

1 **Resilience of Tropical Ecosystems to Ocean Deoxygenation**

2

3 Andrew H. Altieri<sup>1</sup>, Maggie D. Johnson<sup>2</sup>, Sara D. Swaminathan<sup>1</sup>, Hannah R. Nelson<sup>3</sup>, Keryn B.

4 Gedan<sup>4</sup>

5

6 <sup>1</sup>Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL,

7 USA

8 <sup>2</sup>Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

9 <sup>3</sup>Center for Population Biology, University of California, Davis, CA, USA

10 <sup>4</sup>Department of Biology, George Washington University, Washington, DC, USA

11

12 **Keywords:** coral reefs, hypoxia, mangroves, multiple stressors, mutualisms, seagrass

13 **Abstract**

14 The impacts of ocean deoxygenation on biodiversity and ecosystem function are well established  
15 in temperate regions, and here we illustrate how the study of hypoxia in tropical ecosystems can  
16 offer insights of general importance. We first describe how mechanisms of resilience have  
17 developed in response to naturally occurring hypoxia across three tropical ecosystems: coral  
18 reefs, seagrass beds, and mangrove forests. We then suggest that the vulnerability of these  
19 systems to deoxygenation lies in interactions with other stressors that are increasing rapidly in  
20 the Anthropocene. Finally, we advocate for adopting a broader community- and ecosystem-level  
21 perspective that incorporates mutualisms, feedbacks, and mechanisms of self-rescue and  
22 recovery to develop a better predictive understanding of the effects of deoxygenation in coastal  
23 ecosystems.

24

25 **Why Study Deoxygenation in Tropical Ecosystems?**

26 Ocean deoxygenation driven by eutrophication and climate change is accelerating worldwide and  
27 is one of the greatest threats to life in the ocean and to humans that depend on healthy seas [1-4].  
28 However, we have a major blind spot in our understanding of ocean deoxygenation – research on  
29 hypoxia in tropical coastal ecosystems including coral reefs, seagrass meadows, and mangrove  
30 forests has lagged behind temperate systems, despite the large proportion of these systems that  
31 are at risk [5, 6]. This discrepancy has been documented in meta-analyses [7] and reviews [6],  
32 and is evident in publication bias [5]. The few studies that have investigated hypoxia in tropical  
33 systems have focused primarily on coral reefs and organismal perspectives [8, 9]. However, it is  
34 becoming apparent that oxygen limitation (dissolved oxygen concentrations < 3 mg/L, but higher

35 for some taxa) is widespread in tropical ecosystems [6], and is emerging as one of the most  
36 pressing conservation concerns [10].

37

38 Tropical ecosystems differ from temperate regions in several important ways, and understanding  
39 these differences provides insight to the natural capacity of ecosystems to cope with ocean  
40 deoxygenation. Oxygen is more limited in the tropics where warmer temperatures decrease the  
41 saturation capacity of dissolved oxygen in seawater, while simultaneously increasing rates of  
42 aerobic metabolism that consume and deplete oxygen [1]. Moreover, high biodiversity in the  
43 tropics has increased the functional diversity of organisms responding to hypoxia and facilitated  
44 the development of mutualisms in which oxygen can be exchanged between partners [8], such as  
45 corals and their endosymbionts. Finally, tropical coastal ecosystems are typically more tightly  
46 connected to the associated human societies that are dependent on their ecosystem services, and  
47 so these coupled human-natural systems are often more vulnerable to human impacts [11]. For  
48 example, coastal communities in the tropics are disproportionately dependent on healthy  
49 ecosystems needed for fisheries provisions [12], but pollution that fuels deoxygenation via  
50 nutrients and organic matter is often less regulated in the tropics [13].

51

## 52 **Hypoxia as a Natural Feature of Tropical Ecosystems**

53 There are three main drivers of oxygen depletion in coral reefs, mangrove forests, and seagrass  
54 meadows that make them naturally subject to hypoxia at a variety of scales. First, they engineer  
55 landscape-scale biogenic features such as seagrass pools [14], mangrove ponds and channels [15,  
56 16], and coral lagoons and flats [17]. These biogenic features reduce oxygen replenishment by  
57 increasing stratification and reducing flushing rates, and these effects may be exacerbated by

58 tides, seasonal cycles, or climate anomalies (Figure 1). Second, the impounded basins and  
59 complex habitats formed by mangroves, corals, and seagrass habitats are natural traps for organic  
60 matter (e.g., detritus and drift algae), and are themselves sources of copious organic matter, such  
61 as mangrove leaves, seagrass blades, and coral spawn [18], which fuel decompositional  
62 processes that deplete oxygen. Third, respiratory oxygen consumption by seagrass, corals, and  
63 epiphytic algae associated with mangroves at night or in other light-limited conditions,  
64 multiplied by their high biomass, can lead to rapid drawdown of dissolved oxygen in the  
65 surrounding water column (Figure 1). This respiratory drawdown of oxygen from the water  
66 column can be enhanced by the slowing of water flow and dampening of waves by seagrass  
67 canopies, coral reefs, and thickets of mangrove stems and roots [19-21]. This regular depletion is  
68 evident in diel cycling of oxygen concentrations, and offers unique insights into the potential  
69 adaptive responses of resident organisms to dynamic oxygen regimes and their broader  
70 ecological effects (Box 1).

71

72 Anthropogenic deoxygenation is likely to mimic the natural hypoxia regimes of tropical  
73 ecosystems. Based on a synthesis of hypoxia observations in temperate coastal ecosystems,  
74 Rabalais et al. [22] concluded that human influence on oxygen regimes is most apparent at time  
75 scales of hours to weeks and in smaller, semi-enclosed systems such as estuaries, bays, and the  
76 inner shelf. These are the same temporal and spatial scales over which tropical marine  
77 ecosystems are exposed to naturally hypoxic conditions.

78

79 **Natural Mechanisms of Resistance to Hypoxia**

80 Corals, mangroves, and seagrasses all possess physiological and structural mechanisms that  
81 mediate their oxygen environment and can counteract hypoxia (Figure 1). Mangroves have  
82 conspicuous prop roots and pneumatophores that supply atmospheric oxygen to their below-  
83 ground roots and rhizosphere [23]. Similarly, seagrasses transport oxygen from their blades  
84 down to the rhizosphere, creating favorable biogeochemical conditions for nutrient exchange and  
85 root health and release excess photosynthetic oxygen into the canopy [24, 25]. Corals capitalize  
86 on oxygen produced by their endosymbiotic algae to maintain elevated oxygen concentrations  
87 within their tissues and surrounding water [26]. The photosynthetic production of oxygen by  
88 these tropical foundation species, combined with mechanisms that can continue at night  
89 including their ability to utilize oxygen stored in their tissues [27], create oxygenated  
90 microhabitats [25, 26], absorb atmospheric oxygen [23], and/or redistribute oxygen internally  
91 counter to external oxygen gradients [24, 28], provide the potential for “self-rescue” not seen in  
92 the bivalve reefs or infauna-dominated soft-sediments that have been the focus of temperate  
93 hypoxia research.

94  
95 The hypoxia tolerances of marine organisms associated with tropical foundation species are not  
96 well established [7], but evidence points towards widespread adaptation to hypoxia across  
97 taxonomic groups and habitat types. For example, fish from numerous families exhibit high  
98 tolerances to hypoxia in both coral reef [29] and mangrove habitats [30], whereas other fish  
99 overcome low concentrations of dissolved oxygen through surface air gulping [31] or by  
100 crawling out of water to breathe air [32]. Ctenophores and cnidarians thrive in hypoxic mangrove  
101 ponds just as they do in seasonally hypoxic temperate estuaries [15], and lucinid clams reach  
102 their highest abundances in the sulfide-rich, hypoxic sediments of seagrass beds [33]. Other

103 species exhibit phenotypic plasticity in response to hypoxia, such as reef-dwelling fireworms that  
104 can increase the surface area of their respiratory structures [34]. Despite the handful of studies  
105 documenting hypoxia tolerance in tropical species, basic research is needed to elucidate  
106 mechanisms of tolerance, the physiological basis for interspecific variation, and scope for  
107 acclimation to near-term deoxygenation trends. For example, recent research in mangrove forests  
108 has documented distinct fish and benthic communities in forest interiors where oxygen  
109 concentrations are limiting, suggesting community structure may be influenced by hypoxia [35,  
110 36].

111  
112 The tropics are hyperdiverse, and have long been recognized for the ubiquity of mutualisms [37].  
113 This extends to relationships where oxygen serves as a “universal currency” exchanged between  
114 partners to facilitate their persistence in oxygen limiting environments [8]. For example,  
115 photosynthetic endosymbionts (*Symbiodinium* spp.) produce oxygen that is consumed by their  
116 coral hosts [38]. Corals also form facultative mutualisms with “sleep swimming” fish that  
117 mitigate nighttime oxygen depletion by ventilating their sleeping crevice with fin movement  
118 [39]. Seagrasses can tolerate stressful conditions with the aid of lucinid clams. Seagrasses  
119 oxygenate the rhizosphere in exchange for metabolism of toxic sulfides by lucinids, a  
120 relationship that is particularly important in the warmer tropics [33]. Mangroves likewise provide  
121 oxygen to infauna in sediments around pneumatophores, which is important for microbial  
122 biogeochemical cycling [40], and crab burrowing alleviates hypoxic stress in sediments by  
123 enhancing aeration and tidal flushing [41]. These mutualistic interactions are as important for  
124 tolerating deoxygenation at the community level as the physiological mechanisms are at the  
125 organismal level. Future research is likely to reveal other mutualisms, particularly between

126 photosynthetic and non-photosynthetic organisms, and relationships involving the oxygenation  
127 of microhabitats by burrowing or pumping water.

128

129 Adaptations, including metabolic and behavioral traits, mutualisms, and mechanisms of self-  
130 rescue offer protection against deoxygenation. Although hypoxic conditions have been  
131 commonly measured in mangrove forests and seagrass beds, there have been no mass mortality  
132 events attributed solely to naturally occurring hypoxia. Perhaps surprisingly, corals are proving  
133 remarkably tolerant to low oxygen, with common Caribbean reef species capable of tolerating  
134 near-anoxia for over a week [42]. Even in extreme hypoxic events associated with mass  
135 mortality of some coral species (e.g., *Agaricia lamarcki*), other species persisted (e.g.,  
136 *Stephanocoena intercepta*) [5], resulting in community assemblage shifts rather than complete  
137 loss of corals from the ecosystem. Determining the extent to which these adaptations will  
138 translate to tolerance to anthropogenic deoxygenation should be a research priority.

139

#### 140 **Multiple stressors as the Real Culprit**

141 Are tropical ecosystems immune to the effects of anthropogenic deoxygenation? We suggest the  
142 answer is “no”, because hypoxia typically co-occurs with other stressors that exacerbate its  
143 effects. While some of these stressors co-occur with hypoxia naturally, many are directly  
144 intensified by human activity (e.g., ocean acidification, warming, eutrophication), and so they are  
145 increasingly likely to be encountered at detrimental levels alongside hypoxia. Multiple stressors  
146 commonly have negative synergistic effects from the organismal to ecosystem level [43], and  
147 evidence from temperate and pelagic ecosystems suggests that multiple stressor effects involving

148 hypoxia are a general phenomenon and so likely widespread in tropical coastal habitats as well  
149 [44-46].  
150  
151 A recent global analysis identified deoxygenation as one of three major stressors of marine  
152 systems, along with climate change and ocean acidification, whose causes and consequences are  
153 intertwined and increasing in severity at a global scale [2]. Warmer waters increase the  
154 likelihood of deoxygenation by increasing rates of microbial oxygen consumption, promoting  
155 stratification of the water column, and lowering oxygen solubility [1], while at the same time  
156 increasing metabolic demand for oxygen and vulnerability to hypoxia at the organismal scale  
157 through a variety of physiological mechanisms [46, 47]. Hypoxia and low pH are also likely to  
158 co-occur as the microbial respiration that consumes oxygen produces carbon dioxide [48]. Their  
159 co-occurrence is particularly apparent in the shallow impounded habitats formed by tropical  
160 foundation species, where solar insolation, atmospheric warming, and aerobic respiration can  
161 cause warming, deoxygenation, and acidification that exceed global averages by orders of  
162 magnitude (Box 1). The combined effects of multiple stressors, such as low oxygen and  
163 acidification, can have synergistic negative effects on survivorship of corals [49]. Elevated  
164 temperatures have also been identified as a contributing factor to hypoxic seagrass mass  
165 mortality events [50, 51]. Decreased oxygen availability, in turn, is likely to further narrow the  
166 thermal tolerance range of tropical species that is already constrained relative to temperate  
167 counterparts [52]. Even where temperature and oxygen vary independently of one another  
168 spatially, overall warming could increase a system's vulnerability to hypoxic events, as observed  
169 on Panamanian reefs [5]. Based on these observations, we suggest that cases of apparent heat-



170 driven bleaching and mortality of corals and other tropical habitat formers should be re-  
171 examined to consider whether hypoxia was an undetected cofactor.

172

173 Eutrophication, hydrogen sulfide, and harmful algal blooms (HABs) are three stressors likely to  
174 co-occur with deoxygenation since they each have biogeochemical linkages to oxygen depletion  
175 [22]. Excess nutrients can trigger macroalgae blooms that smother coral reefs, seagrass beds, and  
176 mangrove epifaunal communities. Such overgrowth can create microhabitats with low oxygen  
177 concentrations by blocking sunlight needed for photosynthesis, restricting water exchange, and  
178 fueling microbial respiration [26, 53, 54], and can push a system from diel cycling of oxygen to  
179 persistent hypoxia [55]. As microbial communities shift to anaerobic metabolism, hydrogen  
180 sulfide production can lower hypoxia tolerance in corals [49], reduce seedling growth rates of  
181 some mangrove species [40], and cause mass mortality of seagrass [27, 56]. HABs have been  
182 associated with hypoxia and reef mortality, as well as fish kills in mangrove lagoons, likely due  
183 to the production of excess organic matter, shading, toxicity, and smothering of respiratory  
184 surfaces that occurs during phytoplankton blooms [57-59].

185

186 Additional anthropogenic stressors have the potential to exacerbate the impact of deoxygenation  
187 on tropical habitats. Erosional sediments associated with land-use change can blanket nearshore  
188 environments, deplete oxygen, and increase sulfide levels, leading to bleaching and death in  
189 corals [49] and anoxia in seagrass beds [60, 61]. Sediment inputs can also cause high turbidity  
190 that may disrupt the photosynthetic “self-rescue” mechanism for corals and seagrass. Mangroves  
191 are susceptible to oil spills that reduce both oxygen concentrations in sediments and oxygen  
192 uptake by blocking lenticels [62, 63]. Mangroves can also succumb to the combined effects of

193 nutrient limitation and/or sediment starvation that contribute to increasingly hypoxic conditions  
194 associated with altered hydrology [64], in what is likely their greatest oxygen-mediated threat  
195 that has earned the ominous moniker “mangrove heart attack” [65].

196

197 The research capacity of oxygen monitoring programs in tropical marine habitats trails behind  
198 temperate ecosystems [5], and adding dissolved oxygen to the list of commonly measured  
199 stressors (e.g., temperature and pH) is needed to elucidate the separate and interactive effects of  
200 oxygen limitation on biological communities, document the global extent of hypoxia, and  
201 determine the drivers of oxygen depletion to aid resource management decisions [66]. Snapshot  
202 surveys can detect oxygen gradients across a seascape and identify problematic areas, whereas  
203 continuous monitoring programs are logistically more challenging but allow the detection of  
204 hypoxic events that may be otherwise difficult to predict. Where monitoring resources are  
205 limiting, the choice between the two options will depend on the natural history of the system,  
206 existing logistical support, and reliability of biological indicators.

207

### 208 **Mechanisms of resilience to deoxygenation**

209 Understanding the mechanisms underlying ecological resilience is critical for predicting the  
210 impacts of global change factors, such as deoxygenation, and managing natural systems to  
211 maximize ecological function and ecosystem services [67]. We are still in the early stages of  
212 exploring how hypoxic stress interacts with tropical coastal ecosystems, but we can piece  
213 together a preliminary synthesis of factors determining their resilience from existing empirical  
214 observations. In the following sections, we consider resilience through the stages of community  
215 response to hypoxic events: onset of hypoxia and the disruption of mutualisms, acceleration of

216 deoxygenation through feedbacks, and community recovery following disturbance. Finally, we  
217 consider how these stages that comprise the arc of resilience that are likely to vary by ecosystem  
218 with scale dependence.

219

### 220 **Mutualism disruption and ecological destabilization**

221 When mutualisms and their associated feedbacks are overwhelmed by hypoxia and co-occurring  
222 stressors, tropical ecosystems may destabilize and become vulnerable to state change [68]. For  
223 example, the seagrass and lucinid clam mutualism can break down when seagrass mortality  
224 decreases oxygen translocation and elevates sulfide levels, thus leading to mortality of lucinids  
225 and more seagrass [69]. The coral mutualism between cnidarian host and photosynthetic  
226 endosymbionts is likewise vulnerable to multiple stressors, with widespread coral bleaching  
227 preceding coral mortality during severe hypoxia against a backdrop of elevated temperatures [5].  
228 The mutualism that can occur between mangroves and sponges, in which sponges provide  
229 mangroves with nutrients and protection from isopods [70], may be preempted when sponges are  
230 killed by episodic stressful abiotic conditions [71], such as hypoxia. Given that oxygen is an  
231 indicator of overall ecosystem function in tropical ecosystems [8], excessive respiration and  
232 mass mortality associated with hypoxia are signs of destabilization and transition to a new  
233 equilibrium (Table 1).

234

### 235 **Feedbacks and the acceleration of deoxygenation**

236 New feedbacks can emerge with the onset of hypoxia that accelerate and reinforce ecological  
237 state change. This is evident where seagrass mortality leads to the accumulation of dead leaves  
238 that smothers the substrate and fuels microbial respiration, triggering further oxygen depletion,

239 sulfide production, and additional seagrass death [56]. Likewise, decay of reef organisms that  
240 succumb to hypoxia is thought to exacerbate deoxygenation in coral ecosystems [72] and  
241 mangrove epifaunal communities [73]. Another feedback can occur where large-scale hypoxia  
242 makes reefs more susceptible to disease outbreaks [74], and the disease itself generates micro-  
243 scale hypoxia that accelerates its spread over coral colonies [75]. This cycle plays into the larger  
244 DDAM (Dissolved organic carbon, Disease, fleshy Algae and Microbes) feedback model [76]  
245 that was expanded to consider how hypoxia not only perpetuates the cycle, but can also trigger it  
246 [8]. Humans can also play a direct role in hypoxia feedback loops, such as when aquaculture  
247 ponds in cleared mangroves become degraded by hypoxia, triggering disease outbreaks, forcing  
248 abandonment and subsequent clearing of additional ponds [77, 78]. Hypoxic conditions in  
249 coastal habitats are likely to abate when feedbacks are broken, either by the depletion of organic  
250 matter that fuels microbial respiration, or by reoxygenation through changed oceanographic  
251 conditions (e.g., wave mixing, tidal flushing) [22].

252

### 253 **Recovery potential and the scale-dependence of resilience**

254 The ability to revert to the previous ecosystem state once hypoxia subsides is likely to vary  
255 among tropical foundation species for several reasons (Table 1). First, they differ in the amount  
256 physical structure remaining after mortality that has the potential to promote recovery. Living  
257 mangroves and their associated structure will likely persist through hypoxic events, and when  
258 corals die, their skeletons function as habitat for recolonization [79]. Seagrass that suffers  
259 mortality, however, is rapidly degraded or swept away [50]. Second, recovery of tropical  
260 ecosystems is dependent on recolonization and/or regrowth of survivors. Corals that survive  
261 hypoxia can serve as the basis for gradual colonial regrowth, whereas seagrass seeds that survive

262 hypoxic seagrass die-offs can generate rapid recolonization, accelerated by vegetative expansion  
263 [51, 80]. Given that hypoxia is most likely to occur in stagnant areas, local connectivity to source  
264 populations in adjacent habitats may foster recovery more than larval resupply from distant  
265 sources by ocean currents [81]. Third, community-level interactions will play important roles  
266 that differ by habitat, such as on coral reefs where grazers keep dead coral substrate free of algae  
267 and available for coral recruitment following hypoxia [82], or in seagrass beds where facilitative  
268 successional interactions of rhizophytic algae modify sediments to promote seagrass regrowth  
269 [83, 84]. Due to the general lack of long-term datasets incorporating dissolved oxygen  
270 observations, there is uncertainty as to how these various mechanisms of natural resilience and  
271 recovery potential of tropical ecosystems will meet the challenges of the increasing frequency,  
272 size, and intensity of hypoxia events occurring with anthropogenic deoxygenation [6].

273

274 However, there is accumulating evidence that illustrates how feedback processes and  
275 mechanisms of recovery can play out as a function of spatial and temporal scale, particularly  
276 when considering instances where the ecosystem recovery timeline can exceed the return time of  
277 conditions that trigger hypoxic events [42]. This has important implications for the recurrence of  
278 hypoxia in systems where the biomass of habitat dominants themselves drive oxygen depletion,  
279 such as with seagrass where die-offs have been attributed to high biomass which increases  
280 metabolic demand for oxygen [50, 56] and further exacerbates oxygen depletion by slowing  
281 water flow [20]. The recovery time for seagrass populations to reestablish high biomass could  
282 limit when hypoxia is likely to recur, even if other contributing factors that would otherwise  
283 trigger establishment of hypoxia are in place, in a negative feedback loop. On the other hand,  
284 mutualisms that normally ameliorate low-oxygen conditions could break down and remain

285 impaired for years following extreme events, as observed when drought diminished oxygenation  
286 of sediments by seagrass which led to loss of lucinid clams and their potential to ameliorate  
287 sulfide stress [69]. Such systems where a key mutualist has been functionally lost are predicted  
288 to be less resilient [85], and represent a positive feedback that could leave a system more  
289 vulnerable to subsequent hypoxic stress.

290

291 Positive and negative feedbacks are not mutually exclusive and may contribute to variable  
292 system dynamics by operating at different scales, resulting in spatially patchy mortality and  
293 multi-year intervals between die-off events, consistent with seagrass dynamics in Florida Bay,  
294 USA [50]. Other systems, such as coral reefs, offer a contrast because hypoxia can develop  
295 independently of the living biomass of biogenic habitats, and recovery periods can extend over  
296 decades rather than years. Under such circumstances, communities may not have the chance to  
297 recover to historic compositions due to the increasing frequency of deoxygenation events, and  
298 may shift towards more tolerant species [5, 42]. Additional research is needed to fill gaps in our  
299 understanding of how disturbance, feedbacks, and mutualisms interact to determine whether the  
300 trend of increasingly frequent hypoxic events is likely to drive a system toward cycles of  
301 disturbance and recovery or, rather, toward novel ecosystem states.

302

### 303 **Concluding remarks**

304 We emphasize the importance of incorporating hypoxia in tropical ecosystems into our global  
305 understanding of ocean deoxygenation because these systems offer general lessons about  
306 ecological responses and resilience. We suggest many tropical taxa have developed tolerances in  
307 response to naturally occurring hypoxia, and that the most severe impacts associated with

308 hypoxia stem from interactions with co-stressors. These impacts follow the breakdown of  
309 mutualisms and shifts in feedbacks that push systems past thresholds and reinforce ecosystem  
310 state changes. Mass die-offs in tropical ecosystems signal extreme conditions and ecosystem  
311 dysfunction, and their rarity to date is indicative of the natural resistance of these systems to  
312 deoxygenation. However, the increasing occurrence of hypoxic events globally and re-  
313 occurrence in some tropical systems is worrisome, particularly given long recovery times [42,  
314 50]. Hypoxia is both a cause and consequence of other interacting marine stressors (e.g.,  
315 warming, acidification, eutrophication), and oxygen is the basis for mutualisms and feedbacks  
316 that underpin the resilience of these ecosystems. The vital importance of mutualisms to hypoxia  
317 resilience and recovery presents rich areas for future research which are likely to provide  
318 addition insights for not only tropical, but also temperate ecosystems (see Outstanding  
319 Questions). We advocate that monitoring programs in the tropics include dissolved oxygen, and  
320 that research on the effects of tropical ocean deoxygenation build on the foundation of  
321 organismal studies to include community- and ecosystem-level perspectives across ecosystem  
322 types.

323

#### 324 **Acknowledgements**

325 This paper is the result of work funded by the National Oceanic and Atmospheric  
326 Administration's National Centers for Coastal Ocean Science Competitive Research Program  
327 under award NA18NOS4780170 to AHA and MDJ through the University of Florida. This is  
328 CHRP Contribution XXX. This material is also based upon work supported by the National  
329 Science Foundation Graduate Research Fellowship Program to SDS under Grant No. DGE-  
330 1842473, and a Postdoctoral Scholarship at Woods Hole Oceanographic Institution to MDJ. Any

331 opinions, findings, and conclusions or recommendations expressed in this material are those of  
332 the author(s) and do not necessarily reflect the views of the National Science Foundation.

333

#### 334 **References**

335 1. Altieri, A.H. and Gedan, K.B. (2015) Climate change and dead zones. *Glob. Change Biol.* 21,  
336 1395-1406.

337 2. Breitburg, D. *et al.* (2018) Declining oxygen in global ocean and coastal waters. *Science* 359,  
338 eaam7240.

339 3. Diaz, R.J. and Rosenberg, R. (2008) Spreading dead zones and consequences for marine  
340 ecosystems. *Science* 321, 926-929.

341 4. Laffoley, D. and Baxter, J.M., eds. (2019) Ocean deoxygenation: Everyone's problem -  
342 Causes, impacts, consequences and solutions. Full Report., IUCN.

343 5. Altieri, A.H. *et al.* (2017) Tropical dead zones and mass mortalities on coral reefs. *Proc. Natl*  
344 *Acad. Sci. USA* 114, 3660-3665.

345 6. Altieri, A.H. *et al.* (2019) Tropical ecosystems - corals, seagrasses, and mangroves. In Ocean  
346 deoxygenation: Everyone's problem - Causes, impacts, consequences, and solutions. (Laffoley,  
347 D. and Baxter, J.M. eds), pp. 401-429, IUCN.

348 7. Vaquer-Sunyer, R. and Duarte, C.M. (2008) Thresholds of hypoxia for marine biodiversity.  
349 *Proc. Natl Acad. Sci. USA* 105, 15452-15457.

350 8. Nelson, H.R. and Altieri, A.H. (2019) Oxygen: the universal currency on coral reefs. *Coral*  
351 *Reefs* 38, 177-198.

352 9. Hughes, D.J. *et al.* (2020) Coral reef survival under accelerating ocean deoxygenation. *Nat.*  
353 *Clim. Chang.* 10, 296-307.



- 354 10. Sutherland, W.J. *et al.* (in press) A 2021 horizon scan of emerging global biological  
355 conservation issues. *Trends Ecol. Evol.* 36.
- 356 11. Costanza, R. *et al.* (2014) Changes in the global value of ecosystem services. *Glob. Environ.*  
357 *Change* 26, 152-158.
- 358 12. Golden, C. *et al.* (2016) Fall in fish catch threatens human health. *Nature* 534, 317-320.
- 359 13. Lu, C.Q. and Tian, H.Q. (2017) Global nitrogen and phosphorus fertilizer use for agriculture  
360 production in the past half century: shifted hot spots and nutrient imbalance. *Earth Syst. Sci.*  
361 *Data* 9, 181-192.
- 362 14. van der Laan, B. and Wolff, W.J. (2006) Circular pools in the seagrass beds of the Banc  
363 d'Arguin, Mauritania, and their possible origin. *Aquat. Bot.* 84, 93-100.
- 364 15. Gedan, K.B. *et al.* (2017) Community composition in mangrove ponds with pulsed hypoxic  
365 and acidified conditions. *Ecosphere* 8, e02053.
- 366 16. Camp, E.F. *et al.* (2017) Reef-building corals thrive within hot-acidified and deoxygenated  
367 waters. *Sci. Rep.* 7, 2434.
- 368 17. Andrefouet, S. *et al.* (2015) Mass mortality events in atoll lagoons: environmental control  
369 and increased future vulnerability. *Glob. Change Biol.* 21, 195-205.
- 370 18. Gillis, L.G. *et al.* (2014) Potential for landscape-scale positive interactions among tropical  
371 marine ecosystems. *Mar. Ecol. Prog. Ser.* 503, 289-303.
- 372 19. Chamberlain, J.A. and Graus, R.R. (1975) Water-flow and hydromechanical adaptation of  
373 branched reef corals. *Bull. Mar. Sci.* 25, 112-125.
- 374 20. Koch, E.W. and Gust, G. (1999) Water flow in tide- and wave-dominated beds of the  
375 seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* 184, 63-72.

- 376 21. Peters, R. *et al.* (2020) The interplay between vegetation and water in mangroves: new  
377 perspectives for mangrove stand modelling and ecological research. *Wetl. Ecol. Manag.* 28, 697-  
378 712.
- 379 22. Rabalais, N.N. *et al.* (2010) Dynamics and distribution of natural and human-caused hypoxia.  
380 *Biogeosciences* 7, 585-619.
- 381 23. Pi, N. *et al.* (2009) Root anatomy and spatial pattern of radial oxygen loss of eight true  
382 mangrove species. *Aquat. Bot.* 90, 222-230.
- 383 24. Borum, J. *et al.* (2007) Oxygen movement in seagrasses. In *Seagrasses: biology, ecology and*  
384 *conservation* (Larkum, A.W.D. *et al.* eds), pp. 255-270, Springer.
- 385 25. Long, M.H. *et al.* (2020) Ebullition of oxygen from seagrasses under supersaturated  
386 conditions. *Limnol. Oceanogr.* 65, 314-324.
- 387 26. Haas, A.F. *et al.* (2013) Visualization of oxygen distribution patterns caused by coral and  
388 algae. *PeerJ* 1, e106.
- 389 27. Borum, J. *et al.* (2005) The potential role of plant oxygen and sulphide dynamics in die-off  
390 events of the tropical seagrass, *Thalassia testudinum*. *J. Ecol.* 93, 148-158.
- 391 28. Curran, M. (1985) Gas movements in the roots of *Avicennia marina* (Forsk.) Vierh. *Aust. J.*  
392 *Plant Physiol.* 12, 97-108.
- 393 29. Nilsson, G.E. and Ostlund-Nilsson, S. (2004) Hypoxia in paradise: widespread hypoxia  
394 tolerance in coral reef fishes. *Proc. Royal Soc. B* 271, S30-S33.
- 395 30. Dubuc, A. *et al.* (2019) Hypoxia in mangroves: occurrence and impact on valuable tropical  
396 fish habitat. *Biogeosciences* 16, 3959-3976.
- 397 31. Kramer, D.L. (1983) The evolutionary ecology of respiratory mode in fishes: an analysis  
398 based on the costs of breathing. *Environ. Biol. Fishes* 9, 145-158.

- 399 32. Turko, A.J. and Wright, P.A. (2015) Evolution, ecology and physiology of amphibious  
400 killifishes (Cyprinodontiformes). *J. Fish Biol.* 87, 815-835.
- 401 33. van der Heide, T. *et al.* (2012) A three-stage symbiosis forms the foundation of seagrass  
402 ecosystems. *Science* 336, 1432-1434.
- 403 34. Lucey, N.M. *et al.* (2020) Oxygen-mediated plasticity confers hypoxia tolerance in a  
404 corallivorous polychaete. *Ecol. Evol.* 10, 1145-1157.
- 405 35. Mattone, C. and Sheaves, M. (2017) Patterns, drivers and implications of dissolved oxygen  
406 dynamics in tropical mangrove forests. *Estuar. Coast. Shelf Sci.* 197, 205-213.
- 407 36. Sheaves, M. *et al.* (2016) Biotic hotspots in mangrove-dominated estuaries: macro-  
408 invertebrate aggregation in unvegetated lower intertidal flats. *Mar. Ecol. Prog. Ser.* 556, 31-43.
- 409 37. Schemske, D.W. *et al.* (2009) Is there a latitudinal gradient in the importance of biotic  
410 interactions? *Annu. Rev. Ecol. Evol. Syst.* 40, 245-269.
- 411 38. Al-Horani, F.A. *et al.* (2003) The mechanism of calcification and its relation to  
412 photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Mar. Biol.* 142,  
413 419-426.
- 414 39. Goldshmid, R. *et al.* (2004) Aeration of corals by sleep-swimming fish. *Limnol. Oceanogr.*  
415 49, 1832-1839.
- 416 40. McKee, K.L. (1993) Soil physicochemical patterns and mangrove species distribution:  
417 reciprocal effects. *J. Ecol.* 81, 477-487.
- 418 41. Kristensen, E. (2008) Mangrove crabs as ecosystem engineers; with emphasis on sediment  
419 processes. *J. Sea Res.* 59, 30-43.
- 420 42. Johnson, M.D. *et al.* (in review) Catastrophic cascading effects of deoxygenation on coral  
421 reef communities.

- 422 43. Crain, C.M. *et al.* (2008) Interactive and cumulative effects of multiple human stressors in  
423 marine systems. *Ecol. Lett.* 11, 1304-1315.
- 424 44. Rosa, R. and Seibel, B.A. (2008) Synergistic effects of climate-related variables suggest  
425 future physiological impairment in a top oceanic predator. *Proc. Natl Acad. Sci. USA* 105,  
426 20776-20780.
- 427 45. Gunderson, A.R. *et al.* (2016) Multiple Stressors in a changing world: the need for an  
428 improved perspective on physiological responses to the dynamic marine environment. In Annual  
429 Review of Marine Science, Vol 8 (Carlson, C.A. and Giovannoni, S.J. eds), pp. 357-378.
- 430 46. Vaquer-Sunyer, R. and Duarte, C.M. (2011) Temperature effects on oxygen thresholds for  
431 hypoxia in marine benthic organisms. *Glob. Change Biol.* 17, 1788-1797.
- 432 47. Portner, H.O. (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for  
433 integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213, 881-893.
- 434 48. Wallace, R.B. *et al.* (2014) Coastal ocean acidification: The other eutrophication problem.  
435 *Estuar. Coast. Shelf Sci.* 148, 1-13.
- 436 49. Weber, M. *et al.* (2012) Mechanisms of damage to corals exposed to sedimentation. *Proc.*  
437 *Natl Acad. Sci. USA* 109, E1558-E1567.
- 438 50. Hall, M.O. *et al.* (2016) Recurrence of *Thalassia testudinum* seagrass die-off in Florida Bay,  
439 USA: initial observations. *Mar. Ecol. Prog. Ser.* 560, 243-249.
- 440 51. Plus, M. *et al.* (2003) Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced  
441 full mortality. *Aquat. Bot.* 77, 121-134.
- 442 52. Payne, N.L. and Smith, J.A. (2017) An alternative explanation for global trends in thermal  
443 tolerance. *Ecol. Lett.* 20, 70-77.

- 444 53. Smith, J.E. *et al.* (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced  
445 coral mortality. *Ecol. Lett.* 9, 835-845.
- 446 54. McGlathery, K.J. (2001) Macroalgal blooms contribute to the decline of seagrass in nutrient-  
447 enriched coastal waters. *J. Phycol.* 37, 453-456.
- 448 55. van Tussenbroek, B.I. *et al.* (2017) Severe impacts of brown tides caused by *Sargassum* spp.  
449 on near-shore Caribbean seagrass communities. *Mar. Pollut. Bull.* 122, 272-281.
- 450 56. Koch, M.S. *et al.* (2007) Conceptual model of seagrass die-off in Florida Bay: Links to  
451 biogeochemical processes. *J. Exp. Mar. Biol. Ecol.* 350, 73-88.
- 452 57. Guzman, H.M. *et al.* (1990) Coral mortality associated with dinoflagellate blooms in the  
453 Easter Pacific (Coast Rica and Panama). *Mar. Ecol. Prog. Ser.* 60, 299-303.
- 454 58. Dupont, J.M. *et al.* (2010) Ecological impacts of the 2005 red tide on artificial reef  
455 epibenthic macroinvertebrate and fish communities in the eastern Gulf of Mexico. *Mar. Ecol.*  
456 *Prog. Ser.* 415, 189-200.
- 457 59. Mancera, J.E.P. and Vidal V., L.A. (1994) Florecimiento de microalgas relacionado con  
458 mortandad masiva de peces en el complejo lagunar Cienaga Grande de Santa Maria, Caribe  
459 Colombiano. *Bol. Invest. Mar. Cost.* 23, 103-117.
- 460 60. Brodersen, K.E. *et al.* (2017) Sediment Resuspension and Deposition on Seagrass Leaves  
461 Impedes Internal Plant Aeration and Promotes Phytotoxic H<sub>2</sub>S Intrusion. *Front. Plant Sci.* 8.
- 462 61. Folmer, E.O. *et al.* (2012) Seagrass-sediment feedback: an exploration using a non-recursive  
463 structural equation model. *Ecosystems* 15, 1380-1393.
- 464 62. Dicks, B. (1986) Oil and the black mangrove, *Avicena marina* in the Northern Red Sea. *Mar.*  
465 *Pollut. Bull.* 17, 500-503.

- 466 63. Suprayogi, B. and Murray, F. (1999) A field experiment of the physical and chemical effects  
467 of two oils on mangroves. *Environ. Exp. Bot.* 42, 221-229.
- 468 64. Krauss, K.W. *et al.* (2018) Ghost forests of Marco Island: Mangrove mortality driven by  
469 belowground soil structural shifts during tidal hydrologic alteration. *Estuar. Coast. Shelf Sci.*  
470 212, 51-62.
- 471 65. Lewis, R.R. *et al.* (2016) Stress in mangrove forests: Early detection and preemptive  
472 rehabilitation are essential for future successful worldwide mangrove forest management. *Mar.*  
473 *Pollut. Bull.* 109, 764-771.
- 474 66. Levin, L.A. and Breitburg, D.L. (2015) Linking coasts and seas to address ocean  
475 deoxygenation. *Nat. Clim. Chang.* 5, 401-403.
- 476 67. Thrush, S.F. *et al.* (2009) Forecasting the limits of resilience: integrating empirical research  
477 with theory. *Proc. Royal Soc. B* 276, 3209-3217.
- 478 68. Kiers, E.T. *et al.* (2010) Mutualisms in a changing world: An evolutionary perspective. *Ecol.*  
479 *Lett.* 13, 1459-1474.
- 480 69. de Fouw, J. *et al.* (2016) Drought, mutualism breakdown, and landscape-scale degradation of  
481 seagrass beds. *Curr. Biol.* 26, 1051-1056.
- 482 70. Ellison, A.M. and Farnsworth, E.J. (2001) Mangrove communities. In *Marine Community*  
483 *Ecology* (Bertness, M.D. *et al.* eds), pp. 423-442, Sinauer Associates.
- 484 71. Wulff, J. (2012) Ecological interaction and the distribution, abundance, and diversity of  
485 sponges. In *Advances in Sponge Science: Phylogeny, Systematics, Ecology* (Becerro, M.A. *et al.*  
486 eds), pp. 273-344.
- 487 72. Simpson, C.J. *et al.* (1993) Destruction of corals and other reef animals by coral spawn slicks  
488 on Ningaloo Reef, Western Australia. *Coral Reefs* 12, 185-191.

- 489 73. Goodbody, I. (1961) Mass mortality of a marine fauna following tropical rains. *Ecology* 42,  
490 150-155.
- 491 74. Onton, K. *et al.* (2011) Distribution and drivers of coral disease at Ningaloo reef, Indian  
492 Ocean. *Mar. Ecol. Prog. Ser.* 433, 75-84.
- 493 75. Glas, M.S. *et al.* (2012) Biogeochemical conditions determine virulence of black band  
494 disease in corals. *ISME Journal* 6, 1526-1534.
- 495 76. Dinsdale, E.A. and Rohwer, F. (2011) Fish or germs? Microbial dynamics associated with  
496 changing trophic structure on coral reefs. In *Coral Reefs: An Ecosystem in Transition* (Dubinsky,  
497 Z. and Stambler, N. eds), pp. 231-240, Springer.
- 498 77. McLeod, E. and Salm, R.V., *Managing mangroves for resilience to climate change*, Gland,  
499 Switzerland, 2006, p. 64.
- 500 78. Kautsky, N. *et al.* (2000) Ecosystem perspectives on management of disease in shrimp pond  
501 farming. *Aquaculture* 191, 145-161.
- 502 79. Nelson, H.R. *et al.* (2016) The resilience of reef invertebrate biodiversity to coral mortality.  
503 *Ecosphere* 7, e1399.
- 504 80. Greve, T.M. *et al.* (2005) Means of rapid eelgrass (*Zostera marina* L.) recolonisation in  
505 former dieback areas. *Aquat. Bot.* 82, 143-156.
- 506 81. Seemann, J. *et al.* (2018) The importance of sponges and mangroves in supporting fish  
507 communities on degraded coral reefs in Caribbean Panama. *Peerj* 6, e4455.
- 508 82. Kuempel, C.D. and Altieri, A.H. (2017) The emergent role of small-bodied herbivores in pre-  
509 empting phase shifts on degraded coral reefs. *Sci. Rep.* 7, 39670.
- 510 83. Thayer, G.W. *et al.* (1994) Responses of plant-communities in western Florida Bay to the  
511 die-off of seagrasses. *Bull. Mar. Sci.* 54, 718-726.

- 512 84. Williams, S.L. (1990) Experimental studies of Caribbean seagrass bed development. *Ecol.*  
513 *Monogr.* 60, 449-469.
- 514 85. Stone, L. (2020) The stability of mutualism. *Nat. Commun.* 11, 2648.
- 515 86. Rivest, E.B. *et al.* (2017) The role of natural variability in shaping the response of coral reef  
516 organisms to climate change. *Curr. Clim. Change Rep.* 3, 271-281.
- 517 87. Price, N.N. *et al.* (2012) Diel variability in seawater pH relates to calcification and benthic  
518 community structure on coral reefs. *Plos One* 7, e43843.
- 519 88. Camp, E.F. *et al.* (2016) Mangrove and seagrass beds provide different biogeochemical  
520 services for corals threatened by climate change. *Front. Mar. Sci.* 3, 52.
- 521 89. Boyd, P.W. *et al.* (2016) Biological responses to environmental heterogeneity under future  
522 ocean conditions. *Glob. Chang. Biol.* 22, 2633-2650.
- 523 90. Camp, E.F. *et al.* (2018) The future of coral reefs subject to rapid climate change: Lessons  
524 from natural extreme environments. *Front. Mar. Sci.* 5, 4.
- 525 91. Baumann, H. *et al.* (2015) Large natural pH, CO<sub>2</sub> and O<sub>2</sub> fluctuations in a temperate tidal  
526 salt marsh on diel, seasonal, and interannual time scale. *Estuaries Coasts* 38, 220-231.
- 527 92. Hofmann, G.E. *et al.* (2011) High-Frequency Dynamics of Ocean pH: A Multi-Ecosystem  
528 Comparison. *Plos One* 6, e28983.
- 529 93. Schoepf, V. *et al.* (2015) Limits to the thermal tolerance of corals adapted to a highly  
530 fluctuating, naturally extreme temperature environment. *Sci. Rep.* 5, 17639.
- 531 94. Oliver, T.A. and Palumbi, S.R. (2011) Do fluctuating temperature environments elevate coral  
532 thermal tolerance? *Coral Reefs* 30, 429-440.
- 533 95. Palumbi, S.R. *et al.* (2014) Mechanisms of reef coral resistance to future climate change.  
534 *Science* 344, 895-898.



- 535 96. Safaie, A. *et al.* (2018) High frequency temperature variability reduces the risk of coral  
536 bleaching. *Nat. Commun.* 9, 1671.
- 537 97. Comeau, S. *et al.* (2014) Diel pCO<sub>2</sub> oscillations modulate the response of the coral  
538 *Acropora hyacinthus* to ocean acidification. *Mar. Ecol. Prog. Ser.* 501, 99-111.
- 539 98. Camp, E.F. *et al.* (2016) Acclimatization to high-variance habitats does not enhance  
540 physiological tolerance of two key Caribbean corals to future temperature and pH. *Proc. Royal*  
541 *Soc. B* 283, 20160442.
- 542 99. Johnson, M.D. *et al.* (2014) Acclimatization of the crustose coralline alga *Porolithon*  
543 *onkodes* to variable pCO<sub>2</sub>. *Plos One* 9, e87678.
- 544 100. Johnson, M.D. *et al.* (2019) pH variability exacerbates effects of ocean acidification on a  
545 Caribbean crustose coralline alga. *Front. Mar. Sci.* 6, 150.
- 546 101. Cornwall, C.E. *et al.* (2018) Resistance of corals and coralline algae to ocean acidification:  
547 physiological control of calcification under natural pH variability. *Proc Royal Soc B* 285,  
548 20181168.
- 549 102. Rossi, G.S. *et al.* (2020) Fluctuating environments during early development can limit adult  
550 phenotypic flexibility: insights from an amphibious fish. *J. Exp. Biol.* 223 (16).
- 551 103. Long, M.H. *et al.* (2019) Closing the oxygen mass balance in shallow coastal ecosystems.  
552 *Limnol. Oceanogr.* 64, 2694-2708.
- 553 104. Hendriks, I.E. *et al.* (2014) Photosynthetic activity buffers ocean acidification in seagrass  
554 meadows. *Biogeosciences* 11, 333-346.
- 555 105. Cyronak, T. *et al.* (2018) Short-term spatial and temporal carbonate chemistry variability in  
556 two contrasting seagrass meadows: implications for pH buffering capacities. *Estuaries Coasts*  
557 41, 1282-1296.

558 106. Rosentreter, J.A. *et al.* (2018) Seasonal and temporal CO<sub>2</sub> dynamics in three tropical  
559 mangrove creeks - A revision of global mangrove CO<sub>2</sub> emissions. *Geochim. Cosmochim. Acta*  
560 222, 729-745.

561 107. Takeshita, Y. *et al.* (2018) Coral reef carbonate chemistry variability at different functional  
562 scales. *Front. Mar. Sci.* 5, 175.

563 108. Takeshita, Y. *et al.* (2016) Assessment of net community production and calcification of a  
564 coral reef using a boundary layer approach. *J. Geophys. Res.* 121, 5655-5671.

565 109. Van Dam, B.R. *et al.* (2019) Net heterotrophy and carbonate dissolution in two subtropical  
566 seagrass meadows. *Biogeosciences* 16, 4411-4428.

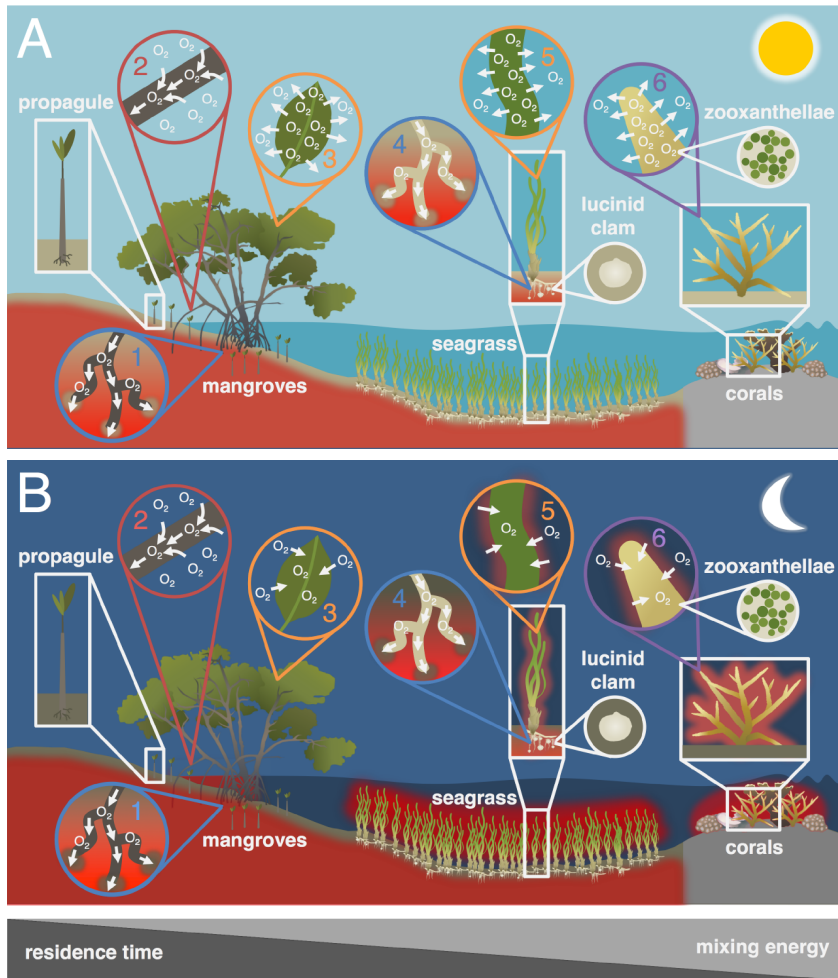
567 110. Calhoun, S.K. *et al.* (2020) Evidence for a biological source of widespread, reproducible  
568 nighttime oxygen spikes in tropical reef ecosystems has implications for coral health. bioRxiv  
569 <https://doi.org/10.1101/2020.03.08.982645>

570 111. Koopmans, D. *et al.* (2018) The response of seagrass (*Posidonia oceanica*) meadow  
571 metabolism to CO<sub>2</sub>-levels and hydrodynamic exchange determined with aquatic eddy  
572 covariance. *Biogeosciences Discuss.* 1-23.

573

574 **Figure 1: Interactions of Mangroves, Seagrasses, and Corals with Oxygen Across the**  
575 **Coastal Tropical Seascape.**

576 (A) During the day, under high light conditions, the photosynthetic production of oxygen  
577 exceeds respiratory demand, as mangroves, seagrasses, and corals act as net producers of  
578 oxygen, which can alleviate hypoxic conditions (indicated in red) in tissues and the surrounding  
579 environment. Both mangroves and seagrasses can translocate oxygen to roots and into the  
580 rhizosphere, and mangroves have specialized structures, such as prop roots of red mangroves (A-  
581 2), that possess numerous tiny pores (lenticels) to uptake air for transport to belowground areas  
582 (A-1). (B) At night, respiration continues but photosynthesis ceases, so mangroves (B-2,3),  
583 seagrasses (B-5), and corals (B-6) must draw oxygen from their environment, which can locally  
584 deplete oxygen. Mangroves (B-1) continue to supply oxygen to their roots and rhizosphere  
585 during darkness, and seagrass does as well (B-4) so long as there is a sufficient supply of oxygen  
586 in the water column. Mutualisms between seagrass and lucinid clams, and between cnidarian  
587 host and zooxanthellae of corals, as well as facilitation of propagules by established mangrove  
588 tress, play an important role in alleviating oxygen limitation and alleviating associated stressors  
589 such as hydrogen sulfide (see Table 1 for details). Mangroves, seagrasses, and coral can also  
590 indirectly mediate oxygen concentrations in adjacent habitat by controlling factors such as water  
591 movement and supply of nutrients and organic matter.



592

593

594 **Table 1. Mechanisms of Resilience to Ocean Deoxygenation in Tropical Ecosystems**

595 The dominant foundation species that define tropical coastal ecosystems vary in their resilience  
596 to hypoxia in the water column due to a combination of physiological mechanisms, feedbacks,  
597 and functional diversity. The result is variation in the potential for initial resistance to hypoxic  
598 conditions, hysteresis in shifts of community state, and overall impact of hypoxia on ecological  
599 function. For example, seagrass is resistant to modest hypoxia due to a self-rescue ability through  
600 photosynthetic oxygen production and mutualisms with lucinid clams, but once a hypoxia  
601 threshold is crossed, the mutualism breaks down and mass mortality occurs due to deoxygenation  
602 feedback and synchronized mortality in low diversity meadows. Coral on the other hand do not  
603 have the same oxygen production capability, and the species diversity of the coral community  
604 will exhibit wider variation in oxygen tolerances, resulting in onset of mortality at less severe  
605 hypoxia and a more graded relationship between oxygen and loss of reef species. Mangroves are  
606 relatively unimpacted by low oxygen conditions because of their high self-rescue potential and  
607 minimal dependence on oxygen-mediated mutualisms.

Ecosystem	Self-rescue ability	Diversity of foundation species	Mutualisms and resilience feedbacks	Deoxygenation feedbacks	Hysteresis potential
(i) Seagrass meadows	<b>Medium</b> Photosynthetic oxygen production with sufficient light.	<b>Low</b> Beds dominated by one or a few species of grass.	Seagrasses provide oxygen, shelter to lucinids and detritus that fuels production of sulfide consumed by lucinids. Lucinid clams oxidize sulfides that are toxic to seagrass.	Seagrass death, organic matter production, hypoxia, sulfide production and intrusion, seagrass death.	
(ii) Coral reefs	<b>Low</b> Photosynthetic oxygen production with sufficient light and with varying susceptibility to bleaching.	<b>High</b> Reefs comprised of diverse stony corals along with sponges and gorgonians.	Corals provide shelter and resources for zooxanthellae and sleep-swimming fish. Zooxanthellae provide oxygen and sleep swimming fish ventilate crevices with oxygenated water.  Coral shelter fish. Fish promote coral by limiting algae.	Bleaching and coral respiration, coral death, organic matter production, sulfide production and hypoxia.  Algal overgrowth and disease, hypoxia, coral death.	
(iii) Mangrove forests	<b>High</b> Uptake and redistribution of atmospheric oxygen to submerged structures.	<b>Low</b> Seaward margin of mangal characterized by monotypic zones.	Sponges provide mangroves with nitrogen and protection against isopods. Mangroves provide sponges with attachment substrate and carbon.  Mature mangroves provide propagules with aerated soils with less sulfides.	Mortality of epibionts, organic matter production, hypoxia.	

608  
609

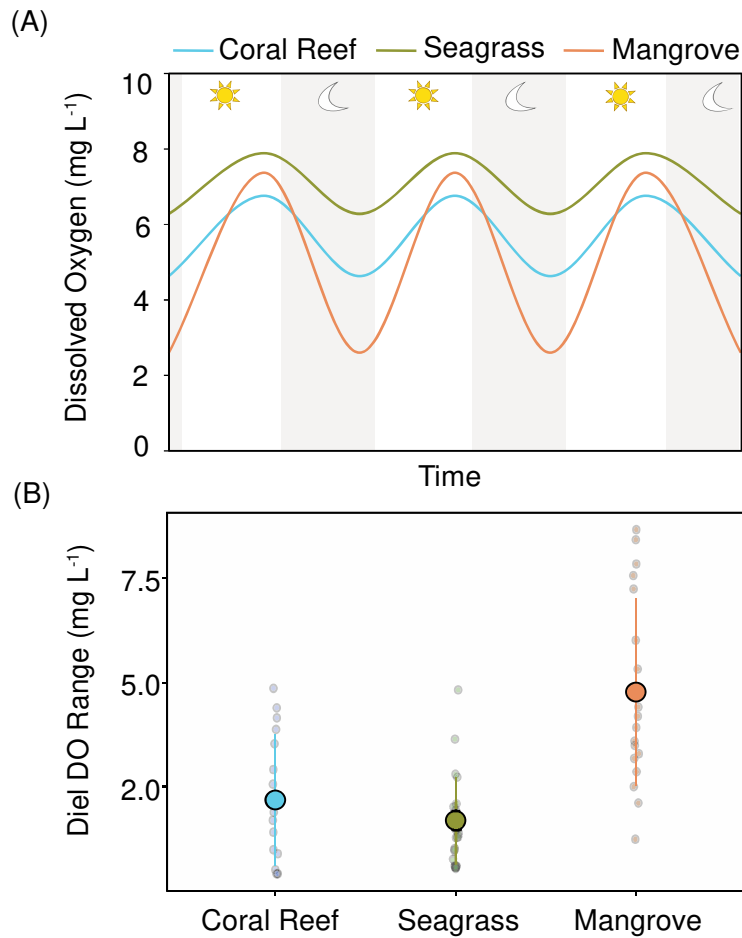
610 **Box 1. The Role of Diel Cycling in Responses to Deoxygenation**

611 Physicochemical properties of seawater can fluctuate over predictable temporal scales. In  
612 tropical coastal habitats, diel cycling of dissolved oxygen (DO), pH, and temperature (Figure  
613 IA), driven by abiotic conditions (e.g., solar radiation) and the metabolism of tropical foundation  
614 species, is one of the clearest examples of this periodicity [86]. Though the capacity to  
615 continuously monitor environmental parameters has greatly improved over the last two decades,  
616 there remain relatively few time series in tropical habitats that incorporate DO, which limits our  
617 understanding of the magnitude of natural DO fluctuations. From a handful of published studies,  
618 the average range in DO concentrations over 24 hours is roughly equivalent across coral reef and  
619 seagrass habitats. That same pattern is amplified in mangroves, where conditions can range from  
620 near-anoxic to hyperoxic in just one day (Figure IB). The magnitude of variability in a given  
621 environmental parameter, including optima and critical values, often differ spatially within the  
622 same habitat type. Fluctuations that exceed projected conditions for the near-future open ocean  
623 occur regularly on shallow coral reefs [34, 87], seagrass meadows [88], and tropical mangrove  
624 ponds [15], and these habitats provide an opportunity to explore the role of contemporary  
625 exposure to environmental variability in mediating organismal tolerances to stress.  
626 Characterizing variability regimes by habitat and location is an essential first step to providing  
627 accurate context to individual organismal tolerances.

628  
629 Exposure to environmental variability can dramatically alter organismal responses to subsequent  
630 stress [89]. Though our limited knowledge of baseline DO variability in the tropics hinders our  
631 ability to understand how variability influences response to deoxygenation, prior work with other  
632 diel cycling stressors (e.g., temperature and pH) provides a clue that such natural variability

633 could mediate organismal responses to sustained hypoxia. Recent studies have documented both  
634 the extent of natural variability in pH and temperature in tropical habitats [86, 90-92] and how  
635 natural thermal and pH variability can either enhance resilience or heighten sensitivity of  
636 resident organisms to near-future ocean conditions (i.e., warming, ocean acidification). For  
637 example, high variability can increase coral thermal tolerance [93, 94] and lower bleaching  
638 susceptibility [95, 96]. In corals, prior exposure to diel pH cycling has limited effects on  
639 responses to sustained pH stress [86, 97, 98], and in some tropical algae exposure to pH  
640 variability can enhance performance [99], increase sensitivity [100], or have no effect during  
641 subsequent exposure to low pH [101]. Analogous studies have yet to explore similar  
642 relationships with oxygen dynamics in tropical foundation species. We hypothesize that naturally  
643 variable oxygen regimes in mangroves, seagrasses, and coral reefs could enhance the resistance  
644 or sensitivity of organismal responses to sustained hypoxic stress, although it is also possible that  
645 response to extreme oxygen conditions could be primarily affected by the actual value of oxygen  
646 concentration relative to established critical values rather than prior exposure to variability as has  
647 been suggested for temperature stress [52]. Recent evidence from fish that inhabit mangroves  
648 suggests that exposure to variable oxygen environments early in life promotes tolerance to  
649 hypoxia as adults [102]. These systems should be utilized and closely studied to understand how  
650 diel cycling may facilitate resilience of key taxa to anthropogenic deoxygenation.





651

652 **Figure I: Dissolved oxygen diel cycling in tropical coastal habitats.**

653 (A) A conceptual framework of diel cycling between average minimum and maximum DO from  
 654 tropical coral reef, seagrass, and mangrove habitats, parameterized using published data. (B) The  
 655 diel range in DO across habitats, with large, solid circles representing the average ( $\pm$  SD) of  
 656 separate diel cycles per habitat, and smaller, light circles showing the raw data points. Data were  
 657 mined from 4 shallow coral reef studies, 4 seagrass studies, and 2 tropical mangrove studies with  
 658 continuous DO data from at least 2 cycles [15, 103-111].

659

660