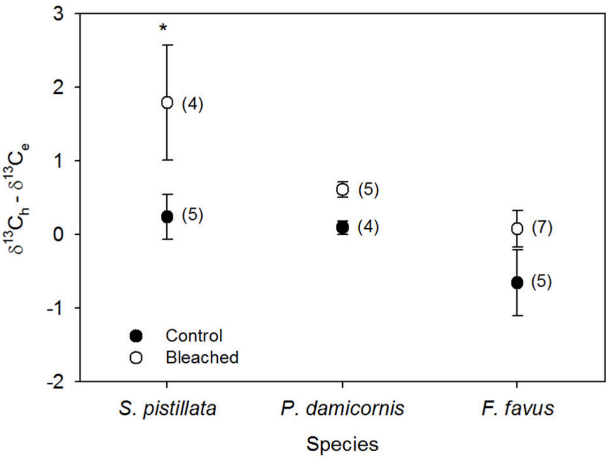

FIGURE 4 | Average difference between host ($\delta^{13}C_h$) and endosymbiont ($\delta^{13}C_e$) stable carbon isotope values in bleached (open circles) and control (black circles) *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia favus* corals from **Figures 3C,D**. Heterotrophy contributes more to the fixed carbon pool when the difference is <0, while photosynthesis contributes more when the difference is ≥0. Averages are plotted ±1 standard error calculated through error propagation and are reported in permil (‰) relative to V-PDB. Sample sizes for each average are in brackets. Significant differences between control and bleached within each species are indicated with *. Corresponding ANOVA results are given in **Table 3**.

TABLE 4 | One-way ANOSIMs of physiological, isotopic, and both physiological and isotopic variables combined where each individual species and treatment was a factor allowing for pairwise tests of each species and treatment combination.

Comparison	Physiology	Isotopes	Physiology + Isotopes
Global	0.44 (<0.001)	0.67 (<0.001)	0.65 (<0.001)
S. pistillata 26 vs. 32	0.56 (0.008)	0.79 (0.018)	0.66 (0.008)
P. damicornis 26 vs. 32	0.14 (0.200)	0.01 (0.450)	0.26 (0.143)
F. favus 26 vs. 32	0.66 (0.001)	0.29 (0.025)	0.64 (0.001)

Shown are the comparisons of interest. The models were all run with 999 permutations. R values are listed with corresponding p-values in brackets. Note two samples had to be removed from the models with isotopes due to missing values.

its heterotrophic intake under bleaching stress. Work by Ziegler et al. (2014) shows that *Pocillopora* are not heterotrophically plastic in response to changes in light, which may indicate that they would not be heterotrophically plastic in response to temperature changes either.

Schoepf et al. (2013) also found no changes in energy reserves and biomass in *P. damicornis* under control and elevated temperature conditions (26.5 vs. 29°C). This is surprising since corals of this genus are often among the most sensitive to thermal stress in other regions (Hueerkamp et al., 2001; Obura, 2001; McClanahan et al., 2004; Guest et al., 2012; Foster et al., 2014; Pisapia et al., 2016) and even suffer lipid losses when bleached (Rodriguez-Troncoso et al., 2016). But there are also cases where *Pocillopora* corals do not readily bleach compared to other species (Sebastian et al., 2009; Guest et al., 2012). Some evidence suggests that *Pocillopora* corals are beginning to acclimatize or adapt to thermal stress in Australia (Ulstrup et al., 2006; Maynard et al., 2008) and may have high acclimatization potential in northern

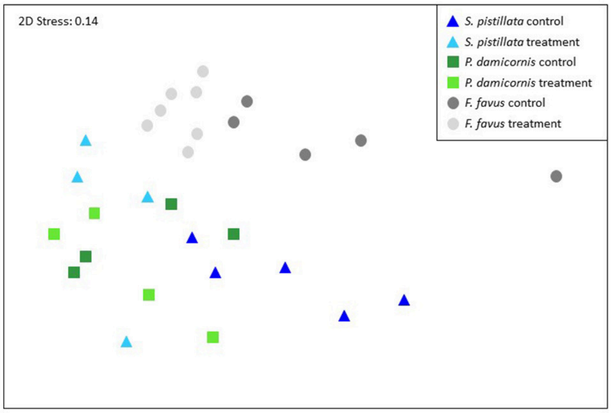

FIGURE 5 | Non-parametric multi-dimensional scaling ordination using the physiological and isotopic variables from 29 of the 31 corals. Two corals were not included because they did not have complete isotope data sets. The NMDS plots and corresponding ANOSIMS patterns were similar when build from just the physiology data (all 31 corals) or just the isotopic data (29 corals). Corresponding ANOSIMs results are given in **Tables 4, 5**.

TABLE 5 | Two-way ANOSIMs of physiological, isotopic, and both physiological and isotopic variables combined where species (*S. pistillata, P. damicornis, F. favus*) and treatment (26°C, 32°C) were the factors.

Comparison	Physiology	Isotopes	Physiology + Isotopes
Global	0.35 (0.001)	0.71 (0.001)	0.68 (0.001)
S. pistillata vs. *P. damicornis*	0.21 (0.034)	0.43 (0.001)	0.33 (0.012)
P. damicornis vs. *F. favus*	0.24 (0.012)	0.82 (0.001)	0.72 (0.001)
S. pistillata vs. *F. favus*	0.55 (0.001)	0.79 (0.001)	0.84 (0.001)
26°C vs. 32°C	0.51 (0.001)	0.37 (0.002)	0.57 (0.001)

The models were all run with 999 permutations. R values are listed with corresponding p-values in brackets. All p-values were significant. Note two samples had to be removed from the models with isotopes due to missing values.

Red Sea populations (Sawall et al., 2015), though not through heterotrophic plasticity mechanisms (Ziegler et al., 2014). These findings suggest that *P. damicornis* in Eilat is a more resilient population to temperature-induced bleaching than those in other locations because (1) they can maintain their energy reserves, biomass, and calcification, and (2) appear to not be dependent on heterotrophy for meeting metabolic demand when bleached.

Favia favus

Bleached *F. favus* suffered declines in more physiological variables than either of the other two species with significant decreases in endosymbiotic algal density, mitotic divisions, protein, carbohydrates, total energy reserves, and biomass (**Figures 1**, **2**), yet still maintained Chl *a* concentrations (**Figure 1B**). Even though photochemical efficiency (F_v/F_m) tends to decline at elevated temperatures for *F. favus* from Eilat (Winters et al., 2006; Kuguru et al., 2007; Fine et al., 2013), the observed increase in $\delta^{13}C_e$ (**Figure 3D**) and maintained Chl *a* levels suggests that some level of photosynthesis persisted while bleached. At the same time, *F. favus* catabolized its protein and carbohydrate reserves, which underlie the significant declines in total energy reserves and biomass (**Figures 2B–E**), presumably to compensate for losses in photosynthetically fixed C. Increases in $\delta^{13}C_h$ (**Figure 3C**) suggest that the protein and carbohydrates catabolized during bleaching (**Figures 2B,C**) were isotopically depleted, or that in the absence of isotopically depleted zooplankton in the diet, coral tissues became progressively enriched. Further research is needed to evaluate the isotopic composition of protein and carbohydrates. However, since these corals were not supplied zooplankton during the experiment, it is likely that the enrichment in $\delta^{13}C_h$ observed here is at least in part a result of a lack of zooplankton availability. Although the $\delta^{13}C_{h-e}$ did not change with bleaching in *F. favus* (**Figure 4**), it was lower overall than in *S. pistillata* and *P. damicornis* indicating a higher contribution of heterotrophic C to its tissues in general, irrespective of bleaching, than in the other two species (**Figure 4**). This is consistent with field-based findings showing that *F. favus* allocates a higher proportion of heterotrophic C to its lipids than does *S. pistillata* (Alamaru et al., 2009). In addition, some species are able to meet up to 36% of metabolic demand when bleached through the heterotrophic acquisition of dissolved and particulate organic carbon (Levas et al., 2013, 2016). The lower overall $\delta^{13}C_{h-e}$ of *F. favus* suggests that when bleached it was able to take up dissolved and/or particulate organic carbon during the tank experiment to meet at least part of its metabolic demand heterotrophically. But any uptake in heterotrophic C was not enough to prevent large losses in protein and biomass. Had the corals been fed zooplankton, it is possible that *F. favus* might have maintained its energy reserves and biomass.

Finally, the skeletal isotopic signature in *F. favus* was unaffected by bleaching (**Figures 3A,B**), suggesting that calcification was maintained or at least did not decrease dramatically (Rodrigues and Grottoli, 2006). This is also consistent with the interpretation that some level of photosynthesis was maintained, since calcification is tightly linked to photosynthesis (see review by Allemand et al., 2011). Furthermore, in healthy corals, $\delta^{18}O_s$ decreases by ~0.2 ‰ per 1°C seawater warming (Weber and Woodhead, 1972; Wellington et al., 1996). Here a non-significant trend of a 0.36 ‰ decline in $\delta^{18}O_s$ ($P < 0.085$) suggests that *F. favus* skeletal isotopic signature recorded the seawater warming event, though not the ~1.2 ‰ decline that would have be expected if it had accurately recorded the full 6°C increase in temperature. Nevertheless, the fact that a warming trend was recorded is further support that *F. favus* calcified throughout the experiment.

Overall, *F. favus* suffered significant declines in energy reserves and biomass, but maintained Chl *a*, appears to have maintained calcification, and appears to have high baseline rates of heterotrophic C contributions to its tissues. The maintenance of Chl *a* and the apparent high baseline heterotrophic capacity of this coral could explain why this genus experiences little to no mortality following bleaching events (McClanahan, 2004; Sutthacheep et al., 2013). In Hawaii, the mounding coral *Porites lobata* can also bleach severely, but recovers quickly due to a high baseline contribution of heterotrophic carbon to the diet (Palardy et al., 2008; Levas et al., 2013). Thus, the high baseline heterotrophic capacity of the mounding coral *F. favus* may facilitate the rapid recovery and low mortality of this species following bleaching stress, and allow it to persist into the future, despite its initial dramatic energy reserve and biomass losses when bleached.

SUMMARY

The corals found in the northern tip of the Gulf of Aqaba are able to tolerate temperatures well above their thermal summer maximum for extended periods of time without bleaching, making them temperature-tolerant super-corals. Unlike most corals that bleach after a 4-DHW exposure and experience significant mortality after 8-DHW, all three species of corals here bleached only after being exposed to the equivalent of 32-DHW. However, the physiological and biogeochemical responses to bleaching were species-specific. *P. damicornis* and *S. pistillata* maintained their total energy reserves and biomass while *F. favus* lost total energy reserves and biomass. Interestingly, total energy reserves in all three species of Eilat corals, irrespective of bleaching status, were higher than levels found in corals that were the most susceptible to repeat bleaching in the Caribbean (Grottoli et al., 2014) and consistent with findings that high energy reserves is a common trait found among the most thermally tolerant corals (Rodrigues and Grottoli, 2007; Anthony et al., 2009; Grottoli et al., 2014; Schoepf et al., 2015). While, we found no isotopic evidence of increases in heterotrophy as a mechanism for coping with the declines in photoautotrophically fixed carbon supply in bleached corals, the isotopic signature of *F. favus* suggests that it has a high baseline input of heterotrophic C, which could underlie its low mortality rate following bleaching events (McClanahan, 2004; Sutthacheep et al., 2013), despite its energy reserve and biomass losses. In addition, endosymbiont type switching or shuffling to acquire or increase thermally tolerant *Symbiodinium* clade D is probably not an underlying trait to Eilat super-coral thermal tolerance as *Symbiodinium* D has never been detected in this population of corals (Fine et al., 2013) even though it is present in more southern regions of the Red Sea (Baker et al., 2004; Ziegler et al., 2014). These findings support our hypothesis that energy reserves, biomass, and heterotrophic capacity are central traits to bleaching tolerance in all corals including northern Gulf of Aqaba super-corals, though corals need not have all of these traits to be thermally resilient. In addition, these resilience traits have been identified in a number of coral species throughout the world, suggesting that these phenotypic traits for thermal tolerance may be universal. But, Eilat coral can tolerate much more severe warming events than other populations of corals with similar phenotypic traits, supporting the finding that the Eilat coral thermal tolerance is also driven by the underlying genetics of these coral populations (Fine et al., 2013). Additional study is needed to confirm these findings where the corals are provided zooplankton throughout the experiment. Irrespective of the underlying mechanism for thermal tolerance, super-corals from the northern portion of the Gulf of Aqaba could be used for restocking reefs in other regions where bleaching events have dramatically reduced coral abundance. This may be particularly relevant for *Stylophora* and *P. damicornis* corals as they are among those most likely to die following bleaching events in some regions (e.g., Glynn, 1984; Glynn et al., 2001; McClanahan, 2004).

AUTHOR CONTRIBUTIONS

AG conceived of the study and secured the funding. DT and GW executed the experiment. AG analyzed the samples, statistically analyzed the data, interpreted the results, and wrote the manuscript. DT contributed to the revising of the manuscript.

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Fine-Scale Biogeographical Boundary Delineation and Sub-population Resolution in the *Symbiodinium thermophilum* Coral Symbiont Group From the Persian/Arabian Gulf and Gulf of Oman

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The adaptation of tropical coral communities to the world's hottest sea, the Persian/Arabian Gulf (PAG), has recently been associated with ecological selection acting on a group of coral-associated algal symbionts, the *Symbiodinium thermophilum* group. Previous studies have shown that considerable genetic diversity exists within the group and that group members found within the PAG are significantly differentiated from those found externally, in the Gulf of Oman and wider waters. However, little is known about this genetic diversity. As an initial step towards understanding whether this diversity could represent niche adapted, selectable populations within the *S. thermophilum* group that may act as natural sources of stress tolerant associations to Indo-Pacific reefs, we investigate whether the diversity is structured between populations and where the location of the internal-external genetic partition lies. We use regions of the nuclear ribosomal DNA (ITS1-5.8S-ITS2) and chloroplastic *psbA* gene (non-coding region) from >100 *S. thermophilum* group-harbouring *Porites* spp. (*P. lobata, P. lutea, and P. harrisoni*) sampled across steep temperature and salinity gradients to conduct analyses of variance and create maximum parsimony networks to assess genetic structure and (dis)similarity within and between populations of *S. thermophilum* found within the PAG and externally in the Gulf of Oman. Our analyses resolve a sharp genetic boundary between *Symbiodinium* populations in the western Strait of Hormuz and identify significant genetic structure between populations with as little as 20 km between them demonstrating that differentiation between populations is likely due to factors other than limited connectivity. Further, we hypothesize that genotypes identified outside of the PAG in the Gulf of Oman existing in near-oceanic salinities, yet thermally challenging waters, putatively represent candidates for stress-tolerant symbionts that could act as natural seed populations of stress tolerant genotypes to the wider indo-Pacific.

Keywords: adaptation, biogeography, climate change, coral reefs, ITS2, Persian/Arabian Gulf, salinity, thermal tolerance

INTRODUCTION

The Persian/Arabian Gulf (PAG) is a thermally extreme and hypersaline body of water with temperatures regularly exceeding 34°C during summer in its southern and hottest part (Hume et al., 2013; Shuail et al., 2016; **Figure 1**, Figure S1), temperatures that prove fatal to most tropical corals (Coles and Riegl, 2013; Hume et al., 2013). Yet, thriving coral communities are found along its coastline (Coles, 2003). These exceptional coral communities are gaining attention as model systems to inform on how corals globally might adapt to increasing sea surface temperatures (SSTs; Hume et al., 2013; Burt et al., 2014; D'Angelo et al., 2015). Such increases are causing more frequent and severe coral bleaching events (Logan et al., 2014) during which the obligate symbiotic relationship between coral and algal symbiont (genus *Symbiodinium*) breaks down leading to symbiont loss, and if recovery is not timely, death of the host (Hughes et al., 2003). Temperature thresholds at which these bleaching events occur are dependent on host and symbiont genotypes but typically lie 1°C above the average maximum summer temperature for a reef (Goreau and Hayes, 1994; Shuail et al., 2016).

Given that the maximum mean temperature of the majority of coral reefs is ≤30°C (Hume et al., 2013), the ability of corals from the southern PAG to withstand temperatures in excess of 35°C without bleaching is truly exceptional (Coles and Riegl, 2013; Hume et al., 2013; Shuail et al., 2016). This exceptional thermal tolerance may be in part due to their algal associations given that hosting certain *Symbiodinium* types may confer an increased thermal tolerance to the coral host (LaJeunesse et al., 2010; Silverstein et al., 2015). Specifically, corals of the southern PAG predominantly form year-round associations with the recently described *Symbiodinium thermophilum* (Hume et al., 2015). The prevalence of this symbiont within PAG corals suggests it is at least partially responsible for their thermotolerance (D'Angelo et al., 2015; Hume et al., 2015, 2016).

S. thermophilum was defined using four genetic markers including specific sequences of the mitochondrial *cytochrome b* (*cob*; K234522) and chloroplastic ribosomal 23S (cp23S; KP234523) (Hume et al., 2015). In addition, genetic characteristics of the nrDNA second internal transcribed spacer regions (ITS2) were used. This non-coding region is multicopy in character with multiple genetic variants of different but closely related sequences present in an individual *Symbiodinium* genome (Thornhill et al., 2007; Arif et al., 2014). Within *S. thermophilum,* an 8bp duplication insert (called *S. thermo.*-indel) in a minority proportion of intragenomic ITS2 variants (∼15%) in an otherwise C3 type sequence (KP234524 & KM487748) was described and its presence has been used as an effective means of screening for this symbiont species (D'Angelo et al., 2015; Hume et al., 2016). The last genetic marker used in the description, the highly variable chloroplastic *psbA* non-coding region (*psbA^{ncr}*), resolves at a subspecies level in the *Symbiodinium* genus (Thornhill et al., 2014). As such, multiple haplotypes were recovered from the *S. thermophilum* symbionts (Hume et al., 2015). Critically, all sequences resolved within a monophyletic grouping separated from other ITS2 C3 type symbionts by considerable genetic distance (Hume et al., 2015). Since the formal description of *S. thermophilum*, additional samples containing the characteristic ITS2 *S. thermo.*-indel have been genotyped using the psbA^{ncr} (D'Angelo et al., 2015; Hume et al., 2016). These recovered psbA^{ncr} sequences showed a considerably larger diversity than the diversity seen in the original *sensu strictu S. thermophilum* definition. Hence, these symbionts are identified as members of the "*S. thermophilum* group" (D'Angelo et al., 2015).

The extreme conditions and exceptional coral-algal associations found in the PAG are a product of the regions unique geography. The PAG is connected to the adjacent Gulf of Oman by the ∼40 km wide Strait of Hormuz that navigates the Musandam Peninsula and is fed by a dominant surface inflow of near-oceanic salinity water (**Figure 1**). Due to high evaporation rates and minimal freshwater input, the PAG is characterised by a net inflow with only a minor deep water outflow of heavier, more saline water through the Strait (Yao and Johns, 2010). This surface inflow is strongest in summer month with the cooler, lower salinity surface water moving northwest towards Qatar or south into the main basin forming an overall cyclonic circulation in the southern Gulf (Yao and Johns, 2010). Despite this lower salinity inflow, salinities in the southern PAG remain high year round (>41.5) resulting in a gradual decrease in salinity from the southern PAG towards the tip of the Musandam Peninsula into the Gulf of Oman (D'Angelo et al., 2015; **Figure 1a**). Temperature gradients along the same coast are seasonally dependent. In summer, the inflow has a cooling effect and the resultant temperature gradient decreases from the southern PAG to the Gulf of Oman whereas in winter month the southern PAG is considerably cooler (winter averages ∼21°C) than the inflowing water (∼24°C; **Figures 1a,b**).

Although cooler than the PAG, the coral-harbouring waters immediately external to it, in the Gulf of Oman, represent an environment with salinities closer to those of the wider Indo-Pacific but with thermal regimes still greater than are found in the majority of coral-containing waters globally. In addition to the relatively large annual thermal ranges of the region (max ∼31°C, min ∼23°C), coral communities in these waters may experience acute hypothermal shocks due to local upwelling events (Coles, 2003). As such the coral communities of these waters should also be considered extraordinarily stress tolerant.

Recently, the abundance of *S. thermophilum* group symbionts was investigated at a range of sites spanning from within the PAG to Muscat, in the neighbouring Gulf of Oman. Along the southern coast of the PAG from Dalma to Ras Al-Khaimah, the association of *Porties* spp. corals with members of the *S. thermophilum* group was complete (100% of associations) despite considerable changes in salinity and temperature (D'Angelo et al., 2015; Hume et al., 2015, 2016). However, immediately external to the PAG off the coast of the Musandam Peninsula in the Strait of Hormuz an increasing number of the *Porites* spp. corals were found in association with symbiont types other than *S. thermophilum*, namely ITS2 type C15 and *S. trenchii* (ITS2 type D1a or D1-4). This decrease in *S. thermophilum* group associations continues with increasing distance from the PAG until associations are almost undetectable in reefs off Muscat. Interestingly, this low level abundance of *S. thermophilum* group associations has been documented as widely distributed as the northern Red Sea (Hume et al., 2016).

Phylogenetic analyses conducted as part of these studies using the psbA^{ncr} revealed a greater genetic diversity of *S. thermophilum* group symbionts external to the PAG than within (Hume et al., 2016). Investigation into the age of this diversity (>several million years), and the group members themselves (∼13 Mya), demonstrated them to be considerably older than the age of the PAG (∼12.5 kya; Purkis et al., 2010; D'Angelo et al., 2015; Hume et al., 2016). These findings led to the hypothesis that positive selection for thermal and salinity tolerance acting on the diversity of group members found external to the PAG, facilitated the colonisation of the physically extreme PAG by a subset of Indo-Pacific corals. Other ecological mechanisms including founder or bottleneck effects were also considered in the explanation of the group's prevalence and relative genetic homogeneity in the PAG. However, the PAG's dominant inflow (Yao and Johns, 2010), the presence of several other thermally tolerant symbiont types within the PAG (Baker et al., 2004; LaJeunesse et al., 2014; Hume et al., 2015) and the fact that *Symbiodinium* can disperse rapidly over large distances (Baird et al., 2009; Pettay et al., 2015) make these mechanisms unlikely.

In the same way that members of the *S. thermophilum* group underwent ecological selection to proliferate in the extreme conditions of the PAG, these members may be selected to enrich reefs in the Gulf of Oman and wider Indo-Pacific with tolerant symbionts. Such an enrichment may afford these reefs greater resilience to perturbations that may arise from predicted increases in SSTs. However, to better understand the capacity for such ecological selection to occur we must first better understand the genetic diversity that exists within the *S. thermophilum* group to know which populations are available for selection. Here, we specifically investigate whether the genetic diversity of the *S. thermophilum* group is structured between populations as a first indication towards whether niche adapted, selectable populations exist. To assess for genetic structure within the group, we use a novel approach analysing the diversity of intragenomic variants in the ITS1-5.8S-ITS2 region of the nrDNA as well as the psbA^{ncr} to compute ϕst indices and create maximum parsimony networks to identify population groupings and assess genetic (dis)similarity within and between individual populations. Our findings identify significant genetic differentiation between *S. thermophilum* group populations and further resolve the coral-symbiont biogeographical boundary in the Strait of Hormuz.

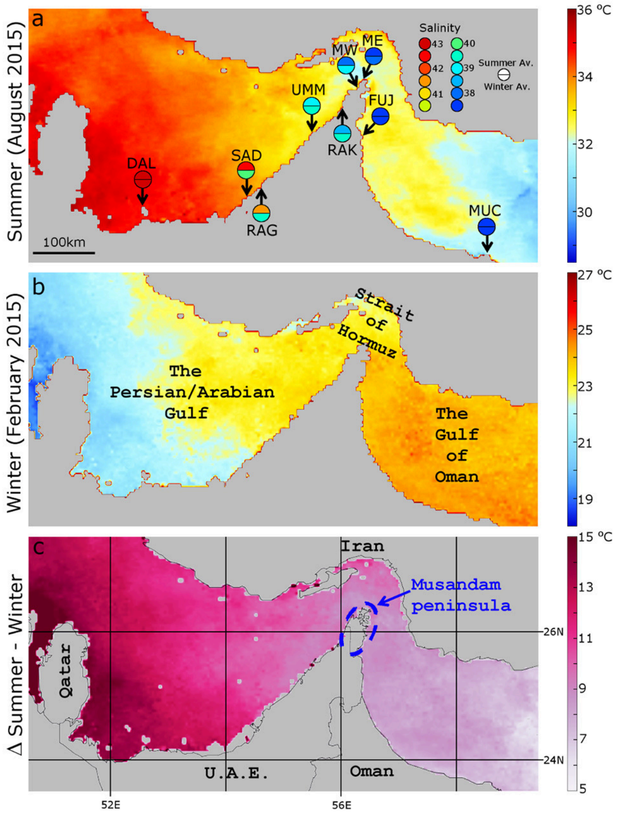

FIGURE 1 | Sampling sites across temperature and salinity gradients of the Persian/Arabian Gulf, Strait of Hormuz, and Gulf of Oman. **(a)** Monthly average (August 2015; warmest month) sea surface temperatures (SSTs) representative of a summer thermal profile. Sampling locations are denoted according to three or two letter codes: DAL, Dalma Island; SAD, Saadiyat reef; RAG, Ras Ghanada; UMM, Umm Al-Quwain; RAK, Ras Al-Khaimah; MW, Musandam peninsula West; ME, Musandam peninsula East; FUJ, Fujairah; & MUC, Muscat. Modelled seasonal (summer, J-A-S; winter, J-F-M) salinities from Yao and Johns (2010) for sampling sites are denoted. **(b)** Monthly average (February 2015; coolest month) SSTs representative of a winter thermal profile. **(c)** Difference in monthly average SSTs between **(a and b)** representative of a regular seasonal temperature range. Remotely sensed SST data of **(a,b)** are Aqua MODIS Sea Surface Temperature (11 μ daytime), monthly, 4 km resolution accessed through the level 3 data browser of OceanColor Web (oceancolor.gsfc.nasa.gov/cgi/l3). netCDF libraries were viewed and images exported using Panoply 4.3 (gis.nasa.gov/tools/panoply). Panel **(c)** was created using Panoply's combine plot function subtracting the winter profile from the summer.

MATERIALS AND METHODS

Sample Collection and Genotyping by nrDNA and psbA^{ncr}

S. thermophilum group-containing coral samples of *P. lobata*, *P. lutea*, and *P. harrisoni* were collected and underwent nrDNA (ITS1-5.8S-ITS2) and psbA^{ncr} genotyping as part of D'Angelo et al. (2015). Field identification relied on local experts to differentiate between *Porites* spp. The relatively low diversity of *Porites* spp. found in the PAG and Gulf of Oman simplified the identification (Bauman et al., 2013). Fragments of *P. lobata* and *P. lutea* were bleached in sodium hypochlorite solution and inspected under a microscope (MZ10, Leica). Analysis of the corallite structure (Veron, 2000) confirmed the field identification of these samples. The *P. lobata* samples were distinguishable from *P. lutea* by the lack of a protruding ring of five tall pali, and from *P. solida* by the lack of a flattened columella. However, it should be noted that *Porites* spp. corals are notoriously difficult to identify from skeletal morphology alone (Forsman et al., 2009). *P. harrisoni* was differentiated from *P. lobata* and *P. lutea* by its gross morphology being more columnar in form. Unfortunately for samples collected at Ras Al Khaimah (RAK) and the one sample collected in Muscat, field identification by an expert was not available. Rather than omit these samples from the study they were identified conservatively as *Porites* spp.

In summary, corals were sampled at between 2 and 7 m in September 2012 and March 2013 from sites within the PAG, the Strait of Hormuz and the Gulf of Oman (**Figure 1**; Figure S2). Throughout this study two or three character length codes (e.g., DAL—Dalma) will be used to refer to sampling sites as denoted in **Figure 1a**. Genomic DNA extractions were performed using a CTAB protocol and the PCR amplification of the nrDNA and psbA^{ncr} markers was achieved using the SYM_VAR_FWD/SYM_VAR_REV and psbAFor_1/psbA_Rev_1 primer pairs. nrDNA amplicons were cloned using a StrataClone PCR cloning kit before sequencing (universal primer T7) whilst psbA^{ncr} amplicons were directly sequenced using the internal primer psbA_int_Fwd. Sequences were aligned in MEGA 6 (Tamura et al., 2013) with nrDNA sequences' unsupported nucleotides (nucleotides divergent from the alignment consensus that were not found in more than one PCR amplicon library) reverted to the consensus to minimise incorporation of genetic diversity generated through PCR error. A full list of psbA^{ncr} sequences used in this study may be found in Table S1, Supplementary Material (106 sequences). The number of colonies nrDNA sequenced as well as the average sequencing depth can be found in Table S2, Supplementary Material. A multiple sequence alignment of the ITS1-5.8S-ITS2 nrDNA sequences used in this study has been submitted to the Dryad Repository (675 sequences).

Assessment of Host-Effect on *Symbiodinium* Sequence

Porites spp. abundance between sites was heterogeneous and uneven sampling across sites was unavoidable (Figure S2). To assess whether any signature of genetic structure found in this study might be an artefact caused by host species distribution due to different species of *Porites* hosting different *Symbiodinium* types, rather than other factors (e.g., environmental conditions), cluster-based correlation analysis between *Symbiodinium* sequence recovered and host species was conducted. For both markers, genetic distances between all unique sequences were calculated in MOTHUR 1.36.1 (Schloss et al., 2009) using the "pairwise.seqs" function. Column-based distances were converted to matrices using a custom PYTHON script before being plotted in two dimensional space through multidimensional scaling using the R package bios2mds. K-means clustering was conducted in R (3 clusters; one per species) using the function "kmeans" with the initial seed set to 20 and with an nstart equalling 50.

If host species had no effect on sequence recovered, sequences should be randomly distributed between the three groups irrespective of host. A two-way table (species, cluster) and chi-square test were employed to test if there was a significant difference between the distribution of sequences amongst the three k-means determined clusters according to either: observed distribution by species, or expected random distribution disregarding species. The counts of sequences from each of the three identified species (unidentified *Porites* sp. were discounted from the analysis) associated within each of the determined clusters were calculated alongside frequencies representative of the null hypothesis of no association between species and cluster. A chi-squared test was performed and results were compared to critical values at 4 degrees of freedom (3 species, 3 clusters).

Inclusion of Its1 and 5.8S nrDNA Regions in Genetic Analyses

Biogeographical and phylogenetic analyses of *Symbiodinium* populations often use only one region of the nrDNA, commonly the ITS2. To maximise possible inferences on genetic structure and investigate possible improvements in phylogenetic resolution within the *S. thermophilum* group the ITS1 and 5.8S regions of the nrDNA were included in all analyses in this study.

Population Genetic Structure Inference by Analysis of Variance

To offer an improved resolution of the previously described biogeographic boundary (located in the Strait of Hormuz) to *S. thermophilum* group-containing coral populations (D'Angelo et al., 2015; Hume et al., 2016) three group configurations were tested for variance. Specifically, two groups of populations were defined as "internal" and "external" (approximate to PAG and Gulf of Oman populations). Within these groupings the sites, Dalma, Saadiyat, Ras Ghanada, Umm Al-Quwain, and Ras Al-Khaimah were always placed in the internal groups whilst Fujairah and Muscat were always in the external group. The three permutations of these groups with the addition or lack of one or both of the Musandam West or Musandam East sites were then tested for among group variance in WinArl 3.5.1.3 (Excoffier and Lischer, 2010) using the complete ITS1-5.8S-ITS2 region of the nrDNA (611 bp) and the partial psbA^{ncr} (495 bp). By this means, the two populations in proximity to the Strait with the greatest haplotypic difference may be identified. These two populations will be the most easterly and westerly population in the internal and external groupings that have largest among group variance.

In addition to the calculation of among groups variance (Va), among populations within groups (Vb), and within populations variances (Vc) were calculated along with their associated fixation indices (φ_{CT}, φ_{SC}, and φ_{ST}, respectively). In this analytical scenario, the among group variance (Va) represents the variance between individual gene sequences that are grouped as belonging to either an internal or external site. When calculating the among group variance, the population to which a sequence belongs is not taken into account. That is, individual gene comparisons are only constrained by which group they belong to. The among populations within groups variance (Vb) represents the average variance found amongst populations that belong to the same group. Here, population comparisons are nested hierarchically within the groups so that only gene sequences found within populations that are found within the same groups will be compared. Within population variance (Vc) represents the variance found between sequences for each population. Here, which group the population belongs to is not taken into account and one Vc value is calculated for each population (i.e., sequences from different populations are not compared). For each of the comparison types listed above, the respective fixation indices are calculated using the same grouping constraints. These fixation indices represent a measure of population differentiation due to genetic structure (i.e., gene flow isolation) with a value closer to 1 representing greater isolation and therefore structure.

Population Genetic Structure Inference by Population Pairwise Distance

To test for genetic dissimilarity between populations, population pairwise genetic distances were also calculated in WINARL in the form of pairwise ϕst values. A null distribution of pairwise ϕst under the hypothesis of no difference between the populations is obtained by permuting haplotypes between populations as part of WINARL's "compute pairwise difference" function. The outputted probability values represent the proportion of permutations leading to a ϕst value larger or equal to the observed one (Excoffier and Lischer, 2010). Whilst one psbA^{ncr} sequence per sample was used in the pairwise analyses, further considerations were taken in the appropriate use of the nrDNA sequences. Whilst not a traditional genetic marker used in population biology, the nrDNA's heritability and complex character states (in the form of multiple intagenomic variants due to the nrDNA's multicopy character) enable its use as such a marker (Sunnucks, 2000). In fact, given that approximations to ecologically relevant species level descriptions in *Symbiodinium* are commonly made according to the sequence and predominance of intragenomic variants of the nrDNA (LaJeunesse et al., 2010; Arif et al., 2014), quantifying dissimilarity between individuals and populations according to these intragenomic abundances is likely an effective means of identifying ecologically significant units. Thus, to ensure the consideration of all available nrDNA intragenomic variants and their frequencies within individual corals and populations each sequence was treated as an individual rather than creating a single "inclusivity consensus sequence" (Barshis et al., 2010) by incorporating IUPAC ambiguity nucleotides representative of polymorphisms detected within clone libraries into the consensus sequence from that individual; a method that cannot take into consideration the frequency of polymorphism-containing intragenomic variants as previously discussed by Barshis et al. (2010). Additionally, the treatment of intragenomic variants as individuals enables the incorporation of samples that are represented by a considerable number of clones but from a low number of individuals (e.g., Muscat site; only one sample with 14 nrDNA clones). Whilst such a low sampling is not ideal, further sampling is limited by the rarity of *S. thermophilum* group external to the PAG. The single Muscat sample is potentially highly informative given its rarity and the considerable distance to its next nearest sampling site (Fujairah 363 km). As such Muscat was included in the pairwise ϕst analyses using the nrDNA marker but excluded using the psbA^{ncr} marker due to the direct sequencing approach used (i.e., returning only a single sequence). Pairwise differences were considered significant at $P < 0.05$.

To test for significant correlation between distances and pairwise genetic dissimilarities between populations a Mantel test (test of correlation between two matrices) was additionally calculated using WINARL (the distance matrix may be found in Table S3).

Creation of Maximum Parsimony Networks

Maximum parsimony networks were created using the ITS2 and the complete ITS1-5.8S-ITS2 region of the nrDNA and the partial psbA^{ncr} using TCS (Clement et al., 2000). For the nrDNA networks, sequences with frequency of 1 were not plotted. TCSbu (Múrias dos Santos et al., 2015) was used to aesthetically arrange the network before further manual manipulation for aesthetic purposes only. To account for extreme variability in the psbA^{ncr}, sequences were clustered to a distance of 0.04 (empirically determined to cluster groups of sequences separated by large mutational distances) using the *cluster* command and average neighbour algorithm in MOTHUR 1.36.1 (Schloss et al., 2009).

Script Access

Access to R and PYTHON scripts used in this study may be found in Code S1 in Supplementary Material.

RESULTS

Assessment of Host-Effect on *Symbiodinium* Sequence

To test for an effect of host species on *Symbiodinium* sequence recovered, a χ^2 analysis was conducted to assess whether sequences were distributed independent of host species amongst three k-means clustered groupings on a 2D plot of sequence pairwise distances. A non-significant interaction was found between species and cluster [$\chi^2_{(4)} = 5.94, p > 0.05$] for the nrDNA regions. In contrast, a significant interaction between species and cluster was identified [$\chi^2_{(4)} = 21.99, p < 0.05$] for the psbA^{ncr} marker. However, 80.4% of the divergence from expected was attributable to a single species, *P. harrisoni,* with a single cluster representing 55.9% of this variance.

TABLE 1 | Pairwise population ϕst *P*-values.

	Internal sites					External sites			
	DAL	**SAD**	**RAG**	**UMM**	**RAK**	**MW**	**ME**	**FUJ**	**MUC**
DAL		0.000	0.000	0.000	0.000	0.000	0.000	0.027	
SAD	0.180		0.612	0.198	0.432	0.018	0.000	0.009	
RAG	0.207	0.000		0.198	0.216	0.045	0.000	0.000	
UMM	0.063	0.018	0.702		0.838	0.000	0.000	0.018	
RAK	0.225	0.126	0.333	0.297		0.000	0.000	0.000	
MW	0.036	0.000	0.279	0.649	0.189		0.000	0.000	
ME	0.000	0.000	0.000	0.000	0.000	0.000		0.216	
FUJ	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
MUC	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.072	

Significant difference at $P < 0.05$ is denoted by an underlined value. Top right = psbA^{ncr}; bottom left = nrDNA.

Population Genetic Structure Inference

To determine into which population groupings (internal or external) the Musandam sites were best allocated to maximise between group variance, multiple combinations were assessed. Allocation of the Musandam West and Musandam East populations to the internal and external groups, respectively, were supported by the highest "among group" (Va and ϕct) and lowest "among population within group" (Vb and ϕsc) variances and fixation indices (Va = 11%, 29%, ϕct = 0.108, 0.294; Vb = 3%, 7%, ϕsc = 0.039, 0.097; nrDNA and psbA^{ncr}, respectively). Pairwise ϕst analysis of the 9 populations corroborated the strong genetic dissimilarity between the external (ME, FUJ, and MUC; **Table 1**) and internal (all other populations) populations in both genetic markers.

For both markers, "among individuals within populations" (population = site) accounted for the majority of variance (86 and 63% for the nrDNA and psbA^{ncr}, respectively) whilst relatively low "among populations/within groups" (3 and 7%) and relatively high "among group" (11 and 29%; group = internal or external) variances supported the groupings of internal and external populations as characterised by the associated high and low fixation indices (ϕct = 0.108, 0.294; ϕsc = 0.039, 0.097). Inclusion of MW within the external grouping did not increase "among group" variance (5 vs. 11 and 9 vs. 29% for the nrDNA and psbA^{ncr} markers, respectively).

Despite the well-supported genetic disparity between internal and external populations and relatively low ϕsc indices, some populations within each group were found to have significant genetic disparity (**Table 1**) from each other. Within the external grouping, disparity was seen amongst the majority of sites. Within the internal grouping, MW showed disparity to all populations with the psbA^{ncr} marker but to only two in the nrDNA marker whilst DAL showed complete disparity to all sites with the psbA^{ncr} and SAD demonstrated dissimilarity to neighbouring DAL, RAG, and UMM with the nrDNA marker.

Mantel tests for both genetic markers recovered insignificant P (rand. >= obs.) values >> than 0.05; 0.222 and 0.219, nrDNA and psbA^{ncr}, respectively.

The maximum parsimony networks for both markers resolved phylogenetic groupings that corresponded well to the pairwise ϕst matrices and population groupings (**Figures 2**, **3**). Within the nrDNA network the external sequences shared no haplotypes with internal sequences except for sequences containing the 8bp *S. thermo.*-indel mutation (**Figure 3A**). In addition, the strong genetic disparity between the DAL population and all other populations is exemplified by a monophyletic grouping of approximately half of the DAL sequences in the psbA^{ncr} phylogeny. MW sequences grouped exclusively with high frequency haplotypes comprising internal and external sequences within the nrDNA phylogeny and yet with the psbA^{ncr} sequences resolved at considerable distance from the main internal grouping, although some haplotypes were shared.

Maximum parsimony networks of the nrDNA regions were clearly divided into two groupings; those with and those without the 8bp *S. thermo.*-indel insert (**Figure 3**). The inclusion of the ITS1 and 5.8S regions of the nrDNA greatly improved phylogenetic resolution within the *S. thermophilum* group samples evidenced by the further separation of a single large haplotype in the ITS2 only network into 6 haplotypes with further minor satellite haplotypes in the combined ITS1-5.8S-ITS2 analysis (**Figure 3**).

DISCUSSION

Host-Effect on *Symbiodinium* Sequence

To assess whether any signature of genetic structure found in this study might be an artefact of host species distribution due to different species of *Porites* hosting different *Symbiodinium* types, cluster-based correlation analysis between *Symbiodinium* sequence recovered and host species was conducted. Whilst a significant result of the psbA^{ncr} chi-squared test suggests a significant interaction between species and cluster for this marker it should be noted that the majority of the divergence was driven by the lower than expected abundance of *P. harrisoni* in the most populace cluster (55.9% of divergence). The large difference between the expected and observed values in this cluster is likely an artefact caused by the high sampling frequency of *P. lutea* (raising the expected value in the cluster in question) and the smaller number of more western sites at which *P. harrisoni* was sampled (lowering the recovered genetic diversity for *P. harrisoni*; *P. harrisoni* sampled at 3 vs., 6 and 5 sites for *P. lutea* and *P. lobata*, respectively; Figure S2) rather than a true species effect of *P. harrisoni* on sequence recovered. Given the likely artefactual cause of this significant result for the psbA^{ncr} marker and the lack of significant correlation between coral host and sequence for the nrDNA marker, *Symbiodinium* sequences and any associated genetic structure identified in this study will be discussed independent of host-species.

Genetic Diversity of the *S. thermophilum* Group

S. thermophilum sensu stricto was originally described from *Porites* spp. samples collected from the DAL, SAD and UMM regions of the southern PAG (Hume et al., 2015). Since this initial description considerable additional genetic diversity has been uncovered from samples collected outside of Southern PAG. This increase in genetic diversity has

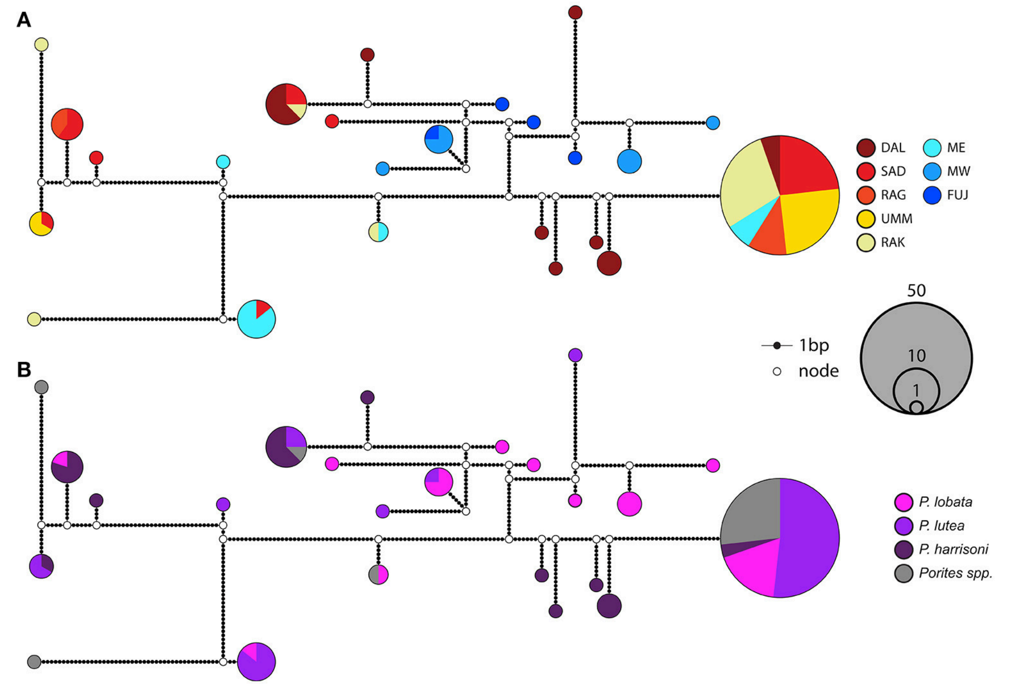

FIGURE 2 | Maximum parsimony network using the psbA^{ncr} genetic marker. Populated nodes are representative sequences of operational taxonomic units (OTUs) created by clustering at a distance of 0.04. Nodes are colored according to both site **(A)** and host species **(B)**.

led to the use of the term *S. thermophilum* group due to the fact that such diversity may be indicative of additional species.

Whilst all of the samples used in the initial *S. thermophilum* description resolved with a single dominant ITS2 type C3 sequence, a range of psbA^{ncr} haplotypes were recovered (Hume et al., 2015). The majority of these psbA^{ncr} sequences (17/22) cluster within the largest OTU of the psbA^{ncr} maximum parsimony network created in this study with the remaining 5 clustering amongst the monophyletic DAL grouping also from this study (**Figure 2**). The majority of internal samples (from DAL, SAD, RAG, UMM, RAK, and MW) analysed in this study also cluster within the same psbA^{ncr} OTU and display a limited diversity of closely related intragenomic ITS1-5.8S-ITS2 variants that share only 3 out of 38 haplotypes with external samples (ME, FUJ, MUC; **Figures 2**, **3**). Taken together, these findings suggest that the majority of *S. thermophilum* group symbionts found within the southern PAG are *S. thermophilum sensu stricto* but that additional *S. thermophilum* group diversity is also present, such as the PAG *Acropora* spp.—specific symbiont (C3V1; KM487747) identified in Hume et al. (2015). In contrast, whilst this study's external *S. thermophilum* group populations also return ITS2 type C3 and *S. thermo*-indel containing sequences characteristic of the *S. thermophilum* group, their lack of shared haplotypes with internal PAG symbionts (both non-*S. thermo*-indel-containing nrDNA and psbA^{ncr} sequences) suggest that they are either a genetically distinct subpopulation of *S. thermophilum* or represent a separate species. Indeed, the quantification of genetic distances between members within the group by Hume et al. (2016) as comparable to those observed between other *Symbiodinium* types estimated to have diverged more than 10 Mya would also support the likely existence of multiple subpopulations within the group.

Genetic Resolution of *S. thermophilum* Sub-taxa

The consideration of nrDNA intragenomic sequence variants in *Symbiodinium* ITS2 phylogenetics has enabled the further resolution of types originally designated only according to their predominant ITS2 sequence, for example the distinction between D1, D1-4 (*S. trenchii*) and D1-4-6 (LaJeunesse et al., 2010). Whilst the consideration of such intragenomic variants has enabled the distinction of *S. thermophilum* group symbionts from other ITS2 type C3 symbionts, neither the presence nor frequency of specific intragenomic variants has yet been able to resolve different populations of *S. thermophilum* group symbionts to the same extent as the inclusion of additional regions of the nrDNA has in this study (**Figure 3A** vs. **Figure 3B**). This inclusion of the 5.8S and ITS1 region has effectively brought the resolution of the rDNA marker closer to that of the psbAncr marker, a marker generally considered hypervariable (Thornhill et al., 2014). However, by sequencing nrDNA ITS2 PCR amplicons to a greater depth using NGS technologies (*sensu* (Arif et al., 2014), Smith et al., 2017) fine scale assessment of differences in the presence and proportion of intragenomic sequence variants will likely result in a significant increase in the resolving power of this marker.

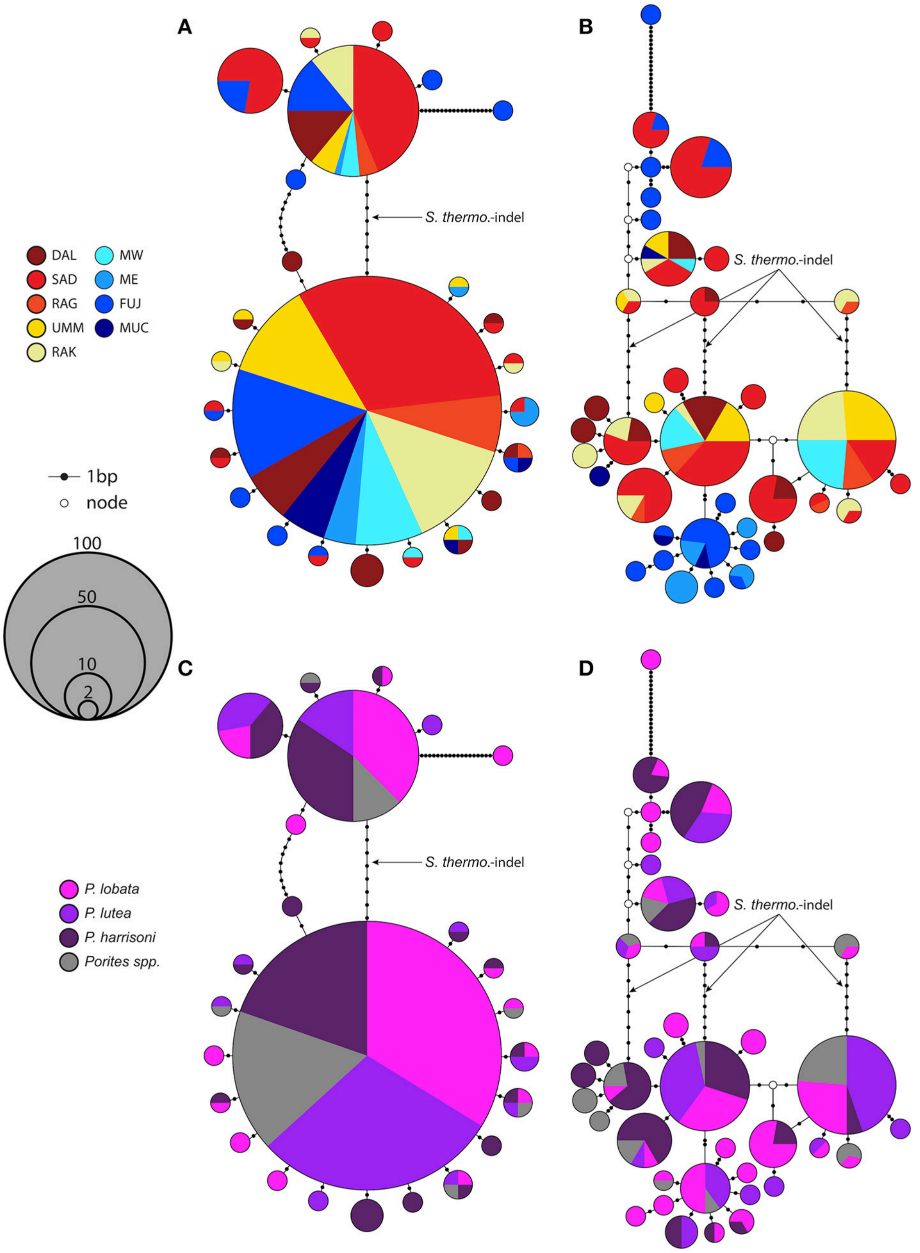

FIGURE 3 | Maximum parsimony networks using the nrDNA. Populated nodes are representative of nrDNA sequences of either the ITS2 region only **(A + C)** or the complete ITS1-5.8S-ITS2 region **(B + D)**. Nodes supported by only a single sequence are not displayed. Nodes are colored by site **(A + B)** and host-species **(C + D)**. The link representing the 8 bp *S. thermo*.-indel is annotated.

Identification of *S. thermophilum* Sub-populations

Whilst *S. thermophilum* group symbionts have been documented throughout reefs on the south coast of the PAG and to a lesser extent externally in the Strait of Hormuz and Gulf of Oman (D'Angelo et al., 2015) it is unclear whether the diversity of physical environments over which they are found has led to a range of genetically disparate sub-populations. Here we further resolve the previously described biogeographical boundary to coral holobiont distribution found in the Strait of Hormuz and identify genetically disparate populations either side of it.

D'Angelo et al. (2015) first documented the host-symbiont biogeographical boundary at the Strait of Hormuz through noting a gradual decrease in the predominance of *S. thermophilum* group associations moving from the western Strait of Hormuz out into the Gulf of Oman. The significant effect of this boundary upon a large number of taxa is qualified by the limited diversity found within the PAG compared to the wider Indo-Pacific (Coles, 2003; D'Angelo et al., 2015). Given the large among group variance between internal and external populations, location either side of the boundary, rather than distance between study sites, would be expected to explain genetic disparity. As such, insignificant results from the mantel test also corroborates the presence of this boundary.

The genetic structure identified in this study would suggest that the western edge of the Strait of Hormuz (i.e., site MW) may represent a specific area where the decrease in genetic diversity from the Gulf of Oman to the PAG is greatest. This is demonstrated through the significant genetic difference of MW to all outer sites in concert with an only mixed differentiation from internal sites (**Table 1**). In addition, the fact that the two significantly differentiated Musandam sites (i.e., MW, ME) have only ∼20 km between them may point to an sudden spatial divide between the internal and external symbiont biomes in this region. Such a small distance between genetically differentiated sites could suggest that local adaptation to specific local conditions, rather than allopatric diversification due to limited connectivity, is responsible for the genetic heterogeneity observed.

Given that the surface inflow into the PAG effectively acts to buffer thermal extremes by cooling in the summer and warming in the winter, a gradient of seasonal thermal range exists that correlates with the penetrative distance of this inflow (**Figure 1c**). As such, coral communities within the southern and more westerly PAG experience the coolest winters and warmest summers in conjunction with the highest year round salinities (∼42; **Figure 1**). Remotely sensed estimated upper bleaching thresholds of reefs in this southern region reflect this with a difference of more than 0.5°C between DAL and SAD (35.05 and 34.53°C, respectively; Shuail et al., 2016). The genetic disparity seen between DAL and to a lesser extent SAD with other internal sites may therefore be due to local adaptation to different thermal histories. However, further population genetic data would be required to verify this.

S. thermophilum Group Symbionts as Stress Tolerant Genetic Resources

As coral reef ecosystems become increasingly under threat so do the natural systems and human populations that rely upon them (Hughes et al., 2003). Coupled with the advanced state of reef degradation these ecosystems are therefore increasingly the focus of conservation efforts (Burt et al., 2014). With their extraordinary stress tolerance, coral associations of the PAG have been suggested as potential candidates to seed thermally degraded reefs in order to accelerate reef recovery and increase future stress tolerance through the integration of genetic resources (Coles and Riegl, 2013). However, mesocosm-based studies by D'Angelo et al. (2015) demonstrated that whilst some *S. thermophilum*-associated corals from the PAG were able to survive in waters of normal oceanic salinity, their growth was reduced and their exceptional thermal tolerance lost. As such, due to the trade-offs associated with the local adaptations to the higher salinity of the PAG, corals from this waterbody appear to have a small potential to colonise reefs elsewhere that are characterised by a more oceanic salinity.

However, the presence of genetically distinct sub populations of the *S. thermophilum* group identified in this study would suggest that a considerable pool of group member symbionts upon which natural selection could act exist. Specifically, group members in the Gulf of Oman surviving in waters characterised as thermally challenging yet with oceanic-like salinities, would appear to be model candidates to act as natural sources of stress tolerant associations to Indo-Pacific reefs. The modification of symbiont associations by corals to those of a more stress tolerant type has been demonstrated (Ortiz et al., 2013; Silverstein et al., 2015) and such mechanisms could allow for the ecological proliferation and integration of *S. thermophilum* group symbionts amongst reefs, especially considering the broad range of cnidarians *S. thermophilum* group symbionts have been identified in association with (more than 40 genera; Hume et al., 2016). Indeed, the spread of a stress-tolerant coral generalist *Symbiodinium trenchii* throughout Caribbean reefs in a period of possibly only several decades has recently been documented and would imply that such an ecological proliferation could occur in a time frame relevant to the slowing of further reef degradation due to future warming (Pettay et al., 2015). Nevertheless, the almost undetectable abundance of *S. thermophilum* group symbionts external to the PAG (found in ∼4% of corals in the Red Sea and Gulf of Oman, often at low within coral abundances; Hume et al., 2016) would suggest that *S. thermophilum* group associations are not competitive given current environmental conditions and extant symbiont populations.

As coral reef ecosystems continue to be degraded by increasingly stressful conditions, and typical associations begin to breakdown, stress tolerant *S. thermophilum* group associations may become more competitive conferring increased tolerances to reefs in future conditions (Pettay et al., 2015). However, many other biotic and abiotic factors that will influence whether these symbionts will be able to acquire a niche and thus proliferate must be taken into account. In particular, trade-offs such as reduced calcification rates that can be associated with thermal tolerance must also be considered (Jones and Berkelmans, 2010). The ability of *S. thermophilum* group associations to be able to confer increased tolerances will be dependent on the maximal retention of genotypes within the group from which better adapted and resilient symbionts may gain predominance and enable reef adaptation to warming waters. As such, reduction of any reef stressors other than rising SSTs that may negatively affect this biodiversity must be prioritised in conservation strategies (D'Angelo and Wiedenmann, 2014).

DATA ACCESSIBILITY

Genbank accession numbers for psbA^{ncr} sequences analysed as part of this study are listed in Table S1. A multiple sequence alignment of the ITS1-5.8S-ITS2 nrDNA sequences used in this study has been submitted to the Dryad Repository. MOTHUR, R, and PYTHON scripts used in this study are available at https://github.com/didillysquat/PAG-Code.

AUTHOR CONTRIBUTIONS

BH: Conceived and conducted the analysis; BH, CD, and JW: Planned and conceived the project; BH: Wrote the initial report; BH, CD, and JW: Revised final versions of the report. JB: Sponsored fieldwork to collect samples and along with JW contributed resources to the analysis.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00138/full#supplementary-material

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Distinct Bacterial Microbiomes Associate with the Deep-Sea Coral *Eguchipsammia fistula* from the Red Sea and from Aquaria Settings

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Microbial communities associated with deep-sea corals are beginning to be studied in earnest and the contribution of the microbiome to host organismal function remains to be investigated. In this regard, the ability of the microbiome to adjust to prevailing environmental conditions might provide clues to its functional importance. In this study, we characterized bacterial community composition associated with the deep-sea coral *Eguchipsammia fistula* under natural (*in situ*) and aquaria (*ex situ*) settings using 16S rRNA gene amplicon sequencing. We compared freshly collected Red Sea coral specimens with those reared for >1 year at conditions that partially differed from the natural environment, in particular regarding increased oxygen and food availability under *ex situ* conditions. We found substantial differences between the microbiomes associated with corals under both environmental settings. The core microbiome comprised only six bacterial taxa consistently present in all corals, whereas the majority of bacteria were exclusively associated either with freshly collected corals or corals under long-term reared aquaria settings. Putative functional profiling of microbial communities showed that corals in their natural habitat were enriched for processes indicative of a carbon- and nitrogen-limited environment, which might be reflective of differences in diet under *in situ* and *ex situ* conditions. The ability of *E. fistula* to harbor distinct microbiomes under different environmental settings might contribute to the flexibility and phenotypic plasticity of this cosmopolitan coral. Future efforts should further assess the role of these different bacteria in holobiont function, in particular since *E. fistula* is naturally present in markedly different environments.

Keywords: phenotypic plasticity, microbial community profiling, 16S rRNA gene, deep-sea ecosystems, climate change, acclimation

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INTRODUCTION

Corals are metaorganisms, so-called coral holobionts, consisting of the cnidarian animal host and a suite of microorganisms, most notably endosymbiotic algae of the genus *Symbiodinium* that provide nutrition via photosynthates (Muscatine and Porter, 1977) and a diverse array of bacteria (Rohwer et al., 2002). The acclimation capacity of a coral holobiont to environmental changes is determined by the coral animal (Todd, 2008), by *Symbiodinium* (in zooxanthellate corals; Brown, 1997), and likely by other associated microbes. In particular, adjustment of associated bacteria to prevailing environmental conditions has been suggested to support acclimatization of the coral holobiont (Reshef et al., 2006). This notion is supported by recent studies that show, at least in part, flexible bacterial microbiomes of the coral holobiont to environmental change (Jessen et al., 2013; Roder et al., 2015; Hernandez-Agreda et al., 2016; Röthig et al., 2016; Ziegler et al., 2016, 2017). However, our knowledge on the role of the bacterial microbiome to coral holobiont function is still limited (Bourne and Webster, 2013; Bourne et al., 2016), although bacteria are shown to contribute to coral health (Rosenberg et al., 2007; Krediet et al., 2013) and are involved in nutrient cycling (Rädecker et al., 2015; Bourne et al., 2016).

Deep-sea corals, similar to their shallow coral counterparts, provide structural habitats that are considered biodiversity hotspots (Roberts et al., 2006). However, they are generally restricted to light-limited and highly productive waters at low temperatures ($<14°C$) and are therefore commonly used synonymous with cold-water corals (Roberts et al., 2006; Naumann et al., 2014). The major differences between deep-sea corals and their shallow-water counterparts are consequently their temperature preference (shallow coral $<30°C$ vs. deep coral $<15°C$ in most places) and that deep-sea corals are azooxanthellate, which might be partially related to the temperature preference. Lacking *Symbiodinium*, the role of bacteria may be more substantial compared to shallow corals. For example, deep-sea coral associated bacteria are likely involved in fixing and recycling of nitrogen and carbon (Neulinger et al., 2008; Middelburg et al., 2015). However, mainly due to their limited accessibility, the knowledge on deep-sea corals is still scarce, especially in regard to their associated microbial communities. Few studies characterized deep-sea coral associated bacterial communities, focusing mainly on octocorals (Penn et al., 2006; Gray et al., 2011; Kellogg et al., 2016; Lawler et al., 2016) and two reef-building scleractinian corals, namely *Lophelia pertusa* and *Madrepora oculata* (Yakimov et al., 2006; Neulinger et al., 2008, 2009; Hansson et al., 2009; Kellogg et al., 2009, 2017; Schöttner et al., 2009, 2012; Galkiewicz et al., 2011; Emblem et al., 2012; van Bleijswijk et al., 2015; Meistertzheim et al., 2016). Findings include species-specific microbiomes, but also considerable spatial and temporal variations. Only very recently, the microbiomes of three further scleractinian corals (i.e., *Eguchipsammia fistula*, *Dendrophyllia* sp., and *Rhizotrochus typus*) from the Red Sea have been characterized (Röthig et al., 2017). The deep Red Sea with low oxygen (1–2 mg O_2 L^{-1}) and limited nutrient availability due to warm temperatures ($>20°C$) features markedly different conditions than otherwise common for deep-sea coral habitats (Roder et al., 2013). In line with other studies, Röthig et al. (2017) showed that these coral microbiomes were species-specific and suggested functional adaptation to their environment. These adaptations include in particular the presence of anaerobe bacterial taxa and potential hydrocarbon degraders. Interestingly, at least two of the three species investigated (i.e., *E. fistula* and *R. typus*) are not endemic to the Red Sea (van der Land, 2008). In line with its global presence (van der Land, 2008) and as a potential explanation to its wide distribution, *E. fistula* from the Red Sea shows a remarkable physiological plasticity displaying substantial tissue (re)growth and polyp budding during long-term rearing (>1 year) under conditions that only in part reflect its natural Red Sea habitat (Roik et al., 2015). More specifically, in comparison to their highly oligotrophic and low oxygen (i.e., 1–2 mg L^{-1}) natural habitat in the Red Sea (Quadfasel, 2001; Roder et al., 2013; Qurban et al., 2014), aquaria-reared colonies of *E. fistula* were provided with a continuous but uniform diet under high oxygen conditions (i.e., >8 mg L^{-1}). Besides assessment of phenotypic differenes, Roik et al. (2015), however, did not assess whether long-term aquaria rearing resulted in differences in bacteria associated with *E. fistula* that could either contribute to the acclimatization or be a result of it.

In this study, we set out to characterize bacterial community structure associated with the Red Sea deep-sea coral *E. fistula* after successful long-term (>1 year) rearing under aquaria settings and compared it to the bacteria associated with *E. fistula* in their native environment. This allowed us to assess coral microbiome differences under different environments and the putative capacity to adjust to markedly different environmental settings. In turn, this may provide insights to the functional importance of the bacterial microbiome to the coral host.

MATERIALS AND METHODS

Coral Collection and Rearing

All *E. fistula* specimens used in this study were sampled by ROV from the central Red Sea in May 2013 on the R/V Aegaeo (KRSE2013L6). The Saudi Coastguard Authority under the auspices of KAUST issued sailing permits that include sample collection. In total, 6 coral samples from *E. fistula* were used for the bacterial microbiome analysis, three from their natural environment and three from long-term rearing in aquaria facilities. Each specimen consisted of one coral colony (∼5–10 cm) of similar biomass, harboring several polyps and the coenosarc.

As described in Röthig et al. (2017), coral samples used to assess the native microbiome (*in situ*) were collected from between 314 and 320 m depth (N22°17.837, E38°53.811) with a custom-made scoop, transferred into a specifically designed two-compartment container, and preserved in RNAlater at depth. About 90 min later upon retrieval, samples were rinsed with sterile-filtered seawater, crushed on liquid nitrogen, and stored at $-80°C$. To assess the *in situ* microbiome 3 of the 4 *E. fistula* samples described in Röthig et al. (2017) were used in this study. To ensure an evenly distributed sample set and a high sequencing depth, one *in situ* sample from Röthig et al. (2017) presenting the lowest coverage was disregarded. Further, a water sample from the corals' direct vicinity was taken using Niskin bottles. One liter of the water sample was filtered over a 0.22 μm Durapore filter (Millipore, Billerica, USA), and filters were stored at $-80°C$ until DNA extraction.

Corals for long-term rearing were collected in close proximity on a separate ROV dive during the same expedition (KRSE2013L6). Coral specimens were retrieved from the same habitat using the scoop and transferred into a plastic basket (Roik et al., 2015). The live *E. fistula* specimens were transferred into an aquaria system and transported to aquaria facilities at the King Abdullah University of Science and Technology (KAUST). Coral polyps were then attached onto reef cement sockets (Reef Construct, Aqua Medic) and transferred into an open flow batch system equipped with chiller, skimmer, trickling filter, and current pumps. Temperature was set to 21.3 ± 0.3°C and water was exchanged regularly. While water temperature resembled the *in situ* environment, oxygen levels were markedly higher (7.7–8.7 mg L^{-1} *ex situ* vs. 1–2 mg L^{-1} *in situ*) and corals were fed with *Mysis* and *Artemia* twice a week. The corals were reared for >1 year with prominent tissue and polyp growth (Roik et al., 2015). To assess bacterial communities associated with long-term reared (*ex situ*) *E. fistula*, three coral specimens were selected for DNA extraction. Feeding was ceased for 5 days, corals were rinsed with filtered seawater, wrapped in aluminum foil, and flash frozen in liquid nitrogen and transferred to −80°C. A one liter water sample was taken from the aquaria system and processed as described above.

DNA Isolation and Sequencing

DNA from flash frozen *ex situ* coral specimens was isolated using the AllPrep DNA/RNA Mini kit (Qiagen, Hilden, Germany). To do this, frozen specimens were unwrapped on ice, transferred to sterile zip lock bags, and dosed in 5 mL Qiagen RLT buffer. Buffer and coral tissue was carefully blasted off using tap air pressure and barrier pipette tips. The tissue-buffer mixture was then transferred into 15 mL Falcon tubes and vortexed. A 500 µL aliquot was used for DNA extraction following the manual (AllPrep Mini kit). DNA from crushed *in situ* corals was isolated according to the same manual. Water filters were cut in strips, Qiagen RLT buffer was added (1,200 µL to the deep-sea and 400 µL to the aquaria water samples), the samples were incubated for 20 min on a wheel, and further extraction followed the Qiagen AllPrep manual.

DNA libraries were generated according to the Illumina 16S metagenomics library preparation manual (Illumina, San Diego, CA, USA). The primers 784F and 1061R (Andersson et al., 2008) with Illumina adapter overhangs (underlined below) were used to amplify the variable regions 5 and 6 of the 16S rRNA gene: forward [5′-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGAGGATTAGATACCCTGGTA-3′] and reverse (5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGCRRCACGAGCTGACGAC-3′). These primers are shown to amplify well with coral DNA (Bayer et al., 2013b). All PCRs were performed in triplicates using ∼1–5 ng DNA from water samples and ∼50–100 ng DNA from coral samples, Qiagen Multiplex PCR master mix, and 0.25 µM of each primer. The total volume was adjusted to 20 µL with RNAse-free water. The amplification PCR was one cycle at 95°C for 15 min, 25 cycles each at 95°C for 30 s, 55°C for 90 s, and 72°C for 30 s; a final extension step at 72°C for 10 min. Successful amplification was visualized on the Bioanalyzer (Agilent Technologies, Santa Clara, USA) for the *in situ* samples, and 10 µL from each of the *ex situ* coral samples was used for a visual check via gel electrophoresis. The triplicate PCRs were pooled and cleaned with the Agencourt AMPure XP magnetic bead system (Beckman Coulter, Brea, CA, USA). Following the Illumina metagenomics sequencing library preparation protocol, PCR products underwent indexing PCR amplification. A 2% ultrapure agarose gel (Ultrapure Agarose, Life Technologies) was used for final size selection with the Zymoclean DNA large fragment recovery kit (Zymo Research, Irvine, USA) with two elutions at 10 µl to purify the PCR products from the gel. The libraries were sequenced with 25% phiX control on the Illumina MiSeq, 2 × 300 bp paired-end version 3 chemistry according to the manufacturer's specifications at the KAUST Bioscience Core Lab. Of note, PCR-based bacterial metabarcoding methods are amenable to potential bias by choice of primer selection, differences in 16S rRNA gene copy number across bacterial taxa, and length of the amplicon.

Bacterial Community Analysis

We used mothur (v.1.36.1; Schloss et al., 2009) for amplicon analysis. Sequence reads were split according to barcodes, assembled to contigs, and quality trimmed. Unique sequences were identified and counted, and the number of total sequences for each sample was determined using the "count.seqs" command. Singleton sequences (i.e., sequences that occurred only once over all samples) were removed. The remaining sequences were aligned to the SILVA reference set (release 119; Pruesse et al., 2007) and sequences that did not align were disregarded. A pre-cluster step with 3 bp difference was performed (Huse et al., 2010), and chimeras were detected using UCHIME as implemented in mothur (Edgar et al., 2011). Chimeras were removed and remaining sequences were classified with the Greengenes database (release 13_5) using a bootstrap of 60 (McDonald et al., 2012). Next, chloroplasts, mitochondria, archaea, eukaryotes, and unknown sequences were removed, and the bacterial composition of samples was compared on the taxonomic level of bacterial families using R (R Core Team, 2014). For further analyses, all samples were subsampled to 10,000 sequences and then clustered into OTUs with a cutoff $\leq$0.03. Alpha diversity indices [i.e., Chao1 (Chao, 1984), Simpson Evenness, and Inverse Simpson Index (Simpson, 1949)], beta diversity analyses [i.e., Principle Coordinate Analysis (PCoA) calculated with a Bray-Curtis dissimilarity matrix], and Analysis of MOlecular VAriance (AMOVA; Excoffier et al., 1992) were performed in mothur. PCoA results were plotted using SigmaPlot 11 (SYSTAT Software, Point Richmond, CA, USA).

To characterize the core microbiome of *E. fistula*, only OTUs present in all coral samples (including all *in situ* and all *ex situ* coral samples) were considered. For the *in situ*, microbiome, OTUs present in all coral samples collected from the natural environment were considered, and accordingly, for the *ex situ* microbiome, OTUs present in all corals from the long-term rearing were selected. Of note, members from the *in situ* and the *ex situ* microbiome are not exclusive and can be present in both the *in situ* and *ex situ* microbiome.

We used METAGENassist (Arndt et al., 2012) for automated taxonomic-to-phenotypic mapping in order to assess putative functional profiles based on the 16S community composition of the coral samples. Input files were created in mothur ("make.shared" and "classify.otu"). During data processing in METAGENassist, all OTUs in the six coral samples were assigned, mapped, and condensed into 372 functional taxa. After filtering based on interquartile range (Hackstadt and Hess, 2009), the remaining 335 functional taxa were normalized over sample by sum and over taxa by Pareto scaling. Subsequently, we analyzed the data for "metabolism by phenotype" using Euclidean distance measure and a complete clustering algorithm to visualize in a heatmap the top 15 features selected by random forest classification.

Please refer to **Supplementary Data Sheet 1** for commented workflows for analyses with mothur, METAGENassist, and R.

RESULTS

Microbiome Composition in Corals and Water

To assess differences of the coral microbiome after long-term rearing (>1 year) in comparison to the *in situ* microbiome of *E. fistula*, we analyzed 8 16S rRNA gene libraries from 3 freshly collected corals (*in situ*), 3 long-term reared (*ex situ*) corals, 1 water sample from the corals' natural habitat (*in situ*), and 1 water sample from the rearing water (*ex situ*). The libraries yielded 1,260,862 sequences, which were subsequently trimmed, filtered, and error-corrected (i.e., removal of chimeras, singletons, and chloroplasts, among others) resulting in 363,265 sequences with an average length of 293 bp.

For visualization of the bacterial composition in coral and water samples, we classified all sequences to the family level in a stacked column plot and summarized over replicates in pie charts (**Figure 1**). The bacterial communities of freshly collected (*in situ*) and reared (*ex situ*) corals were different from each other. In the bacterial communities of *in situ* corals, families of unclassified Gammaproteobacteria, Vibrionaceae, Rhodospirillaceae, and an unclassified family of Proteobacteria comprised on average about half (46%) of all sequences. Conversely, *ex situ* corals harbored different abundant families. Here, Brevibacteriaceae, Alteromonadaceae, Flavobacteriaceae, and Oceanospirillaceae constituted on average about half (48%) of all sequences. Both water samples were markedly different from the coral samples. The *in situ* water sample had >70% of the sequences belonging to only two bacterial families, namely Alteromonadaceae and Pseudoalteromonadaceae. The *ex situ* water sample was more diverse with bacteria from the Alteromonadaceae, Flavobacteriaceae, and Rhodobacteraceae making up >80% of the bacterial diversity.

To assess differences between bacterial communities of freshly collected (*in situ*) corals, reared (*ex situ*) corals, and water samples in more detail, we subsampled to 10,000 sequences and clustered into operational taxonomic units (OTUs). We identified 2,017 distinct OTUs across all samples, of which 1,750 OTUs were associated with corals and 458 with water samples (**Supplementary Data Sheet 2**). We next calculated alpha diversity indices. All coral samples contained more OTUs than the water samples, and alpha diversity indices on average were higher in *in situ* corals compared to their *ex situ* counterparts (**Table 1**). However, there were no significant differences for any alpha diversity measure between *in situ* and *ex situ* coral samples (all $P_{\text{t-test}} > 0.05$), which might be due to coral colonies displaying a pronounced inter-individual variability in alpha diversity indices. In particular, *in situ* reared specimens were highly variable, suggesting flexible microbial association (**Table 1**).

To further assess differences in the bacterial communities of coral specimens and seawater samples, we plotted all samples in a principle coordinate analysis (PCoA) based on Bray-Curtis dissimilarity (**Figure 2**). We found the *in situ* and *ex situ* coral samples to cluster together. Further, they grouped away from each other and from the seawater samples. Both seawater samples were not clustering closely with any coral sample indicating distinct bacterial communities for corals and water. To assess differences between coral samples in more detail, we excluded both water samples from subsequent analyses.

Distinct Bacterial Communities Associated with *in situ* and *ex situ* Corals

Based on OTU abundance, *in situ* corals and *ex situ* corals were significantly different from each other ($P_{\text{AMOVA}} < 0.05$). Of the 1,750 coral associated OTUs, we found 70 to be present in samples from both groups. These shared OTUs generally displayed pronounced differences in their abundance between conditions, indicating strong dependence on environmental context (e.g., variability and composition of diet). Only 10 of these 70 OTUs were among the 50 most abundant OTUs. Further, the OTU abundances differed at least six-fold between both conditions (**Supplementary Data Sheet 2**). Hence, the majority of coral-associated bacterial taxa was present either in *in situ* or in *ex situ* samples, but not in both.

We identified 1,251 distinct OTUs associated with *in situ* corals, while reared specimens contained only 568 OTUs. Thus, bacterial richness was much higher in corals in their natural habitat, potentially reflecting the more stable environment and less diverse diet (with a consequently less diverse gut microbiome) under reared conditions (**Supplementary Data Sheet 2**). The 36 most abundant coral-associated OTUs (average abundance >50) included 26 that were exclusively associated with either the *in situ* or *ex situ* samples. The low number of shared taxa was even more pronounced among rare OTUs (<10 sequence counts across all coral samples). From 1,368 OTUs with an abundance <10 over all coral samples, 962 OTUs were only found associated with *in situ* corals, 388 exclusively in *ex situ* corals, and only 18 OTUs occurred in both groups (**Supplementary Data Sheet 2**).

To identify stable bacterial associates in *E. fistula* we determined the core microbiome, as defined by all OTUs that were present in all coral samples. The core microbiome comprised only 6 OTUs and was numerically dominated by Gammaproteobacteria (>73%), namely OTU0001 (*Alteromonas* sp.) and OTU0003 (*Photobacterium angustum*). The remaining 4 OTUs were less abundant and included Spirochaetes (OTU0013, unclassified Borreliaceae), Nitrospira (OTU0067, unclassified Nitrospiraceae), Betaproteobacteria (OTU0086, *Pelomonas puraquae*), and Cytophagia (OTU0111, *Reichenbachiella* sp.),

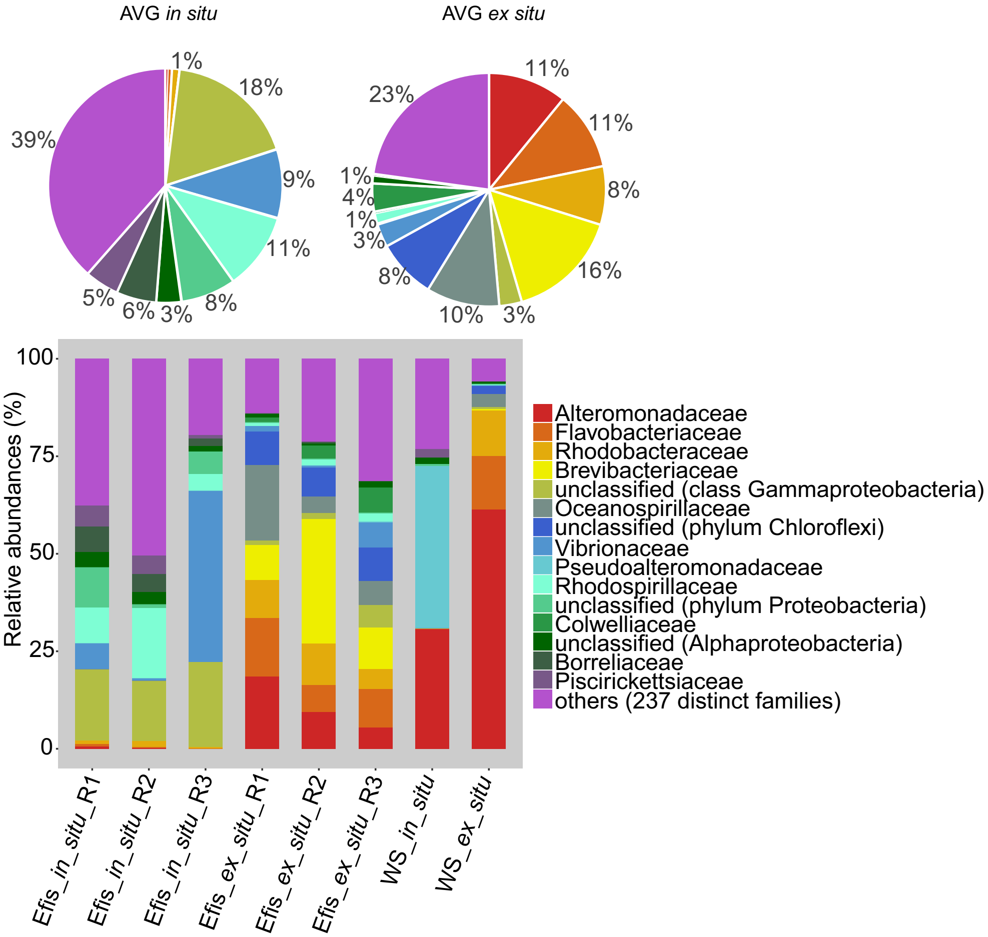

FIGURE 1 | Bacterial diversity from freshly collected (*in situ*) and long-term reared (*ex situ*) *Eguchipsammia fistula* deep-sea corals from the Red Sea on the phylogenetic level of family (Greengenes database, bootstrap ≥60). Each color represents one of the 15 most abundant families across all samples. Less abundant taxa (comprising 237 distinct families) are grouped under the category "others." Pie charts display average bacterial community composition of *in situ* (left) and *ex situ* (right) corals. Sequences that could not be classified on the family level are denoted at the next higher classified taxonomic level. AVG, average; Efis, *E. fistula*; WS, water sample; R, replicate.

which together comprised <27% of abundance counts of the core microbiome (**Figure 3**, **Supplementary Data Sheet 2**). Despite their consistent presence, core microbiome members were highly variable in abundance across coral samples (from 3 to 1,337 sequence counts, **Supplementary Data Sheet 2**).

In the coral holobiont, distinct bacterial taxa may be functionally important under different environmental conditions (Roder et al., 2015; Röthig et al., 2016). This may impede the delineation of functionally relevant bacteria based on abundance, since rare bacteria under one environmental condition may become abundant under another. For this reason, we chose to look for bacterial taxa consistently present in all *in situ* or all *ex situ* samples (irrespective of relative abundance) to identify bacterial taxa that may provide functional insights. In all *in situ* corals, we identified 146 common OTUs, of which only 19 also occurred in reared samples. Similarly, in all *ex situ* corals, we found 143 common OTUs, of which only 27 occurred in freshly collected corals (**Figure 3**). OTUs exclusive to either condition comprised abundant and rare members. The pronounced differences in the microbiomes of *in situ* and *ex situ* corals highlight the flexibility of microbiome composition of *E. fistula* and suggest that abundant and rare bacterial members can change under prevailing environmental conditions, including taxa of putative functional importance.

Taxonomy-Based Functional Profiling of Bacterial Communities in *E. fistula*

To gain further insight into the functional importance of the pronounced microbiome differences, we assessed putative functional changes underlying the distinct bacterial communities in the freshly collected (*in situ*) and long-term reared (*ex situ*) corals using METAGENassist. As anticipated based on results from the OTU-based PCoA analysis (**Figure 2**), *in situ* coral samples clustered together and away from *ex situ* corals indicating functional differences between both groups as well as similarities within each group (**Figure 4**). Functional groups

TABLE 1 | Summary statistics of 16S rRNA gene amplicon sequencing of *in situ* and *ex situ Eguchipsammia fistula* and water samples.

Sample	No. of raw sequences	No. of OTUs	Chao 1	Inverse Simpson index	Simpson evenness
Efis_*in_situ*_R1	59,064	757	987	38.3	0.039
Efis_*in_situ*_R2	21,415	657	717	43.8	0.061
Efis_*in_situ*_R3	10,585	338	347	6.2	0.018
AVG_*in_situ*	**30,355**	**584**	**684**	**29.4**	**0.039**
Efis_*ex_situ*_R1	50,602	314	647	12.8	0.024
Efis_*ex_situ*_R2	39,276	291	452	8.3	0.020
Efis_*ex_situ*_R3	60,680	377	686	23.4	0.036
AVG_*ex_situ*	**50,186**	**327**	**595**	**14.8**	**0.027**
WS_*in_situ*	31,035	289	391	4.5	0.011
WS_*ex_situ*	90,608	178	448	6.3	0.015
AVG_WS	**60,822**	**234**	**419**	**5.4**	**0.013**

Efis, E. fistula; WS, water sample; R, replicate; AVG, average.

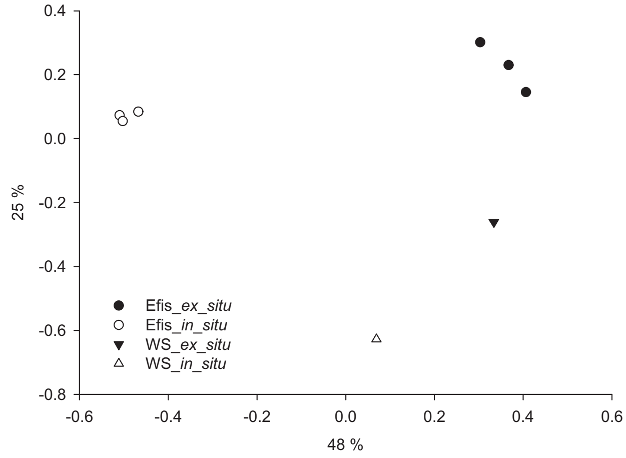

FIGURE 2 | Differences in microbial communities of *in situ* and *ex situ* *Eguchipsammia fistula* and seawater based on Bray–Curtis dissimilarity of microbial taxon abundances in a principal coordinate analysis (PCoA) ($R^2 = 0.91$). Efis, *E. fistula*; WS, water sample. Percentages on axes indicate variation explained by the two coordinates.

of *in situ* samples were represented by an enrichment of the processes “carbon fixation,” “chlorophenol degrading,” “napthalene degrading,” “sulfur metabolizing,” “dinitrogen-fixing,” and “chitin degradation.” In contrast, in *ex situ* corals we identified pronounced enrichment of the functions “sugars fermentor,” “lignin degrader,” “stores polyhydroxybutyrate,” “dehalogenation,” and “nitrite reducer.” Other processes like “xylan degrader,” “iron oxidizer,” and “sulfide oxidizer” were enriched for individual samples, but did not show overall trends related to the environment of origin.

DISCUSSION

In this study, we assessed differences in bacterial communities associated with the deep-sea coral *E. fistula* from the Red Sea from freshly collected (*in situ*) specimens and after >1 year rearing (*ex situ*) in aquaria facilities that only partly resemble natural conditions. We identified a major restructuring of the bacterial microbiome that aligns with distinct underlying putative functional profiles, suggesting that the bacterial compartment adjusts to prevailing environmental conditions. Whether this is a consequence of functional restructuring of the coral holobiont or a parallel response of the associated bacterial communities to differences in environmental conditions remains to be determined. Of note, *in situ* coral samples were preserved in RNAlater, whereas *ex situ* corals were flash frozen in liquid nitrogen, and it has been shown that RNAlater can bias samples regarding recovery of some bacterial taxa (Gray et al., 2013; Salter et al., 2014). Accordingly, some of the differences we found may be due to the different preservation methods used.

Microbiome Differences in *E. fistula* between Native Red Sea and Long-Term Rearing Environment

Studies on mucus microbiomes of shallow-water corals (Kooperman et al., 2007; Pratte et al., 2015) and on the microbiome of deep-sea corals (Schöttner et al., 2009) show that transfer and rearing of corals from their native environment to aquaria settings resulted in changes of the associated bacteria, but these were not accompanied by alterations in the appearance of the coral. In contrast, our previous study comparing *in situ* and *ex situ* long-term reared coral specimens of *E. fistula* (Roik et al., 2015) showed substantial morphological differences (i.e., enhanced tissue growth and polyp budding) of *E. fistula* under *ex situ* conditions that were characterized by higher oxygen and nutrition levels (among other parameters). Concomitant with the morphological changes, we hypothesized that long-term rearing may result in microbiome changes in *E. fistula*. Indeed, here we found pronounced differences in the coral bacterial microbiome of *in situ* and *ex situ E. fistula*. Changes in the microbial community based on environmental differences were shown before by Roder et al. (2015) where the microbiome of *Ctenactis echinata* was less structured and more diverse in lower populated coral habitats, indicating that preferred habitats align with more structured bacterial communities. A more extreme case of environmental adjustment was observed by Röthig et al. (2016) where associated bacteria of *Fungia granulosa* changed under high salinity exposure over 29 days and suggested a shift toward increased osmolyte production, sulfur oxidation, and nitrogen fixation. Similarly, Ziegler et al. (2017) reported on changes of the bacterial microbiome of *Acropora hyacinthus* in a highly variable and warm environment that align with increased heat tolerance of the coral host. In the current study, differences in the bacterial microbiome between *in situ* collected and *ex situ* reared corals were substantial and were representative of differences in prevailing environmental conditions.

In line with substantial differences between microbial community structure of *in situ* and *ex situ* coral specimens, we identified only 6 OTUs comprising the core microbiome (i.e., OTUs that were present in every coral sample). The core microbiome included abundant [OTU0001: average abundance (AVG) 161, OTU0003: AVG 786, and OTU0013: AVG 220] but also comparably rare members (OTU0067: AVG 24, OTU0086:

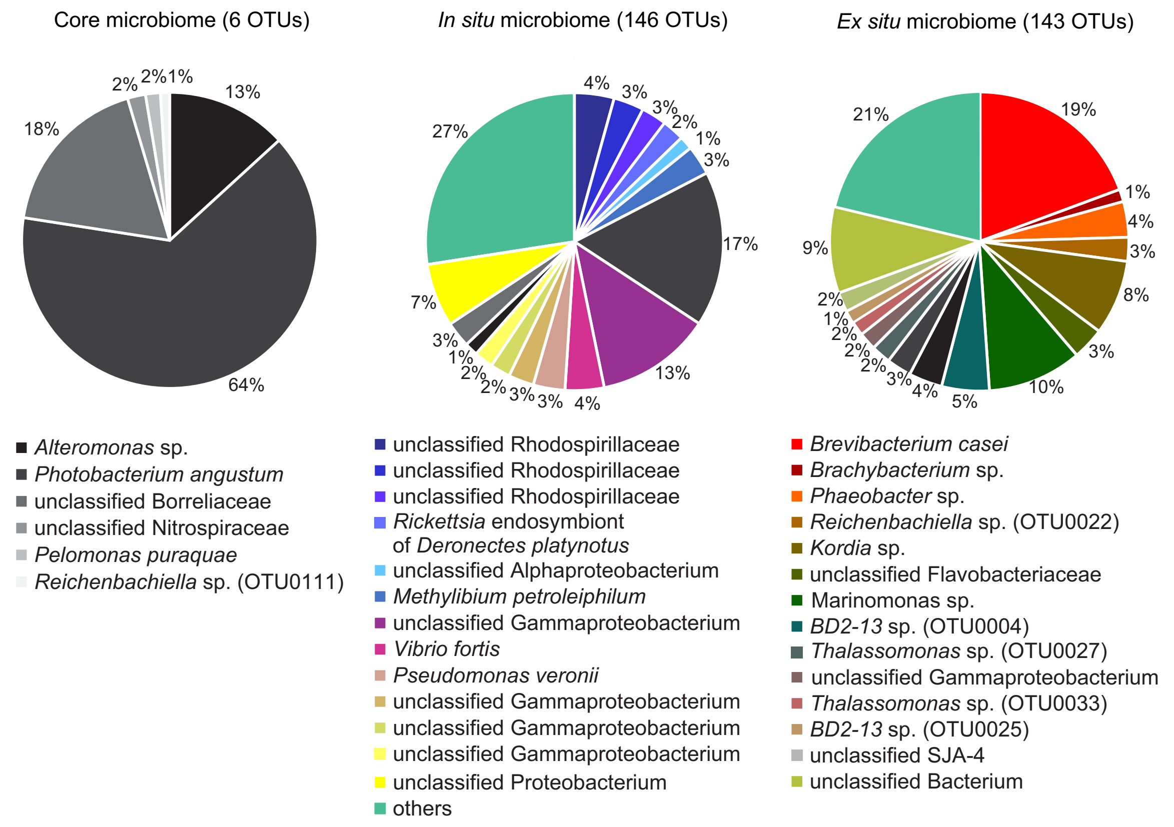

FIGURE 3 | *Eguchipsammia fistula* core microbiome and microbiomes of freshly collected (*in situ*) and long-term reared (*ex situ*) coral specimens. Bacterial members were determined by assessing presence of OTUs over samples. OTUs present in all coral samples were considered to be members of the core microbiome, taxa represented in all *in situ* samples to be members of the *in situ* microbiome, and those occurring in all *ex situ* samples were considered taxa of the *ex situ* microbiome. Each color represents a distinct OTU, including all core microbiome members and the 16 most abundant taxa each of the *in situ* and *ex situ* microbiomes; 130 (*in situ*) and 127 (*ex situ*) rare OTUs have been summarized in the category "others," respectively.

AVG 20, and OTU0111: AVG 12; **Supplementary Data Sheet 2**). OTU0003 (*P. angustum,* previously *Vibrio angustum/fischeri*) was previously described as a squid endosymbiont and closely related taxa are shown to inhibit virulence gene expression (Thompson et al., 2009; Mansson et al., 2011), at least hypothetically indicating functional importance and a potential to form a symbiotic relationship with a metazoan host as suggested by Hernandez-Agreda et al. (2016). OTU0086 (*P. puraquae*) has been identified as a coral-derived endophytic bacterium (Deng et al., 2015). The previous occurrence of OTU0003 and OTU0086 in close relationship with marine metazoans provides a context of functional importance and/or a putatively symbiotic relationship.

All core microbiome members varied in their abundance between freshly collected and long-term reared corals. For example, OTU0001 displayed an average abundance of 320 in *ex situ* and only 3 in *in situ* corals, whereas the trend was reversed for OTU0003 with 236 reads in *ex situ* and 1337 in *in situ* coral samples (**Supplementary Data Sheet 2**). The small and highly variable core microbiome in *E. fistula* potentially indicates a limited functional importance of its members and highlights the microbiome flexibility of the *E. fistula* coral holobiont. Our analysis of *in situ* and *ex situ* microbiomes suggests that *E. fistula* is associated with largely different microbial communities, pending on the prevailing environmental conditions. More importantly, these microbiomes align functionally to the different environments (see below). As such, the notion of species-specific core microbiomes that are consistent over large geographical and environmental scales (Bayer et al., 2013a; Ainsworth et al., 2015; Roder et al., 2015; Hernandez-Agreda et al., 2016, 2017; Ziegler et al., 2016; Neave et al., 2017) is in contrast to the highly variable core microbiome in *E. fistula*. Rather, it may suggest a limited association with obligate bacterial symbionts and/or a high flexibility in regard to bacterial symbionts. At the same time, our ability to detect rare conserved OTUs is directly related to sequencing depth. Hence, we cannot positively exclude that we are missing conserved associations of OTUs that would become visible at a higher sequencing depth.

Putative Functional Differences between Native Red Sea and Long-Term Rearing Bacterial Microbiomes

To gain insight into putative functional differences associated with microbiome differences, we conducted taxonomy-based

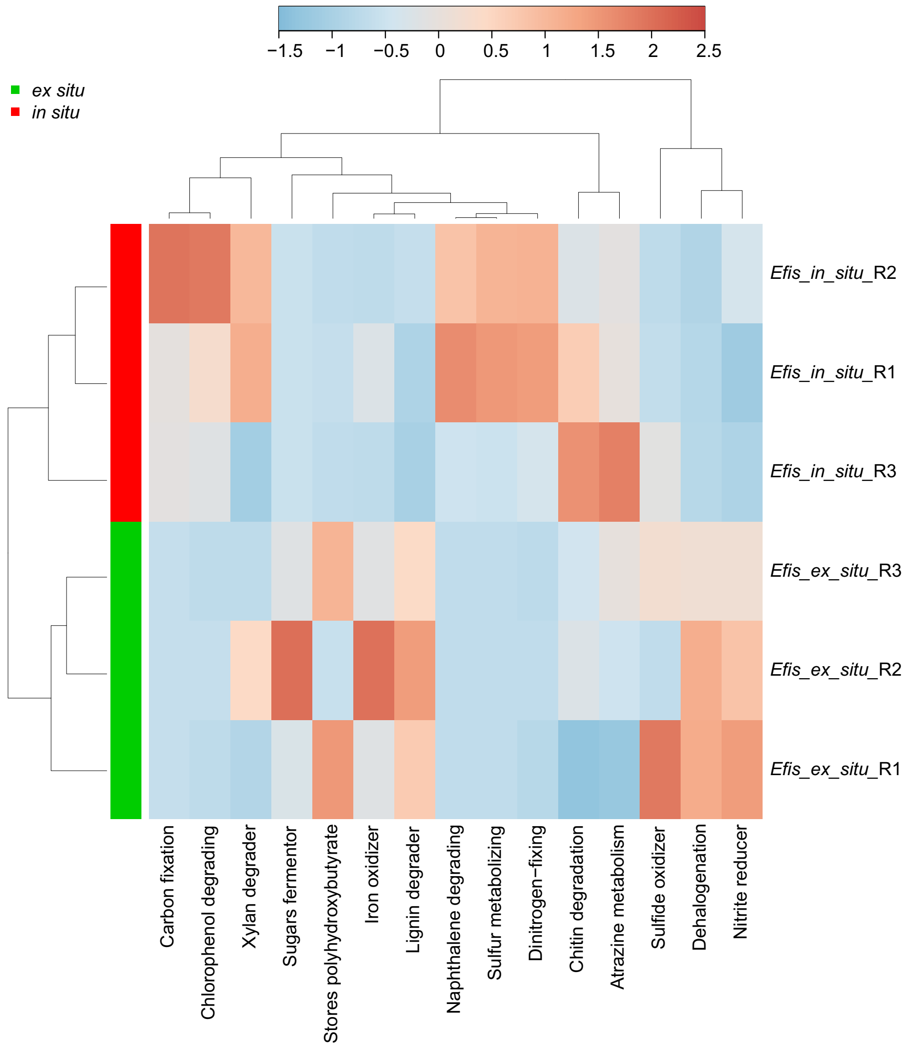

FIGURE 4 | Taxonomy-based functional profiling of bacterial communities from freshly collected (*in situ*) and long-term reared (*ex situ*) *Eguchipsammia fistula* deep-sea coral specimens from the Red Sea. The heat map shows functional differences on a relative scale with enrichment in red and depletion in blue. Data were analyzed for "metabolism by phenotype" with Euclidean distance measure and a complete clustering algorithm. Efis, *E. fistula*; R, replicate.

functional profiling. The identified differentially enriched processes revealed functional differences that might support the coral holobiont under two distinct environments. In particular changes in nutrition levels align with a decrease of "carbon fixation," "dinitrogen-fixing," and "chitin degradation," but an increase in "nitrite reducer" in long-term reared *ex situ* corals. Deep-sea corals are dependent on heterotrophic feeding and therefore generally limited not only in nitrogen, but also in carbon supply (Kiriakoulakis et al., 2004; Roberts et al., 2006). To cover their demands, corals utilize a wide range of food sources including phytodetritus, phytoplankton, zooplankton, dissolved organic matter (Dodds et al., 2007; Gori et al., 2014), and even chemoautotrophic carbon-fixing has been suggested (Middelburg et al., 2015). In line with this, the bacterial microbiome of *in situ E. fistula* included bacterial taxa with the potential to fix nitrogen and carbon directly (i.e., "dinitrogen-fixing," "carbon fixation") or indirectly, e.g., from crustacean prey (i.e., "chitin degradation"). In captivity, an increased food supply may lead to increased growth as shown for *M. oculata* (Orejas et al., 2011) and *E. fistula* (Roik et al., 2015). The long-term reared *E. fistula* were fed regularly with crustaceans *ad libitum* (Roik et al., 2015). The stable supply of readily available nitrogen and carbon at least hypothetically reduced the need for bacterial fixed nitrogen and carbon from other sources, and enriched nitrite reducing bacterial taxa (i.e., "nitrite reducer") in *ex situ* conditions might also be influenced by the provided nutrition. Expulsion of nitrogen (i.e., ammonium, nitrite, and nitrate) has been observed in *L. pertusa* (Maier et al., 2009, 2011), a process that may be increased by regular feeding in reared *E. fistula*. In this study, increased nitrite availability might enrich denitrifying bacteria in the microbiome. Taken together, microbiome differences correspond at least partly with the distinct environment and provide putative beneficial functions that might support the coral holobiont under the respective prevailing conditions. Future efforts should target analysis of the active fraction of bacteria, e.g., via RNA-based 16S gene profiling, and compare these data to DNA-based 16S gene profiling in order to disentangle active from total bacterial community composition.

Microbiome Flexibility Aligns with Phenotypic Plasticity

The microbiome is thought to adjust and support the coral holobiont under changing environmental conditions (Reshef et al., 2006). Coral microbiomes are shown to vary to a degree across spatial, depth, and environmental distributions (Pantos et al., 2015; Roder et al., 2015; Hernandez-Agreda et al., 2016; Glasl et al., 2017). Rapid adjustment of the microbiome has also recently been reported under stressful environmental conditions and suggested to support holobiont functioning (Röthig et al., 2016; Ziegler et al., 2017). Studies on deep-sea corals are scarcer, but findings are similar and indicate that environmental conditions influence coral-associated bacterial communities. For instance, diet of deep-sea corals is thought to influence the coral microbiome (Neulinger et al., 2008; Meistertzheim et al., 2016) and in turn the microbiome can unlock nutrient resources for the holobiont (Middelburg et al., 2015). In this context, *L. pertusa* has been suggested to be a more opportunistic feeder (based on fatty acid and $\delta^{15}N$ analyses) than *M. oculata* (Meistertzheim et al., 2016). This may be based on a more variable bacterial microbiome compared to *M. oculata*, which also aligns with a higher flexibility and phenotypic plasticity reflected by higher thermal tolerance and a larger distribution range (Neulinger et al., 2008; Meistertzheim et al., 2016).

E. fistula possesses a wide distribution range including the Red Sea, Indo-Pacific, Australia, and New Zealand (van der Land, 2008). These deep-sea habitats differ substantially in their environmental conditions, specifically in temperature and oxygen level (Roder et al., 2013) suggesting a high flexibility of the coral *E. fistula*. The high phenotypic plasticity of *E. fistula* has recently been demonstrated by long-term rearing at conditions that only partly resemble the natural Red Sea habitat (Roik et al., 2015). After >1 year rearing under increased oxygen level and consistent food supply, *E. fistula* corals displayed enhanced skeletal and tissue growth. Our data shows that this phenotypic plasticity is accompanied by a remarkably flexible bacterial microbiome associated with *E. fistula*. The microbiome changes include the loss of and acquisition of hundreds of OTUs with only comparably few taxa occurring under both conditions (albeit at different abundances), to a point where the concept of a conserved core microbiome remains to be re-examined. As a notion of caution, at the same time, it is posited that rare taxa in particular respond to environmental changes (Jessen et al., 2013; Hernandez-Agreda et al., 2016), and our ability to detect those are directly related to sequencing depth. In their natural habitat, *E. fistula* may host a highly diverse microbiome to utilize a wide range of nutrients. Moreover, the more diverse diet under *in situ* conditions may be a source of microbial diversity itself (*sensu* Meistertzheim et al., 2016), and certain microbiome members may proliferate in response to carbon sources that become episodically available. By comparison, *ex situ* coral specimens were reared under highly stable environmental conditions and provided with a uniform diet, where the less diverse microbiome may reflect the uniform diet or may be a direct consequence of it. Taken together, phenotypic plasticity of *E. fistula* may be supported by its microbiome flexibility and more specifically by its ability to associate with distinct bacteria under different environmental conditions. However, specific implications of microbiome stability on coral holobiont functioning are still unknown at large for deep-sea and for shallow-water corals. Even though putative functional profiles indicate that microbiome changes support holobiont function in the respective environments, it remains to be determined if these changes are driven by the environment or a result of selection by the holobiont.

CONCLUSIONS

The bacterial microbiome of *E. fistula* is remarkably flexible and distinct between *in situ* and *ex situ* conditions. This is also reflected in the underlying putative functional profiles of the microbiomes that align at least in part with the environmental conditions. The associated bacterial communities may therefore be a result of or contribute to the high flexibility, phenotypical plasticity, and wide distribution of *E. fistula*. In this context it will be interesting to assess specific contributions of the different bacteria to holobiont functioning.

DATA ACCESSIBILITY

Sequence data determined in this study have been deposited on NCBI under BioProject accession no. PRJNA354830 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA354830) for *in situ* samples (Accession no.: Efis_*in_situ*_R1 = SRR5051585, Efis_*in_situ*_R2 = SRR5051579, Efis_*in_situ*_R3 = SRR5051575, WS_*in_situ* = SRR5051584) and under PRJNA383322 (https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA383322) for *ex situ* samples (Accession no.: Efis_*ex_situ*_R1 = SRR5458549, Efis_*ex_situ*_R2 = SRR5458548, Efis_*ex_situ*_R3 = SRR5458547, WS_*ex_situ* = SRR5458546).

AUTHOR CONTRIBUTIONS

TR, AR, and CRV designed and conceived the experiments. TR, AR, and LY generated the data. TR and CRV analyzed and interpreted the data. CRV contributed reagents/materials/analysis tools. TR and CRV wrote the manuscript. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00259/full#supplementary-material

Supplementary Data Sheet 1 | Commented workflow for the mothur and METAGENassist analysis; commented R script for stacked column charts plotting (**Figure 1**).

Supplementary Data Sheet 2 | OTU abundance counts over samples with annotation, reference OTU sequence, and affiliation to core microbiome. Core microbiome members are displayed in **bold**. Efis, *E. fistula*; WS, water sample; R, replicate.

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Environmental Extremes Are Associated with Dietary Patterns in Arabian Gulf Reef Fishes

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Climate change is affecting the trophic ecology of reef fishes through changes in reef-associated food availability and fish feeding behavior. The southern Arabian Gulf is a thermally extreme environment, providing an opportunity to study fish diets on reefs with summer temperatures representative of next-century conditions elsewhere. Using 18S metagenomic analyses of stomach contents, we provide the first description of the dietary composition of three abundant reef fishes (*Pomacanthus maculosus*, *Pomacentrus aquilus*, and *Pomacentrus trichrourus*) from the thermally extreme southern Arabian Gulf, with five sampling periods across 1 year used to assess seasonal variation in diet. In total, 146 stomach content samples were sequenced, resulting in 9.6 million filtered reads that aligned to 17 classes in 14 phyla. Corals (Cnidaria, Anthozoa) dominated stomach contents of all three fishes (overall mean: 74.6, 40.6, and 21.2% of stomach reads, respectively), suggesting coral consumption to be characteristic of reef fish diet in the region. Sanger sequencing validated the presence of corals in the stomach contents and identified two common genera in the region, *Porites* and *Platygyra,* as part of the diet. Other common phyla included sponges and annelid worms (*P. maculosus*: 14.9%, 4.1%; *P. aquilus*: 5.9%, 16.7%; *P. trichrourus*: 8.2%, 14.7%, respectively), with the remainder comprised of 11 other phyla. Algae were virtually absent in diets of all three species. The *P. maculosus* diet was consistently coral/sponge dominated across the year, but there was substantial seasonal variation in the damselfishes, with diets dominated by coral in the hottest month (August; *P. aquilus*: 89.4%, *P. trichrourus*: 51.5%) but broadest in spring (March, May) when corals became less common (<19.8% each) and bivalves, free living ascidians, and various arthropods increased; parasitic cestodes were also abundant in damselfish stomachs in spring (mean: >16.4%). These results suggest that these fishes have developed a feeding ecology responsive to the fluctuating and extreme environmental conditions of their region. These results broaden our understanding of the diets of these three species and document the nature, complexity and temporal dynamics of reef fish diets in the most thermally extreme coral reef environment on earth.

Keywords: 18S rRNA, angelfish, damselfish, Arabian Gulf, diet, Persian Gulf, trophic

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INTRODUCTION

Coral reefs are one of the most diverse, ecologically complex and economically significant ecosystems in the world (Moberg and Folke, 1999). Corals provide essential habitat and food resources for an array of organisms, with coral reef fishes being among the most diverse and functionally important of these reef-associated groups (Moberg and Folke, 1999; Coker et al., 2014). Due to their close association with reefs, fish assemblages are strongly influenced by the topographic complexity and abundance of corals (Graham and Nash, 2013; Rogers et al., 2014), and the amount and variety of food items available on reefs further affects reef fish community structure and functional ecology (Chong-Seng et al., 2012; Glynn et al., 2014; López-Pérez et al., 2016). Reef fishes also influence their habitat, with their feeding activities directly or indirectly affecting the abundance of key benthic groups on reefs, such as algae, sponges and corals (Hixon, 1997; Hill, 1998; Cole et al., 2011). As such, the trophic ecology of reef fishes is strongly interlinked with the functioning of the wider coral reef community.

Climate change represents a growing threat to coral reefs and associated fish communities. Elevated sea surface temperature (SST) in recent decades has been associated with mass coral bleaching events around the world (Hughes et al., 2017), resulting in long-term shifts in the composition of benthic communities on many reefs (Baker et al., 2008; de Bakker et al., 2017). The resultant changes in habitat structure have been shown to strongly influence the composition and abundance of reef fishes (Wilson et al., 2006; Munday et al., 2008; Pratchett et al., 2008), and there is increasing evidence that shifts in the availability of food items on these changing reefs are influencing both the composition of reef fish feeding guilds (Pratchett et al., 2008; Wilson et al., 2008) as well as the items selected as food (Floeter et al., 2004; Berumen and Pratchett, 2006). Increasing temperatures also have direct effects on fish feeding activity itself. Fishes are ectotherms, and so changes of a few degrees Celsius can influence their behavior and metabolism (Wood and McDonald, 1997), affecting feeding-related parameters, such as swimming speed (Johansen and Jones, 2011), bite rates (Smith, 2008), and attack/escape dynamics (Allan et al., 2015), with increased feeding necessary to support the greater metabolic demand at higher temperatures (Nowicki et al., 2012). It is, thus, likely that climate change will have substantial but largely underappreciated effects on the trophic ecology of reef fishes in the future.

The Arabian/Persian Gulf represents a natural laboratory in which to investigate the influence of extreme temperatures on the trophic ecology of reef fishes. Coral reefs in the Arabian Gulf experience the highest summer maxima (>35°C) and the greatest range of temperatures (ca. 20°C annually) known for reefs anywhere in the world (Sheppard and Sheppard, 1991; Coles, 1997, 2003; Hume et al., 2013), with summer conditions in the Gulf today representative of conditions projected for many tropical reef environments in the next century (Riegl, 1999; Collins et al., 2013; Wernberg et al., 2013). As a result of these extreme conditions, coral reefs in the Gulf are less structurally complex and less diverse than in most other parts of the Indo-Pacific (Coles, 2003), with benthic communities distinct from those in even the biogeographically connected Indian Ocean (Sheppard et al., 1992; Bauman et al., 2012). As a result of this extreme environment as well as variation in habitat structure and food resources, reef fish assemblages in the Arabian Gulf are also structurally and functionally distinct from those in more benign reef environments (Feary et al., 2010, 2012), with trophic guild structure that differs markedly from even adjacent seas (Feary et al., 2010; Burt et al., 2011b; Hoey et al., 2016), and broader ranges of food consumed in at least some guilds (Pratchett et al., 2013).

Only limited research is available on the trophic ecology of Arabian Gulf reef fish. Other than studies of diet-related pollutant accumulation in commercially important fish species (e.g., Saei-Dehkordi et al., 2010; Monikh et al., 2012, 2013), only a few other studies have explored reef fish feeding ecology in the Arabian Gulf. Pratchett et al. (2013) used *in situ* observations of feeding habits to discern selectivity and rates of feeding in corallivorous butterflyfishes, while Burt et al. (2011b) inferred the trophic structure of reef fish communities based on field surveys and literature reviews. Both of these studies suggested that reef fish feeding activities in the Arabian Gulf were distinct from that of less extreme reef environments. Similarly, related studies on the composition of the wider reef fish communities or specific trophic groups have suggested that variation in abundance and composition of certain guilds likely substantially influences trophic ecology in the Arabian Gulf (Feary et al., 2010, 2012; Hoey et al., 2016). However, to date there have been no studies that have directly explored the diets of reef fishes in the Arabian Gulf. Given the environmental conditions and benthic composition of these reefs, such information and more long-term studies would be very useful for developing an understanding of the adaptability of trophic ecology of reef fish communities in other regions to future climate change. In addition, due to reefs here also having the largest range of temperatures known to be experienced by reef fish anywhere in the world (approximately 20°C annually; winter minimum <20°C, summer maximum >35°C) (Sheppard and Sheppard, 1991; Coles, 1997, 2003; Hume et al., 2013), reef fish in the Arabian Gulf also provide an opportunity to understand the plasticity of diets under highly variable environmental conditions (Pratchett et al., 2013).

Traditional techniques for quantifying dietary habits have typically been based on microscopic analysis of stomach, gut or fecal contents (Carreon-Martinez and Heath, 2010). These traditional morphological techniques, however, can be biased and inaccurate as identifiable characters can be lost in digestion and morphological similarities between food items can lead to misidentification (Carreon-Martinez and Heath, 2010; Paquin et al., 2014). To account for these limitations, there has been increasing use of molecular techniques to describe the composition of fish diets (e.g., Budarf et al., 2011; Paquin et al., 2014; Miyake et al., 2015). With recent improvements in technology, high-throughput sequencing techniques now provide a rapid and low cost means by which to characterize diets, with bioinformatic approaches applied to the resultant metagenomic data allowing for a much more robust, reliable and deep understanding of diet composition than had previously been possible using microscopy-based techniques (Clare, 2014). In general, this approach is more qualitative than quantitative. Qualitatively, the metabarcoding approach can reveal dietary items that may not be discoverable from traditional morphological techniques, such as small organisms or highly digested items (Leray and Knowlton, 2015; Albaina et al., 2016; Harms-Tuohy et al., 2016). Quantitatively, however, the number of sequences may not correspond to the abundance of the DNA or the food item in the stomach since the amplicon region may present in different numbers of copies in different organisms (Albaina et al., 2016). Also of note is that the metagenomics approach cannot identify whether a food item is a primary target of the fish feeding or is accidentally ingested in general foraging or indirectly consumed along with the primary items (Harms-Tuohy et al., 2016).

Here we use a metagenomics approach to examine stomach content of three abundant coral reef fishes from the southern Arabian Gulf, *Pomacanthus maculosus* (Arabian angelfish), *Pomacentrus aquilus* (dark damsel), and *Pomacentrus trichrourus* (pale-tail damsel). The goal of this study is to provide an unbiased and detailed account of the diet and its seasonal variation in the three species. The results of this study provide the first record of the diets of reef fishes in this understudied region and revealed important insights into how the diet of reef fishes changes in response to extreme environmental conditions.

METHODS

Sample Collection and Processing

Collection permit and IACUC approval were obtained from Environmental Agency Abu Dhabi and New York University Abu Dhabi, respectively. Three reef-associated fish species were collected from Saadiyat reef in Abu Dhabi, UAE (N 24.59900° E054.42150°): the Arabian angelfish, *P. maculosus*, the dark damsel, *P. aquilus*, and the pale-tail damsel, *P. trichrourus* (**Figure 1A**). These species are among the most abundant coral reef fishes in the southern Arabian Gulf, and among the most important species driving reef fish community divergence from those in adjacent seas (Feary et al., 2010; Burt et al., 2011b, 2013). Although little is known of the dietary habits of these species in the northeastern Arab region, data from other regions suggest that *P. maculosus* feeds mainly on sponges and algae, *P. aquilus* primarily on zooplankton, and *P. trichrourus* mainly on benthic algae (Masuda and Allen, 1993; ter Hofstede, 1998).

To determine the influence of seasonality on dietary content, collections were performed over five sampling periods across a year from summer (August 2015) to spring (May 2016), when mean monthly sea-bottom temperatures ranged over 15°C (**Figure 1B**). During each sampling period between 8 and 10 individuals of each species were collected by SCUBA using 30% clove oil (Clove bud oil, Sigma-Aldrich) emulsified with 95% ethanol as an anesthetic for hand-netting (Munday and Wilson, 1997). Anesthetized individuals were immediately transferred to the surface and euthanized in an ice-water slurry before being preserved at −80°C until processing.

To obtain stomach contents, individual fish were thawed and immediately dissected to avoid potential microbial degradation. The gastrointestinal tract was removed and the liver immediately separated and discarded to avoid contaminating the stomach content DNA with any enzymes that could aggravate DNA degradation. The stomach was separated from the intestines and the stomach contents were removed and immediately processed for DNA extraction.

DNA Extraction and Sequencing

DNA extraction was performed on the stomach content using the ZR Soil Microbe DNA MiniPrep (Zymo Research, The Epigenetics Company, USA) following the manufacturer's protocol. DNA samples were eluted in 80 uL of elution buffer. DNA quality was assessed using a Nanodrop 8000 instrument and DNA concentration measured using a Qubit instrument with the *High Sensitivity* dsDNA assay kit.

A 730 bp 18S rRNA gene fragment was amplified using PCR and purified using Agencourt AMPure XP beads (Beckman Coulter). Purified DNA fragments were then used to construct an 18S library following the Illumina 16S Metagenomic Sequencing Library Preparation workflow adapted for Illumina's MiSeq

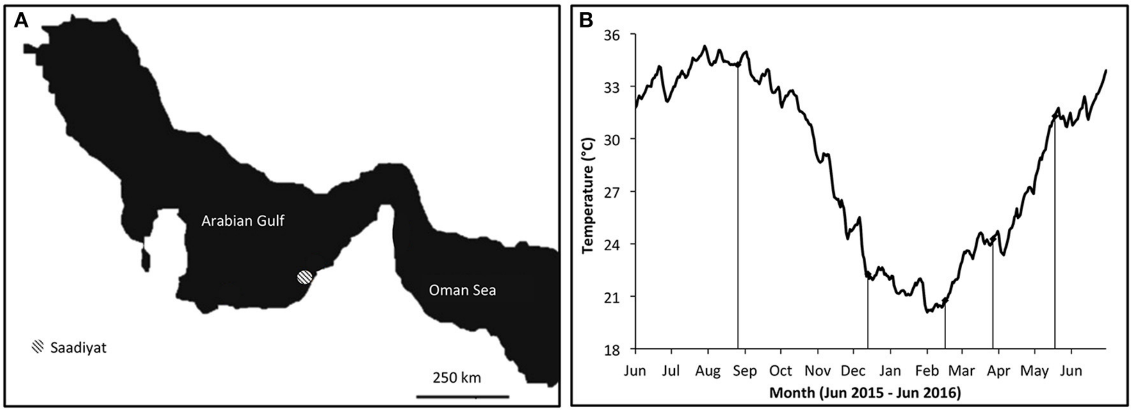

FIGURE 1 | (A) Map of the Saadiyat reef study location (adapted from Howells et al., 2016). **(B)** Mean daily seawater temperatures on Saadiyat reef. Lines indicate collection periods.

System (Illumina, 2017). The protocol was adapted for 18S metagenomic profiling by replacing 16S primers with 18S primers 574*f and 1132r (Hugerth et al., 2014; Supplementary Table S1) and using 56°C as annealing temperature:

5′ TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCGGTAAYTCCAGCTCYV 3′,

5′ GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGCCGTCAATTHCTTYAART 3′.

Samples amplified using 18S primers were indexed and purified following the Illumina 16S Metagenomic Sequencing Library Preparation protocol. The libraries were quantified using a Qubit instrument and average library size calculated by measuring amplicon size of 4 random samples using a DNA 7500 kit and a 2100 Bioanalyzer (Agilent Technologies). Library concentration was estimated using the following formula:

[(Concentration in ng/μl)/(660 g/mol × average library size)] × 106 = concentration in nM

Equimolar quantities of 18S libraries were then pooled and sequenced using MiSeq Reagent Kit v3 (Illumina) and a MiSeq instrument. The 18S metagenomic data is deposited in BioProject NCBI (Accession: PRJNA393758).

Bioinformatics and Statistical Analyses

Raw sequencing data (fastq files) were subject to quality control following standard protocols recommended by Illumina and were demultiplexed using the bcl2fastq 1.8.4 program (Illumina). Individual sample sequences were trimmed using the program Trimmomatic v0.32 to remove (i) sequencing primers/indexes, (ii) low quality reads and (iii) reads of length below 36 bp (Bolger et al., 2014). Quality control of trimmed reads was performed using FastQC 0.11.4 (Andrews, 2010). Resulting high quality reads (R1 only) were used for downstream analysis, including OTU clustering and taxonomy assignment, using USearch 8.1.1861 (Edgar, 2013), and QIIME 1.9.1 (Caporaso et al., 2010) (based on Pylro et al., 2014). Using USearch the following steps were performed: (i) removal of low quality reads, (ii) dereplication of sequences, (iii) removal of chimeric sequences, and (iv) OTU clustering based on 99% similarity. Taxonomy assignment of the OTUs was performed using QIIME based on a QIIME compatible version of Silva 111. Stringent filtering was done by keeping only OTUs supported by at least two reads and by limiting downstream analysis to OTUs found in at least 50% of a species' stomach samples to ensure that only truly representative dietary items were included in further analyses. To compare relative abundance of OTUs between samples, number of reads were normalized by converting them to fractions over the total number of reads within each individual sample. We note that a number of reads aligned to "Eukaryota, Metazoa, Craniata, and ∗," as expected, given that DNA from the fishes themselves would be extracted and amplified. These reads were removed from the analysis prior to normalization. In the overview of the diet at the phylum level, the cutoff for contribution to the stomach content was 90% and the remaining $\leq$10% were grouped into the category "Other" (**Figure 2**).

For the purposes of exploring the taxonomic composition of stomach contents across seasons, the data were aligned and processed at multiple taxonomic levels. Accordingly, statistical and visual analyses were performed on the lowest possible taxonomic classification that did not result in a major loss of data and resolution.

Principal component analysis (PCA) and variance component analysis (VCA) were performed using JMP Genomics 8.0. In all VCAs, the variation required to be explained was across principal components (PC) PC1 to PC3 and the PCAs were based on Pearson correlation with scaled and centered data. SIMPER and PERMANOVA statistical analyses were carried out in Primer-e v7. For these analyses, read proportion data was transformed using the transformation $\text{asin}[\text{sqrt}(P_i)]$, and abundance values were back-transformed using the formula $[\sin(T_i)]$ then converted to percentages. SIMPER analysis was

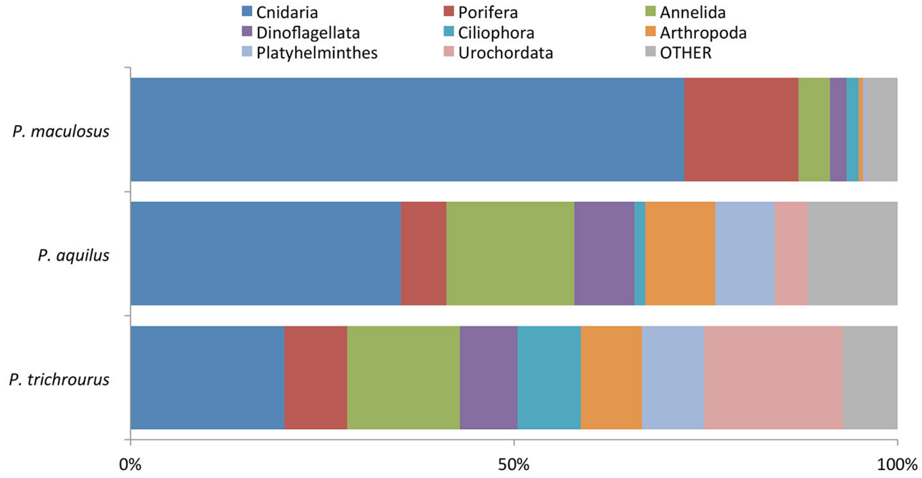

FIGURE 2 | Breakdown of phyla observed in the stomach contents of three reef fish species in Abu Dhabi, UAE, averaged across all sampling periods. The "Other" category is comprised of Cercozoa, Echinodermata, Mollusca, Bryozoa, Apicomplexa and Bolidomonas, each of which was observed in all three fish species at low abundance. See Supplementary Table S3 for means, variances and standard errors.

performed with the following parameters: resemblance based on S17 Bray-Curtis similarity and cut off for low contributions was 70.00%. The PERMANOVA parameters were resemblance also based on S17 Bray-Curtis similarity, sums of squares Type III (partial), fixed effects sum to zero for mixed terms, permutation method was permutation of residuals under a reduced model with 999 permutations (PERMANOVA works with any distance measure that is appropriate to the data and uses permutations to make it distribution free; Primer-e, 2017)[1]. Sampling groups/periods were considered significantly different if $p < 0.05$ (PERMANOVA). For the alignment of Sanger sequences, the identified coral was based on the top hit in BLAST with the highest *E*-value (nucleotide collection nr/nt database; megablast).

RESULTS

A total of 146 individual fish samples were collected over the course of this study, including 48 *P. maculosus*, 50 *P. aquilus* and 48 *P. trichrourus*, representing between 8 and 10 individuals per species per sampling period (Supplementary Table S2, S4). Most DNA samples had a yield > 400 ng and a SpeedVac instrument was used to concentrate eight samples that had a yield <20 ng. DNA samples were used as a template for 18S library preparation. Four samples were randomly chosen for amplicon size measurement using a Bioanalyzer 2100 instrument. Average amplicon size was approximately 735.5 bp as expected.

In total, 27,555,995 reads remained after trimming of 28,419,461 raw reads. Approximately 68% of the reads remained after USearch filtering and 35% of reads remained after dereplication. In total, 192,341 Operational Taxonomic Units (OTUs) (at 99% sequence identity) with minimum cluster size of 2 were identified from these filtered sequence reads of which 2,292 remained after applying the "minimum 2" filter and those were used for classification.

Overall, between 3 and 8 phyla accounted for approximately 90% of the stomach content (averaged across all samples in each species), with 6 to 11 rare phyla making up the remaining 10%. Stomach contents in *P. maculosus* were heavily dominated by animals from the phyla Cnidaria (72.2% of contents), Porifera (14.9%), and Annelida (4.1%), with the remaining 8.8% composed of organisms from 11 other phyla (**Figure 2**). Cnidarians also dominated the stomach content of *P. aquilus*, but to a lesser degree (35.3% of contents), with relatively important contributions (totaling 47.3% of contents) from the phyla Annelida, Arthropoda, Dinoflagellata, Platyhelminthes, and Porifera (**Figure 2**), with 8 additional phyla making up the remaining 17% of the stomach contents. There was a much more even composition of stomach contents in *P. trichrourus*, with 8 phyla each contributing between 7 and 19% of stomach contents (**Figure 2**; Cnidaria, Urochordata, Annelida, Ciliophora, Porifera, Platyhelminthes, Arthropoda, and Dinoflagellata), with six additional phyla comprising the remaining 7% (**Figure 2**). Phyla mean, variance, and standard error values are shown in detail in Supplementary Table S3. To further explore the taxonomic composition of stomach contents across seasons, the data were next processed at the Class level; due to the stringency of the alignment analysis, lower taxonomic classification (i.e., assigning OTUs to Family or Order levels) resulted in loss of resolution.

Seasonal changes in the relative abundance of dietary items in the stomachs of the three fish species is illustrated in **Figure 3**. *P. maculosus* showed the highest consistency in diet among individuals and across seasons (**Figure 3A**). The dominant component of their stomach content across the entire study was Anthozoa (corals), reflecting the heavy weighting of Cnidarians in the Phylum-based analyses above (**Figure 2**), with corals making up 74.6% of stomach content reads averaged across all seasons. Sponges (Demospongiae) were the second-most common dietary item, but this was mainly due to a spike in sponge abundance in the stomachs of many *P. maculosus* in December when it made up 48.0% of stomach contents, which coincided with a relative decrease in corals in many individuals (December coral: 44.6% on average). However, excluding December, sponges were a minor component of stomach contents in the remaining sampling periods (mean: 10.4%). Other taxa made very minor contributions to the overall diet for *P. maculosus* (each class <8.6% of reads in a

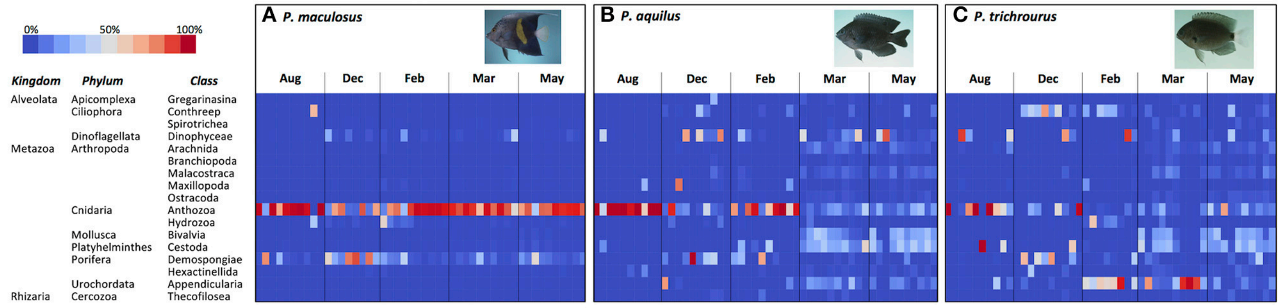

FIGURE 3 | Heatmap illustrating stomach content composition in three species of reef fish (**A**, *P. maculosus*; **B**, *P. aquilus*; **C**, *P. trichrourus*) collected over five sampling periods in Abu Dhabi, UAE. Each cell in the heatmap represents the relative abundance (percent of reads from stomach contents; see key) of a class of organisms in a sample's stomach at a particular sampling period (month). Fish images from http://www.fishbase.org (Randall, unpublished).

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[1] http://www.primer-e.com/permanova.htm (Accessed Jun 28, 2017).

given season), and mainly represented minor variation among individuals.

The two *Pomacentrus* species each showed a greater variety of dietary items and a greater degree of temporal variability in stomach contents than were observed in *P. maculosus*, with more variability among individual fishes (**Figure 3**). The main contributors to the stomach content of *P. aquilus*, averaged across the year, were Anthozoa (40.6%), Dinophyceae (12.1%), Cestoda (11.8%), Demospongiae (7.3%), and Bivalvia (7.1%) with all other classes each contributing <5.9% to the overall diet. However, there was considerable temporal variation in stomach content composition (**Figure 3B**). While corals (Anthozoa) heavily dominated the *P. aquilus* diet in the hottest month (August) and the coldest month (February) where it made up 89.4 and 67.6% of stomach contents, respectively, it became relatively less common in the transitional months of December, March, and May when other organisms became major dietary contributors (**Figure 3B**). In December, corals (Anthozoa) declined to 18.8% of contents, while dinoflagellates (Dinophycaeae) and sponges (Demospongiae) became major contributors across the population (22.5 and 20.5% of stomach contents, respectively). Dietary variety was greatest in the spring (March and May), when *P. aquilus* diets included relatively equal contributions of bivalve molluscs (Bivalvia: 17.7%), dinoflagellates (Dinophyceae: 14.6% of stomach content, averaged across March and May), free-swimming ascidians (Appendicularia: 10%), sea-spiders (Arachnida: 5.2%), and crustaceans (Malacostraca: 4.6%), with corals (Anthozoa) also making an important contribution (13.7%). Interestingly, parasitic flatworms (Cestoda) were very abundant in virtually all *P. aquilus* individuals in both March and May (25.4 and 24.8% of stomach contents, respectively). Various other Classes of organisms were also present in stomachs at low but meaningful levels, and this dietary heterogeneity was consistent across individuals throughout the *P. aquilus* population in March and May (**Figure 3B**).

Like *P. aquilus*, the stomach content of *P. trichrourus* had considerable variability in dietary items, and these varied seasonally (**Figure 3C**). In August, corals (Anthozoa) dominated the stomach content of *P. trichrourus* (51.5% on average), although a few individual fish had substantial contributions from a small number of other taxa (e.g., Dinophyceae and Demospongiae). As temperatures cooled through the autumn and transitioned into the winter and spring, *P. trichrourus* diets shifted (**Figure 3C**). In December, corals became less common (20.2%), while the ciliate protozoan group CONThreeP and the sponges (Demospongiae) became the dominant items in stomachs (24.7 and 24.1% on average, respectively). By February, the coldest month, corals and sponges became minor components of the stomach contents as the free-swimming ascidians, Appendicularia, came to dominate the stomachs of *P. trichrourus* (49.4%, on average), with CONThreeP remaining a major contributor as well (14.5%; **Figure 3C**). Similar to what was observed in *P. aquilus*, the diet of *P. trichrourus* markedly diversified in the spring, with stomach contents made up of a broader assortment of taxa in generally comparable abundance (**Figure 3C**). While the free-swimming ascidians (Appendicularia) were among the most common stomach items in March (43.5%), this was mainly due to high abundance in just a few individual fish, with the majority of the fish stomachs containing a diverse assortment of taxa (**Figure 3C**). By May, there was broader representation among a large number of taxa (9 Classes each had >4% representation in stomach contents), with parasitic flatworms (Cestoda), corals and bivalves being the most common stomach contents (21.5, 19.5, and 16.9%, respectively); cestodes were also relatively common in *P. trichrourus* stomachs in March (16.4%; **Figure 3C**).

Next, multivariate analyses were used to explore variation in the composition of stomach content among species and sampling periods. PCA of the full dataset across the three fish species and all sampling periods was performed to examine the correlation structure in the data and relationships between individual fish samples relative to taxonomic status and sampling period (**Figure 4A**). This analysis revealed a high correlation structure in the data with PC1-3 explaining 64% of total observed variation and highlighted the distinctiveness of *P. maculosus*‘s stomach content driving the variation observed along PC1 while *P. aquilus* and *P. trichrourus* are largely overlapping. The relatively tight grouping of *P. maculosus* samples reflects a high degree of temporal similarity while the broader spread of samples across both axes for the two *Pomacentrus* species indicates more variable stomach contents in these species among sampling periods (**Figure 4A**). VCA was performed to quantify the relative contribution of species, sampling period and their interaction to the observed variance. This analysis revealed that 59.9% of the total variance is explained of these three effects (**Figure 4B**) with most of the variance explained by the species effect (29.3%) followed by species∗sampling period interaction (17.7%) and sampling period (12.9%).

Next, PCA was used to quantify the influence of seasonality on stomach contents for each species separately (**Figures 5A–C**). PC1-3 explain 69, 58, and 53% of the total variation in the data in *P. maculosus, P. aquilus*, and *P. trichrourus*, respectively. While the first three PCs explain similar proportions of the variance in each species, PC plots shown in **Figures 5A–C** highlight both patterns that are shared among the three species as well as species-specific patterns. For example, the March-May samples in each species largely cluster together along one axis (PC1: *P. aquilus* and *P. trichrourus*; PC2: *P. maculosus*). The overall effect of seasonality on each individual species was quantified using VCA and revealed that sampling period accounted for 37.8, 57.7, and 47.1% of the combined PC1-3 variance in *P. maculosus, P. aquilus*, and *P. trichrourus*, respectively (**Figure 5D**). These results are consistent with the patterns visible in **Figures 2**, **3** further highlighting the more seasonally structured data in *P. aquilus* and *P. trichrourus* relative to *P. maculosus.*

SIMPER analyses were used to determine the diet components driving the observed variation in each species and to quantify their relative contribution. SIMPER showed 72.3% similarity in stomach contents across all seasons in *P. maculosus*, reflecting relatively limited temporal variability in this species. In *P. maculosus* there was no difference in stomach composition in the spring sampling periods (March and May) nor between the two most thermally extreme sampling periods (August and February); there was also no difference between February

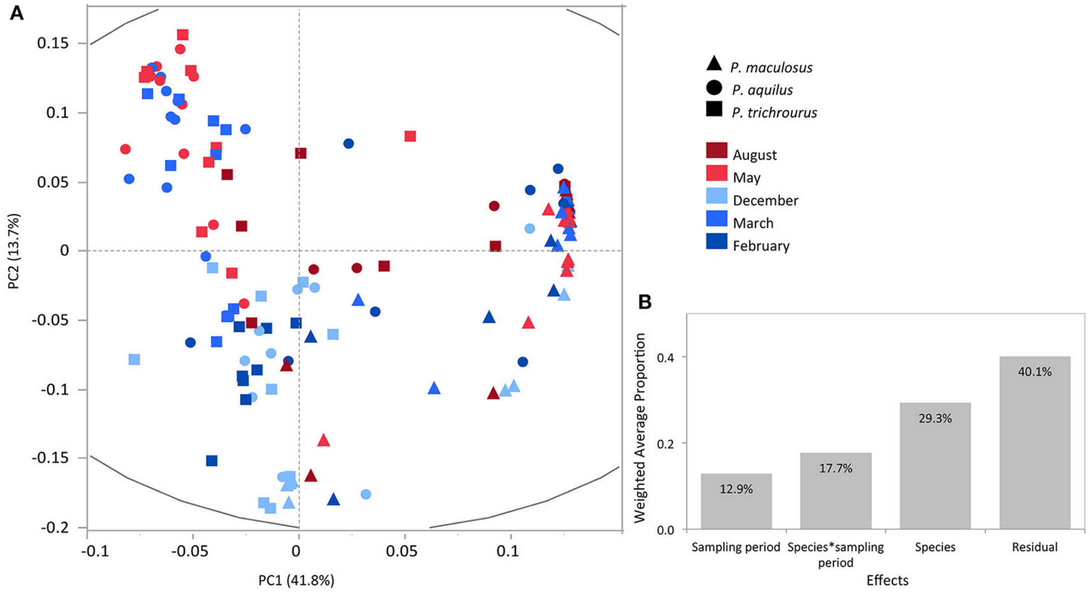

FIGURE 4 | Principal component (PC) and variance component (VC) analyses of the combined dataset. **(A)** PC1 and PC2 together explain 54.5% of the total variance. **(B)** VC analysis of PC1-3 for species, sampling period and the interaction between species and sampling period.

and May (PERMANOVA $p > 0.05$ each). All other pairwise comparisons between seasons were significant (PERMANOVA $p < 0.05$) for *P. maculosus*. primary taxa characterizing *P. maculosus* stomach content were corals and sponges, which together contributed 83% to the similarity in the stomach contents for this species. The greater overall variability in stomach content in the two *Pomacentrus* species was reflected with lower similarity values in SIMPER (*P. aquilus*: 54.7%; *P. trichrourus*: 42.8%, compared with 72.3% in *P. maculosus*, **Table 1**), and each of these species were shown to have significant seasonal shifts in diet with PERMANOVA. In *P. aquilus*, only August and February samples and March and May samples did not differ significantly (pairwise PERMANOVA $p > 0.05$ each), while in *P. trichrourus* all sampling periods differed significantly (pairwise PERMANOVA $p < 0.05$ each). The primary taxa characterizing *P. aquilus* were corals, cestodes and bivalves, which together contributed over 54.7% to similarity in stomach content in this species in SIMPER, while corals, appendicularians, cestodes, CONThreeP, and bivalves were strongly associated with *P. trichrourus*, together contributing 42.8% to similarity.

In addition to exploring taxonomic composition within species, SIMPER was used to identify taxa driving differences in stomach contents between species. All pairwise comparisons showed moderately strong dissimilarity in stomach contents between species (55–68% dissimilarity, **Table 2**), but the only significant difference was between *P. maculosus* and *P. trichrourus* (PERMANOVA $p < 0.05$, **Table 2**); stomach contents did not differ between the two *Pomacentrus* species nor between *P. maculosus* and *P. aquilus* (PERMANOVA $p > 0.05$ each, **Table 2**). The primary driver of divergence between *P. maculosus* and *P. trichrourus* was coral (Anthozoa), which was more than five times more abundant in *P. maculosus* stomachs, and contributed nearly a third of the dissimilarity between these groups (**Table 2**). Sponges (Demospongiae) were also four times more common in *P. maculosus*, while the free-swimming ascidians (Appendicularia) were virtually nonexistent in the angelfish, but made up nearly 12% of the diet of *P. trichrourus*, with these prey items together contributing another 25% to dissimilarity between these fishes. See Supplementary Tables S5 and S6 for detailed SIMPER and PERMANOVA results in pairs of sampling periods.

One of the surprising observations was the dominance of Anthozoa (corals) in stomach content across the entire study (**Figures 2**, **3** and SIMPER analysis). To confirm this observation, we performed an independent non-NGS based validation exercise using Sanger sequencing with different primers and genetic loci. DNA was extracted from two *P. maculosus* stomach samples and two *P. aquilus* samples, all collected in August. DNA was PCR amplified using two pairs of primers: the first targets the nuclear ribosomal ITS region in *Porites* corals (Forsman et al., 2009) and the second targets the NAD mitochondrial loci in corals (primer pair ND51a; Concepcion et al., 2006). Amplified PCR fragments were verified using gel electrophoresis and purified using QIAquick Gel Extraction Kit (Qiagen, USA). The amplified fragments had the expected sizes. Forward and reverse sequencing was performed on an ABI PRISM 3730xl Genetic Analyzer (Applied Biosystems, USA) instrument using standard protocols. Sequence files were viewed and cleaned using FinchTV software. All four samples yielded good quality sequences that were subject to BLAST alignment (NCBI). The sequences aligned mainly to *Porites* and *Platygyra* species (**Table 3**). In both *P. maculosus* samples, the *Porites*-specific fragment aligned exclusively to *Porites lutea*,

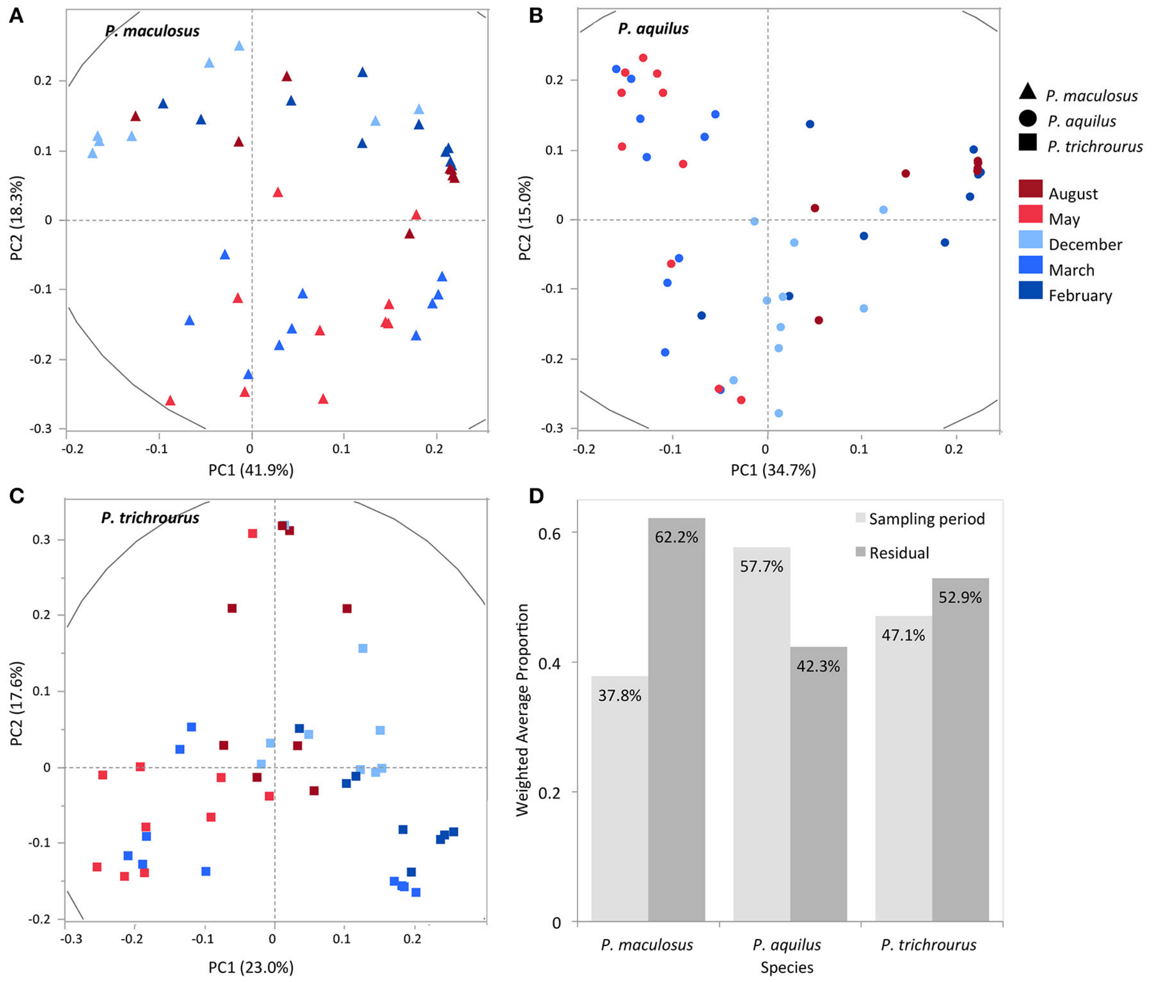

FIGURE 5 | Principal component (PC) and variance component (VC) analysis across each species' dataset. **(A)** PC1 and PC2 together explain 60.2% of the total variance in *P. maculosus*, **(B)** 49.7% in *P. aquilus*, and **(C)** 40.6% in *P. trichrourus*. **(D)** VC analysis of PC1-3 in each species group for sampling period.

TABLE 1 | Results of SIMPER analysis of similarity within each species group showing top stomach content contributors (cut off 70%).

Species	Avg. similarity (%)	Class	Avg. abundance (%)	Contribution (%)	Cumulative contribution (%)
P. maculosus	72.25	Anthozoa	77.78	67.68	67.68
		Demospongiae	12.41	15.54	83.22
P. aquilus	54.74	Anthozoa	40.52	53.44	53.44
		Cestoda	6.12	12.17	65.62
		Bivalvia	2.54	7.55	73.17
P. trichrourus	42.79	Anthozoa	15.16	24.89	24.89
		Appendicularia	11.76	20.69	45.57
		Cestoda	6.12	12.09	57.67
		Conthreep	3.21	9.48	67.14
		Bivalvia	1.95	8.05	75.19

while the fragment from both *P. aquilus* samples aligned to both *P. lutea* and "*Porites* spp." (N.B. *Porites* spp. represents a group of *Porites* that cannot be resolved to species level). *Porites* spp. were also observed in both fish species using the NAD marker, while *P. maculosus* was shown to also have *Platygyra* and/or *Montastrea* in some stomach samples (the difference cannot be resolved based on the data, but presumably represents the regionally common *Platygyra* as *Montastrea* is not known for the Arabian Gulf) (Riegl et al., 2011; **Table 3**).

TABLE 2 | Results of SIMPER and PERMANOVA analyses of dissimilarity (dsim) between pairs of groups of species, showing the top contributors to the total dissimilarity in each group (cut off 70%).

Groups compared	Mean dsim (%)	P (perm)	Class	Group 1 abundance	Group 2 abundance	Contribution of dsim (%)	Cumulative dsim (%)
P. maculosus and *P. aquilus*	55.03	0.069	Anthozoa	77.78	40.52	26.74	26.74
			Demospongiae	12.41	2.23	15.04	41.78
			Dinophyceae	1.00	4.76	9.67	51.45
			Cestoda	0.36	6.12	9.38	60.83
			Bivalvia	0.04	2.54	5.72	66.55
			Appendicularia	0.01	2.23	5.49	72.03
P. aquilus and *P. trichrourus*	58.51	0.469	Anthozoa	40.52	15.16	23.56	23.56
			Dinophyceae	4.76	2.86	12.78	36.35
			Appendicularia	2.23	11.76	12.59	48.94
			Demospongiae	2.23	2.23	8.99	57.93
			Cestoda	6.12	6.12	8.35	66.28
			Conthreep	0.36	3.21	8.15	74.42
P. maculosus and *P. trichrourus*	68.04	0.001	Anthozoa	77.78	15.16	30.39	30.39
			Appendicularia	0.01	11.76	12.53	42.92
			Demospongiae	12.41	2.23	11.62	54.54
			Cestoda	0.36	6.12	7.99	62.53
			Dinophyceae	1.00	2.86	7.84	70.38

TABLE 3 | Corals identified from Sanger sequencing of two *P. maculosus* samples and two *P. aquilus* samples.

Primer	Sample type*	Bases covered**	Coral identified	*E*-value (BLAST)
Porites ZITS	*P. maculosus*	41-651	*Porites lutea*	1.00×10^{-140}
	P. maculosus	41-661	*Porites lutea*	0.00
	P. aquilus	41-541	*Porites lutea*	4.00×10^{-145}
	P. aquilus	32-196	*Porites* spp.	3.00×10^{-77}
NAD mitochondrial marker	*P. maculosus* +	60-490	*Porites* spp.	0.00
	P. maculosus −	49-270	*Platygyra* spp. *Montastraea* spp.	2.00×10^{-109}
	P. maculosus +	39-491	*Porites* spp.	0.00
	P. maculosus −	34-266	*Platygyra* spp.	4.00×10^{-117}
	P. aquilus	81-491	*Porites* spp.	0.00

All samples were from the August collection. The Expect value (E) parameter describes the number of hits expected to be seen by chance when searching a database of a particular size (i.e., the random background noise).

**(+) indicates the larger band and (-) indicates the smaller band on the gel.*

*** all based on the reverse read.*

DISCUSSION

Coral reefs have undergone considerable change in recent decades as a result of local anthropogenic pressure and SST anomalies (Hughes et al., 2003). Climate change models predict that coral bleaching will increase in both severity and frequency in the future (Diaz-Pulido et al., 2009). Resultant changes in the benthic composition of reefs will likely affect structural and functional attributes of reef fish communities (Wilson et al., 2006; Baker et al., 2008; Munday et al., 2008; Pratchett et al., 2008; de Bakker et al., 2017), with particular effects likely to occur in the feeding ecology of this diverse and important group of organisms (Floeter et al., 2004; Berumen and Pratchett, 2006; Pratchett et al., 2008; Wilson et al., 2008). The Arabian Gulf is the most thermally extreme coral reef environment on earth (Riegl et al., 2011), and as such represents a unique natural laboratory in which to examine the trophic ecology of reef fishes in an extreme environment. The current study is the first to examine the diets of coral reef fishes in the region, with the metagenomics approach used here allowing for a much more comprehensive assessment of the diets of these three reef fish species than has historically been available globally. Our results provide important data on the diet of reef fishes in this thermally extreme environment, which may be useful in shaping further studies and questions on reef fish adaptability to climate change and highly variable seasonal fluctuations in temperature in other regions.

The metagenomics approach employed here allowed for an unbiased and much broader assessment of the dietary items in the stomachs of these fishes than would be possible with traditional approaches. The small size and partially digested nature of stomach contents can lead to bias, inaccuracy and misidentification in traditional microscopy-based stomach content surveys (Carreon-Martinez and Heath, 2010; Paquin et al., 2014). The sequencing-based approach used here, however, requires only minute quantities of genetic material, allowing not only classification of food items that are partially digested, but also items that are individually microscopic and/or unidentifiable but contribute substantially to the overall variety and/or volume of items in stomachs (Budarf et al., 2011; Paquin et al., 2014;

Miyake et al., 2015). One limitation of the metagenomics approach is the inability to differentiate between primary food items and incidental food items (Harms-Tuohy et al., 2016). A high abundance of dinoflagellates was observed in the fish diets here, but these are living within corals as well as free-living in sediments so it cannot be determined whether they were consumed as free living or incidentally when consuming corals (Carpenter et al., 1997). Nonetheless, if the item is consistently observed across samples then it is a component of the diet, regardless of the means of consumption. Additionally, while the 18S amplicon approach results in a loss of taxonomic resolution, it allows a much broader coverage that is preferable in diet assessment (Albaina et al., 2016). Limited feeding observations and traditional stomach content analyses from other regions has suggested that *P. maculosus* feed mainly on sponges and algae, *P. aquilus* on zooplankton, and *P. trichrourus* on benthic algae (Allen and Randall, 1980; Masuda and Allen, 1993; ter Hofstede, 1998; Salameh et al., 2012). Our results greatly expand the knowledge of the composition of diets for these species, showing that each of these species is consuming a much wider array of prey items than had previously been appreciated. We observed 17 distinct taxonomic classes across 10 phyla in the stomach contents of the three fish species examined, in addition to 5 phyla where the OTUs did not align to lower taxonomic classifications. Overall, only a small fraction of these food items would have been identifiable under a microscope, with the majority of the taxa occurring in the stomachs extremely difficult or impossible to identify using traditional visual approaches (e.g., a wide variety of microscopic protozoans, heavily fragmented arthropod parts, morphologically indistinct pieces of coral tissue). The better representation of these morphologically indistinct but taxonomically diverse food items validates our use of genomics-based approaches to provide a more comprehensive and taxonomically rich understanding of the food items consumed by these reef fishes.

Perhaps the most interesting observation of this study was that corals are a major dietary component of all three of these species, despite none being considered corallivores, and corals not previously reported as important components of their diet (Masuda and Allen, 1993; Carpenter et al., 1997; ter Hofstede, 1998; Froese and Pauly, 2017). Of note, the genera of corals observed in the diet, as shown using Sanger sequencing, largely reflect the dominant corals observed on reefs in the southern Gulf, namely *Porites* and *Platygyra* (70.4% and 13.3% of live coral at Saadiyat reef, respectively; Burt et al., 2011a). Supplementary Figure S1 shows the breakdown of the benthos in the Saadiyat region, where coral makes up over 60% of the overall benthos. Corals likely represent an important but underappreciated nutritional resource for many reef fishes that are not considered corallivores. For example, coral gametes are known to provide substantial benefits to diverse groups of coral reef fishes that opportunistically consume them during coral spawning (Pratchett et al., 2001; McCormick, 2003). In addition, coral mucous coats trap organic detrital material from the surrounding water column, with such enriched material likely representing a substantial food resource for many reef fishes (Wilson et al., 2003). Thus, coral likely represents an important component of the diet of many reef fishes, but its role has previously been underappreciated due to the difficulty of detecting coral in partially digested stomach contents using traditional techniques (Zekeria et al., 2002; Pratchett et al., 2008).

While it could be argued that the prevalence of corals in the stomachs of the fish studied here is due to incidental consumption, with coral tissues being ingested accidentally while foraging for other items, the high proportion of corals in the overall diet and over various sampling periods among virtually all individuals suggests otherwise. Remarkably, *P. maculosus* in the southern Arabian Gulf appears to be somewhat of a coral-specialist in terms of its diet, with corals making up 45–85% of its diet in a given sampling period, on average. In other regions, the family of Pomacanthidae is generally known to be omnivorous feeders, with sponges and algae dominating their diets (Andréa et al., 2007; Batista et al., 2012), with corals typically making up <2% of their stomach contents (ter Hofstede, 1998). It is also noteworthy that this family is highly diverse in its feeding ecology (Konow and Bellwood, 2011). While our results show that sponges are consumed by *P. maculosus* throughout the year in the Arabian Gulf, sponges are generally a minor component of the *P. maculosus* diet (16% overall) relative to coral (75% overall). Sponges are relatively rare in this region (<1% of reef benthos, Burt et al., 2011a), perhaps due to the extreme nature of the environment and/or as a result of overgrazing due to the unusually high abundance of *P. maculosus* on these reefs (>400 ha^{-1} in the southern Gulf, Burt et al., 2011b). Regardless of the cause, *P. maculosus* in the sampled region have focused their diet toward corals, and this is consistent across all individuals and seasons we examined.

The two damselfishes generally had a more varied and flexible diet than the angelfish (within species average similarity of stomach contents across seasons ca. 49%, compared to 72% in the angelfish). Although corals also appear to be a major food source for the damselfish, particularly in summer when it made up >50% of the diet of each damselfish species, there was a shift away from coral dominance and instead a broadening of the food items incorporated into the *Pomacentrus* diets in December, March and May when corals made up <20% of their diets, suggesting that corals may not be a preferred food source. Corals are generally considered an energy-poor resource (Aeby, 2002), with higher costs related to handling time that further decrease the relative value of these foods for smaller bodied fishes, such as the two damselfish examined here (Tricas, 1989). While these damselfishes may need to rely on coral to supplement their diet in the hot summer months when their metabolic demands will be at their highest (Nilsson et al., 2009), the relative decrease of corals in their diets in December, March and May suggests that their diet is shifting as a result of temperature-related differences in preference and/or food availability. The spring season (March and May) is the time of rapid population growth and spawning of many reef-associated organisms in the southern Gulf (Alsaffar and Lone, 2000; George, 2012; Grandcourt, 2012; Howells et al., 2016), and the broadening of damselfish diets to include large contribution from bivalves, ascidians, sponges and other taxa during these months may simply reflect increased abundance of food items available, or a shift in preference.

Interestingly, there is also a notable increase in the parasitic cestode worms in the stomachs of both damselfish species in March and May (*P. aquilus*: spring mean = 25 vs. 3% mean in all other seasons; *P. trichrourus* spring mean = 19 vs. 8% mean in all other seasons). While this may represent increased ingestion of cestodes from the surrounding environment, the observed increase in these parasites in stomachs in spring may also reflect weakened host immune systems following several months of cold winter temperatures. A diverse array of cestodes are known to occur in the Arabian Gulf, and the prevalence and intensity of infection in fishes here is generally considered to be high compared with other regions (e.g., 27.2% of individuals infected across a suite of commercial fish species; El-Naffar et al., 1992; Al Kawari et al., 1996). It is unclear why the incidence of cestodes would be substantially higher in the two *Pomacentrus* species as opposed to the *P. maculosus*, but earlier surveys of infection rates across various fishes in the Arabian Gulf have shown higher infection rates in species with broader diets (El-Naffar et al., 1992), suggesting that the more coral/sponge-specific diet of *P. maculosus* may reduce opportunity for infection.

In addition to the general commonness of corals in the diet of these three fish species, the virtual absence of algae in the diets of these fishes is also notable. In other regions, available dietary reports have indicated various algae as contributors to the diet of *P. maculosus* (ter Hofstede, 1998), and *in situ* bite observations suggest that algae is a major component of the diet of *P. trichrourus* (Masuda and Allen, 1993). Algae (mainly turf and CCA) are among the most common benthos on reefs in the southern Gulf, occupying more space than corals on many reefs (Burt et al., 2011a). Various classes of algae (Chlorophyta) were observed in all three fish species in all sampling periods, but at abundance so low that it was removed during the data treatment and filtering process as it did not meet minimum cut-off standards for inclusion in this study (see methods), possibly indicating that while present in abundance on Saadiyat reef it was not being preferentially consumed by any of the fish species examined, suggesting that algae here have low palatability. Various algae are known to produce secondary metabolites that can deter feeding by reef fishes (Hay et al., 1987), and it is possible that algae here are employing such chemical defenses. It is also possible that the heavy sediment loads experienced on these reefs plays a role. Wind-induced sediment resuspension is common on the shallow (<6 m) reefs of the southern Gulf (Riegl, 1999), and these sediments can become trapped in the epilithic algal matrix (EAM). Higher sediment loads have been shown to decrease the energetic value of detrital material trapped in the EAM (Purcell and Bellwood, 2001; Gordon et al., 2016) and reduce reef fish grazing rates (Bellwood and Fulton, 2008; Goatley and Bellwood, 2012), providing another plausible reason for the limited algal consumption by the three fish species examined here.

In the coming century climate change is expected to induce SST increases that will result in many parts of the tropics developing a thermal environment similar to the summer temperatures experienced in the Arabian Gulf today (Riegl, 1999; Collins et al., 2013; Wernberg et al., 2013). These temperature increases are likely to have profound impacts on fish communities, with shifts in benthic communities having indirect influence on the structure and function of fish assemblages (Baker et al., 2008; de Bakker et al., 2017) and thermal stress directly affecting the physiology and behavior of fishes themselves (Floeter et al., 2004; Berumen and Pratchett, 2006; Wilson et al., 2006; Munday et al., 2008; Pratchett et al., 2008). This study examined the diet of three common reef fish in the most thermally extreme environment on earth, providing unique insights into how reef fish have adapted trophically. Overall, our results indicate a greater variety and degree of flexibility in diets in these reef fishes than is generally appreciated, indicating that dietary plasticity has allowed these species to respond to the unique resource and environmental constraints placed on them in the Gulf. Since the metagenomic approach limits the dietary taxonomic resolution, we may also be overestimating their dietary commonality (Longenecker, 2007). Higher taxonomic resolution might demonstrate further trophic diversity and food specialization between fish species (Longenecker, 2007). However, the variety and flexibility presented here also suggests that reef fish species with more flexible and/or generalist diets are likely to be more successful on future reefs in other regions. While the broader flexibility in diets at first glance appears to be of benefit, this flexibility may also come at a cost. For example, our results show that *P. maculosus* in the Arabian Gulf is feeding primarily on coral, but coral is known to have low nutritional value (Tricas, 1989; Aeby, 2002) and it is unknown whether its focus on corals—rather than the expected sponge/algae diet—has an energetic cost that translates into lower performance at the individual or population level. Additionally, over the long-term the degree of corallivory by the hyper-abundant *P. maculosus* and the very common *P. aquilus* and *P. trichrourus* populations on these reefs (Burt et al., 2011b) may contribute to the further depletion of corals that are already under pressure from recurrent bleaching events and localized development activities (Sheppard et al., 2010; Sale et al., 2011). Further research is needed to examine the broader implications of the unique feeding habits of coral reef fishes living in this extreme environment. In future studies, to compensate for the quantitative and taxonomic shortcomings of the metagenomics approach, it may also be useful to pair the approach with traditional stomach volume observations and a reference amplicon library specific to the region (e.g., Albaina et al., 2016).

AUTHOR CONTRIBUTIONS

The following contributions were made by authors: Project conception and design: JB, YI, and RS. Sample collection, processing and sequencing: GV, DM, RS, and MD. Data analyses and interpretation: JB, YI, MD, MV, and RS. Writing and revision of manuscript: RS, JB, and YI.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2017.00285/full#supplementary-material

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Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships

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An 18-year database of coral reef fish expatriation poleward in South East Australia was used to estimate persistence of coal reef fish recruits on temperate reefs. Surveys have identified over 150 coral reef fish species recruiting to temperate reefs at latitudes of 34°S (Sydney) and 60 species to 37°S (Merimbula) with 20 and 5 species respectively overwintering in at least 1 year over the study duration. We developed indices of vulnerability of key species to drops in water temperatures, by relating drops in abundances of species to temperature drops. Twenty species were ranked according to their temperature vulnerability. Overall, the families Chaetodontidae (butterflyfishes), Acanthuridae (surgeonfishes), Labridae (wrasses) and Pomacetnridae (damselfishes) had similar cold-water tolerance. However, there was considerable variability within families, for instance in the Pomacentridae, species from the genus *Abudefduf* appeared to have better cold-temperature tolerance than the other species. Predicted minimum overwintering temperature varied from 15.6°C to 19.8°C, with some species showing lower Tzero at Merimbula, the more poleward location. There was general concordance between a species' tolerance to cold-water and its tendency to occur as an overwinter but also notable exceptions. So while this work demonstrates the potential utility of tolerance to seasonal temperature drops as a means to predict range expansion capacity of vagrant species, the exceptional cases serve to highlight alternative factors. Specifically, tolerance to seasonal cooling of water is not the only important factor when predicting the range expansion capacity of a species. Factors affecting the general abundance of the vagrants, such as habitat suitability and competitor/predator environments will also be critical where overwinter survival becomes a lottery.

Keywords: Acanthurid surgeonfishes, Chaetodontid butterflyfish, overwintering, Pomacentrid damselfish, water temperature drop, vagrant coral reef fishes

INTRODUCTION

The future of species globally, both in terrestrial and aquatic environments, is under threat through human-caused climate change (Chen et al., 2011; Poloczanska et al., 2013). Colonization of new, more climatically-suitable, habitat is a key coping strategy used by organisms, and understanding this process is critical to guide conservation strategies (Gilman et al., 2010). Not surprisingly, species' range expansions are difficult to accurately predict (HilleRisLambers et al., 2013; Bates et al., 2014), since they require detailed knowledge of dispersal mechanisms and physiological tolerance of species to the receiving environment. Range expansion is also problematic to measure empirically since it requires longer-term detailed fish observations.

As a result of strengthening western boundary currents under climate change, many coral reef fishes are expected to expand their ranges polewards (Figueira and Booth, 2010; Wernberg et al., 2012; Feary et al., 2014; Vergés et al., 2016). This influx into temperate ecosystems may lead to novel interactions and affect the structure and function of temperate marine communities (Vergés et al., 2014; Luiz et al., 2016). To date, there is still relatively little understanding of factors that constrain or facilitate species' geographic responses to climate change, including those of marine fishes (Li et al., 2011; Yang et al., 2011; Blois et al., 2013; Liancourt et al., 2013). Feary et al. (2014) and Booth et al. (2018a,b) showed that species metrics such as large body size, high swimming ability, large size at settlement and pelagic spawning behavior are more likely to occur in species expatriating into temperate habitats.

Low winter water temperatures are thought to act as a bottleneck for tropical fish survival polewards, with a threshold identified of approximately 18°C, below which few coral reef fish survive (Figueira et al., 2009; Figueira and Booth, 2010). Additionally, temperate waters exhibit short-term drops in temperature (at the scale of days to weeks) which can stress the tropical species. A species that copes better with drops in water temperature may be more able to exploit range-edge habitats, and such species may be more resilient to lower winter temperatures and thus more able to expand their ranges poleward.

The southeast coast of Australia is a known ocean warming hotspot (Ridgway, 2007) and is therefore likely to be particularly susceptible to the process of tropicalization. Every year, tropical fish larvae are expatriated south from the Great Barrier Reef (GBR) via the East Australian Current (EAC), where they arrive and settle in recruitment pulses from January to May (Booth et al., 2007). Our 18-year dataset of coral reef fish abundances across seasons in temperate locations can be used to identify key abundance fluctuations.

Here, we explore the idea that an indicator of a species' resilience under climate change scenarios is how they cope with drops in water temperature. Oliver et al. (2015) note the importance of resilience metrics to help assess possible range shifts and future biodiversity loss. Our aim was to see if we can identify species which are more or less sensitive to water temperature changes at extreme temperate latitudes, and use this to predict which species may do better or worse in the future, both in these extreme poleward habitats, and also in their coral reef natal habitats.

Specifically, we aimed to evaluate the utility of short-term abundance change with temperature as a metric for cold-temperature tolerance. We explore how this metric links to overwintering and whether it depends on location, which might indicate local adaptation or selection during transport. We then rank existing vagrant coral reef fish species as to their cold-temperature tolerance, and identify patterns by taxonomic groups (family).

METHODS

Vagrant Fish Surveys

Since 2002, seasonal surveys of tropical fish expatriates have been conducted at sites in South East Australia (e.g., Booth et al., 2007). Surveys involve a snorkeler navigating a known area systematically and identifying, counting and sizing all tropical fish observed. Surveys were conducted at four sites around Sydney (34°S) and one in Merimbula (37°S) approximately every 1–3 weeks during the peak recruitment period (December–May) dropping off to approximately every 4–6 weeks for the rest of the year (**Table 1**). Shelly Beach East and West sites in Sydney as well as the Bar Beach Site in Merimbula have been surveyed since 2002. Two Sydney Harbour sites, Little Manly and Collins Beach, have been surveyed since 2009.

Water Temperature

The water temperature at all sites was logged at 30 min intervals with duplicate loggers (HOBO Pendant UA-001-08) placed within each site at 2–3 m depth. Logger data for Shelly Beach was not available for the entire data series so instead we used logger data from nearby Long Reef which is highly correlated ($r^2 = 0.97$). Daily averages for all sites were extracted from the full time series. From this we computed the average temperature over the interval between individual surveys (typically 7–14 days).

TABLE 1 | Number of surveys conducted at each site between January and June of each summer recruitment season.

Season	Sydney-shelly beach	Sydney-collins beach	Sydney-little manly	Merimbula-bar beach
2002–2003	4			18
2003–2004	17			17
2004–2005	19			29
2005–2006	21			19
2006–2007	12			15
2007–2008	10			13
2008–2009	5			10
2009–2010	18	3	13	16
2010–2011	15	11	11	10
2011–2012	13	12	12	4
2012–2013	13	14	14	11
2013–2014	14	14	14	11
2014–2015	17	17	17	5
2015–2016	11	11	11	6

There are occasional gaps in the temperature series at both sites due to logger failures. With exception of a period of 1 year from July 2012 to July 2013 in Merimbula, most periods are only a few weeks in duration and not during the key period of January-June considered here (see below). Analysis of abundance series (as described below) was not conducted where no temperature data was available.

Identifying Resilient Species

We based our assessment of the resilience of vagrant coral reef fish species on three general characteristics; (1) has the species been observed to overwinter at either location, (2) how common are overwinterers for the species and (3) how sensitive to temperature is the abundance of each species? The status as an overwintering species was based on the observation of at least one overwinter survivor (adult present in surveys after August) in the data series for each location. To evaluate how common overwintering was, we established the relative occurrence of overwinterers for each species as the ratio of the average abundance (per survey for the whole dataset) of overwinter sized individuals (as defined by Figueira and Booth, 2010) at any time of year to the average abundance (per survey for the whole dataset) of recruits (any non-overwinter sized fish) during the main recruitment season (January–May).

Our general approach to characterizing thermal sensitivity for each species was to evaluate the absolute and relative rates of decline in abundance of different species with temperature across all the sites and seasons available within this dataset. Here we define the term "abundance series" as the data series of abundance values for a given species at a given site in a given season. In order to achieve our objective, we first narrowed our list of species to only the top 20 most commonly occurring ones (high density per survey but also represented by at least five abundance series across the whole data set) at these sites based on long-term averages (Table S1). We next normalized each abundance series by the maximum value in the series such that all values varied between zero and one (**Figure 1A**). When doing this, we excluded, based on size, any fish which would not have recruited during the season in question (and would thus be overwinter survivors). We then identified the "decline period" of each abundance series from its peak (1.0) to its lowest value, typically zero (as numbers reduced through the season). Since these are surveys of rare species in large areas, it is not uncommon for decline periods to show some fluctuations. Where multiple peak values were observed, the start of the decline period was taken to be the latest peak value. We also included up to two zero abundance values in a row (surveys which found no individuals of that species) at the end of the decline period (as opposed to stopping at the first zero) to ensure a true zero had been reached (see **Figure 1A**).

We next regressed the proportional abundance for a survey against the average temperature over the interval between that survey and the previous one for all decline periods (see **Figure 1B**). We only included decline periods where the peak abundance had at least 3 individuals observed and consisted of at least 4 survey data points. As indicated above, periods where no temperature data was available were not considered in this analysis. We then excluded relationships where large fluctuations in numbers from one survey to the next led to slopes that deviated wildly from the positive relationship we observed for most of the decline periods. The abundance series which had these issues were typically those which only barely met the criteria for inclusion. In total this lead to exclusion of 19 of the 380 initial abundance series (5%, see Table S1 for summary of number of series by species).

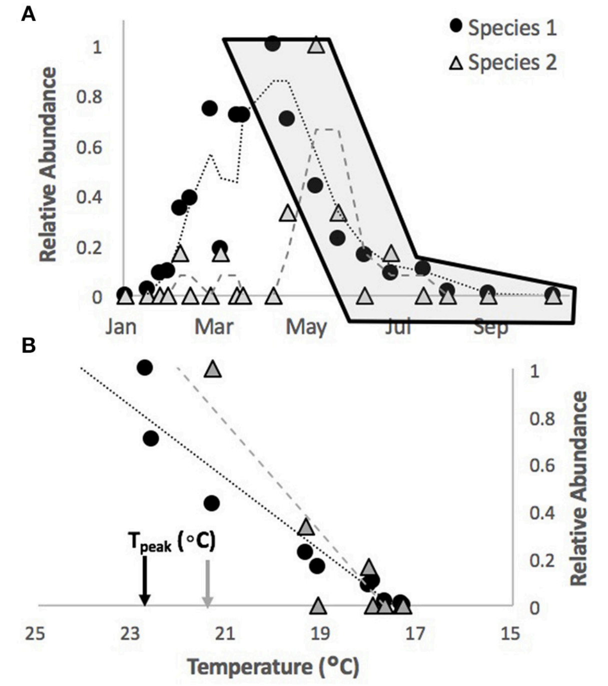

FIGURE 1 | Illustration on methodology for extracting abundance-temperature relationships. From normalized abundance series over time (**A**, illustrated for two random species here) data are extracted for the region of decline, starting with normalized relative abundance value of one (the point in the gray shaded area of **A**). For each survey in this period the relative abundance on that survey is plotted against the temperature between that survey and the previous **(B)**. The best fit line to this data (dashed line in **B**) is used to estimate the slope and temperature at which relative abundance was 1.0 (Tpeak, identified on the X-axis for each species).

From the best-fit line to each of these 361 decline periods, we extracted two metrics which describe the sensitivity of abundance to temperature for given species at each site and season:

(a) **T_{peak}**: The temperature at which the species had its peak abundance for the series (proportional abundance of 1.0). This is the temperature after which it started to decline in abundance. Lower values would suggest a more cold-tolerant species.

(b) **Slope**: This is the slope of the relationship between temperature and proportional abundance. This relationship is positive and thus a lower value suggests a more cold-tolerant species whose abundance drops off more slowly with reductions in temperature.

RESULTS

Over the whole period of this dataset there was a relatively consistent pattern of incursion of tropical fish recruits in

January/February, stable populations through March/April and then a drop off in May or June which occurred more rapidly in Merimbula than in Sydney (**Figure 2**). Tropical fish were very rarely observed after June in Merimbula but were found more commonly through August in Sydney.

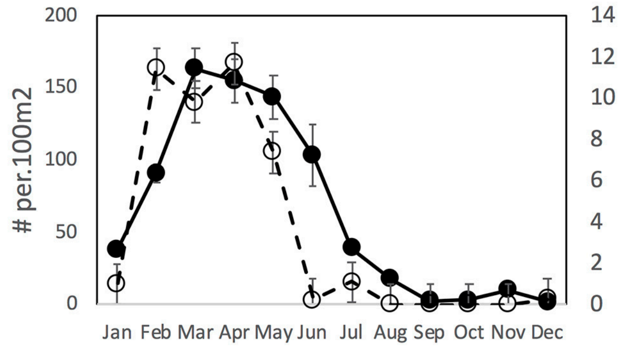

FIGURE 2 | Mean (±SE) density of tropical vagrant fishes overall in Sydney (solid line, solid symbol curve, left Y axis) and Merimbula (dashed line, open symbol, right Y axis) over 12 months, $n = 14$ years.

Overwinter survival was generally much more common in Sydney than in Merimbula (**Figure 3A**) with the highest ratio observed for the territorial damselfish *Stegastes gascoynei*, although overwintering was much more limited for the other Pomacentridae aside from *Chromis nitida*. *Naso unicornis* was relatively abundant as an overwinterer amongst the Acanthuridae and overwintering was very uncommon for the *Chaetodontiade*. Both labrid species had high overwintering ratios in Sydney, but not in Merimbula.

Temperatures at the peak of abundance (T_{peak}) differed between 18 and 24°C across the dataset and were generally lower at Merimbula than Sydney for the same species (**Figure 3B**) although there was a large overlap in error bars suggesting that this is not a significant effect. There was considerable variation across the Pomacentridae with members of the genus *Abudefduf* showing relatively high cold-water tolerance (low T_{peak}). *S. gascoynei* and *C. nitida* had moderate T_{peak} values within this family while *Pomacentrus bankanensis* had the

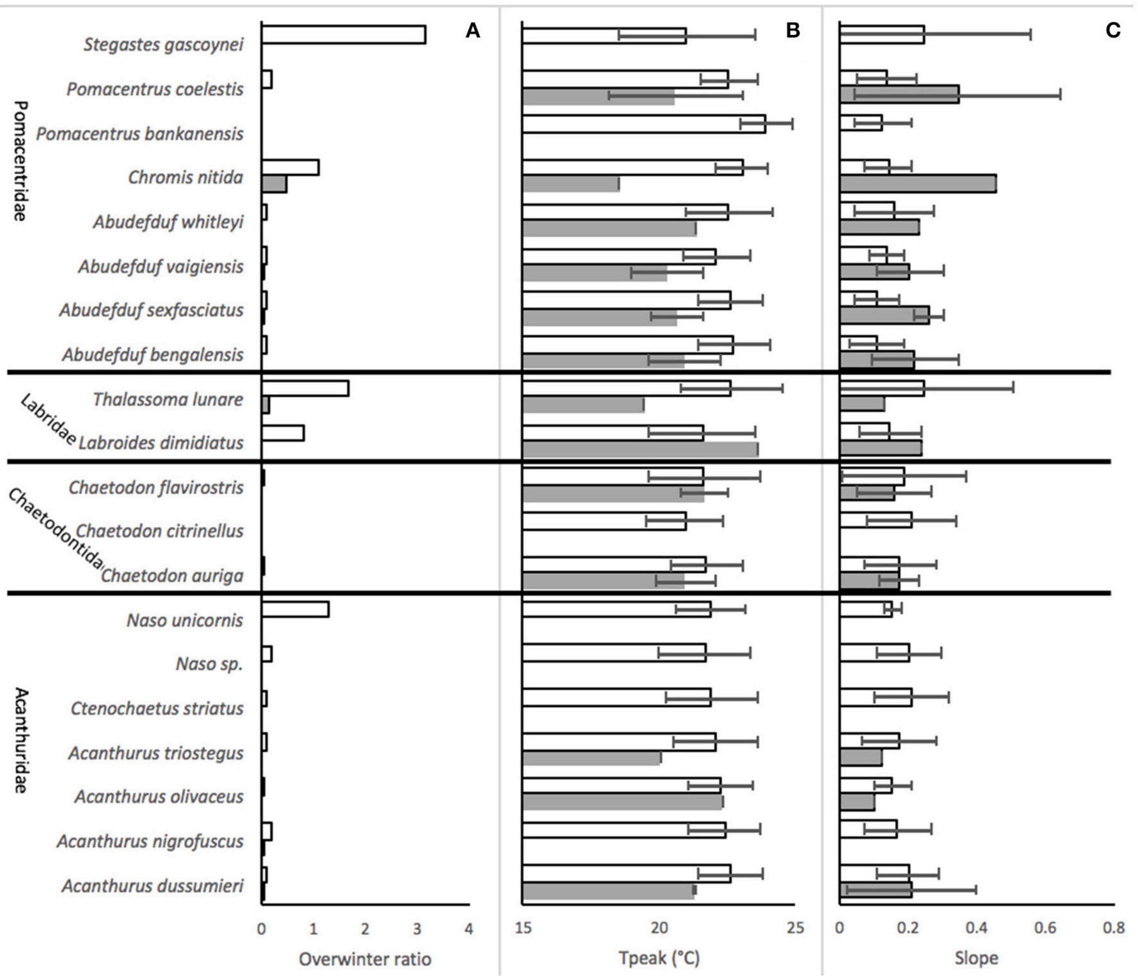

FIGURE 3 | Performance of 20 species of expatiating coral reef fish in SE Australia, (mean ± SD of values derived from all abundance series in the 2002–2017 dataset), at Sydney (empty bars) and Merimbula (filled bars), for **(A)** the ratio of average over winterers to recruits, **(B)** temperature after which abundance started to fall (T_{peak}), and **(C)** slope of relationship between temperature and proportional abundance.

highest value of in the whole dataset. The chaetodontids had generally lower T_{peak} values than the than any of the other families as a whole, but only by a half a degree or so. Acanthurids tended to have T_{peak} values which were intermediate to those of Pomacentrids and Chaetodontids, while the Labrids, represented by only two species had quite variable values (**Figure 3B**). Cold water tolerance expressed by the slope of the temperature-abundance relationships generally matched that suggested by T_{peak} values (**Figures 3C**, **4**).

Families were overall similar in their cold water tolerance ranking. Acanthuridae (surgeonfishes), Labridae (wrasses) and Pomacentridae (damselfishes) were similarly represented across the rankings, each having around 50% of member species considered here in the top 50% of rankings. There is some evidence that the Chaetodontidae (butterflyfishes) may be less cold-tolerant since all three species were in the bottom 50% of rankings, although two of them were at positions 11 and 12, so the generalization is weak.

However, there was again considerable variability within the Pomacentrids with the *Abudefdufs* appearing to have better cold-temperature tolerance than the other species. Of note here is the very low slope value for *P. bankanensis* which is not consistent with its very high T_{peak} value, though this was not a very common species, with only 5 abundance series upon which to base the analyses.

Based on the average of ranked values for each of the metrics, *Naso unicornis* is indicated as the most cold-tolerant while *Pomacentrus bankensis* the least (**Table 2**). While there is a very general concordance with these rankings and the categorization of a species as an overwinterer based on observations, there are certainly notable exceptions. We expected to see the species which have been observed to overwinter at both sites ranked consistent near the top. While this pattern holds for *A. vaigiensis*, which is the most commonly observed tropical vagrant fish in the dataset, the other two species in this category, *C. nitida* and *Thalasomma lunare* are ranked 11 and 16 out of 20, respectively. However, the species that are not known to overwinter at either location are ranked near the bottom of the list, as expected, including *P. bankanensis*, which is ranked lowest.

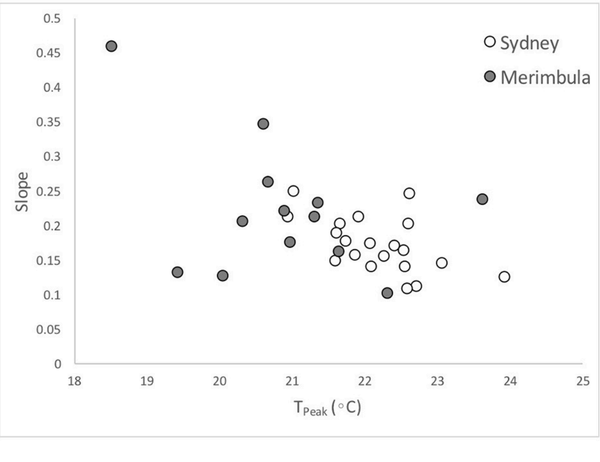

FIGURE 4 | Relationship between predicted T_{peak} and slope of temperature-drop, fish abundance drop curves, for the 20 species. Each point is average of all values available for each species. Not all species occurred in Merimbula.

DISCUSSION

How coral reef fishes respond to key stressors such as water temperature will determine their ability to cope with the projected effects of human-caused climate change. For the tropical vagrant species considered here there were strong and consistent drops in abundance as water temperature changed through the season. The nature of these changes, as characterized by the T_{peak} and slope values, allows us to characterize the relative cold-temperature tolerance of the more common tropical vagrant species. Importantly, the tolerance suggested by these metrics is broadly supported by the characterization of a species as an "overwinterer" but provide a much greater resolution amongst species. The species that occur as vagrants quite commonly and in high abundance, such as *A. vaigiensis* and *P. coelestis* did appear near the top of the list of cold-tolerance. And of course many of the rare species, such as *P. bankanensis* and *T. lunare* appeared near the bottom of the list.

This work also highlights the interplay between two important factors which help to determine the probability of overwinter survival, thermal tolerance and abundance. There are species such as *Chaetodon auriga*, *A. sexfasciatus*, *A. whitleyi,* and *A. dussumieri* which are all relatively common vagrants at these sites (occurring most years and in moderate numbers) but who would appear to have relatively low capacity to deal with seasonal temperature drops. For these species, in absence of adaptation/acclimation, range expansion may depend strongly on high recruitment numbers. Conversely species such as *L. dimidiatus* and *Naso sp*. may do well into the future not because of their high numbers (they tend to be rare) but because of their high tolerance to cold-temperatures.

While there was not strong evidence of a of a location effect (Sydney 34°S vs. Merimbula 37°S) which would support local adaptation or selection during transport, it appears that T_{peak} was lower overall in Merimbula (e.g., **Figure 4**). This may indicate either local adaptation to colder waters, or selection of more cold-resistant individuals (this may occur during advection from tropical waters) at this higher latitude location.

How might these metrics indicate the resilience of these species and their ability to range shift poleward? That is, can a short term performance metric predict long term changes? While this is unclear at present, such metrics have been established in other systems (e.g., McLeod, 2009; Fogarty et al., 2017). There seems to be more variability in the T_{peak} than Slope value. However, a suite of factors including likelihood of advection of larvae to a location (e.g., Booth and Parkinson, 2011; Feary et al.,

TABLE 2 | Key temperature resilience metrics for 20 species of expatriating coral reef fish in SE Australia.

Sci Name	Com. Name	Family	n	Recruit density	Overwinter		Overwinter ratio	Tpeak (°C)	Slope	AVG rank
					SYD	MER				
Naso unicornis	Bluespine unicornfish	Acanthuridae	6	0.2	Y	N	1.34	21.86	0.16	5.00
Labroides dimidiatus	Cleaner wrasse	Labridae	7	0.1	Y	N	0.81	21.89	0.16	6.33
Abudefduf vaigiensis	Sergeant major	Pomacentridae	43	35.5	Y	Y	0.10	21.76	0.15	7.67
Stegastes gascoynei	Coral sea gregory	Pomacentridae	6	0.2	Y	N	3.21	21.01	0.25	7.67
Naso sp.	Unicornfish	Acanthuridae	7	0.1	Y	N	0.20	21.66	0.20	8.67
Pomacentrus coelestis	Neon damsel	Pomacentridae	30	2.7	Y	N	0.19	22.23	0.17	10.00
Abudefduf bengalensis	Bengal's sergeant	Pomacentridae	33	1.6	Y	N	0.11	22.44	0.13	10.00
Acanthurus triostegus	Convict surgeon	Acanthuridae	21	1.1	Y	N	0.10	21.98	0.17	10.33
Acanthurus nigrofuscus	Dusky surgeon	Acanthuridae	18	1.0	Y	N	0.18	22.40	0.17	10.33
Chromis nitida	Yellow-back puller	Pomacentridae	7	0.5	Y	Y	1.05	22.42	0.19	10.67
Chaetodon flavirostris	Dusky butterflyfish	Chaetodontidae	15	0.7	Y	N	0.02	21.63	0.18	11.00
Chaetodon auriga	Threadfin butterflyfish	Chaetodontidae	29	0.3	Y	N	0.01	21.58	0.17	11.00
Abudefduf sexfasciatus	Scissor-tail sergeant	Pomacentridae	35	3.0	Y	N	0.08	22.47	0.12	11.33
Acanthurus olivaceus	Yellow surgeon	Acanthuridae	14	0.2	N	N	0.01	22.26	0.15	11.33
Thalassoma lunare	Moon wrasse	Labridae	6	0.1	Y	Y	0.71	22.08	0.23	11.67
Chaetodon citrinellus	Speckled butterflyfish	Chaetodontidae	5	0.1	N	N	0.00	20.95	0.21	12.50
Abudefduf whitleyi	Whitley's sergeant	Pomacentridae	34	4.1	Y	N	0.10	22.50	0.16	13.33
Ctenochaetus striatus	Lined bristletooth	Acanthuridae	9	0.3	Y	N	0.09	21.92	0.21	13.67
Acanthurus dussumieri	Pencil surgeon	Acanthuridae	16	2.3	Y	N	0.11	22.43	0.20	13.67
Pomacentrus bankanensis	Speckled damsel	Pomacentridae	5	0.1	N	N	0.00	23.92	0.12	13.83

Each value is derived from all available abundance series (n) for each species. Recruit density (1,000 m^{-2}) is per survey during the peak settlement period (January–May). "Overwinter" refers to that species being recorded to survive at least one winter in Sydney (SYD) or Merimbula (MER). The overwinter ratio is the average density of overwintering adults divided by average recruit density at all sites. T_{peak} is the temperature after which abundance started to decline. Slope describes the rate at which abundance dropped with falling temperature. Species are sorted according to the average of the ranked value for each of the three metrics (AVG rank) with a lower value indicating higher overall resilience to dropping temperatures. Color coding indicates High resilience (darker blue) to low resilience (deeper red) for each metric.

2014; Fogarty et al., 2017) and local habitat effects (e.g., Beck et al., 2017) must also be considered in prediction a species' persistence.

Annual settlement of surgeonfishes is rapidly increasing, and has been suggested to indicate a "tropicalization" phenomenon similar to that occurring in the Mediterranean (Vergés et al., 2014). Our results suggest that several of these may be among the most cold-tolerant species (lower T_{peak}, lower Slope) which has implications for their invasiveness in future.

A recent review of range shifts of young-of-the-year of many of the species considered here (Fowler et al., 2017) shows that even less resilient species had shifted. Of our "High Ranked" species, 2 of 5 species showed recruitment further poleward (recruitment, not overwintering) while 3 of 5 species of "Low Ranked" species had shifted. However, this does not indicate establishment or even temperature tolerance, rather offshore advection of larvae and early survival. How species respond to temperature drops at the temperate habitat (as reported here) would be more indicative of range shift potential (i.e. establishment). For instance, in Austral summer 2016, EAC activity and warmer waters lead to unprecedented arrivals of acanthurids and *Abudefduf whitleyi* at the southern location (Merimbula), however these species quickly disappeared once temperatures dropped (Booth unpub. data).

Future extensions of this study would investigate responses of key tropical species in their natal habitats to ambient temperature drops, and linking more- and less-resilient species to overwinter success. As noted by Shoo et al. (2006), investigation of fine grained responses to climate, such as how expatriating reef fishes respond to short-term temperate changes, may increase our ability to predict range shifts.

ETHICS STATEMENT

Animal ethics approval for this project was granted by the University of Technology, Sydney (UTS) Animal Care and Ethics Committee (ACEC) under the ethics permit of DB (Permit ETH17 – 1117). Collections were under NSW DPI F94/696.

AUTHOR CONTRIBUTIONS

DB contributed in leading the study, gathering data, analysing data and writing the manuscript. WF contributed in gathering data, analysing data and writing the manuscript. GB contributed in gathering data and writing the manuscript. LB contributed in gathering data and 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.2018.00031/full#supplementary-material

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