


Insights from extreme coral reefs in a changing world

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Abstract Coral reefs are one of the most biodiverse and economically important ecosystems in the world, but they are rapidly degrading due to the effects of global climate change and local anthropogenic stressors. Reef scientists are increasingly studying coral reefs that occur in marginal and extreme environments to understand how organisms respond to, and cope with, environmental stress, and to gain insight into how reef organisms may acclimate or adapt to future environmental change. To date, there have been more than 860 publications describing the biology and/or abiotic conditions of marginal and extreme reef environments, most of which were published within the past decade. These include systems characterized by unusually high, low, and/or variable temperatures (intertidal, lagoonal, high-latitude areas, and shallow seas),

turbid or urban environments, acidified habitats, and mesophotic depth, and focus on reefs geographically spread throughout most of the tropics. The papers in this special issue of Coral Reefs, entitled *Coral Reefs in a Changing World: Insights from Extremes*, build on the growing body of literature on these unique and important ecosystems, providing a deeper understanding of the patterns and processes governing life in marginal reef systems, and the implications that these insights may have for the future of tropical coral reefs in our rapidly changing world.

Keywords Marginal reef · Lagoon · Intertidal · Turbid · Urban reef · Extreme temperature

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Introduction

Coral reefs are one of the most biodiverse and economically important ecosystems in the world, but they are increasingly under threat from anthropogenic activities (Mora and Sale 2011; Hughes et al. 2017a, 2018a, b; Pörtner et al. 2019). Land-use changes and coastal development have increased sedimentation, eutrophication, and pollution in many nearshore areas (Maina et al. 2013; Burt and Bartholomew 2019). Declining water quality, along with overharvesting of functionally important fishes, have led to the degradation of reef habitats (Hughes et al. 2007; Kroon et al. 2016; Burt and Bartholomew 2019). These localized pressures have been greatly compounded by global stressors, namely ocean warming and acidification resulting from enhanced greenhouse gas emissions (Baker et al. 2008; Riegl et al. 2009; Hoey et al. 2016b; Hoegh-Guldberg et al. 2017) and growing extent and severity of oxygen-depleted ‘dead zones’ (Diaz and Rosenberg 2008) and hypoxia events (Hughes et al. 2020). Importantly, the

increasing frequency and intensity of marine heatwaves have led to thermally induced mass fish mortalities and coral bleaching events (Pearce et al. 2011; Hughes et al. 2017b; Holbrook et al. 2019), declines in coral cover globally (Gardner et al. 2003; De'ath et al. 2012; Perry and Morgan 2017; Hughes et al. 2018b), shifts in coral assemblages (Hughes et al. 2018a; Pratchett et al. 2020), and the subsequent recruitment failure of coral populations (Riegl et al. 2018; Burt and Bauman 2019; Hughes et al. 2019).

Reef scientists are increasingly studying coral reefs that inhabit marginal and extreme environments to develop an understanding of how reef organisms elsewhere in the tropics may respond to future environmental change (Perry and Larcombe 2003; Burt et al. 2014; Camp et al. 2018; Glynn et al. 2018; Schleyer et al. 2018). Reefs occurring in thermally extreme habitats (e.g., Howells et al. 2016a; Camp et al. 2019), or thermally variable high-latitude environments (e.g., Krueger et al. 2017; Thomas et al. 2017), highly turbid or urban areas (e.g., Loya et al. 2016; Morgan et al. 2016; Bauman et al. 2017), mesophotic depths (e.g., Loya et al. 2016; Semmler et al. 2017), near volcanic vents (e.g., Fabricius et al. 2011; Enochs et al. 2015), or lagoons where multiple abiotic parameters vary (Camp et al. 2019), among others, act as natural laboratories in which researchers can examine the response of reef organisms to unabated environmental stressors.

These marginal reef sites are particularly valuable because they represent exposure to extreme conditions for durations greatly in excess of what can be replicated in the lab; they incorporate environmental complexity, subjecting organisms to naturally co-occurring stressors; and they involve diverse community interactions and complicated ecological processes that can be difficult to simulate in experimentally. Ultimately, this understanding of how reef species and communities are coping with extreme environments is shedding light onto how they may acclimate or adapt to changing conditions elsewhere in the world in the coming decades.

A search of the literature relating to four marginal or extreme environments from 1965 to 2019 (Web of Science: topic=coral AND (marginal OR peripheral OR subtropical OR turbid OR mesophotic OR vent) returned >2500 records. These publications were then filtered for relevance, with 867 being conducted in such environments. The total number of publications relating to extreme temperature (including subtropical reefs), turbid or urban, and mesophotic environments was broadly comparable (316, 223, and 292 publications, respectively), with far fewer being conducted in extreme pH settings (29 studies). There were, however, considerable differences in the spatial and temporal distribution of publications arising from these environments (Fig. 1). The vast majority of studies that

have examined the effects of extreme and/or variable temperatures on coral reefs have been conducted in subtropical regions or areas of extensive upwelling (i.e., the Tropical East Pacific), while those examining turbid reefs have been concentrated around the inshore reefs of Australia's Great Barrier Reef, and reefs in urbanized areas of Indonesia and Singapore (Fig. 1a, b). Studies of extreme pH waters have been concentrated around Japan and southeast Asia (Fig. 1c), while studies of mesophotic reef environments were broadly spread across most tropical locations, with higher concentrations of studies in the Atlantic, Hawaii, and Gulf of Aqaba (Fig. 1d). There were also marked differences in the temporal distribution of publication among extreme environments, with the number of publications conducted in unusually warm, cold, and turbid environments increasing relatively gradually since the 1990s (Fig. 1a, b). In contrast, there has been a rapid increase in the number of publications relating to mesophotic environments since 2010 (Fig. 1d), likely reflecting technological advancements (e.g., rebreathers) that have facilitated access to these environments (e.g., Loya et al. 2019). The 25 papers included in this special issue *Coral Reefs in a Changing World: Insights from Extremes* build on these previous studies to provide new insights into the ecology of extreme reefs through investigation of intertidal, lagoon, turbid, urban, acidified, and thermally anomalous environments.

Intertidal and shallow reefs

Shallow and coastal reef environments are often subject to marginal environmental conditions including variable and high temperatures and pH, high turbidity and sedimentation, and fluctuating salinity (Camp et al. 2018). For example, in the back reef tide pools on Ofu Island, American Samoa, sea surface temperatures can reach >35 °C during low tides, and fluctuations of up to 10 °C across tidal cycles (Oliver and Palumbi 2011a). Such systems provide a useful model system to understand how organisms respond to highly variable environmental stress. The continued and increasing interest in thermally extreme environments (Fig. 1a) is not surprising given increasing water temperature is seen as the greatest threat to the structure and functioning of coral reefs globally (Hoey et al. 2016b; Hughes et al. 2018b). There has been a long history of coral reef research in thermally extreme environments that initially focused on the environmental conditions that limited the distribution of corals and coral reefs (Kinsman 1964; Glynn and Wellington 1983; Shepard et al. 1992). However, the increased frequency and intensity of marine heatwaves (Holbrook et al. 2019) have led to a renewed focus to understand how corals in these

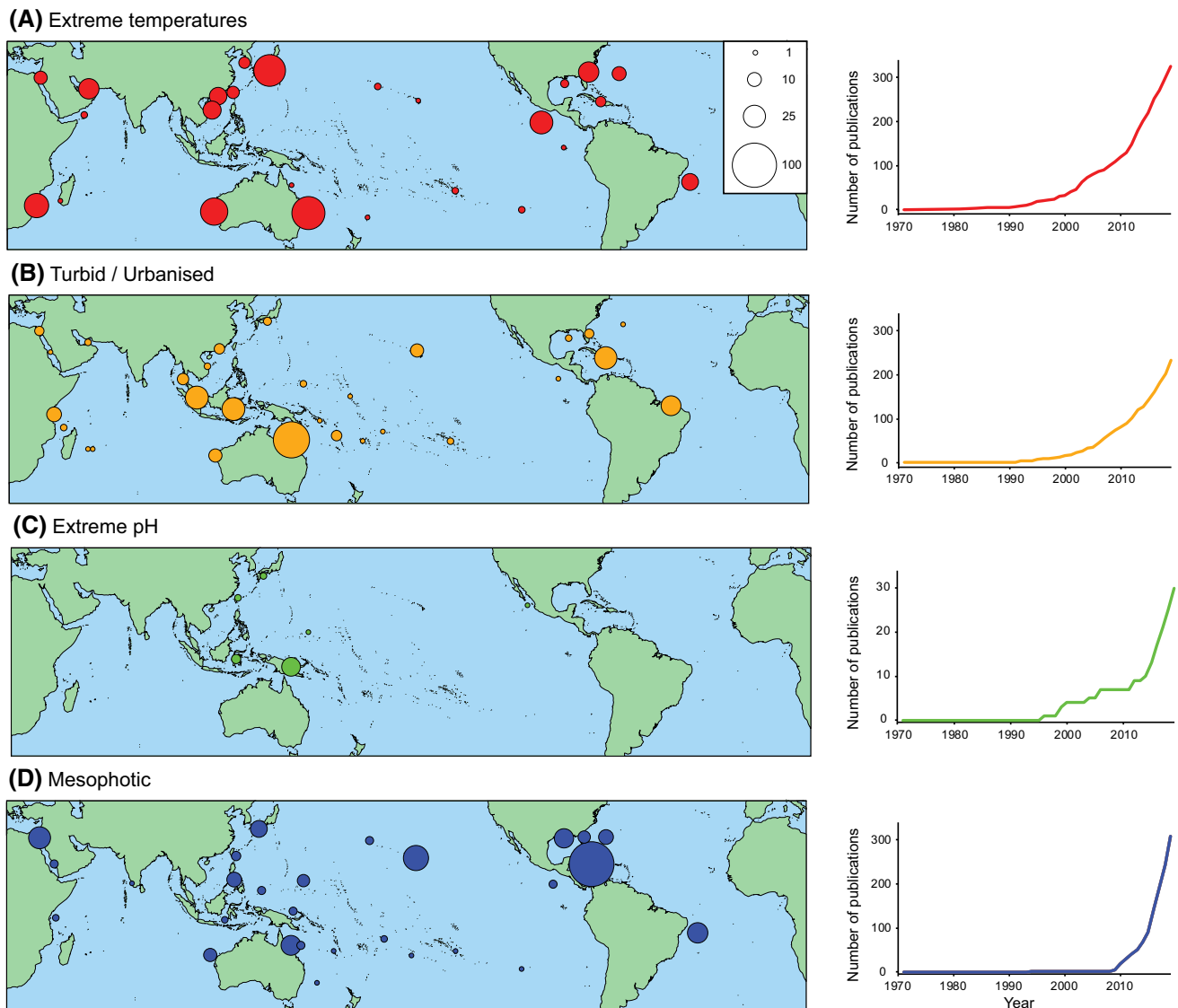


Fig. 1 Spatial and temporal distribution of publications reporting on the biology and/or abiotic conditions of four marginal or extreme reef environments. The number of publications was determined based on a

Web of Science search (topic=coral AND marginal OR peripheral OR subtropical OR turbid OR mesophotic OR vent); year=1965–2019, with each publication examined for relevance

areas acclimate and/or adapt to extreme temperatures through examination of intertidal reefs, lagoonal coral communities, and reefs in thermally stressful seas (Glynn 1983, 1984; Riegl et al. 2011; Glynn et al. 2016; Camp et al. 2018).

Despite the hostile environmental conditions in shallow and intertidal reef environments, they have been demonstrated to house diverse and abundant coral communities (Craig et al. 2001), including a range of bleaching-resistant corals (Safaie et al. 2018). These coral communities have demonstrated enhanced thermal tolerance that is underpinned by association with heat-tolerant symbionts (Oliver and Palumbi 2011b), unique bacterial communities (Ziegler et al. 2017), and acclamatory and adaptive mechanisms

in the coral host itself (Barshis et al. 2013; Bay and Palumbi 2014; Thomas et al. 2018).

While research indicates that corals from highly variable intertidal environments have enhanced resilience to thermal stress, they are not immune to extreme conditions. In the Kimberley region of northwestern Australia where tidal amplitude can be > 10 m, intertidal coral assemblages, often dominated by *Acropora*, are regularly experiencing water temperatures as high as 37 °C, and aerial exposure for several hours a day (Richards et al. 2015). Despite being seemingly adapted to these extreme conditions, these intertidal corals are also susceptible to elevated temperatures with up to 80% of coral colonies bleaching following prolonged exposure to elevated temperatures (4.5–9.3 Degree Heating Weeks,

DHW) in 2015/2016 (Le Nohaïc et al. 2017). An experimental study demonstrated that intertidal corals from the Kimberley region are highly sensitive to relatively small increases in water temperature above the typical range for this region, with several species experiencing more pronounced bleaching and *Acropora* spp. experiencing up to 75% mortality after only a few days of exposure to a 1 °C increase in water temperature (Schoepf et al. 2015). This result indicates that while they may be resilient to the short-term temperature variation and extremes that occur over tidal cycles (e.g., through short-term changes in gene expression over tidal cycles, Ruiz-Jones and Palumbi 2017), they have limited capacity to contend with thermal stress over longer durations (i.e., days to weeks).

Consistent with these findings from the Kimberley region, Buckee et al. (2019) reported the recent loss of large areas of intertidal corals in the Houtman Abrolhos Islands, a high-latitude reef system off Western Australia in 2018. Three months of recurrent low water levels exposed intertidal coral communities to aerial conditions in the middle of the day and resulted in a ca. 30% loss of total coral cover, due entirely to mortality of *Acropora*. This mortality of shallow *Acropora* occurred despite these corals being regularly exposed during spring tides, with no previous records of bleaching (Webster et al. 2002). The unusually low mid-day water levels that occurred in the spring of 2018 were due to the confluence of diurnal spring tides, seasonal sea-level minima, and El-Nino-Southern Oscillation-related interannual variability in sea levels (Buckee et al. 2019). These results indicate that the effects of the El-Nino-Southern Oscillation on coral reefs extend beyond the well-documented influence on temperatures, and that while intertidal corals are able to cope with high diurnal variations in temperature, they (like their subtidal counterparts) are susceptible to prolonged exposure to elevated temperatures.

Lagoonal reefs

Another environmentally extreme reef system that is drawing increasing attention is that of mangrove lagoons. Due to the shallow depth, restricted flushing in these systems, coral communities are often subject to extreme and highly variable temperatures (diel range: 7.7 °C, Camp et al. 2019). High metabolic demands drive frequent exposure to low dissolved oxygen (<3 mg L⁻¹), and recurrent reduced pH (<7.3 pH_T) across seasonal and tidal cycles (Manzello et al. 2012; Camp et al. 2017), making them one of the most extreme coral habitats identified to date. Several recent studies have shown that lagoon coral communities tend to have increased respiration accompanied by reduced net photosynthesis (Camp et al. 2017, 2019, 2020), indicating that heterotrophic energy

acquisition is likely an important mechanism of physiological plasticity that allows corals to survive in these extreme conditions. These are similar to patterns reported for turbid reefs (Guest et al. 2016b; Teixeira et al. 2019), suggesting that heterotrophy may be a broadly utilized strategy across marginal environments. In mangrove lagoons, reduced coral species diversity and lower calcification rates relative to adjacent reefs demonstrate some of the costs and trade-offs of survival into suboptimal environmental conditions (Camp et al. 2016, 2017, 2019).

There is increasing recognition of the role that the microbiome plays in supporting the coral holobiont, especially in lagoon systems. Lagoon coral communities have repeatedly been shown to be associated with unique assemblages of algal symbionts compared with adjacent open-water reefs (Camp et al. 2019, 2020). Several studies have now reported that rather than hosting a prevalence of stress-tolerant *Durussdinium*, lagoon corals are often dominated by novel unexpected symbiont partners (Smith et al. 2017b; Camp et al. 2020), suggesting that flexibility in symbiont associations supports coral persistence under the unique metabolic demands in these lagoon systems. Recent development of analytical tools that use next-generation sequencing data of the ITS2 rDNA to exploit intragenomic variants now allows identification of ITS2-type profiles representative of putative Symbiodiniaceae taxa that were unresolved using earlier methods (Hume et al. 2019). Such techniques have the capacity to show fine-scale divergence in algal genotypes that may represent highly niche-adapted coral-Symbiodiniaceae associations (Howells et al. 2020a, b; Hume et al. 2020) and will allow further insights into the role of algal symbionts in the survival of corals in extreme lagoon environments.

There is also increasing interest in understanding how host-associated bacterial communities support coral survival in such extreme conditions. Camp et al. (2020) showed divergent bacterial communities associating with corals in lagoon habitats compared with open reef habitats, suggesting species-specific plasticity in altering bacterial composition in relation to the prevailing environmental conditions. Such flexibility may offer opportunity for rapid holobiont acclimation or adaptation to environmental stress through bacterial microbiome changes (e.g., Ziegler et al. 2017, 2019) and thus may represent a currently understudied mechanism for corals to cope with environmental extremes and future climate change.

Thermally extreme seas

In addition to specific habitat types, research has also grown rapidly on larger marginal marine systems for the insights that they can provide into how reef fauna and

ecosystems cope with environmental extremes, in particular in the Persian/Arabian Gulf and the Red Sea (Riegl et al. 2011; Berumen et al. 2013; Burt 2013; Vaughan and Burt 2016). Large areas of both the Persian/Arabian Gulf and the Red Sea are characterized by extreme sea surface temperatures in summer (>35 °C and >33 °C, respectively), large seasonal temperature ranges (>15 °C and >10 °C, respectively), and by persistent hyper-salinity (>44 and >41 PSU, respectively) (Ateweberhan et al. 2006; Riegl and Purkis 2012; Carvalho et al. 2019; Vaughan et al. 2019). Despite these conditions, corals occur in all eight nations bordering the Persian/Arabian Gulf, and the Red Sea harbors one of the most diverse and endemic-rich reef assemblages in the world (Carvalho et al. 2019; Vaughan et al. 2019).

Recent research has shown that the superior thermal tolerance of corals in the Persian/Arabian Gulf is the result of a suite of mechanisms including prevalent and persistent association with a novel species of thermally tolerant symbiodinium, *Cladocopium thermophilum* (Hume et al. 2015, 2018; Howells et al. 2020a, b), genetic adaptations in both the algal symbionts and the coral host (Howells et al. 2016a; Smith et al. 2017a), enhanced transcription of host stress response genes during thermal extremes (Kirk et al. 2018), and heritable epigenetic modifications through DNA methylation that can promote acclimatization within generations and the transfer of these modifications between generations (Liew et al. 2020). Similarly, corals in the northern Red Sea have an exceptionally high bleaching threshold that may have been shaped by the selective thermal barrier presented in the southern Red Sea, resulting in coral genotypes that have lower susceptibility to thermal stress (Fine et al. 2013), and able to resist bleaching even after >15 DHW (Osman et al. 2018).

Despite the superior thermal tolerance of reef organisms in this region, there is increasing evidence that life in these extremes comes at a cost. It is well documented that species richness of reef fauna declines dramatically in relation to environmental stress in the Persian/Arabian Gulf (471 vs. 1171 fish species and 40 vs. 140 coral species in the adjacent Sea of Oman; Burt et al. 2011; Riegl et al. 2012; Bauman et al. 2013a; Buchanan et al. 2019; Claereboudt 2019), but more subtle pictures have emerged in recent years. Compared with conspecifics in the neighboring Sea of Oman, corals in the Persian/Arabian Gulf have smaller colony size (Bauman et al. 2013b), reduced fecundity in some species (Howells et al. 2016b), and, depending on the species and local environmental conditions, can have reduced calcification rates (Howells et al. 2018), suggesting trade-offs are incurred to survive in these extreme conditions, as also reported in lagoonal systems (e.g., Camp et al. 2017). Recent surveys of coral disease in the southern Gulf have shown that white syndrome outbreaks

consistently occur in early summer and increased exponentially with cumulative heat exposure (Howells et al. 2020a, b), suggesting that thermal stress may also compromise coral immune systems and/or enhance virulence of the disease pathogens. The occurrence of these outbreaks, despite a near absence ($<5\%$) of bleaching when daily temperatures were >35 °C, indicates that disease presents as a primary signal of thermal stress that would not otherwise be readily discernable (Howells et al. 2020a, b). These observations are complimented by a larger-scale survey across 17 reefs in Persian/Arabian Gulf and adjacent water bodies which showed that disease prevalence was more than 4–8 times higher in Gulf (2.05%) than in the adjacent seas, with disease prevalence primarily related to extreme temperature ranges (Aeby et al. 2020). These findings indicate that disease-related costs of thermal stress are likely a common feature across species and reefs in this extreme environment.

Similar environmental constraints also apply to reef fishes. Although less studied than coral, research over the past decade has shown that reef fish communities in the Persian/Arabian Gulf are low in species richness (241 species), abundance and biomass, and are comprised of smaller individuals than conspecifics that occur in adjacent seas (Feary et al. 2010; Burt et al. 2011; Buchanan et al. 2016). These communities also function differently, being largely dominated by small-bodied herbivores, omnivores, and generalist predators and containing relatively few planktivores, corallivores, and large herbivores (e.g., parrotfishes) that are common to reefs elsewhere (Burt et al. 2011; Pratchett et al. 2013; Hoey et al. 2016a, 2018). Dietary patterns are also divergent. For example, butterflyfish communities are largely dominated by facultative corallivores, while obligate corallivores are rare or absent (Pratchett et al. 2013), and several species of fishes have been shown to consume unusual food resources relative to their typical diets, particularly during the metabolically challenging summer season (Shraim et al. 2017), suggesting that they are resorting to dietary flexibility to support seasonally dynamic and sometimes extreme energetic demands for survival.

The results of a recent behavioral study suggest that reef fishes may also use behavioral changes to downregulate costly activities during extreme seasons and upregulate activities that enhance energy stores during more benign seasons. Using a combination of field observations and aquaria experiments, D'Agostino et al. (2019) showed that during the metabolically challenging summer and winter seasons, the damselfish *Pomacentrus trichourous* substantially reduced their feeding rates and movement, but increased feeding and activity during the shoulder seasons when conditions are most benign, presumably to maximize energy intake when physiological demands were more

optimal. Individuals also switched diets in a manner that suggest behavioral modification to maximize energy budgets, feeding mainly on plankton in the cooler seasons, but on a combination of plankton and a variety of benthic resources during the hottest time of year when energetic demands would be greatest (D'Agostino et al. 2019). Together, these studies suggest that adopting a more flexible behavioral and dietary lifestyle may be necessary to support the physiological and energetic demands presented in thermally extreme seas.

Turbid reefs

In addition to thermally extreme or variable systems, turbid reefs have drawn increasing attention in recent years for their role as a potential climate change refuge due to the shading effect of turbid water for benthic organisms (Cacciapaglia and Van Woesik 2016). While turbid reefs have historically been considered marginal for coral growth due to high suspended sediment loads and low light levels, causing reduced depth distribution, photosynthesis, growth rates and juvenile survival (Rogers 1990; Erftemeijer et al. 2012; Jokiel et al. 2014), there is a growing body of evidence that these systems, under certain conditions, can support coral communities with cover that is comparable to or exceeds that of clear-water reefs (e.g., Browne et al. 2010; Guest et al. 2016a; Morgan et al. 2016; Schleyer and Porter 2018). Over the past decade, a number of field studies have documented lower levels of bleaching and mortality on turbid inshore reefs compared with clear-water offshore reefs, despite being exposed to similar or higher temperatures (Wagner et al. 2010; van Woesik et al. 2012; Morgan et al. 2017; van Woesik and McCaffrey 2017). The resilience of some turbid reefs to thermal stress has been suggested to be due to a combination of factors including the dominance of existing communities by stress-tolerant species, pre-adaptation to thermal stress as a result of chronic exposure to high and variable temperature regimes, and the attenuation of light by high suspended sediment loads that reduces the additive stress of solar irradiance on corals during high-temperature events (van Woesik et al. 2012; Morgan et al. 2017; Teixeira et al. 2019). Recent modeling studies suggest that turbidity may mitigate against high-temperature bleaching for 12% of the world's reefs, with 30% of these reefs located in the species-rich Coral Triangle (Sully and van Woesik 2020). Furthermore, corals in turbid waters have also been shown to have faster recovery and lower mortality following bleaching, likely as a result of enhanced heterotrophic capacity (Guest et al. 2016b; Banha et al. 2019), a process that has also been shown to confer resilience against ocean acidification (Towle et al. 2015).

However, natural turbidity processes on nearshore reefs, such as sediment resuspension or planktonic light attenuation, are often becoming elevated by terrigenous sediment run-off and dredging activities (Friedlander et al. 2005). Terrigenous run-off is typically accompanied by a multitude of anthropogenic pollutants (nutrients, pathogens, pesticides, insecticides, oil, waste, sewage) that are known to have deleterious effects on corals and associated fish and invertebrate biota (Field et al. 2007; Stender et al. 2014; Hess et al. 2017; Johansen et al. 2017) and has been correlated with severely reduced fish abundance and yields on affected reefs (including loss of corals and herbivores typically seen as critical for a productive and resilient ecosystem) (Mallela et al. 2007; DeMartini et al. 2013; Jokiel et al. 2014). Our current limited understanding shows suspended sediment to impair vision and olfaction in fishes looking for shelter and food (Wenger et al. 2011, 2012), and their response to predators (Bauman et al. 2019; Hess et al. 2019). Gill damage may occur after short-term sediment exposure and bacterial and pathogens may accumulate on the gills (Au et al. 2004) and limit capacity to extract oxygen needed to support high energetic demands (Hess et al. 2015). These data highlight the complexity of turbidity impacts on reefs, and why sedimentation and run-off is recognized as a major threat to many inshore coral reefs (e.g., Gombos et al. 2010).

Urban reefs

One subset of turbid reefs that has received growing attention are urban reefs. About 25% of the global human population live within 50 km of a coastline (UNEP 2002). This concentration of human populations and economic activity, coupled with associated changes in land-use, coastal modification, and dredging is leading to increasingly urbanized coral reef environments (Burt 2014; Guest et al. 2016a; Browne et al. 2019; Burt et al. 2019a). Importantly, impacts from turbidity are often compounded by additional anthropogenic pressure from eutrophication, pollution, fishing pressure, and related stressors (Heery et al. 2018; Burt and Bartholomew 2019; Todd et al. 2019; Figueroa-Pico et al. 2020). While these extreme environmental conditions come at a cost (e.g., low carbonate accretion and coral growth rates, Browne et al. 2015; Januchowski-Hartley et al. 2020), urban reefs are typically heavily dominated by robust, stress-tolerant corals that are relatively resistant to bleaching and/or are able to recover rapidly from stressors (Guest et al. 2016b; Brown et al. 2020).

Numerous studies are beginning to elucidate the role that the coral-associated microbial communities may play in the resilience of turbid-water urban corals to

environmental stress. Flexible host–bacterial associations have been suggested to provide opportunity for dynamic microbiome adjustment under environmental change (Ziegler et al. 2019), permitting corals to optimize their bacterial complement to reflect prevailing conditions and enhance survival. Röthig et al. (2020) tested this hypothesis by examining the microbiome of *Oulastrea crispata* across the water quality gradient presented by Hong Kong’s highly urbanized coastline. Despite dramatic differences in environmental conditions among reefs, *O. crispata*’s microbiome was relatively stable, even at sites with very poor water quality. These results suggest that *O. crispata* maintains a conserved microbiome, and that environmental flexibility in its bacterial complement does not underpin robustness of the coral, but rather its wide environmental tolerance may be largely due to acclamatory or adaptive mechanisms in the coral host itself (Röthig et al. 2020). These findings are in contrast to the findings of Wainwright et al. (2019) who examined the bacterial communities of *Pocillopora acuta* across the urbanized reef environment of Singapore. They showed that coral microbiomes diverged sharply among sites and that small-scale (<1 km) differences in environmental factors were responsible for these patterns (Wainwright et al. 2019). It is unclear to what extent the flexibility of these bacterial associations is responsible for the success of *P. acuta* in Singapore, suggesting that additional research is needed to discern its functional role in environmental tolerance.

In addition to bacteria, there is also growing attention to the role that algal symbionts play in supporting coral survival in turbid urban environments (e.g., Poquita-Du et al. 2020; Tan et al. 2020). Smith et al. (2020) used next-generation sequencing and the SymPortal analytical framework to explore Symbiodiniaceae communities in five coral species across Singapore. In contrast to earlier suggestions that stress-tolerant *Durusdinium* strains likely play a crucial role in supporting the resilience of Singapore’s corals (Guest et al. 2016b; Tanzil et al. 2016), they showed that symbiont communities were instead heavily dominated by *Cladocopium*, adding to a growing list of studies showing that prevalence of *Durusdinium* is not a prerequisite for survival in marginal and extreme environments (e.g., Smith et al. 2017b; Hume et al. 2018; Camp et al. 2020; Osman et al. 2020). They also showed that, in contrast with other marginal reef environments, Singapore’s reefs contained remarkably low diversity and a lack of host specificity in the symbiont communities (Smith et al. 2020), suggesting that while these reefs support diverse coral assemblages, the strong selective pressure exerted by the extreme turbidity likely limits the diversity of the associated symbiont community. The observations from this and related studies suggest that as high-resolution ITS2 analyses become more widespread and the usage of

SymPortal framework increases, it will be possible to develop a deeper and more nuanced understanding of important aspects of coral–algal symbioses in marginal reef environments.

Volcanic CO₂ vents

Beyond thermally extreme and turbid reefs, coral communities associated with ojos and volcanic CO₂ vents have drawn attention due to potential acclimation of resident corals to ocean acidification. While volcanic reefs have long been studied for successional processes and disturbance/recovery dynamics (Grigg and Maragos 1974; Tomascik et al. 1996; Starger et al. 2010; Vroom and Zgliczynski 2011; Smallhorn-West et al. 2019), it is only recently that the focus has shifted toward using acidified waters near volcanic CO₂ vents as natural laboratories to understand how tropical reef organisms may respond to future ocean acidification (Hall-Spencer et al. 2008; Fabricius et al. 2011; Inoue et al. 2013; Enochs et al. 2015; Januar et al. 2017). These studies have shown various ecological consequences of exposure to acidified waters near these vents, including shifts from hard corals to soft coral or macro-algal dominance (Inoue et al. 2013; Enochs et al. 2015), reduced coral diversity (Fabricius et al. 2011; Enochs et al. 2015), and enhanced colonization by bioeroders (Enochs et al. 2016a, b), providing insights into possible future changes to tropical reefs under ocean acidification. However, a recent study of a volcanically acidified vent site documented pronounced resilience of some coral colonies that are periodically exposed to extreme low pH (frequently <7.0). The persistence of these corals was likely related to rapid flushing of low pH waters during tidal cycles, indicating that temporal dynamics in stress exposure can strongly influence response patterns (Enochs et al. 2020; see also Oprandi et al. 2019).

To date, volcanic CO₂ vent studies for tropical coral reefs have focused on a small number of geographic regions within the Pacific, including Papua New Guinea (Fabricius et al. 2011), Indonesia (Oprandi et al. 2019), Japan (Inoue et al. 2013), and the Mariana Islands (Enochs et al. 2015), but the first ecological assessment of volcanically acidified coral reef in the Caribbean was recently described (Enochs et al. 2020), and non-volcanic CO₂ vents at fault lines are being discovered in other parts of the tropics (e.g., Oporto-Guerrero et al. 2018). This suggests that our understanding of the patterns and processes governing reef communities in naturally acidified environments will continue to improve with expanded geographic scope.

Conclusion

Coral reefs around the globe are being modified at an unprecedented rate as a result of local anthropogenic pressures and global climate change (Hoegh-Guldberg et al. 2017; Hughes et al. 2017a). Since the devastating 1998 global bleaching event, there has been growing research interest on marginal and extreme reef systems for the role that they might play as potential refugia for reefs elsewhere in the tropics, and the insights that they provide on how reef organisms might respond to the increasingly marginal nature of coastal environments in the future (Perry and Larcombe 2003; Camp et al. 2018). This research growth has largely occurred in just the past decade, suggesting that we are only beginning to understand where these marginal reefs occur and how they function; as time goes on we will continue to learn from these unique ecosystems.

The articles in this special issue add to the growing body of literature exploring how organisms in marginal reef environments are able to cope with extreme environmental conditions. A common emerging theme across marginal systems is the importance of ecological plasticity in allowing reef fauna to persist under conditions that might otherwise be lethal. From flexible bacterial and symbiont associations in corals in marginal inshore environments (e.g., Camp et al. 2020; Smith et al. 2020), to enhanced heterotrophic capacity in light-limited turbid reefs (e.g., Guest et al. 2016b; Banha et al. 2019), to behavioral, physiological and dietary plasticity in fishes in thermally extreme seas (e.g., Shraim et al. 2017; D'Agostino et al. 2019), there is growing evidence that such ecological flexibility may be a broadly utilized, but still underappreciated, strategy for persistence of reef fauna in extreme and variable environments. Evidence also continues to grow that there are trade-offs for survival across many marginal systems. Despite long-term persistence, observations that corals can have reduced calcification (e.g., Camp et al. 2017; Howells et al. 2018), enhanced bioerosion (e.g., Enochs et al. 2016a; Al-Mansoori et al. 2019), more prevalent disease (e.g., Aeby et al. 2020), and various other negatively affected traits (Perry and Larcombe 2003) suggests that there are significant costs to living in marginal environments that are still not yet fully appreciated. There is also growing recognition that the potential for marginal and extreme systems to serve as refugia for other tropical reefs is increasingly coming under question. While there is much evidence that reef fauna in marginal systems have developed important acclamatory and adaptive mechanisms to allow their survival under environmental extremes (Coles and Brown 2003), these organisms often live very close to their physiological limits and are vulnerable to

being pushed over this threshold (Kleypas et al. 1999; Camp et al. 2018). As a result, the same pressures that are affecting reef fauna on more benign reef systems are affecting marginal reefs, including recent devastating bleaching events on intertidal reefs (Le Nohaïc et al. 2017), turbid reefs (Lafratta et al. 2017), mesophotic reefs (Frade et al. 2018), and those in the world's hottest sea, the Persian/Arabian Gulf (Burt et al. 2019b). Instead of singularly focusing attention on their potential role as refugia under climate change, there is a growing consensus that marginal and extreme reef systems should be recognized for their importance in their own right, as biodiverse and highly unique ecosystems that are important assets for climate change science (Burt et al. 2014; Loya et al. 2016; Camp et al. 2018; Soares 2020). As research continues to grow we will gain a broader understanding of the patterns and processes governing life in extremes and allowing for improved conservation and management of these ecosystems. Increasing research will also deepen insights into what the future may hold for reefs elsewhere in the tropics as environmental conditions become increasingly marginal for reef fauna globally in our rapidly changing world.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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