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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 >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

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

37 **Keywords**

38 Marginal reef; Lagoon; Intertidal; Turbid; Urban reef; Extreme temperature

39

40 **Introduction**

41 Coral reefs are one of the most biodiverse and economically important ecosystems in the world,
42 but they are increasingly under threat from anthropogenic activities (Mora and Sale 2011;
43 Hughes et al. 2017a; 2018; Pörtner et al. 2019). Land-use changes and coastal development have
44 increased sedimentation, eutrophication, and pollution in many nearshore areas. Declining water
45 quality, along with overharvesting of functionally important fishes, have led to the degradation
46 of reef habitats (Hughes et al. 2007; Maina et al. 2013; Kroon et al. 2016; Burt and Bartholomew
47 2019). These localized pressures have been greatly compounded by global stressors, namely
48 ocean warming and acidification resulting from enhanced greenhouse gas emissions (Baker et al.
49 2008; Riegl et al. 2009; Hoey et al. 2016b; Hoegh-Guldberg et al. 2017) and growing extent and
50 severity of oxygen-depleted ‘dead zones’ (Diaz and Rosenberg 2008) and hypoxia events
51 (Hughes et al. 2020). Importantly, the increasing frequency and intensity of marine heat waves
52 have led to thermally-induced mass fish mortalities and coral bleaching events (Pearce et al.
53 2011; Hughes et al. 2017b; Holbrook et al. 2019), declines in coral cover globally (Gardner et al.

54 2003; De'ath et al. 2012; Perry and Morgan 2017; Hughes et al. 2018b), shifts in coral
55 assemblages (Hughes et al. 2018a; Pratchett et al. 2020), and the subsequent recruitment failure
56 of coral populations (Riegl et al. 2018; Burt and Bauman 2019; Hughes et al. 2019).

57 Reef scientists are increasingly studying coral reefs that inhabit marginal and extreme
58 environments to develop an understanding of how reef organisms elsewhere in the tropics may
59 respond to future environmental change (Perry and Larcombe 2003; Burt et al. 2014; Camp et al.
60 2018; Glynn et al. 2018; Schleyer et al. 2018). Reefs occurring in thermally extreme habitats
61 (e.g. Howells et al. 2016a; Camp et al. 2019), or thermally variable high-latitude environments
62 (e.g. Krueger et al. 2017; Thomas et al. 2017), highly turbid or urban areas (e.g. Loya et al. 2016;
63 Morgan et al. 2016; Bauman et al. 2017), mesophotic depths (e.g. Loya et al. 2016; Semmler et
64 al. 2017), near volcanic vents (e.g. Fabricius et al. 2011; Enochs et al. 2015), or lagoons where
65 multiple abiotic parameters vary (Camp et al. 2019), among others, act as natural laboratories in
66 which researchers can examine the response of reef organisms to unabated environmental
67 stressors.

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

75 A search of the literature relating to four marginal or extreme environments from 1965 - 2019
76 (Web of Science: topic = coral AND (marginal OR peripheral OR sub-tropical OR turbid OR

77 mesophotic OR vent) returned >2,500 records. These publications were then filtered for
78 relevance, with 867 being conducted in marginal or extreme environments. The total number of
79 publications relating to extreme temperature (including sub-tropical reefs), turbid or urban, and
80 mesophotic environments was broadly comparable (316, 223, and 292 publications,
81 respectively), with far fewer being conducted in extreme pH setting (29 studies). There were,
82 however, considerable differences in the spatial and temporal distribution of publications arising
83 from these environments (Figure 1). The vast majority of studies that have examined the effects
84 of extreme and/or variable temperatures on coral reefs have been conducted in subtropical
85 regions or areas of extensive upwelling (i.e., the Tropical East Pacific), while those examining
86 turbid reefs have been concentrated around the inshore reefs of Australia's Great Barrier Reef,
87 and reefs in urbanized areas of Indonesia and Singapore (Figure 1a, b). Studies of extreme pH
88 waters have been concentrated around Japan and southeast Asia (Figure 1c), while studies of
89 mesophotic reef environments were broadly spread across most tropical locations, with higher
90 concentrations of studies in the Atlantic, Hawaii and Gulf of Aqaba (Figure 1d). There were also
91 marked differences in the temporal distribution of publication among extreme environments,
92 with the number of publications conducted in unusually warm, cold and turbid environments
93 increasing relatively gradually since the 1990's (Figure 1a,b). In contrast, there has been a rapid
94 increase in the number of publications relating to mesophotic environments since 2010 (Figure
95 1d), likely reflecting technological advancements (e.g., rebreathers) that have facilitated access
96 to these environments (e.g. Loya et al. 2019). The 25 papers included in this special issue *Coral*
97 *Reefs in a Changing World: Insights from Extremes* build on these previous studies to provide
98 new insights into the ecology of extreme reefs through investigation of intertidal, lagoon, turbid,
99 urban, acidified, and thermally anomalous environments.

100

101 >>INSERT FIG. 1>>>

102

103 **Intertidal and shallow reefs**

104 Shallow and coastal reef environments are often subject to marginal environmental conditions
105 including variable and high temperatures and pH, high turbidity and sedimentation, and
106 fluctuating salinity (Camp et al. 2018). For example, in the back reef tide pools on Ofu Island,
107 American Samoa, sea surface temperatures can reach >35 °C during low tides, and fluctuations
108 of up to 10 °C across tidal cycles (Oliver and Palumbi 2011a). Such systems provide a useful
109 model system to understand how organisms respond to highly variable environmental stress. The
110 continued and increasing interest in thermally extreme environments (Figure 1a) is not surprising
111 given increasing water temperature is seen as the greatest threat to the structure and functioning
112 of coral reefs globally (Hoey et al. 2016b; Hughes et al. 2018b). There has been a long history of
113 coral reef research in thermally extreme environments that initially focused on the environmental
114 conditions that limited the distribution of corals and coral reefs (Kinsman 1964; Glynn and
115 Wellington 1983; Sheppard et al. 1992). However, the increased frequency and intensity of
116 marine heatwaves (Holbrook et al. 2019) has led to a renewed focus to understand how corals in
117 these areas acclimate and/or adapt to extreme temperatures through examination of intertidal
118 reefs, lagoonal coral communities, and reefs in thermally stressful seas (Glynn 1983,1984; Riegl
119 et al. 2011; Glynn et al. 2016; Camp et al. 2018).

120 Despite the hostile environmental conditions in shallow and intertidal reef environments, they
121 have been demonstrated to house diverse and abundant coral communities (Craig et al. 2001),

122 including a range of bleaching-resistant corals (Safaie et al. 2018). These coral communities
123 have demonstrated enhanced thermal tolerance that is underpinned by association with heat-
124 tolerant symbionts (Oliver and Palumbi 2011b), unique bacterial communities (Ziegler et al.
125 2017), and acclamatory and adaptive mechanisms in the coral host itself (Barshis et al. 2013;
126 Bay and Palumbi 2014; Thomas et al. 2018).

127 While research indicates that corals from highly variable intertidal environments have enhanced
128 resilience to thermal stress, they are not immune to extreme conditions. In the Kimberley region
129 of northwestern Australia where tidal amplitude can be > 10 m, intertidal coral assemblages,
130 often dominated by *Acropora*, are regularly experiencing water temperatures as high as 37 °C,
131 and aerial exposure for several hours a day (Richards et al. 2015). Despite being seemingly
132 adapted to these extreme conditions, these intertidal corals are also susceptible to elevated
133 temperatures with up to 80% of coral colonies bleaching following prolonged exposure to
134 elevated temperatures (4.5–9.3 Degree Heating Weeks, DHW) in 2015/16 (Le Nohaïc et al.
135 2017). An experimental study demonstrated that intertidal corals from the Kimberley region are
136 highly sensitive to relatively small increases in water temperature above the typical range for this
137 region, with several species experiencing more pronounced bleaching and *Acropora* spp.
138 experiencing up to 75% mortality after only a few days of exposure to a 1 °C increase in water
139 temperature (Schoepf et al. 2015). This result indicates that while they may be resilient to the
140 short-term temperature variation and extremes that occur over tidal cycles (e.g. through short-
141 term changes in gene expression over tidal cycles, Ruiz-Jones and Palumbi 2017), they have
142 limited capacity to contend with thermal stress over longer durations (i.e., days to weeks).
143 Consistent with these findings from the Kimberley region, Buckee et al. (2019) reported the
144 recent loss of large areas of intertidal corals in the Houtman Abrolhos Islands, a high-latitude

145 reef system off Western Australia in 2018. Three months of recurrent low water levels exposed
146 intertidal coral communities to aerial conditions in the middle of the day and resulted in a ca.
147 30% loss of total coral cover, due entirely to mortality of *Acropora*. This mortality of shallow
148 *Acropora* occurred despite these corals being regularly exposed during spring tides, with no
149 previous records of bleaching (Webster et al. 2002). The unusually low mid-day water levels that
150 occurred in the spring of 2018 were due to the confluence of diurnal spring tides, seasonal sea-
151 level minima, and El-Nino-Southern Oscillation-related interannual variability in sea levels
152 (Buckee et al. 2019). These results indicate that the effects of the El-Nino-Southern Oscillation
153 on coral reefs extend beyond the well documented influence on temperatures, and that while
154 intertidal corals are able to cope with high diurnal variations in temperature, they (like their
155 subtidal counterparts) are susceptible to prolonged exposure to elevated temperatures.

156

157 **Lagoonal reefs**

158 Another environmentally extreme reef system that is drawing increasing attention is that of
159 mangrove lagoons. Due to the shallow depth, restricted flushing in these systems, coral
160 communities are often subject to extreme and highly variable temperatures (diel range: 7.7 °C,
161 Camp et al. 2019). High metabolic demands drive frequent exposure to low dissolved oxygen (<
162 3 mg L⁻¹), and recurrent reduced pH (< 7.3 pH_T) across seasonal and tidal cycles (Manzello et al.
163 2012; Camp et al. 2017), making them one of the most extreme coral habitats identified to date.
164 Several recent studies have shown that lagoon coral communities tend to have increased
165 respiration accompanied by reduced net photosynthesis (Camp et al. 2017; Camp et al. 2019;
166 Camp et al. 2020), indicating that heterotrophic energy acquisition is likely an important
167 mechanism of physiological plasticity that allows corals to survive in these extreme conditions.

168 These are similar to patterns reported for turbid reefs (Guest et al. 2016b; Teixeira et al. 2019),
169 suggesting that heterotrophy may be a broadly utilized strategy across marginal environments. In
170 mangrove lagoons, reduced coral species diversity and lower calcification rates relative to
171 adjacent reefs demonstrates some of the costs and trade-offs of survival into suboptimal
172 environmental conditions (Camp et al. 2016; Camp et al. 2017; Camp et al. 2019).

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

187 There is also increasing interest in understanding how host-associated bacterial communities
188 support coral survival in such extreme conditions. Camp et al. (2020) showed divergent bacterial
189 communities associating with corals in lagoon habitats compared with open reef habitats,
190 suggesting species-specific plasticity in altering bacterial composition in relation to the

191 prevailing environmental conditions. Such flexibility may offer opportunity for rapid holobiont
192 acclimation or adaptation to environmental stress through bacterial microbiome changes (e.g.
193 Ziegler et al. 2017; Ziegler et al. 2019), and thus may represent a currently under-studied
194 mechanism for corals to cope with environmental extremes and future climate change.

195

196 **Thermally extreme seas**

197 In addition to specific habitat types, research has also grown rapidly on larger marginal marine
198 systems for the insights that they can provide into how reef fauna and ecosystems cope with
199 environmental extremes, in particular in the Persian/Arabian Gulf and the Red Sea (Riegl et al.
200 2011; Berumen et al. 2013; Burt 2013; Vaughan and Burt 2016). Large areas of both the
201 Persian/Arabian Gulf and the Red Sea are characterized by extreme sea surface temperatures in
202 summer (>35 °C and >33 °C, respectively), large seasonal temperature ranges (>15 °C and >10
203 °C, respectively), and by persistent hyper-salinity (>44 and >41 PSU, respectively)
204 (Ateweberhan et al. 2006; Riegl and Purkis 2012; Carvalho et al. 2019; Vaughan et al. 2019).
205 Despite these conditions, corals occur in all eight nations bordering the Persian/Arabian Gulf,
206 and the Red Sea harbors one of the most diverse and endemic-rich reef assemblages in the world
207 (Carvalho et al. 2019; Vaughan et al. 2019).

208 Recent research has shown that the superior thermal tolerance of corals in the Persian/Arabian
209 Gulf is the result of a suite of mechanisms including prevalent and persistent association with a
210 novel species of thermally tolerant symbiodinium, *Cladocopium thermophilum* (Hume et al.
211 2015; Hume et al. 2018; Howells et al. 2020), genetic adaptations in both the algal symbionts
212 and the coral host (Howells et al. 2016a; Smith et al. 2017a), enhanced transcription of host

213 stress response genes during thermal extremes (Kirk et al. 2018), and heritable epigenetic
214 modifications through DNA methylation that can promote acclimatization within generations and
215 the transfer of these modifications between generations (Liew et al. 2020). Similarly, corals in
216 the northern Red Sea have an exceptionally high bleaching threshold that may have been shaped
217 by the selective thermal barrier presented in the southern Red Sea, resulting in coral genotypes
218 that have lower susceptibility to thermal stress (Fine et al. 2013), and able to resist bleaching
219 even after >15 DHW (Osman et al. 2018).

220 Despite the superior thermal tolerance of reef organisms in this region, there is increasing
221 evidence that life in these extremes comes at a cost. It is well documented that species richness
222 of reef fauna declines dramatically in relation to environmental stress in the Persian/Arabian
223 Gulf (471 vs 1171 fish species and 40 vs 140 coral species in the adjacent Sea of Oman; Burt et
224 al. 2011; Riegl et al. 2012; Bauman et al. 2013a; Buchanan et al. 2019; Claereboudt 2019), but
225 more subtle pictures have emerged in recent years. Compared with conspecifics in the
226 neighboring Sea of Oman, corals in the Persian/Arabian Gulf have smaller colony size (Bauman
227 et al. 2013b), reduced fecundity in some species (Howells et al. 2016b), and, depending the
228 species and local environmental conditions, can have reduced calcification rates (Howells et al.
229 2018), suggesting trade-offs are incurred to survive in these extreme conditions, as also reported
230 in lagoonal systems (e.g. Camp et al. 2017). Recent surveys of coral disease in the southern Gulf
231 have shown that white syndrome outbreaks consistently occur in early summer and increased
232 exponentially with cumulative heat exposure (Howells et al. In Press), suggesting that thermal
233 stress may also compromise coral immune systems and/or enhance virulence of the disease
234 pathogens. The occurrence of these outbreaks, despite a near absence (<5%) of bleaching when
235 daily temperatures were >35 °C, indicates that disease presents as a primary signal of thermal

236 stress that would not otherwise be readily discernable (Howells et al. In Press). These
237 observations are complimented by a larger-scale survey across 17 reefs in Persian/Arabian Gulf
238 and adjacent water bodies which showed that disease prevalence was more than four to eight
239 times higher in Gulf (2.05%) than in the adjacent seas, with disease prevalence primarily related
240 to extreme temperature ranges (Aeby et al. 2020). These findings indicate that disease-related
241 costs of thermal stress are likely a common feature across species and reefs in this extreme
242 environment.

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

257 The results of a recent behavioral study suggest that reef fishes may also use behavioral changes
258 to downregulate costly activities during extreme seasons and upregulate activities that enhance

259 energy stores during more benign seasons. Using a combination of field observations and aquaria
260 experiments, D'Agostino et al (2019) showed that during the metabolically challenging summer
261 and winter seasons, the damselfish *Pomacentrus trichrourous* substantially reduced their feeding
262 rates and movement, but increased feeding and activity during the shoulder seasons when
263 conditions are most benign, presumably to maximize energy intake when physiological demands
264 were more optimal. Individuals also switched diets in a manner that suggest behavioural
265 modification to maximize energy budgets, feeding mainly on plankton in the cooler seasons, but
266 on a combination of plankton and a variety of benthic resources during the hottest time of year
267 when energetic demands would be greatest (D'Agostino et al. 2019). Together, these studies
268 suggest that adopting a more flexible behavioral and dietary lifestyle may be necessary to
269 support the physiological and energetic demands presented in thermally extreme seas.

270

271 **Turbid reefs**

272 In addition to thermally extreme or variable systems, turbid reefs have drawn increasing attention
273 in recent years for their role as a potential climate change refuge due to the shading effect of
274 turbid water for benthic organisms (Cacciapaglia and Van Woesik 2016). While turbid reefs have
275 historically been considered marginal for coral growth due to high suspended sediment loads and
276 low light levels, causing reduced depth distribution, photosynthesis, growth rates and juvenile
277 survival (Rogers 1990; Erftemeijer et al. 2012; Jokiel et al. 2014), there is a growing body of
278 evidence that these systems, under certain conditions, can support coral communities with cover
279 that is comparable to or exceeds that of clear-water reefs (e.g. Browne et al. 2010; Guest et al.
280 2016a; Morgan et al. 2016; Schleyer and Porter 2018). Over the past decade a number of field
281 studies have documented lower levels of bleaching and mortality on turbid inshore reefs

282 compared with clear-water offshore reefs, despite being exposed to similar or higher
283 temperatures (Wagner et al. 2010; van Woosik et al. 2012; Morgan et al. 2017; van Woosik and
284 McCaffrey 2017). The resilience of some turbid reefs to thermal stress has been suggested to be
285 due to a combination of factors including the dominance of existing communities by stress-
286 tolerant species, pre-adaptation to thermal stress as a result of chronic exposure to high and
287 variable temperature regimes, and the attenuation of light by high suspended sediment loads that
288 reduces the additive stress of solar irradiance on corals during high temperature events (van
289 Woosik et al. 2012; Morgan et al. 2017; Teixeira et al. 2019). Recent modeling studies suggest
290 that turbidity may mitigate against high-temperature bleaching for 12% of the world's reefs, with
291 30% of these reefs located in the species-rich Coral Triangle (Sully and van Woosik 2020).
292 Furthermore, corals in turbid waters have also been shown to have faster recovery and lower
293 mortality following bleaching, likely as a result of enhanced heterotrophic capacity (Guest et al.
294 2016b; Banha et al. 2019), a process that has also been shown to confer resilience against ocean
295 acidification (Towle et al. 2015).

296 However, natural turbidity processes on nearshore reefs, such as sediment resuspension or
297 planktonic light attenuation, are often becoming elevated by terrigenous sediment run-off and
298 dredging activities (Friedlander et al. 2005). Terrigenous run-off is typically accompanied by a
299 multitude of anthropogenic pollutants (nutrients, pathogens, pesticides, insecticides, oil, waste,
300 sewage) that are known to have deleterious effects on corals and associated fish and invertebrate
301 biota (Field et al. 2007; Stender et al. 2014; Hess et al. 2017; Johansen et al. 2017) and has been
302 correlated with severely reduced fish abundance and yields on affected reefs (including loss of
303 corals and herbivores typically seen as critical for a productive and resilient ecosystem) (Mallela
304 et al. 2007; DeMartini et al. 2013; Jokiel et al. 2014). Our current limited understanding shows

305 suspended sediment to impair vision and olfaction in fishes looking for shelter and food (Wenger
306 et al. 2011; Wenger et al. 2012), and their response to predators (Bauman et al. 2019; Hess et al.
307 2019). Gill damage may occur after short-term sediment exposure and bacterial and pathogens
308 may accumulate on the gills (Au et al. 2004) and limit capacity to extract oxygen needed to
309 support high energetic demands (Hess et al. 2015). These data highlight the complexity of
310 turbidity impacts on reefs, and why sedimentation and run-off is recognized as a major threat to
311 many inshore coral reefs (e.g. Gombos et al. 2010).

312

313 **Urban reefs**

314 One subset of turbid reefs that has received growing attention are urban reefs. About 25% of the
315 global human population live within 50 km of a coastline (UNEP 2002). This concentration of
316 human populations and economic activity, coupled with associated changes in land-use, coastal
317 modification, and dredging is leading to increasingly urbanized coral reef environments (Burt
318 2014; Guest et al. 2016a; Browne et al. 2019). Importantly, impacts from turbidity are often
319 compounded by additional anthropogenic pressure from eutrophication, pollution, fishing
320 pressure, and related stressors (Heery et al. 2018; Burt and Bartholomew 2019; Todd et al. 2019;
321 Figueroa-Pico et al. 2020). While these extreme environmental conditions come at a cost (e.g.
322 low carbonate accretion and coral growth rates, Browne et al. 2015; Januchowski-Hartley et al.
323 2020), urban reefs are typically heavily dominated by robust, stress-tolerant corals that are
324 relatively resistant to bleaching and/or are able to recover rapidly from stressors (Guest et al.
325 2016b; Brown et al. 2020).

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

345 In addition to bacteria, there is also growing attention to the role that algal symbionts play in
346 supporting coral survival in turbid urban environments (e.g. Poquita-Du et al. 2020; Tan et al.
347 2020). Smith et al. (Smith et al. 2020) used next-generation sequencing and the SymPortal
348 analytical framework to explore Symbiodiniaceae communities in five coral species across

349 Singapore. In contrast to earlier suggestions that stress-tolerant *Durusdinium* strains likely play a
350 crucial role in supporting the resilience of Singapore's corals (Guest et al. 2016b; Tanzil et al.
351 2016), they showed that symbiont communities were instead heavily dominated by
352 *Cladocopium*, adding to a growing list of studies showing that prevalence of *Durusdinium* is not
353 a prerequisite for survival in marginal and extreme environments (e.g. Smith et al. 2017b; Hume
354 et al. 2018; Camp et al. 2020; Osman et al. 2020). They also showed that, in contrast with other
355 marginal reef environments, Singapore's reefs contained remarkably low diversity and a lack of
356 host-specificity in the symbiont communities (Smith et al. 2020), suggesting that while these
357 reefs support diverse coral assemblages, the strong selective pressure exerted by the extreme
358 turbidity likely limits the diversity of the associated symbiont community. The observations from
359 this and related studies suggests that as high-resolution ITS2 analyses become more widespread
360 and the usage of SymPortal framework increases, it will be possible to develop a deeper and
361 more nuanced understanding of important aspects of coral-algal symbioses in marginal reef
362 environments.

363

364 **Volcanic CO₂ vents**

365 Beyond thermally extreme and turbid reefs, coral communities associated with ojos and volcanic
366 CO₂ vents have drawn attention due to potential acclimation of resident corals to ocean
367 acidification. While volcanic reefs have long been studied for successional processes and
368 disturbance/recovery dynamics (Grigg and Maragos 1974; Tomascik et al. 1996; Starger et al.
369 2010; Vroom and Zgliczynski 2011; Smallhorn-West et al. 2019), it is only recently that the
370 focus has shifted towards using acidified waters near volcanic CO₂ vents as natural laboratories
371 to understand how tropical reef organisms may respond to future ocean acidification (Hall-

372 Spencer et al. 2008; Fabricius et al. 2011; Inoue et al. 2013; Enochs et al. 2015; Januar et al.
373 2017). These studies have shown various ecological consequences of exposure to acidified
374 waters near these vents, including shifts from hard corals to soft coral or macro-algal dominance
375 (Inoue et al. 2013; Enochs et al. 2015), reduced coral diversity (Fabricius et al. 2011; Enochs et
376 al. 2015), and enhanced colonization by bioeroders (Enochs et al. 2016a; Enochs et al. 2016b),
377 providing insights into possible future changes to tropical reefs under ocean acidification.
378 However, a recent study of a volcanically acidified vent site documented pronounced resilience
379 of some coral colonies that are periodically exposed to extreme low pH (frequently < 7.0). The
380 persistence of these corals was likely related to rapid flushing of low pH waters during tidal
381 cycles, indicating that temporal dynamics in stress exposure can strongly influence response
382 patterns (Enochs et al. 2020; see also Oprandi et al. 2019).

383 To date, volcanic CO₂ vent studies for tropical coral reefs have focused on a small number of
384 geographic regions within the Pacific, including Papua New Guinea (Fabricius et al. 2011),
385 Indonesia (Oprandi et al. 2019), Japan (Inoue et al. 2013), and the Mariana Islands (Enochs et al.
386 2015), but the first ecological assessment of volcanically acidified coral reef in the Caribbean
387 was recently described (Enochs et al. 2020), and non-volcanic CO₂ vents at fault lines are being
388 discovered in other parts of the tropics (e.g. Oporto-Guerrero et al. 2018). This suggests that our
389 understanding of the patterns and processes governing reef communities in naturally acidified
390 environments will continue to improve with expanded geographic scope.

391

392 **Conclusion**

393 Coral reefs around the globe are being modified at an unprecedented rate as a result of local
394 anthropogenic pressures and global climate change (Hoegh-Guldberg et al. 2017; Hughes et al.
395 2017a). Since the devastating 1998 global bleaching event, there has been growing research
396 interest on marginal and extreme reef systems for the role that they might play as potential
397 refugia for reefs elsewhere in the tropics, and the insights that they provide on how reef
398 organisms might respond to the increasingly marginal nature of coastal environments in the
399 future (Perry and Larcombe 2003; Camp et al. 2018). This research growth has largely occurred
400 in just the past decade, suggesting that we are only beginning to understand where these marginal
401 reefs occur and how they function; as time goes on we will continue to learn from these unique
402 ecosystems.

403 The articles in this special issue add to the growing body of literature exploring how organisms
404 in marginal reef environments are able to cope with extreme environmental conditions. A
405 common emerging theme across marginal systems is the importance of ecological plasticity in
406 allowing reef fauna to persist under conditions that might otherwise be lethal. From flexible
407 bacterial and symbiont associations in corals in marginal inshore environments (e.g. Camp et al.
408 2020; Smith et al. 2020), to enhanced heterotrophic capacity in light-limited turbid reefs (e.g.
409 Guest et al. 2016b; Banha et al. 2019), to behavioral, physiological and dietary plasticity in
410 fishes in thermally extreme seas (e.g. Shraim et al. 2017; D'Agostino et al. 2019), there is
411 growing evidence that such ecological flexibility may be a broadly utilized, but still
412 underappreciated, strategy for persistence of reef fauna in extreme and variable environments.
413 Evidence also continues to grow that there are trade-offs for survival across many marginal
414 systems. Despite long-term persistence, observations that corals can have reduced calcification
415 (e.g. Camp et al. 2017; Howells et al. 2018), enhanced bioerosion (e.g. Enochs et al. 2016a; Al-

416 Mansoori et al. 2019), more prevalent disease (e.g. Aeby et al. 2020), and various other
417 negatively affected traits (Perry and Larcombe 2003) suggests that there are significant costs to
418 living in marginal environments that are still not yet fully appreciated. There is also growing
419 recognition that the potential for marginal and extreme systems to serve as refugia for other
420 tropical reefs is increasingly coming under question. While there is much evidence that reef
421 fauna in marginal systems have developed important acclamatory and adaptive mechanisms to
422 allow their survival under environmental extremes (Coles and Brown 2003), these organisms
423 often live very close to their physiological limits and are vulnerable to being pushed over this
424 threshold (Kleypas et al. 1999; Camp et al. 2018). As a result, the same pressures that are
425 affecting reef fauna on more benign reef systems are affecting marginal reefs, including recent
426 devastating bleaching events on intertidal reefs (Le Nohaïc et al. 2017), turbid reefs (Lafratta et
427 al. 2017), mesophotic reefs (Frade et al. 2018), and those in the world's hottest sea, the
428 Persian/Arabian Gulf (Burt et al. 2019). Instead of singularly focusing attention on their potential
429 role as refugia under climate change, there is a growing consensus that marginal and extreme
430 reef systems should be recognized for their importance in their own right, as biodiverse and
431 highly unique ecosystems that are important assets for climate change science (Burt et al. 2014;
432 Loya et al. 2016; Camp et al. 2018; Soares 2020). As research continues to grow we will gain a
433 broader understanding of the patterns and processes governing life in extremes and allowing for
434 improved conservation and management of these ecosystems. Increasing research will also
435 deepen insights into what the future may hold for reefs elsewhere in the tropics as environmental
436 conditions become increasingly marginal for reef fauna globally in our rapidly changing world.

437 **Conflict of interest statement**

438 The authors declare no conflicts of interest.

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840 **List of Figures**

841 Figure 1. Spatial and temporal distribution of publications reporting on the biology and/or abiotic
842 conditions of four marginal or extreme reef environments. The number of publications was
843 determined based on a *Web of Science* search (topic = coral AND marginal OR peripheral OR
844 subtropical OR turbid OR mesophotic OR vent); year = 1965-2019), with each publication
845 examined for relevance.

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