Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter

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8.8 The significance of ocean deoxygenation for tropical ecosystems – corals, seagrasses and mangroves

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Summary

- Deoxygenation affects tropical coastal ecosystems but is relatively understudied and poorly understood.
- The number of hypoxic ecosystems may be underestimated by an order of magnitude in the tropics due to lack of research capacity.
- Corals, seagrasses and mangroves themselves are vulnerable to hypoxia, and also have the ability to influence oxygen concentrations in the surrounding water, leading to feedbacks that can influence deoxygenation rates.
- Corals, seagrasses, and mangroves provide habitat to diverse communities of organisms that are vulnerable to low concentrations of oxygen.
- The warmer temperatures typical of tropical ecosystems, combined with the dependence of coral reefs on calcification, suggests that a multiple-stressor perspective is needed for predicting the effects of deoxygenation in this region.

Ocean hypoxia effect	Potential consequences
Hypoxia establishes along gradients of connectivity between terrestrial inputs and oceanic flushing.	• Species may segregate or become restricted to a portion of their former range. • Fisheries catches may decline or be displaced.
Low oxygen can trigger biogeochemical changes that exacerbate hypoxia in feedback loops.	• Low oxygen can foster production of toxic sulphides, leading to further death of benthic plants and algae.
Differential tolerances and abilities to acclimate in foundation species of corals, seagrasses, and mangroves.	• Overall diversity of foundation species may decrease, as seen in reef building corals. • Communities may shift to dominance by stress tolerant species that have lower habitat complexity.
Hypoxia mediates species interactions because of different stress tolerances of interactors.	• Pathogens may gain an advantage over stressed hosts, as in black band disease on corals. • Increased stress may increase dependence on mutualisms, as in sleep-swimming fish that flush hypoxic coral crevices with oxygenated water. • Algae may increase on reefs because they are more tolerant than corals to extremely low oxygen conditions.
Low-oxygen events can cause mass mortality of habitat-forming seagrass and corals.	• Ecosystem services including nursery function are lost. • Structural complexity of habitats simplify with loss of structures such as coral reefs and seagrass beds that are built and maintained by aerobic organisms.
Hypoxia in tropical ecosystems may interact with other global change stressors including ocean acidification and warming.	• The health and survivorship of corals and seagrasses may respond non-linearly to changes in dissolved oxygen concentrations. • Photosynthetic consumption of CO_2 and production of O_2 by corals and seagrasses may alleviate stresses associated with ocean deoxygenation and acidification; on the other hand, increased respiration by photosynthetic organisms, particulary with warming, can have the opposite effect.

8.8.1 Introduction

Oxygen depletion is a worldwide phenomenon. However, deoxygenation in coastal marine ecosystems, which is accelerating due to anthropogenic impacts including eutrophication and climate change, is most widely recognized and studied in temperate ecosystems (Breitburg et al., 2018; Diaz et al., 2011; Diaz & Rosenberg, 2008; Rabalais et al., 2010). Hypoxia (oxygen concentrations < 2.8 mg L^{-1}, Diaz & Rosenberg, 1995) has been documented in tropical coastal marine ecosystems, but to a lesser degree than in temperate counterparts (Figures 8.8.1 and 8.8.2). After correcting for differences in length of shoreline (a basic approximation of potentially hypoxic coastal habitat), the number of documented dead zones in temperate regions outnumbers those in the tropics by an order of magnitude (Altieri et al., 2017). Analysis suggests this disparity is at least partially due to underreporting and a lack of targeted research capacity in the tropics (Figure 8.8.2). In many cases, signs of hypoxic stress and mortality are evident in tropical habitats such as coral reefs, even where the quantitative data to verify the severity of low oxygen stress is unavailable (Altieri et al., 2017; Nelson & Altieri, 2019). In this section, we argue that: (1) it is likely that ocean deoxygenation is more widespread in the tropics than currently recognized, (2) hypoxia has a variety of negative effects on the dominant structure-forming species in coral, seagrass, and mangrove ecosystems, as well as the diverse communities of organisms which they support, and (3) there are a variety of natural and social impacts of hypoxia already documented in the coastal tropics, and more are likely to be identified as the intensity of

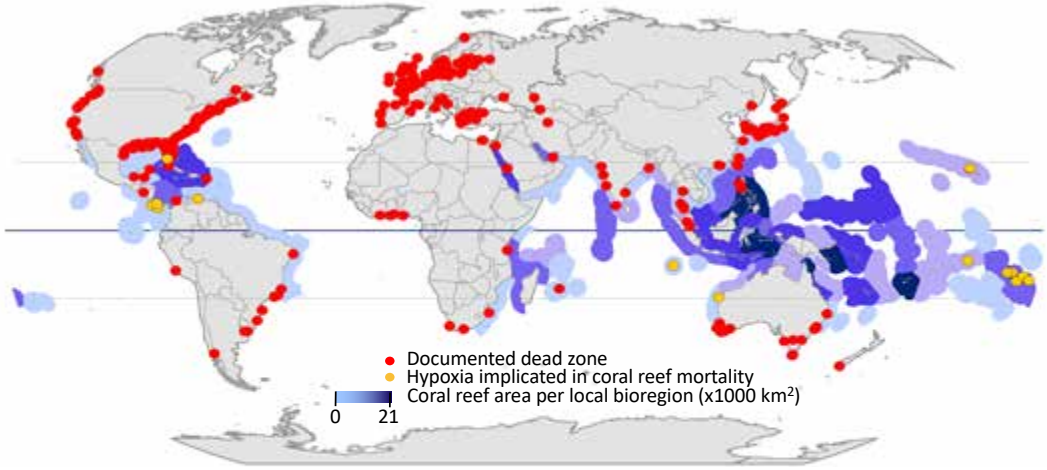

Figure 8.8.1 Map of hypoxic ecosystems worldwide. Red dots are documented hypoxic ecosystems and gold dots are additional tropical sites where hypoxia was inferred from mass mortality events or other signs of stress. Purple represents the relative abundance of coral in various bioregions. From Altieri et al. (2017).

hypoxia research in the coastal tropics approaches that of temperate areas.

Despite the relative lack of attention that deoxygenation in the coastal tropics has received, sufficient studies have accumulated to develop an understanding of its impacts on living systems. In many cases our understanding comes from ecosystems where hypoxia appears to occur naturally, such as the isolation of reef flats by tides (Kinsey & Kinsey, 1967) or accumulation of detritus in seagrass beds (van der Heide et al., 2012). In general terms, the mechanisms that drive the formation of hypoxia in tropical ecosystems, and the biological responses to that stress, are not so different from in temperate ecosystems. However, there are several key features of tropical systems that may make hypoxia of greater concern than in temperate ecosystems. First, tropical ecosystems are typically exposed to warm temperatures year-round. This is important given that higher temperatures decrease water's saturation capacity for dissolved oxygen, increase biological oxygen demand of both the microbes that can generate hypoxic conditions and the metazoans that depend on oxygen, and can stimulate primary productivity that fuels microbial activity (Altieri & Gedan,

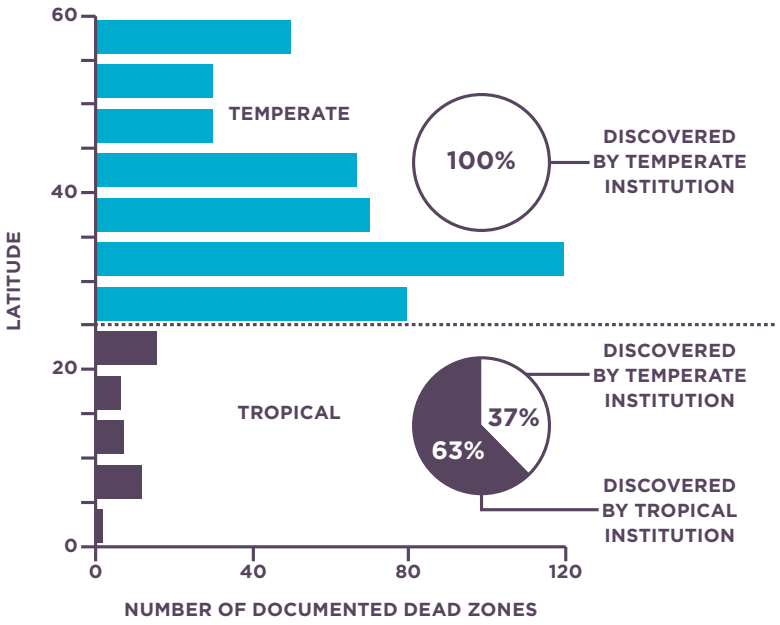

Figure 8.8.2 Distribution of hypoxic ecosystems by latitude. There is approximately an order of magnitude fewer documented dead zones in the tropics than there are in temperate regions. The disparity in research effort, evident by the number of tropical dead zones first identified by a temperate investigator, suggests that the number of tropical dead zones has been underestimated due to a deficit in research capacity. From Altieri et al. (2017).

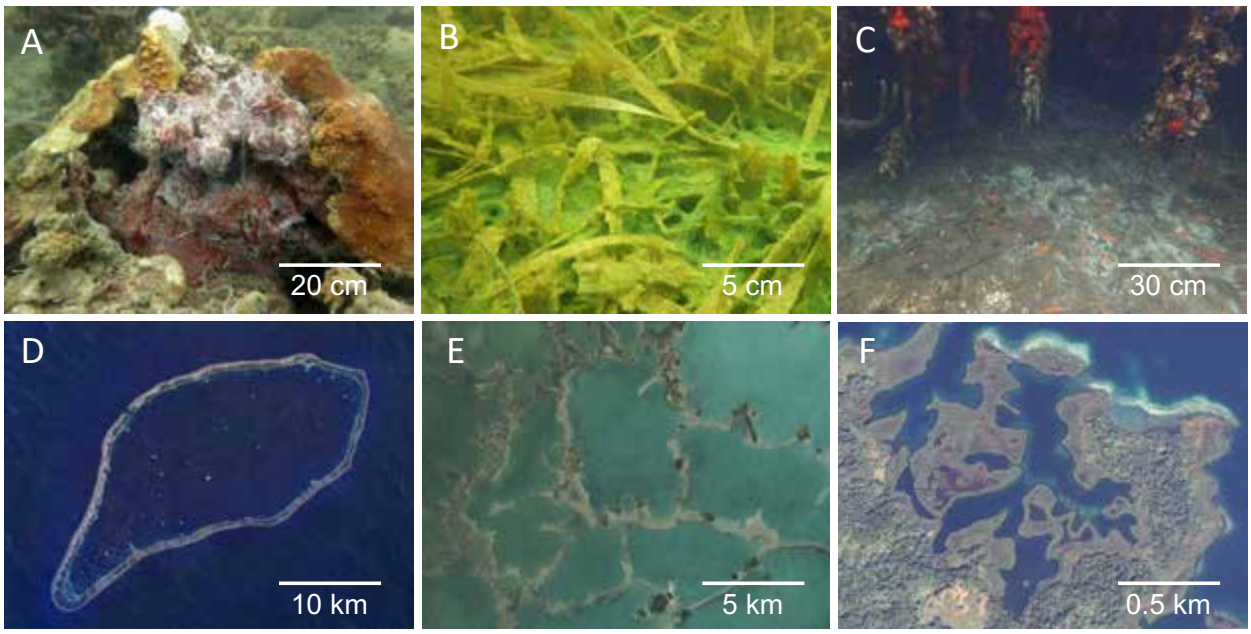

Figure 8.8.3 Photographic evidence of hypoxia in three of the main tropical, coastal ecosystem types: (A) coral reefs: dead urchins and brittlestars strewn atop a dying coral head on the Caribbean coast of Panama, (B) seagrass meadow: dead seagrass coated with microbial mats accumulated during a die-off event associated with concentrations of low oxygen and high hydrogen sulphide in Florida Bay, USA, and (C) mangroves: mats of *Beggiatoa* bacteria below the roots indicating activity of aerobic sulphur reducing bacteria in Bocas del Toro, Panama. Deoxygenation is a common occurrence in each ecosystem with similar indicators including mortality of macro-biota and proliferation of microbial mats. Coral bleaching (A), which is typically associated with thermal stress, can also be triggered by hypoxia. Coral, seagrass, and mangroves can contribute to the creation of hypoxia by forming ponds, channels, and other semi-enclosed basins as seen in (D) coral reef atoll, Manihi Atoll, French Polynesia, (E) basins within a seagrass bed in Florida Bay, USA, and (F) mangrove ponds in Bocas del Toro Panama. (A) © Maggie Johnson, (B) © Brad Furman, (C) © Andrew Altieri, (D-E) © Google, Landsat, (F) © Google, CNES.

2015). Second, many tropical ecosystems are regularly affected by large tropical storms, such as typhoons and hurricanes, that can affect the nutrient and stratification characteristics that generate hypoxic conditions (Herbeck et al., 2011). Third, many coastal, tropical countries are developing nations, where hypoxia drivers and social vulnerabilities are both elevated. In developing nations, fertilizer inputs are increasing at a more rapid rate than in temperate ecosystems, and human population growth and agricultural practices have outpaced growth in their capacity to manage sewage and run-off (Lu & Tian, 2017; MEA, 2005a). Moreover, in many tropical countries, human populations are more reliant on local marine habitats for vital ecosystem services including food, tourism-related income, and shoreline protection. In such places, the negative effects of deoxygenation on coastal ecosystem function will directly affect human well-being (Barbier et al., 2011).

Tropical shorelines are characterized by three key biogenic habitats that define their ecological organization: coral reefs, seagrass meadows, and mangrove forests. Deoxygenation and its effects are observed in all three coastal ecosystems (Figure 8.8.3). Much of our understanding about the structure and function of coastal tropical ecosystems has been developed in the study of these habitats (Bertness et al., 2001). We posit that the study of coral reefs, mangrove forests, and seagrass beds, which has contributed unique insights to general ecological theory, also has the potential to enrich our understanding of ocean deoxygenation. For comparison, the study of hypoxia in temperate ecosystems has been dominated by the study of soft sediment communities (Diaz & Rosenberg, 1995; Levin et al., 2009; Middelburg & Levin, 2009) (but see examples of interactions between oxygen conditions and temperate bivalve reefs: e.g. Altieri & Witman, 2006; Lenihan, 1999). By adopting a perspective focused on habitat-forming species of corals, seagrasses, and mangroves, we offer a globally relevant perspective on deoxygenation in tropical ecosystems that considers the effects of: 1) these species on oxygen conditions, 2) deoxygenation on these species, and 3) hypoxia on the community of species that reside in each habitat.

8.8.2 Definition of species group

Many ecosystems are defined by biomass dominants that create habitat and modify environmental conditions (Altieri & Van De Koppel, 2013). These species are commonly referred to as foundation species (*sensu* Dayton, 1972) because their establishment is the basis

Figure 8.8.4 (A) Coral reef, (B) Seagrass bed, (C) Mangroves. (A) © blue-sea.cz, (B) © Ethan Daniels / Shutterstock, (C) © happystock / Shutterstock.

for diverse communities and numerous secondary ecological interactions (Bruno & Bertness, 2001). For example, coral reefs, which cover less than 1% of the sea floor, host over 25% of known marine species (Reaka-Kudla, 1997). Studying ocean deoxygenation in tropical ecosystems from the perspective of these habitats, and in the context of the foundation species, is particularly insightful because effects on each of these habitats cascade to associated organisms, which, overall, represent a large portion of the earth's marine biodiversity. Moreover, corals, seagrasses, and mangroves are themselves organisms that have their own dependence on oxygen and potential vulnerability to hypoxic conditions.

Corals, seagrasses, and mangroves (Figure 8.8.4) form large aggregated living structures that can influence concentrations of dissolved oxygen through their metabolic activities (Figure 8.8.5). Seagrasses and most corals (along with their zooxanthellae) are submerged autotrophic organisms that exchange gases with the surrounding water column. During the night and other light limiting conditions they are net consumers of oxygen (and producers of CO_2) which can contribute to low oxygen conditions (Shashar et al., 1993). Mangroves differ in that their primary gas exchange structures are in an emergent canopy. Similar to seagrasses, however, they transport oxygen to their roots (to overcome naturally oxygen depleted sediment conditions) which release oxygen into the surrounding sediments (McKee, 1993). Mangroves and seagrasses are highly productive and form large swaths at the land-sea interface capable of intercepting terrigenous nutrients in rivers and other sources of run-off, and thereby reducing eutrophication of neighbouring marine environments and the likelihood of hypoxic conditions that can result (Boto & Wellington,

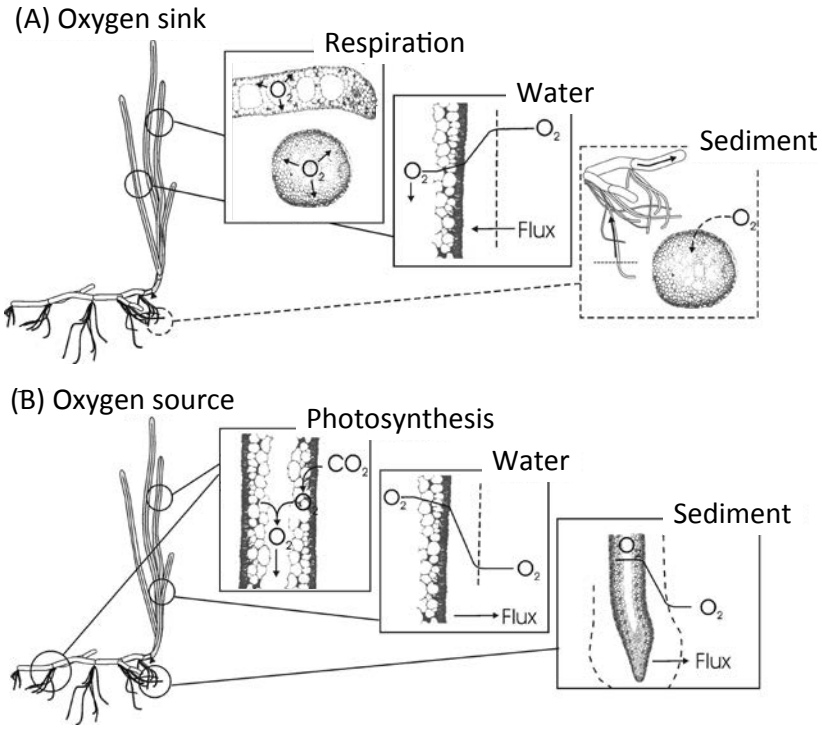

Figure 8.8.5 Diagram of oxygen production, consumption, and exchange in seagrass both in the water column and below ground. Corals and mangroves similarly exchange oxygen with the water column, and mangroves with the sediments. From Borum et al. (2006).

1988; Vonk et al., 2008). However, the detritus and other organic matter trapped by seagrasses, mangroves, and corals (including from their own production) can fuel local oxygen depletion (Bjork et al., 2008).

The physical structure of coral reefs, seagrass beds, and mangrove forests can also influence oxygen dynamics by modifying the movement of water and other materials. They act as barriers that limit water movement and exchange and thereby prevent re-oxygenation of hypoxic waters from open-ocean and surface waters (Figure 8.8.3 D-F). Coral atolls, barrier reefs, and reef flats can create lagoons susceptible to oxygen depletion (Andrefouet et al., 2015; Kinsey & Kinsey, 1967). Likewise, mangroves can form creeks and ponds with limited exchange and vulnerability to oxygen depletion (Mattone & Sheaves, 2017). In some settings, seagrass shoals enclose basins that become hypoxic (Robblee et al., 1991), and more commonly their effect on water chemistry is noticeable within the canopy where water can stagnate and be influenced by gas exchange of the blades and sediments below.

8.8.3 Trends and impacts

8.8.3.1 Coral reefs

Over the last several decades, coral reef ecosystems (Figure 8.8.6) have suffered significant declines in the abundance and diversity of reef-building corals (Bellwood et al., 2004; Bruno et al., 2007; Gardner et al., 2003). While much of this degradation has been attributed to increased temperatures due to climate change (Hoegh-Guldberg et al., 2007; Hughes et al., 2003; Munday et al., 2008), an increase in mass mortality events (i.e. “dead zones”) associated with low oxygen within the last 20 years suggests that hypoxia is another important, but largely overlooked, stressor on reefs (Altieri et al., 2017). Not only are coral tissues and surrounding boundary layers routinely hypoxic in some locations at night (Kinsey & Kinsey, 1967; Niggl et al., 2010; Ohde & van Woesik, 1999; Orr & Moorhouse, 1933), due to the depletion of oxygen by polyp and zooxanthellae respiration (Gardella & Edmunds ,1999; Kuhl et al., 1995; Shashar et al., 1993) (Figure 8.8.7), but entire

Figure 8.8.6 Healthy coral reef. © Vlad61.

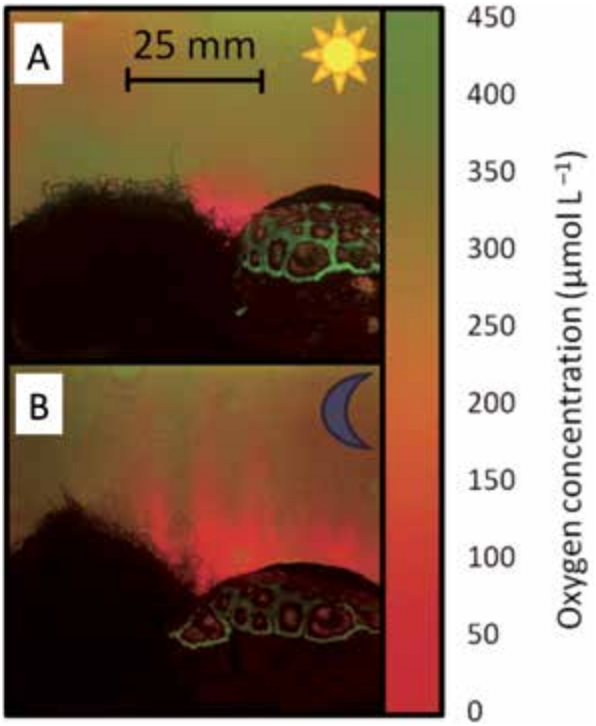

Figure 8.8.7 False colour image of oxygen depletion at the interface of algae (filamentous mat) and coral (polygons with green trim) during both day (A) and night (B). The oxygen depletion contributes to the competitive dominance of algae over coral. From Haas et al. (2013).

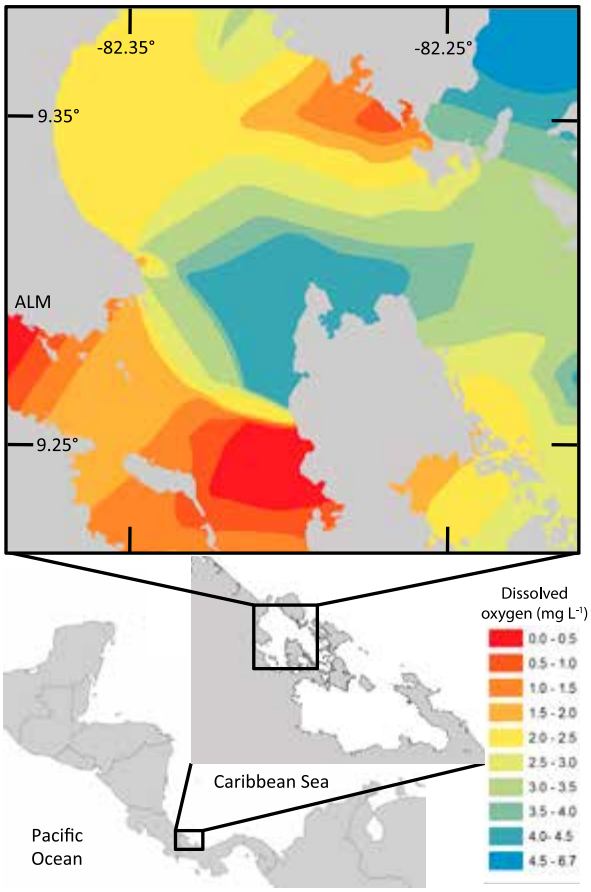

Figure 8.8.8 Map of hypoxia within Bahia Almirante on the Caribbean coast of Panama. Hypoxia (orange and red false colour) developed near human settlements, and led to declines in coral cover and diversity. From Altieri et al. (2017).

reefs can undergo prolonged periods of hypoxia due to natural oceanographic and meteorological processes or the anthropogenic formation of dead zones (Altieri et al., 2017) (Figure 8.8.8). Hypoxia has been implicated in the mass mortality of coral reef organisms in over 20 events around the world (Nelson & Altieri, 2019) (Figure 8.8.1), with the majority of these events occurring within the last two decades (Altieri et al., 2017).

Like other ecosystems, coral reef dead zones occur when processes that increase oxygen demand occur in tandem with processes that prevent the restoration of oxygen in the system (i.e. reoxygenation). Increases in oxygen demand and deoxygenation in reef environments have been attributed to coral spawn slicks (Hobbs & Macrae, 2012; Simpson et al., 1993) (Figure 8.8.9), algal blooms (Dupont et al., 2010; Genin et al., 1995; Guzman et al., 1990; Smith, 1975), higher seawater temperatures due to the seasonal conditions (Andrefouet et al., 2015) or climate change (Altieri & Gedan, 2015), and excess organic matter due to sewage pollution (Jokiel et al., 1993; Pastorok & Bilyard, 1985; Smith et al., 1981), mariculture effluent (Loya, 2004; Villanueva et al., 2005), or the presence of benthic algae (Brown & Carpenter, 2013; Gregg et al., 2013; Haas et al., 2010, 2011). In contrast to the mostly biological processes that increase oxygen demand on reefs, the factors that prevent reoxygenation on reefs are predominately physical. Coral reef dead zones occur more frequently in semi-enclosed or closed basins that exhibit water-column stratification and poor flushing (e.g. Altieri et al., 2017; Andrefouet et al., 2015) and during periods of calm seas with unusually light winds and low swell (e.g. Andrefouet et al., 2015; Hobbs & McDonald, 2010; Hobbs & Macrae, 2012).

In general, the response of organisms to hypoxia is dependent on both the magnitude and duration of deoxygenation (Best et al., 2007). The effects of hypoxia on corals range from reduced photosynthesis (Gardella & Edmunds, 1999) and calcification (Al-Horani et al., 2007; Colombo-Pallotta et al., 2010; Wijgerde et al., 2012, 2014), to bleaching (Altieri et al., 2017; Yonge et al., 1932), and in extreme cases, mortality (Altieri et al., 2017; Yonge et al., 1932). The ability of corals to withstand hypoxia varies among species; corals have been shown to survive severe hypoxic conditions

Figure 8.8.9 Coral spawn slick on surface of water. © Suzanne Long / Alamy stock photo.

(< 5% air saturation) in the laboratory for periods ranging from several hours to at least a week, depending on the species (Altieri et al., 2017; Dodds et al., 2007; Haas et al., 2014; Mayer, 1917; Sassaman & Mangum, 1973; Weber et al., 2012; Yonge et al., 1932). Generally, branching and solitary species typically suffer the highest mortality during severe hypoxic events (Figure 8.8.10), whereas massive, submassive, and encrusting corals are usually less affected (Adjeroud et al., 2001; Genin et al., 1995; Guzman et al., 1990; Laboy-Nieves et al., 2001; Simpson et al., 1993). The response of organisms to hypoxia also depends on the presence of other stressors. There is evidence that some coral communities might be relatively robust to the combination of low pH and deoxygenated waters (Camp et al., 2017), and that the endosymbiotic dinoflagellates belonging to the genus *Symbiodinium* may mitigate some of the impacts of hypoxia and concurrent respiration-driven acidification in cnidarians (Klein et al., 2017). However, additional research is needed to better understand the physiological responses of coral to hypoxia (and co-occurring stressors including acidification and excess nutrients) and to develop a mechanistic explanation of this variation in tolerance among species. Such findings would allow for predicting shifts in community composition with increasing hypoxia and establish the scope for adaptation within species.

8.8.3.2 Seagrass beds

Seagrasses (Figure 8.8.11) are declining globally at an accelerating rate (current loss at 1.5% per year) comparable to loss rates for mangroves, coral reefs, and tropical rainforests (Orth et al., 2006; Waycott et al., 2009). In the tropical Atlantic and Indo-Pacific regions, conservative estimates are that 21% of the 72 known seagrass species exhibit decreasing population trends and 11% of species have been designated as threatened on the IUCN Red List (Short et al., 2011). Several tropical seagrass mass mortality events have been reported in recent decades (Carlson et al., 1994; Hall et al., 1999; Plus et al., 2003; Robblee et al., 1991; Seddon et al., 2000; Zieman et al., 1999). Although causality is rarely established in these events (Ralph et al., 2007), correlative evidence and work from experimental studies suggests that hypoxia is one of the main factors underlying these die-offs (Borum et al., 2005; Carlson et al., 1994; Durako & Kuss, 1994).

One of the primary drivers of repeated, sustained hypoxia in seagrass ecosystems is eutrophication (Burkholder et al., 2007). While some level of nutrient enrichment can result in increased seagrass productivity (Ferdie & Fourqurean, 2004; Short et al., 1985; Short & Wyllie-Echeverria, 1996; Terrados et al., 1999), chronic nutrient enrichment in seagrass meadows causes excessive growth of macroalgae, epiphytes, and phytoplankton, resulting in the development of hypoxic conditions (Bjork et al., 2008). Nutrients and organic matter from both terrestrial watershed inputs and coastal development (e.g. sewage) contribute to chronic nutrient enrichment in seagrass ecosystems (Burkholder et al., 2007). Eutrophication-induced hypoxia in seagrass meadows occurs most often during the warm summer months, especially in calm, poorly flushed bodies of water where nutrient loads are concentrated and frequent (Burkholder et al., 2007; Lapointe & Clark, 1992).

Seagrasses are both a source and sink for oxygen in the surrounding water column and sediments (Figure 8.8.5). During the day, when seagrass is photosynthesizing, oxygen partial pressures within seagrass are primarily dependent on changes in surface irradiance (Borum et al., 2005, 2007; Greve et al., 2003). In contrast, at night,

Figure 8.8.10 A thicket of the endangered staghorn coral *Acropora cervicornis* that succumbed to an acute hypoxia event in Bocas del Toro, Panamá. The coral was one of the few remaining stands of live *A.cervicornis* inside the Bay of Almirante prior to the 2017 hypoxia event. © Dr Maggie D. Johnson.

internal seagrass oxygen partial pressures are linearly related to the oxygen concentration in the water column, so low water column oxygen concentrations often results in hypoxic seagrass tissues (Borum et al., 2005, 2007; Greve et al., 2003). At the same time as tissue and water column concentrations of CO_2 are elevated by night-time respiration. Seagrasses face hypoxic conditions not only in the water column, but also in their sediments (Borum et al., 2007; Pedersen et al., 1998).

Figure 8.8.11 Seagrass bed © Rich Carey / Shutterstock.

In general, coastal marine sediments are mostly anoxic and highly reduced below their surface layer because of the slow oxygen diffusion from the water column and degradation of organic matter within the sediment (Borum et al., 2007). Consequently, seagrass sediments represents a large oxygen sink and seagrasses must supply oxygen to their below-ground tissues through either photosynthesis or by diffusing oxygen from the water column through leaves to rhizomes and roots (Pedersen et al., 1998). Environmental factors that disrupt seagrass oxygen balances, for example by increasing seagrass respiration or increasing the oxygen demand within the sediment, can result in hypoxic seagrass tissues (Borum et al., 2005). Environmental factors that disturb seagrass oxygen balances include hypersalinity, higher water temperatures, and infections by pathogens (Durako & Kuss, 1994; Koch & Erskine, 2001; Zieman et al., 1999).

The tolerance of seagrass to hypoxia differs among species (Koch et al., 2007a; Pedersen et al., 2016), but hypoxia generally has negative effects on seagrass

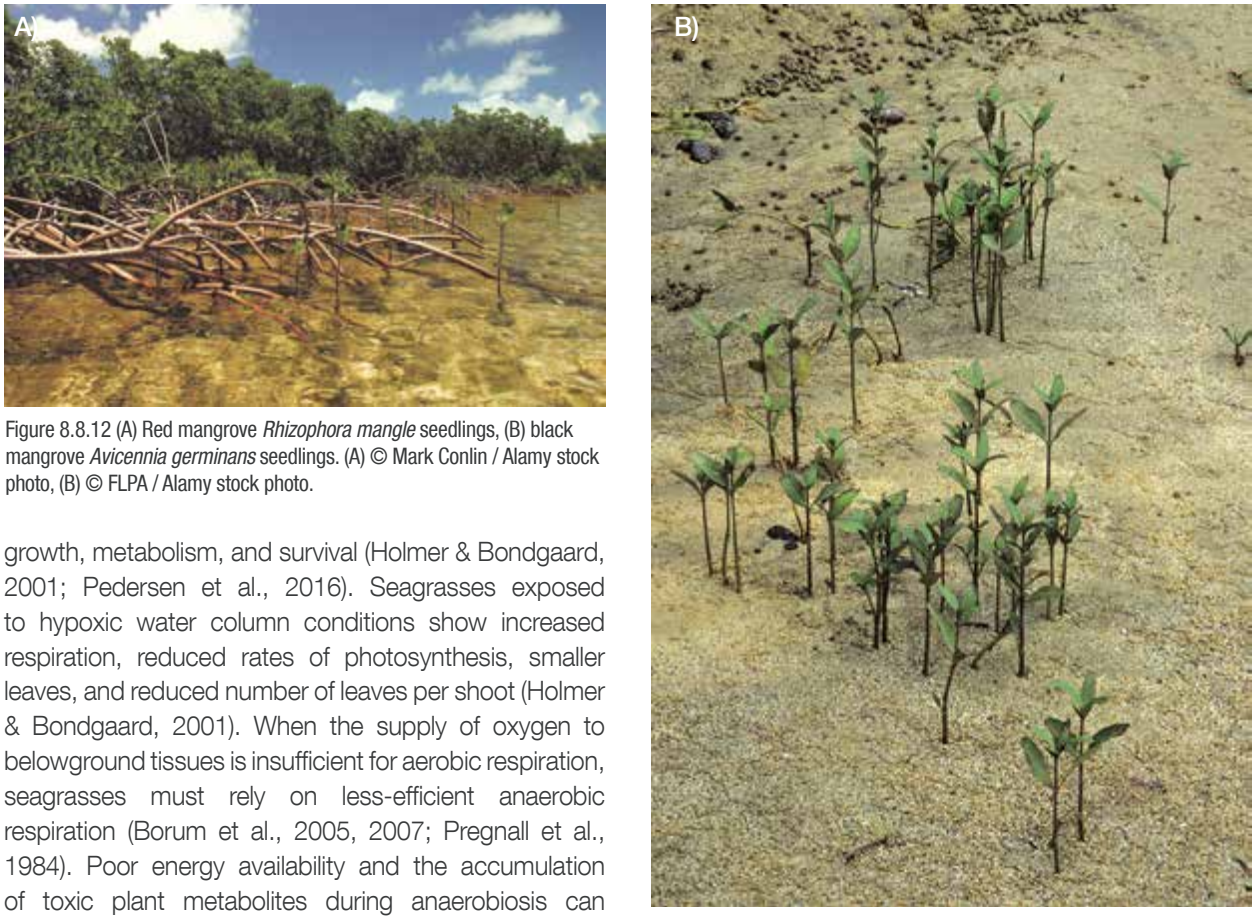

Figure 8.8.12 (A) Red mangrove *Rhizophora mangle* seedlings, (B) black mangrove *Avicennia germinans* seedlings. (A) © Mark Conlin / Alamy stock photo, (B) © FLPA / Alamy stock photo.

growth, metabolism, and survival (Holmer & Bondgaard, 2001; Pedersen et al., 2016). Seagrasses exposed to hypoxic water column conditions show increased respiration, reduced rates of photosynthesis, smaller leaves, and reduced number of leaves per shoot (Holmer & Bondgaard, 2001). When the supply of oxygen to belowground tissues is insufficient for aerobic respiration, seagrasses must rely on less-efficient anaerobic respiration (Borum et al., 2005, 2007; Pregnall et al., 1984). Poor energy availability and the accumulation of toxic plant metabolites during anaerobiosis can eventually result in seagrass morality (Perez et al., 2008). Seagrass die-offs create a positive feedback cycle where mortality begets further mortality as higher ecosystem oxygen demands are created when dead plant material is decomposed (Bjork et al., 2008).

Aside from the direct effects of hypoxia on seagrass tissues, hypoxia also negatively affects seagrass by indirectly mediating the invasion of sulphides in seagrass tissues. Sulphide is a potent phytotoxin, which negatively affects seagrass photosynthesis, metabolism, and growth (Holmer & Bondgaard, 2001). Tropical marine seagrass beds have especially high sulphide concentrations because high temperatures stimulate microbial sulphate reduction rates within sediments and the low availability of iron in the carbonate sediments of tropical seagrass beds reduces their sulphide binding capacity (Chambers et al., 2001; Koch et al., 2007a). Seagrasses are able to prevent sulphide from invading their tissues by supplying sufficient oxygen to below-ground tissues to maintain an oxic microsphere around their roots and rhizomes (Koch et al., 2007b; Pedersen et al., 1998, 2004). When seagrasses are unable to maintain this supply of oxygen to below-ground tissues, sulphides are able to enter and accumulate within the plant tissues, frequently resulting in plant mortality (Borum et al., 2005; Carlson et al., 1994). This process has been implicated as the most likely mechanism responsible for mass die-offs of the tropical seagrass *Thalassia testudinum* in the Florida Bay (Borum et al., 2005) (Figure 8.8.3B).

8.8.3.3 Mangrove forests

Compared to coral reefs and seagrass beds, hypoxia is naturally a more common occurrence in mangrove ecosystems (Figure 8.8.3C), though it is also being exacerbated by anthropogenic nutrient inputs and land use modification. Mangroves themselves are generally tolerant of hypoxic conditions because most of their structure is exposed to the atmosphere, and the roots that encounter hypoxic conditions in the water and sediments are supplied with oxygen from above (McKee, 1993). Like seagrasses, mangrove trees are able to transport oxygen to roots and rhizomes, a process that can locally oxygenate the rhizosphere, reduce sulphide concentrations, and alter microbial communities at the scale of centimetres (McKee, 1993; McKee et al., 1988). However, oxygen can be limiting for mangrove performance, and the effects of hypoxia on mangrove trees varies by species. For example, young

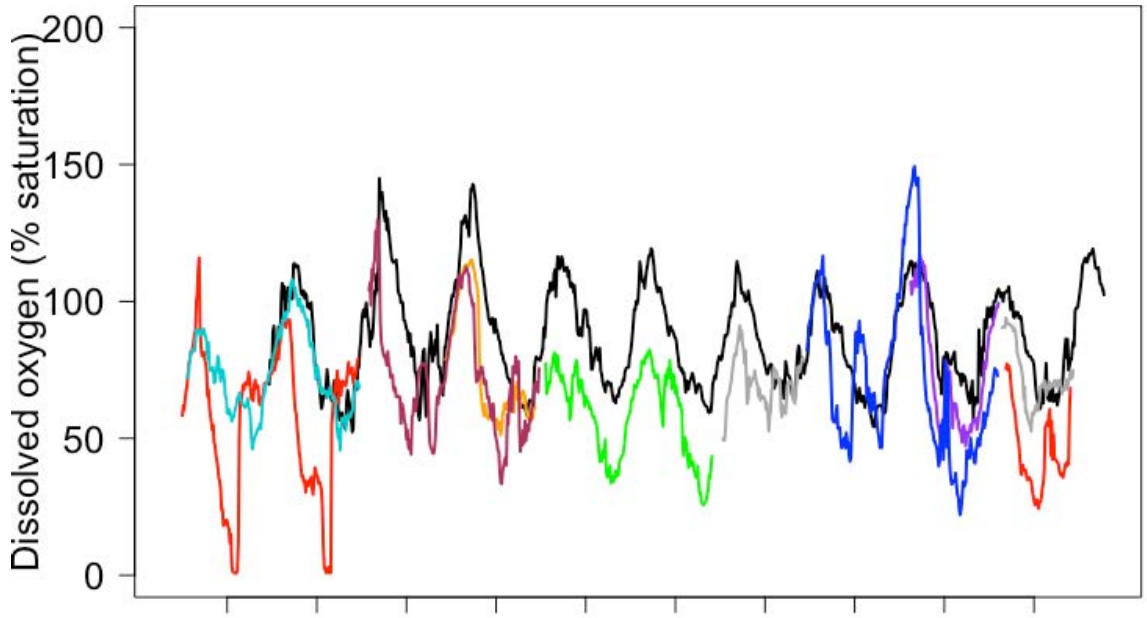

Figure 8.8.13 Diel cycling of oxygen in ponds that are isolated by mangroves. Diel cycling is evidence of biological oxygen demand where a system turns from a net producer of oxygen to a net consumer of oxygen under light limiting conditions. Coloured lines represent a sequence of monitoring periods in several mangrove ponds, and the black line represents conditions in a nearby seagrass bed. From Gedan et al. (2017).

seedlings of the red mangrove *Rhizophora mangle* (Figure 8.8.12A), which lives at frequently inundated depths, can tolerate hypoxia, but seedlings of the black mangrove *Avicennia germinans* (Figure 8.8.12B) and white mangrove *Laguncularia racemosa*, which tend to predominate at higher elevation and more inland areas of neotropical mangrove forests, are less tolerant of hypoxic stress (McKee, 1993, 1996).

Short-duration hypoxia or anoxia naturally occurs in many mangrove subhabitats, as demonstrated by studies of dissolved oxygen patterns in mangrove forests in remote locations and undisturbed watersheds. Diel-cycling hypoxia is common in shallow, aquatic mangrove ponds (Figure 8.8.13) (Gedan et al., 2017) and pools in the mangrove forest interior (Mattone & Sheaves, 2017). The diel-cycling pattern in dissolved oxygen is a reflection of daytime photosynthesis and nighttime respiration that depletes dissolved oxygen concentrations (Baumann et al., 2015; Nixon & Oviatt, 1973). Short duration hypoxia also occurs in high intertidal areas that are submerged for only a portion of the day on flood tides. Tide pools form in these basin interior areas during ebb tides, when most of the dissolved oxygen delivered with the tide is consumed by microbial and benthic communities (Knight et al., 2013; Mattone & Sheaves, 2017).

On monthly time scales, spring flood tides bring more oxygenated water to the hypoxic areas of the mangrove interior than neap tides (Mattone & Sheaves, 2017), although the opposite pattern has also been observed in a Malaysian mangrove estuary, when spring tides were high enough to liberate hypoxic water trapped in tidal creeks and resuspend sulphide-laden sediments that consume dissolved oxygen (Figure 8.8.14) (Okamura et al., 2010). In either case, dissolved oxygen is most readily consumed in the interior of the mangrove forest and hypoxic water is exported towards the mouth of the estuary where it mixes with more oxygenated water. This phenomenon creates a down-estuary dissolved oxygen gradient in many mangrove forests (Figure 8.8.14) (Mattone & Sheaves, 2017; Okamura et al., 2010). As with many coastal and estuarine environments, inundation, connectivity, and tidal flushing alleviate hypoxic conditions towards the edge of mangrove stands, whereas isolation in pools and reduced tidal influence exacerbate hypoxic conditions in the interior of mangrove forests (Figure 8.8.14) (Knight et al., 2013; Mattone & Sheaves, 2017).

This spatial pattern sets up a gradient of environmental stress and can structure the distribution of species living in mangrove ecosystems at various scales. Many more aquatic species can tolerate the dissolved oxygen conditions at the mangrove fringe and mouth of tidal creeks than conditions in the basin interior or heads of tidal creeks, thus establishing gradients in the diversity of macrofauna at the scale of metres or kilometres (Knight et al., 2013; Okamura et al., 2010). The aquatic species that live in the mangrove interior must be extremely

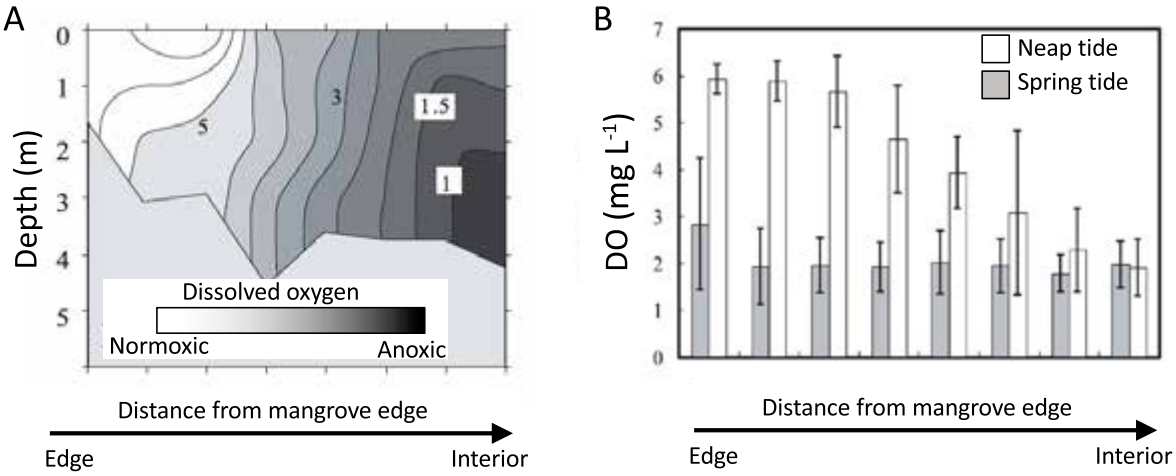

Figure 8.8.14 (A) Spatial gradient of hypoxia in a mangrove forest. Isolation of water in the interior of a mangrove stand inhibits flushing and reoxygenation by surrounding waters. (B) The role of limited water exchange in contributing to hypoxic conditions is evident from the establishment of hypoxic conditions at only at the most interior sites during the neap tides (when the tidal volume is relatively low). During spring tides, hypoxic water was liberated from isolated creek sheds to result in widespread hypoxia in this system. From Okamura et al. (2010).

tolerant of hypoxic conditions. Notable examples include the well-studied amphibious mangrove killifish, *Kryptolebias marmoratus*, which leaves the water to escape episodic hypoxia (Figure 8.8.15), and fish that surface-breathe which are common in mangrove forests (Dunson & Dunson, 1999). Some common mangrove fishes, such as the sailfin molly and sheepshead minnow, can tolerate more than a day at low oxygen saturation (Peterson, 1990). There has been little research into the movement of species in response to hypoxia in mangrove ecosystems, but mobile species likely migrate between various subhabitats to reduce hypoxia exposure as in other ecosystems (Breitburg et al., 2009).

Overlain on these natural dynamics and spatial patterns in mangrove ecosystems, anthropogenic eutrophication and shoreline development can exacerbate hypoxia in mangrove ecosystems. Anthropogenic inputs may exceed the limits of macrofaunal survival in many mangrove microhabitats. For example, sewage effluent in a formerly oligotrophic tidal creek in Darwin, Australia amplified the diel-cycle of hypoxia and reduced dissolved oxygen saturation to half that of a reference creek (Smith et al., 2012). Similarly, Krebs et al. (2014) found a higher frequency of hypoxia in urban mangrove tidal creeks than in non-urban watersheds in Tampa Bay, Florida, USA. Untreated sewage disposal in Brazilian mangrove streams elevated nutrient levels and caused severe hypoxia and regular anoxia with mean DO concentrations below 1 mg L^{-1} (Aguiar et al., 2011).

Figure 8.8.15 The mangrove killifish, *Kryptolebias marmoratus,* leaves water to escape hypoxic conditions that frequently occur in mangrove habitats. Image reprinted with permission from Turko & Wright (2015).

Shrimp ponds (Figure 8.8.16) constructed in mangrove forest are viewed as the greatest anthropogenic threat to mangrove ecosystems (Alongi, 2002; McLeod & Salm, 2006). The tremendous expansion of shrimp aquaculture in the 1980s and 1990s converted an estimated 50% of the mangroves in Thailand and China (Spalding et al., 2010) and 17% in Peru (Mialhe et al., 2013) to ponds. Shrimp ponds reduce estuarine circulation and water quality, and thereby also promote diel-cycling hypoxia within mangroves (Johnston et al., 2002; Stram et al., 2005). The vast majority of these ponds are quickly abandoned when water quality degrades (Ewel et al., 1998; McLeod & Salm, 2006). Moreover, the effluent from shrimp farming, estimated to be 43 billion tons of wastewater in China alone (Biao & Kaijin, 2007), represents a major source of pollution that can promote hypoxia in adjacent habitats (Dierberg & Kiattisimkul, 1996; Paul & Vogl, 2011).

Figure 8.8.16 Shrimp farms in Phang Nga bay, Thailand. © Stephane Bidouze.

8.8.4 Ecosystem consequences

8.8.4.1 Coral reefs

Aside from the direct impacts of hypoxia on coral reef organisms, hypoxia also has indirect effects, such as through the abundance of algae and spread of coral diseases in coral reef ecosystems. While corals in some locations, especially at low flows, routinely experience hypoxia at night (Gardella & Edmunds, 1999; Goldshmid et al., 2004; Kuhl et al., 1995; Nilsson et al., 2004; Ohde & van Woesik, 1999; Shashar et al., 1993; Wild et al., 2008), hypoxic conditions are also present in the interaction zone between corals and algae during the day (Barott et al., 2009; Haas et al., 2013; Smith et al., 2006) (Figure 8.8.7). The hypoxia that develops in coral-algal interfaces can have severe negative consequences for corals, including bleaching (Barott et al., 2009) and death (Smith et al., 2006). Algae, in contrast, are significantly more tolerant to extremely low oxygen conditions (Haas et al., 2014). Therefore, natural or anthropogenic stressors that increase algal biomass or productivity could result in feedbacks that promote further coral mortality and the spread of algae.

This feedback is reinforced by coral diseases, such as black band disease (BDD) (Figure 8.8.17), which kills underlying coral tissue through the high concentrations of sulphide and hypoxic conditions produced by the BBD mat (Carlton & Richardson, 1995; Glas et al., 2012). The rate at which BBD mats spread is correlated with oxygen depletion (Glas et al., 2012). Not only does BBD create localized zones of hypoxia that kill corals, but also BBD is more common at reefs repeatedly stressed by larger-scale hypoxic events (Onton et al., 2011). Thus, reefs that undergo frequent hypoxic events are more likely to have a higher incidence of disease.

Interactions between coral, algae, and disease are integrated within the Dissolved Organic Carbon (DOC), Disease, Algae and Microbes (DDAM) model, which explains how hypoxia, algae, and disease are linked in a positive feedback loop that results in coral degradation (Barott & Rohwer, 2012; Dinsdale & Rohwer, 2011; Gregg et al., 2013). Algae release DOC, which simulates rapid microbial growth, creating localized hypoxic zones, which results in increased coral disease and mortality, leading to bare space for the recruitment of even more algae, thus perpetuating the loop (Barott & Rohwer, 2012; Dinsdale & Rohwer, 2011; Gregg et al., 2013) (Figures 8.8.7 and 8.8.18).

The fish and invertebrates that inhabit coral reefs exhibit a wide variety of behavioural and physiological responses to hypoxia. Mobile reef organisms often respond to hypoxia by moving upward to find more oxygenated water. For example, moray eels and other bottom-dwelling reef

Figure 8.8.17 Progression of black band disease (BBD) sweeping over a coral colony. BBD depletes oxygen at its leading edge which contributes to coral death. BBD is also more prevalent in areas that experience reef-scale hypoxia. Image reprinted with permission from Rogers et al. (2008).

fishes have been observed swimming at the surface of the water during a hypoxic event (Simpson et al., 1993). In response to severe hypoxia, some reef fish enter a phase of metabolic and ventilatory depression (Routley et al., 2002). Mobile reef invertebrates have been observed migrating out of crevices and burrows to the surface of the substratum (Figure 8.8.19) (Altieri et al., 2017; Laboy-Nieves et al., 2001; Simpson et al., 1993) or moving to the tips of arborescent coral colonies (Johnson et al., 2018; Simpson et al., 1993) in severely hypoxic conditions. Relatively little is known about the metabolic adaptations of reef invertebrates to hypoxia, but generally invertebrates demonstrate depression of activity (Diehl et al., 1979), reduced feeding (Bell et al., 2003; Llanso & Diaz, 1994; Tamai, 1993), metabolic depression (Rutherford & Thuesen, 2005), and/or altered heart rates (Harper & Reiber, 1999) in response to low oxygen levels.

Reef fishes that form obligatory associations with living corals and inhabit the nocturnally hypoxic spaces within branching coral colonies (e.g. *Gobiodon histrio*) (Figure 8.8.20) and generally exhibit a greater hypoxia tolerance than other reef fish (Nilsson et al., 2004, 2007). Among coral reef invertebrates, there are limited data on the differences in hypoxic tolerances among species, but there is considerable variation in susceptibility, with some species undergoing mass mortalities during severe hypoxic events while others appeared unaffected (e.g. Adjeroud et al., 2001; Laboy-Nieves et al., 2001). In general, predicting the response of coral reef organisms to hypoxia is challenging given the large variability of lethal and sublethal thresholds among benthic taxa (Vaquer-Sunyer & Duarte, 2008). Under-reporting of hypoxic events in the tropics (Altieri et al., 2017) and the difficulty of sampling reef diversity (Plaisance et al., 2011), suggests the impacts of hypoxia on most coral reefs organisms remains largely undetected or poorly understood.

8.8.4.2 Seagrass beds

Deoxygenation both directly and indirectly affects the biodiversity of seagrass ecosystems. Directly,

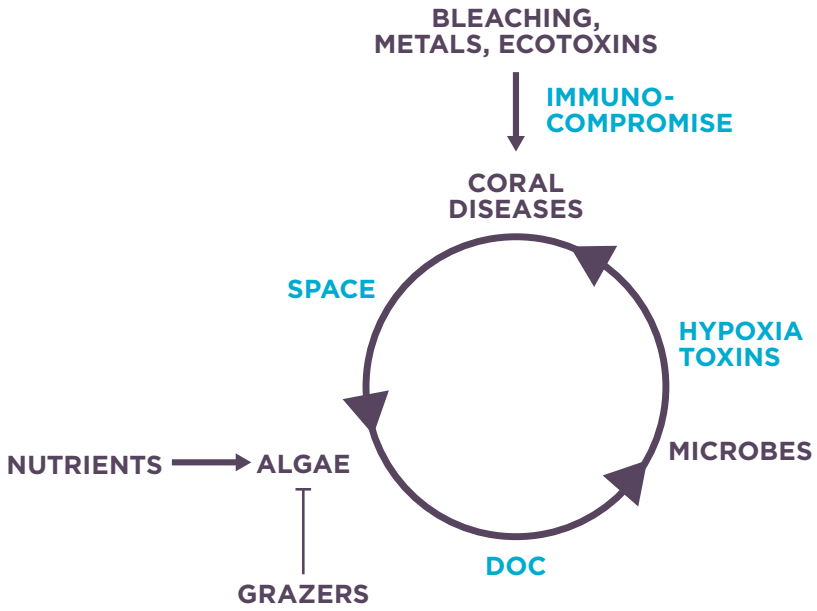

Figure 8.8.18 The 'DDAM loop', in which oxygen depletion plays a critical link in a feedback loop that includes anthropogenic factors such as climate change, overfishing, and eutrophication that leads to coral mortality through algal overgrowth through microbial proliferation. From Dinsdale and Rower (2010).

deoxygenation can reduce the diversity of organisms inhabiting seagrass beds by eliminating species that cannot tolerate low oxygen conditions. For example, experimental anoxia in a *Posidonia oceanica* meadow in north-west Spain resulted in an immediate reduction of metazoan meiofauna richness (Gambi et al., 2009). Indirectly, the loss and degradation of seagrass due to deoxygenation threatens the numerous species that rely on seagrass habitat for shelter or food. Overall, about one third of seagrass-associated species are listed as threatened on the IUCN Red List, in many cases related to a decline in seagrass habitat (Short et al., 2011).

The loss of seagrass affects not only the biological communities that inhabit seagrass ecosystems, but also the physical characteristics and resilience of seagrass ecosystems. For example, die-offs of the dominant seagrass *T. testudinum* in Florida Bay has resulted in elevated nutrient levels and increased turbidity due to available nutrients and suspended sediment that were previously taken up or trapped by seagrass beds (Durako, 1994). Increased turbidity decreases the light available for seagrass photosynthesis (Hemminga & Duarte, 2000), which affects the ability of seagrass to recolonize areas where mass mortality events have occurred.

8.8.4.3 Mangroves forests

Some studies have attributed a low density of aquatic organisms in mangrove forests to hypoxia, and recognized the harsh hypoxic conditions as a barrier to fish moving upstream (Mattone & Sheaves, 2017; Okamura et al., 2010). By comparing mangrove ponds on the Caribbean coast of Panama that varied in magnitude of diel-cycling hypoxia, Gedan et al. (2017) found reduced fish diversity in ponds with higher magnitude diel swings, and noted that echinoderms were largely absent from all ponds. However, they observed a rich community of benthic invertebrates and macroalgae that apparently tolerate regular exposure to short-duration hypoxia (Gedan et al., 2017).

Spatial gradients in hypoxia in mangroves (Figure 8.8.14) shape the landscape of secondary production. Due to the frequent hypoxic conditions, the mangrove forest interior does not provide the fish habitat or fishery benefits of fringe or riverine mangroves (Ewel et al., 1998). When the ecosystem is perturbed to more extreme hypoxia, ecosystem function can collapse. In Australia, eutrophication and hypoxia were associated with higher phytoplankton productivity, accumulation of a dense algal mat, and fish kills (Smith et al., 2012).

Despite the established links between eutrophication and hypoxia, it can be difficult to assess the overall effects of these processes on the fauna associated with mangroves, in part due to the contradictory effects of nutrient enrichment and hypoxia (Breitburg et al., 2009). For example, in the mangrove tidal creeks of Tampa Bay, the body condition and abundance of grass shrimp were higher in developed, relative to undeveloped,

Figure 8.8.19 Brittlestars and gastropods, normally hidden in cryptic spaces on a coral reef, attempting to flee low-oxygen conditions during a hypoxia event that affected coral reefs on the Caribbean coast of Panama in 2017. Hypoxia resulted in the mass mortality of brittlestars, gastropods, and other motile invertebrates. © Dr Maggie D. Johnson.

watersheds, whereas killifish and sheepshead minnows showed the opposite pattern (Krebs et al., 2014).

Overall, mangrove fauna is much more tolerant of environmental stresses including hypoxia than coral reef- and seagrass-associated fauna. In an illustrative example, a stressful upwelling event in a Venezuelan estuary that reduced DO, water temperatures, and salinity annihilated up to 98% of the corals at locations within the estuary, but mangrove prop root communities were unaffected (Laboy-Nieves et al., 2001). This may be a result of the foundation species in mangrove forests, the mangroves themselves, being more resistant to aquatic hypoxic conditions because they are partially exposed to air.

8.8.5 Societal consequences

8.8.5.1 Coral reefs

Around six million people, the majority of whom live in developing countries, depend on coral reef fisheries which can account for 51–94% of the total animal protein consumed (Bell et al., 2009; Teh et al., 2013). Mass die-offs due to extreme hypoxic events can have severe impacts on reef fish populations. For example, a hypoxic event on Ningaloo Reef (western Australia) in 1989 resulted in over one million dead fish washed ashore (Simpson et al., 1993), and over 200,000 dead fish within a couple days in 2012 in the hypoxic lagoon surrounded by the South Keeling Islands (Hobbs & Macrae, 2012). These massive hypoxic fish kills can result in local extirpation of some fishes, as observed on the west Florida shelf where five species of demersal fish failed to recolonize artificial reefs within the two years following a red tide that resulted in massive fish kills (Dupont et al., 2010). In remote settings, such as islands in the Pacific where there is a limited range of crops and animal protein available locally or through import (Bell et al., 2009), the loss of fish due to hypoxic dead zones events presents a serious threat to food security and nutrition.

Aside from providing seafood products, corals reef ecosystems provide a variety of essential ecosystem services, including shoreline protection, nitrogen fixation, waste assimilation, and tourism opportunities (Moberg & Folke, 1999). Given the dependence of such ecosystem goods and services on biodiversity and biomass, the mortality and loss of coral diversity due to hypoxia will likely have a variety of cascading social consequences.

8.8.5.2 Seagrass beds

Seagrasses also provide nursery grounds and habitat for many harvested commercial, recreational, and subsistence fish and shellfish (Beck et al., 2001; de la Torre-Castro & Ronnback, 2004; Heck et al., 2003; Unsworth & Cullen, 2010; Watson et al., 1993). In many tropical regions, such as East Africa and the Indo-Pacific, local people are dependent on seagrass-associated fisheries for their livelihoods and as a source of animal protein (de la Torre-Castro & Ronnback, 2004; Samonte-Tan et al., 2007; Unsworth & Cullen, 2010). The loss and deterioration of seagrass meadows due to stressors, such as hypoxia, could threaten the food security and income of these communities (Unsworth & Cullen, 2010).

In addition to furnishing food, habitat, and nursery grounds for many seagrass-associated species valued by humans, seagrass meadows provide a plethora of ecosystems services including water purification, coastal protection and erosion control via sediment stabilization, nutrient and carbon sequestration, and delivery of trophic subsidies to adjacent marine and terrestrial habitats (Barbier et al., 2011; Heck et al., 2008; Orth et al., 2006). The decline of seagrass habitats due to hypoxia threatens the ability of these ecosystems to provide essential goods and services.

8.8.5.3 Mangrove forests

Given that mangroves themselves are tolerant of low oxygen conditions, ocean deoxygenation will have minimal direct societal impacts through changes in mangrove distributions and abundances. However, hypoxia is likely to affect the organisms that inhabit mangroves, including fish, which can be an important source of food and livelihood for local human populations (Ronnback, 1999). Since mangrove nurseries can supply half or more of the fish on nearby coral reefs (Mumby et al., 2004), deoxygenation of mangrove habitats is likely to affect the ecosystem services of adjacent habitats as well. Moreover, the factors that promote deoxygenation in mangrove ecosystems such as eutrophication, removal of mangroves and associated filtration capacity, and creation of shrimp farms have a number of well-recognized negative effects on human well-being (MEA, 2005b). Even with the apparent localized benefits of some activities such as shrimp farming, which offers substantial employment opportunity (e.g. 10,000 jobs in coastal Peru; Mialhe et al., 2013), the environmental costs grossly outweigh the economic benefits in any comprehensive economic analysis (Gunawardena & Rowan, 2005).

Figure 8.8.20 *Gobiodon histrio* a species that exhibits greater hypoxia tolerance than other reef fish © Roberto Nistri / Alamy stock photo.

8.8.6 Implications of continuing ocean deoxygenation

8.8.6.1 Coral reefs

The continued decline of oxygen in the ocean is worrying because the recovery of reefs following hypoxic mass mortality events can take years (Dupont et al., 2010) to decades (Smith, 1975) due to the slow-growing nature of corals. Compared to many other types of disturbances on coral reefs (e.g. overfishing, crown-of-thorns starfish outbreaks, disease epidemics), the long-term effects of hypoxia on reefs are likely to be more severe because hypoxia simultaneously affects a broad range of taxa including consumers, habitat formers, and microbes (Altieri et al., 2017). Recolonization of some taxa (e.g. benthic algae, polychaetes, fishes) on coral reefs can be relatively rapid, while others (e.g. corals, echinoderms, molluscs) are slower to recover and may take decades (Banner, 1968; Dupont et al., 2010; Smith, 1975). Regardless of the rate of recovery, the community that establishes during recovery from a severe hypoxia event is unlikely to be identical to the community that preceded the deoxygenation due to hysteresis (Diaz & Rosenberg, 2008; Nelson et al., 2016). Whether a reef will shift from a coral-dominated to an algal-dominated state following a hypoxia-driven mass mortality of coral depends, in part, on whether sufficient grazing pressure is present (Kuempel & Altieri, 2017).

Figure 8.8.21 Mangroves converted to shrimp ponds contribute to hypoxic conditions in surrounding waterways and create ideal conditions for oxygen depletion within the ponds themselves. Image credit: Ilka Feller made possible by LightHawk.

8.8.6.2 Seagrass beds

Continued ocean deoxygenation is concerning because the effects of hypoxia will be compounded by climate change, which could accelerate rates of seagrass decline. There is some evidence that seagrass species can recover following prolonged deoxygenation and short-term, extreme anoxia events. For example, increases in seagrass coverage have been linked to significant reductions in anthropogenic nitrogen loads in subtropical Southwest Florida estuaries (Tomasko et al., 2005). Following an anoxic crisis that caused widespread seagrass mortality in Thau Lagoon in the French Mediterranean Sea in 1999, seagrass recovered to previous biomass levels within nine months through colonization by surviving seedlings (Plus et al., 2003). However, consecutive anoxic events are expected to deplete seed banks and limit recovery potential (Plus et al., 2003), particularly in long-lived meadow forming genera such as *Thalassia* that may take decades to recover following disturbance (Walker et al., 2007).

8.8.6.3 Mangrove forests

Global attention to the problem of mangrove destruction for shrimp aquaculture (Figure 8.8.21) has highlighted abandoned ponds as an opportunity for mangrove restoration (McLeod & Salm, 2006). Cessation of shrimp production and restoration of tidal hydrology can alleviate eutrophication and anthropogenic hypoxia from these areas. However, in many areas of the world, mangrove forest destruction for shrimp aquaculture and other land uses continues unimpeded (Lee, 2016). Where shrimp aquaculture is unregulated or poorly regulated, ponds will continue to become anoxic and unsustainable, contributing to hypoxia in mangrove ecosystems and eutrophication in adjacent estuaries (Lee, 2016).

8.8.7 Conclusions / Recommendations

While this review reveals an alarming number of mechanisms and examples by which hypoxia has a negative impact on coral, seagrass, and mangrove habitats, the greater message is that deoxygenation in tropical ecosystems is poorly documented and so many impacts are likely as of yet unrecognized. The actual number of tropical hypoxic ecosystems is likely underestimated by an order of magnitude, and a notable proportion (13%) of coral reefs and associated tropical habitats globally are at risk of being or becoming hypoxic (Altieri et al., 2017) (Figure 8.8.22). Trends in shoreline development, habitat loss, and

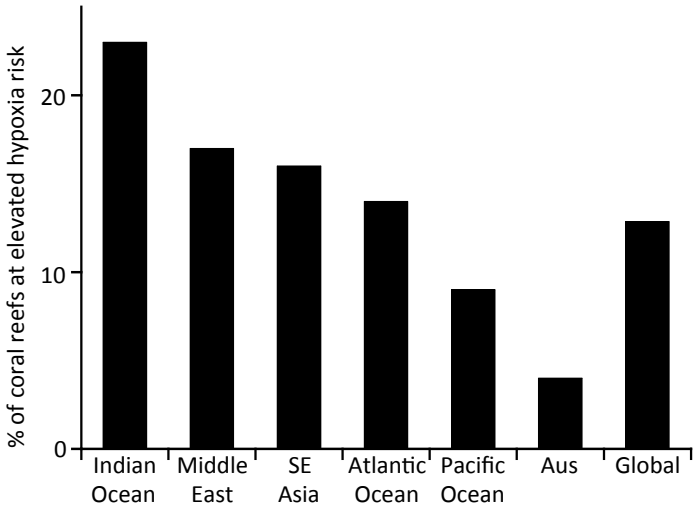

Figure 8.8.22 Percentage of coral reef ecosystems by ecoregions, and worldwide, at risk for hypoxia based on established databases of anthropogenic factors that contribute to hypoxia, including eutrophication and temperature, and coastal geomorphology that promotes stratification and limit exchange with the open ocean. From Altieri et al. (2017).

eutrophication in the tropics, combined with lessons learned from decades of hypoxia development in temperate ecosystems, suggests that the tropics are on a trajectory of increasing deoxygenation impacts but also that the effects are reversible if management efforts can be properly directed (Kemp et al., 2009). There are also some important distinctions regarding hypoxia in the tropics related to temperature, climate dynamics, and the dominant ecological role of biogenic habitats. The deficit of hypoxia research in the tropics and recent documentation of hypoxic events should motivate increased monitoring and research on the topic and its clear links to the well-being of human populations in tropical coastal areas. Below are several important themes to guide future research and management of ocean deoxygenation in tropical ecosystems.

8.8.7.1 Habitat interactions

The focus of this section has been on coral reefs, seagrass beds, and mangrove forests because of their critical role in tropical coastal ecosystems and their importance in mediating the effects of ocean deoxygenation. For simplicity corals, seagrasses, and mangroves are addressed separately in many of the subsections above. However, it is important to recognize that these three habitats often occur in close spatial association and are tightly linked through the exchange of energy, materials, and organisms (Gillis et al., 2014; van de Koppel et al., 2015) (Figure 8.8.23). As a consequence, the spatial configuration of these habitats can influence oxygen dynamics through the import/export of materials and the movement of water. By reviewing these habitats in concert, there are also commonalities that become apparent owing to the structure and function of their foundation species: they are living organisms susceptible to ocean deoxygenation, they have the potential to modify oxygen conditions in and around their structures through their own metabolic gas exchange and modification of flow, and they play host to diverse communities and symbioses that are vulnerable to hypoxia. The generality and fundamental nature of these functions across habitat types suggests tropical ecosystems demand increased management and research to confront the ocean deoxygenation crisis. They also suggest that lessons learned in one habitat may apply to the others which should accelerate further development of a general understanding to govern management and direct future research.

8.8.7.2 Multiple-stressors

A multiple-stressor perspective (Breitburg & Riedel, 2005; Crain et al., 2008) should be applied to ocean deoxygenation in the tropics since hypoxia commonly co-occurs with other stressors. Two co-stressors that are particularly relevant are temperature and acidification because of their interactive physiological effects and their association with the origins of hypoxia, as evident in coral reefs (Nelson & Altieri, 2019). Increased temperatures often drive hypoxic conditions through a variety of mechanisms including decreased oxygen solubility in water and enhanced sediment and macrophyte respiration that consumes oxygen as observed in seagrass beds (Marsh et al., 1986; Zimmerman et al., 1989). The respiration that depletes

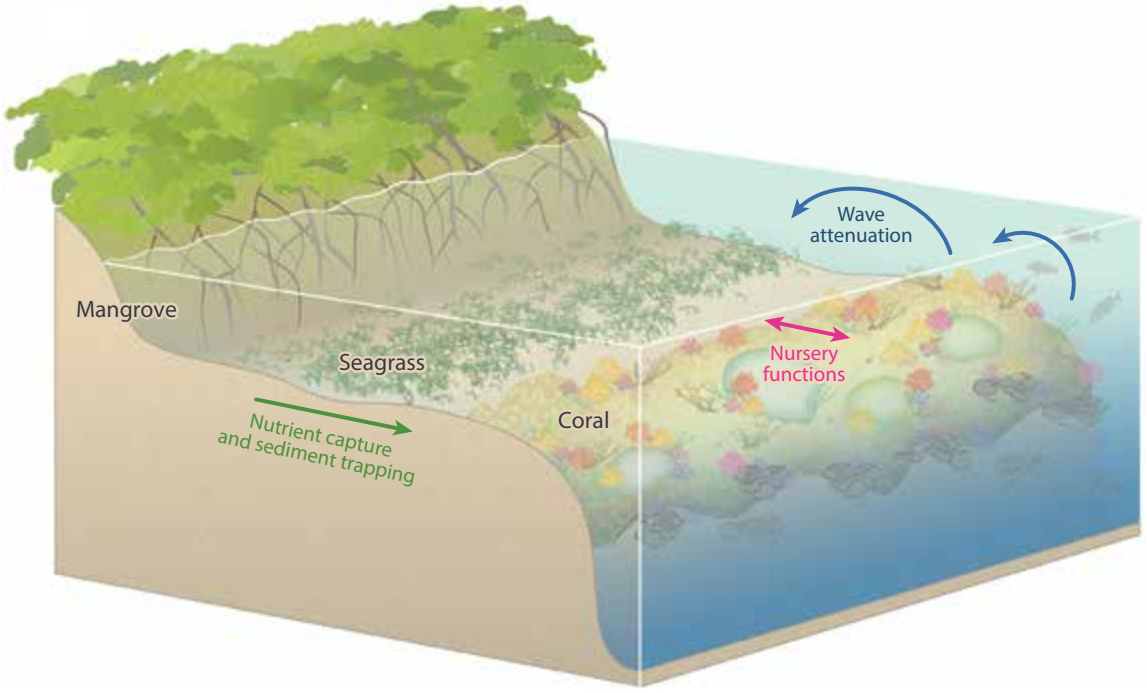

Figure 8.8.23 Various resource exchange and habitat modifications that connects coral reef, seagrass, and mangrove ecosystems. Inputs of nutrients and organic material, as well as the limited exchange from wave attenuation, contribute to oxygen dynamics in each. From van de Koppel et al. (2015).

oxygen also produces carbon dioxide which will locally drive down pH such that oxygen and pH often cycle together, as observed in mangroves (Gedan et al., 2017). The progression of climate change and ocean acidification, and increased vulnerability of organisms to hypoxia under elevated temperatures and increased acidity, suggests that the effects of continuing ocean deoxygenation on tropical marine organisms will become more severe with time.

The synergistic effects of temperature and hypoxic stress have been well documented in temperate organisms as higher temperatures lead to lower tolerance for hypoxia (Vaquer-Sunyer & Duarte, 2011) due in part to increased metabolic demands for oxygen and the oxygen limitation of thermal tolerance (Pörtner, 2010). A first step in developing a broader understanding of the synergisms between temperature and hypoxia tolerance in tropical ecosystems will be establishment of a basic quantitative assessment of their combined effect on mortality as has been done primarily for temperate species (Vaquer-Sunyer & Duarte, 2011). This would determine if the taxa that dominate tropical ecosystems differ in some consistent way, perhaps because of differing evolutionary histories and/or prior exposures to hypoxic environments. Over 90% of documented hypoxic marine ecosystems are in areas predicted to experience over 2 °C warming by the end of this century due to climate change (Altieri & Gedan, 2015). Many tropical species already exist near the edge of their tolerance to oxygen and temperature extremes with narrower tolerances for fluctuations than their temperate counterparts (Johannes & Betzer, 1975). As a consequence, estimates suggest that groups such as tropical seagrasses are at significant risk of local extinction due to combined thermal and low oxygen stress in areas that experience warming (Pedersen et al., 2016).

Ocean acidification (OA) is of particular concern in tropical ecosystems because of the dependence of coral reef construction on calcification that is negatively affected by declines in pH. While a large and growing body of research has considered the synergistic impacts of OA and climate change (Hoegh-Guldberg et al., 2017; Koch et al., 2013; Kroeker et al., 2013), far less has considered the interactions of OA and deoxygenation for coral reefs or other tropical ecosystems. Where they have been examined together experimentally, it was found that hypoxia and low pH acted synergistically to decrease photosynthesis and survivorship of corals (Weber et al., 2012). Dissolved oxygen and pH often co-vary where local respiration rates deplete oxygen and supply carbon dioxide, often reaching or exceeding values not expected in the open ocean for decades or centuries to come (Figure 8.8.24). This local production

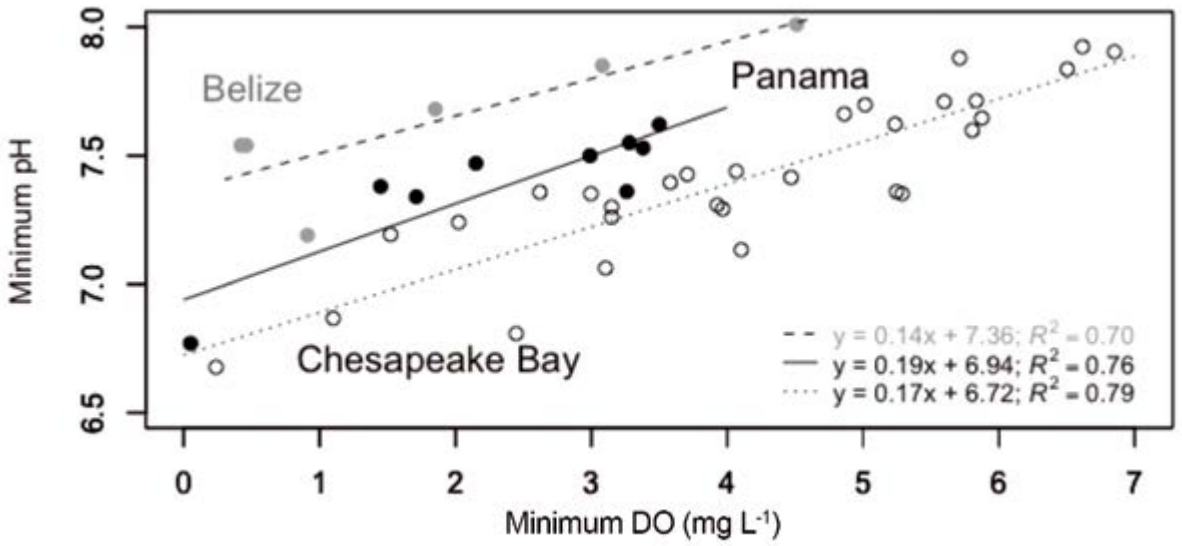

Figure 8.8.24 Correlation between oxygen depletion and pH depression in mangrove ponds. The relationship illustrates the common mechanism (i.e. aerobic respiration) that consumes oxygen and produces carbon dioxide and leads to co-occurring hypoxia and acidification stress. From Gedan et al. (2017).

of carbon dioxide and resultant respiration-driven acidification has the potential to exacerbate the ocean acidification driven by global process, and also offers an opportunity for comparative studies of variation in pH over relatively small spatial and temporal scales. On the other hand, consumption of dissolved carbon dioxide and production of oxygen through photosynthesis by tropical foundation species has the potential to locally counteract the effects of an acidified and hypoxic environment. For example, it has been hypothesized that seagrass beds might provide a local refuge for calcifying organisms such as corals by drawing down carbon dioxide within their canopies, and they may do the same for hypoxic stress if their super-saturation of oxygen in the water column during the day provides at least temporary relief from hypoxic stress (Hendriks et al., 2014). Further research is needed to understand how the physiological effects of oxygen, temperature, and pH (along with salinity and other potential stressors) interact with one another and are modified by foundation species in the tropics.

8.8.7.3 Feedbacks and hysteresis

Mortality and shifts in community composition due to hypoxic conditions at the ecosystem scale can initiate further changes in biogeochemical processes and oxygen depletion. Known examples from tropical

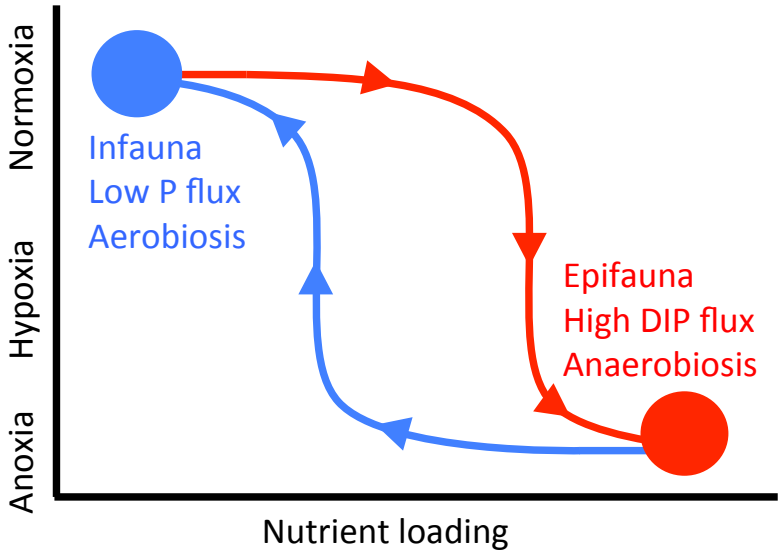

Figure 8.8.25 Diagram of hysteresis in hypoxic ecosystems. Due to feedbacks between oxygen concentration and changes in microbial processes, the return pathway (blue) can differ from the initial impact (red) such that the response to given level of driver can differ and be dependent on prior state. From Conley et al. (2009).

ecosystems include the production of organic material following hypoxia-induced seagrass mortality that fuels further oxygen depletion (Bjork et al., 2008), or the increase in coral death and algal production associated with anaerobic pathogens that further starve environments of oxygen (Dinsdale & Rohwer, 2011) (Figure 8.8.18). These feedbacks can lead to hysteresis in which achieving the threshold value for eutrophication needed to reverse hypoxic conditions may be lower and more difficult to achieve than values that initiated hypoxic conditions (Conley et al., 2009) (Figure 8.8.25). Studies of temperate soft sediment habitats have revealed other feedbacks between sediment oxygen conditions, microbial communities, nutrient cycling and availability, production of organic matter, and development of hypoxic conditions (Middelburg & Levin, 2009). Little is known about such shifts in biogeochemical process in tropical hypoxic ecosystems, and additional research on species tolerances and interactions (for both microbial and metazoan communities) will be necessary for elucidating the full suite of such feedbacks that further modify hypoxic conditions at the local scale.

8.8.7.4 Conclusion

Ocean deoxygenation is affecting tropical coastal ecosystems. Many identified hypoxic ecosystems are in countries at an early stage of economic development where lessons learned about links between agricultural intensification, water treatment, and hypoxia in advanced economies in temperate countries might inform management strategies to avoid future deoxygenation events (Kemp et al., 2009). The dependence of many tropical coastal societies on healthy coral reef, seagrass bed, and mangrove forest ecosystems for services including food provision, storm buffering, and tourism should be motivation for the international community to support the exchange of scientific capacity, management lessons, and intellectual capital. Given the apparent discovery deficit of hypoxic ecosystems in the tropics, it is urgent to document the extent of the problem and the consequences for ecological structure and function. Otherwise there is a risk that hypoxia will alter ecosystems before changes can be quantified, thus leading to "shifting baselines" (*sensu* Dayton et al., 1998) in which our understanding and management of some tropical ecosystems will be distorted by first observations in a degraded state.

Deoxygenation in tropics, by the numbers:

- 75%: Percentage decline in coral diversity in a Panamanian hypoxic dead zone.
- 1,000,000: The number of dead coral reef fish following a single hypoxic event in Australia.
- 13%: Percentage of coral ecosystems worldwide at elevated risk from deoxygenation.
- 8.66 mg O_2 L^{-1}: Swing in dissolved oxygen concentration recorded in a mangrove pond over a 24- hour period from a low of 0.46 to a high of 9.12 mg O_2 L^{-1}.
- USD$127 million: Value of ecosystem services loss from a single event of seagrass die-off associated with hypoxia in Florida.
- 370: Estimated number of undiscovered hypoxic ecosystems in the tropics.

8.8.8 References

Adjeroud, M., Andrefouet, S., & Payri, C. (2001). Mass mortality of macrobenthic communities in the lagoon of Hikueru atoll (French Polynesia). *Coral Reefs*, *19*, 287-291. https://doi.org/10.1007/PL00006962

Aguiar, V.M.D., Neto, J.A.B., & Rangel, C.M. (2011). Eutrophication and hypoxia in four streams discharging in Guanabara Bay, RJ, Brazil, a case study. *Marine Pollution Bulletin*, *62,* 1915-1919. https://doi.org/10.1016/j.marpolbul.2011.04.035

Al-Horani, F.A., Tambutte, E., & Allemand, D. (2007). Dark calcification and the daily rhythm of calcification in the scleractinian coral, *Galaxea fascicularis*. *Coral Reefs, 26,* 531-538. https://doi.org/10.1007/s00338-007-0250-x

Alongi, D.M. (2002). Present state and future of the world's mangrove forests. *Environmental Conservation, 29,* 331-349. https://doi.org/10.1017/S0376892902000231

Altieri, A.H., & Gedan, K.B. (2015). Climate change and dead zones. *Global Change Biology, 21*, 1395-1406. https://doi.org/10.1111/gcb.12754

Altieri, A.H., Harrison, S.B., Seemann, J., Collin, R., Diaz, R.J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America, 114,* 3660-3665. https://doi.org/10.1073/pnas.1621517114

Altieri, A.H., & Van De Koppel, J. (2013). Foundation species in marine ecosystems. In M.D. Bertness, J.F. Bruno, B.R. Silliman, & J.J. Stachowicz (Eds.). pp. 37-56. Marine Community Ecology and Conservation. Sinauer Associates, Sunderland, Massachusetts. https://doi.org/10.1111/maec.12240

Altieri, A.H., & Witman, J.D. (2006). Local extinction of a foundation species in a hypoxic estuary: Integrating individuals to ecosystem. *Ecology, 87,* 717-730. https://doi.org/10.1890/05-0226

Andrefouet, S., Dutheil, C., Menkes, C.E., Bador, M., & Lengaigne, M. (2015). Mass mortality events in atoll lagoons: environmental

control and increased future vulnerability. *Global Change Biology, 21*, 195-205. https://doi.org/10.1111/gcb.12699

Banner, A.H. (1968). A fresh-water "kill" on the coral reefs of Hawaii. Hawaii Institute of Marine Biology, University of Hawaii, Technical Report 15.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., & Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*, 169-193. https://doi.org/10.1890/10-1510.1

Barott, K., Smith, J., Dinsdale, E., Hatay, M., Sandin, S., & Rohwer, F. (2009). Hyperspectral and physiological analyses of coral-algal interactions. *PLoS ONE, 4*, e8043. https://doi.org/10.1371/journal.pone.0008043

Barott, K.L., & Rohwer, F.L. (2012). Unseen players shape benthic competition on coral reefs. *Trends in Microbiology, 20,* 621-628. https://doi.org/10.1016/j.tim.2012.08.004

Baumann, H., Wallace, R.B., Tagliaferri, T., & Gobler, C.J. (2015). Large Natural pH, CO_2 and O_2 fluctuations in a temperate tidal salt marsh on diel, seasonal, and interannual time scale. *Estuaries and Coasts, 38,* 220-231. https://doi.org/10.1007/s12237-014-9800-y

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., … Weinstein, M.R. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience, 51,* 633-641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Bell, G.W., Eggleston, B.B., & Wolcott, T.G. (2003). Behavioral responses of free-ranging blue crabs to episodic hypoxia. I. Movement. *Marine Ecology-Progress Series, 259,* 215-225. https://doi.org/10.3354/meps259215

Bell, G.W., Kronen, M., Vunisea, A., Nash, W.J., Keeble, G., Demmke, A., … Andrefouet, S. (2009). Planning the use of fish for food security in the Pacific. *Marine Policy, 33,* 64-76. https://doi.org/10.1016/j.marpol.2008.04.002

Bellwood, D.R., Hughes, T.P., Folke, C., & Nystrom, M. (2004). Confronting the coral reef crisis. *Nature, 429,* 827-833. https://doi.org/10.1038/nature02691

Bertness, M.D., Gaines, S.D., & Hay, M.E. (Eds.). (2001). *Marine Community Ecology.* Sinauer Associates, Sunderland, Massachusetts.

Best, M.A., Wither, A.W., & Coates, S. (2007). Dissolved oxygen as a physico-chemical supporting element in the Water Framework Directive. *Marine Pollution Bulletin, 55,* 53-64. https://doi.org/10.1016/j.marpolbul.2006.08.037

Biao, X., & Kaijin, Y. (2007). Shrimp farming in China: Operating characteristics, environmental impact and perspectives. *Ocean & Coastal Management, 50,* 538-550. https://doi.org/10.1016/j.ocecoaman.2007.02.006

Bjork, M., Short, F., McLeod, E., & Beer, S. (2008). *Managing seagrasses for resilience to climate change*. Gland, Switzerland.

Borum, J., Pedersen, O., Greve, T.M., Frankovich, T.A., Zieman, J.C., Fourqurean, J.W., & Madden, C. J. (2005). The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology, 93,* 148-158. https://doi.org/10.1111/j.1365-2745.2004.00943.x

Borum, J., Sand-Jensen, K., Binzer, T., Pedersen, O., & Greve, T.M. (2007). Oxygen movement in seagrasses. In A.W.D. Larkum, R.J. Orth, & C.M. Duarte (Eds.). *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, pp. 255-270. https://doi.org/10.1007/1-4020-2983-7_10

Boto, K.G., & Wellington, J.T. (1988). Seasonal-variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated, mangrove waterway. *Marine Ecology Progress Series, 50,* 151-160. https://doi.org/10.3354/meps050151

Breitburg, D., Levin, L.A., Oschlies, A., Gregoire, M., Chavez, F., Conley, D.J., … Zhang, J. (2018). Declining oxygen in global ocean and coastal waters. *Science, 359,* eaam7240. https://doi.org/10.1126/science.aam7240

Breitburg, D.L., Hondorp, D.W., Davias, L.A., & Diaz, R.J. (2009). Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Annual Review of Marine Science, 1,* 329-349. https://doi.org/10.1146/annurev.marine.010908.163754

Breitburg, D.L., & Riedel, G.F. (2005). Multiple stressors in marine systems. In E.A. Norse & L.B. Crowder (Eds.). *Marine Conservation Biology.* pp. 167-182, Island Press, Washington, D.C.

Brown, A.L., & Carpenter, R.C. (2013). Water-flow mediated oxygen dynamics within massive *Porites*-algal turf interactions. *Marine Ecology Progress Series, 490,* 1-10. https://doi.org/10.3354/meps10467

Bruno, J.F., & Bertness, M.D. (2001). Habitat modification and facilitation in benthic marine communities. In M.D. Bertness, S.D. Gaines, & M.E. Hay (Eds.). *Marine Community Ecology*. pp. 201-220, Sinauer Associates, Sunderland, Massachusetts.

Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D., … Melendy, A.M. (2007). Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology, 5,* 1220-1227. https://doi.org/10.1371/journal.pbio.0050124

Burkholder, J.M., Tomasko, D.A., & Touchette, B.W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology, 350,* 46-72. https://doi.org/10.1016/j.jembe.2007.06.024

Camp, E.F., Nitschke, M.R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S.G., Smith, D.J., … Suggett, D.J. (2017). Reef-building corals thrive within hot-acidified and deoxygenated waters. *Scientific Reports, 7,* 2434. https://doi.org/10.1038/s41598-017-02383-y

Carlson, P.R., Yarbro, L.A., & Barber, T.R. (1994). Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bulletin of Marine Science, 54,* 733-746.

Carlton, R.G., & Richardson, L.L. (1995). Oxygen and sulfide dynamics in horizontally migrating cyanobacterial mat: Black band disease of corals. *FEMS Microbiology Ecology, 18*, 155-162. https://doi.org/10.1111/j.1574-6941.1995.tb00173.x

Chambers, R.A., Fourqurean, J.W., Macko, S.A., & Hoppenot, R. (2001). Biogeochemical effects of iron availability on primary producers in a shallow marine carbonate environment. *Limnology and Oceanography, 46,* 1278-1286. https://doi.org/10.4319/lo.2001.46.6.1278

Colombo-Pallotta, M.F., Rodriguez-Roman, A., & Iglesias-Prieto, R. (2010). Calcification in bleached and unbleached Montastraea

faveolata: evaluating the role of oxygen and glycerol. *Coral Reefs, 29,* 899-907. https://doi.org/10.1007/s00338-010-0638-x

Conley, D.J., Carstensen, J., Vaquer-Sunyer, R., & Duarte, C.M. (2009). Ecosystem thresholds with hypoxia. *Hydrobiologia, 629,* 21-29. https://doi.org/10.1007/s10750-009-9764-2

Crain, C.M., Kroeker, K., & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters, 11,* 1304-1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Dayton, P., Tegner, M., Edwards, P., & Riser, K. (1998). Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications, 8*, 309-322. https://doi.org/10.1890/1051-0761(1998)008[0309:SBGARE]2.0.CO;2

Dayton, P.K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos of McMurdo Sound, Antarctica. In B.C. Parker (Ed.). *Proceedings of the Colloquium on Conservation Problems in Antarctica.* Allen Press, Lawrence, KS, pp. 81-95.

de la Torre-Castro, M., & Ronnback, P. (2004). Links between humans and seagrasses - an example from tropical East Africa. *Ocean & Coastal Management*, *47*, 361-387. https://doi.org/10.1016/j.ocecoaman.2004.07.005

Diaz, R.J., & Rosenberg, R. (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology - an Annual Review, 33*, 245-303.

Diaz, R.J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science, 321,* 926-929. https://doi.org/10.1126/science.1156401

Diaz, R.J., Selman, M., & Chique, C. (2011). Global eutrophic and hypoxic coastal systems. World Resources Institute. Eutrophication and hypoxia: Nutrient pollution in coastal waters.

Diehl, W.J., McEdward, L., Proffitt, E., Rosenberg, V., & Lawrence, J.M. (1979). Response of *Ludia clathrata* (Echinodermata, Asteroidea) to hypoxia. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology, 62,* 669-671. https://doi.org/10.1016/0300-9629(79)90122-1

Dierberg, F.E., & Kiattisimkul, W. (1996). Issues, impacts, and implications of shrimp aquaculture in Thailand. *Environmental Management, 20*, 649-666. https://doi.org/10.1007/BF01204137

Dinsdale, E.A., & Rohwer, F. (2011). Fish or germs? Microbial dynamics associated with changing trophic structure on coral reefs. In Z. Dubinsky & N. Stambler (Eds.). *Coral Reefs: An Ecosystem in Transition.* Springer, Netherlands, pp. 231-240. https://doi.org/10.1007/978-94-007-0114-4_16

Dodds, L.A., Roberts, J.M., Taylor, A.C., & Marubini, F. (2007). Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *Journal of Experimental Marine Biology and Ecology, 349,* 205-214. https://doi.org/10.1016/j.jembe.2007.05.013

Dunson, W.A., & Dunson, D.B. (1999). Factors influencing growth and survival of the killifish, *Rivulus marmoratus*, held inside enclosures in mangrove swamps. *Copeia, 1999,* 661-668. https://doi.org/10.2307/1447598

Dupont, J.M., Hallock, P., & Jaap, W.C. (2010). Ecological impacts of the 2005 red tide on artificial reef epibenthic macroinvertebrate and fish communities in the eastern Gulf of Mexico. *Marine Ecology Progress Series, 415,* 189-200. https://doi.org/10.3354/meps08739

Durako, M.J. (1994). Seagrass die-off in Florida Bay (USA) - Changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. *Marine Ecology Progress Series, 110,* 59-66. https://doi.org/10.3354/meps110059

Durako, M.J., & Kuss, K.M. (1994). Effects of *Labyrinthula* infection on the photosynthetic capacity of *Thalassia testudinum*. *Bulletin of Marine Science, 54,* 727-732.

Ewel, K.C., Twilley, R.R., & Ong, J.E. (1998). Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters, 7,* 83-94. https://doi.org/10.2307/2997700

Ferdie, M., & Fourqurean, J.W. (2004). Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. *Limnology and Oceanography, 49*, 2082-2094. https://doi.org/10.4319/lo.2004.49.6.2082

Gambi, C., Bianchelli, S., Perez, M., Invers, O., Ruiz, J.M., & Danovaro, R. (2009). Biodiversity response to experimental induced hypoxic-anoxic conditions in seagrass sediments. *Biodiversity and Conservation, 18,* 33-54. https://doi.org/10.1007/s10531-008-9433-1

Gardella, D.J., & Edmunds, P.J. (1999). The oxygen microenvironment adjacent to the tissue of the scleractinian *Dichocoenia stokesii* and its effects on symbiont metabolism. *Marine Biology, 135*, 289-295. https://doi.org/10.1007/s002270050626

Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A., & Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science, 301,* 958-960. https://doi.org/10.1126/science.1086050

Gedan, K.B., Altieri, A.H., Feller, I.C., Burrell, R., & Breitburg, D. (2017). Community composition in mangrove ponds with pulsed hypoxic and acidified conditions. *Ecosphere, 8*, e02053. https://doi.org/10.1002/ecs2.2053

Genin, A., Lazar, B., & Brenner, S. (1995). Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature, 377*, 507-510. https://doi.org/10.1038/377507a0

Gillis, L.G., Bouma, T.J., Jones, C.G., van Katwijk, M.M., Nagelkerken, I., Jeuken, C.J.L., … Ziegler, A.D. (2014). Potential for landscape-scale positive interactions among tropical marine ecosystems. *Marine Ecology Progress Series, 503*, 289-303. https://doi.org/10.3354/meps10716

Glas, M.S., Sato, Y., Ulstrup, K.E., & Bourne, D.G. (2012). Biogeochemical conditions determine virulence of black band disease in corals. *ISME Journal, 6,* 1526-1534. https://doi.org/10.1038/ismej.2012.2

Goldshmid, R., Holzman, R., Weihs, D., & Genin, A. (2004). Aeration of corals by sleep-swimming fish. *Limnology and Oceanography, 49*, 1832-1839. https://doi.org/10.4319/lo.2004.49.5.1832

Gregg, A.K., Hatay, M., Haas, A.F., Robinett, N.L., Barott, K., Vermeij, M.J.A., … Rohwer, F. (2013). Biological oxygen demand optode analysis of coral reef-associated microbial communities exposed to algal exudates. *PeerJ, 1,* e107. https://doi.org/10.7717/peerj.107

Greve, T.M., Borum, J., & Pedersen, O. (2003). Meristematic oxygen variability in eelgrass (*Zostera marina*). *Limnology and Oceanography, 48,* 210-216. https://doi.org/10.4319/lo.2003.48.1.0210

Gunawardena, M., & Rowan, J.S. (2005). Economic valuation of a mangrove ecosystem threatened by shrimp aquaculture in Sri Lanka. *Environmental Management, 36,* 535-550. https://doi.org/10.1007/s00267-003-0286-9

Guzman, H.M., Cortes, J., Glynn, P.W. & Richmond, R.H. (1990). Coral mortality associated with dinoflagellate blooms in the Easter Pacific (Coast Rica and Panama). *Marine Ecology Progress Series, 60,* 299-303. https://doi.org/10.3354/meps060299

Haas, A.F., Gregg, A.K., Smith, J.E., Abieri, M.L., Hatay, M., & Rohwer, F. (2013). Visualization of oxygen distribution patterns caused by coral and algae. *PeerJ, 1,* e106. https://doi.org/10.7717/peerj.106

Haas, A.F., Jantzen, C., Naumann, M.S., Iglesias-Prieto, R., & Wild, C. (2010). Organic matter release by the dominant primary producers in a Caribbean reef lagoon: implication for in situ O_2 availability. *Marine Ecology Progress Series, 409,* 27-39. https://doi.org/10.3354/meps08631

Haas, A.F., Nelson, C.E., Kelly, L.W., Carlson, C.A., Rohwer, F., Leichter, J.J., … Smith, J.E. (2011). Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS ONE, 6,* e27973. https://doi.org/10.1371/journal.pone.0027973

Haas, A.F., Smith, J.E., Thompson, M., & Deheyn, D.D. (2014). Effects of reduced dissolved oxygen concentrations on physiology and fluorescence of hermatypic corals and benthic algae. *PeerJ, 2,* e235. https://doi.org/10.7717/peerj.235

Hall, M.O., Durako, M.J., Fourqurean, J.W., & Zieman, J.C. (1999). Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries, 22*, 445-459. https://doi.org/10.2307/1353210

Harper, S.L., & Reiber, C. (1999). Influence of hypoxia on cardiac functions in the grass shrimp (*Palaemonetes pugio* Holthuis). *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology, 124,* 569-573. https://doi.org/10.1016/S1095-6433(99)00151-8

Heck, K.L., Carruthers, T.J.B., Duarte, C.M., Hughes, A.R., Kendrick, G., Orth, R.J., & Williams, S.W. (2008). Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems, 11,* 1198-1210. https://doi.org/10.1007/s10021-008-9155-y

Heck, K.L., Hays, G., & Orth, R.J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series, 253,* 123-136. https://doi.org/10.3354/meps253123

Hemminga, M.A., & Duarte, C.M. (2000). *Seagrass Ecology*. Cambridge University Press. https://doi.org/10.1017/CBO9780511525551

Hendriks, I.E., Olsen, Y.S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T.S., … Duarte., C.M. (2014). Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences, 11,* 333-346. https://doi.org/10.5194/bg-11-333-2014

Herbeck, L.S., Unger, D., Krumme, U., Liu, S.M., & Jennerjahn, T.C. (2011). Typhoon-induced precipitation impact on nutrient and suspended matter dynamics of a tropical estuary affected by human activities in Hainan, China. *Estuarine, Coastal and Shelf Science, 93*, 375-388. https://doi.org/10.1016/j.ecss.2011.05.004

Hobbs, J.-P.A., & Macrae, H. (2012). Unusual weather and trapped coral spawn lead to fish kill at a remote coral atoll. *Coral Reefs, 31*, 961-961. https://doi.org/10.1007/s00338-012-0918-8

Hobbs, J.-P.A., & McDonald, C.A. (2010). Increased seawater temperature and decreased dissolved oxygen triggers fish kill at the Cocos (Keeling) Islands, Indian Ocean. *Journal of Fish Biology, 77*, 1219-1229. https://doi.org/10.1111/j.1095-8649.2010.02726.x

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., … Hatziolos, M.E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science, 318,* 1737-1742. https://doi.org/10.1126/science.1152509

Hoegh-Guldberg, O., Poloczanska, E.S., Skirving, W.J., & Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science, 4,* 158. https://doi.org/10.3389/fmars.2017.00158

Holmer, M., & Bondgaard, E.J. (2001). Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. *Aquatic Botany, 70,* 29-38. https://doi.org/10.1016/S0304-3770(00)00142-X

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., … Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science, 301*, 929-933. https://doi.org/10.1126/science.1085046

Johannes, R.E., & Betzer, S.B. (1975). Chapter 1. Introduction: Marine communities respond differently to pollution in the tropics than at higher latitudes. *Tropical Marine Pollution, 12,* 1-12. https://doi.org/10.1016/S0422-9894(08)71106-1

Johnson, M.D., Rodriguez, L.M., & Altieri, A.H. (2018). Shallow-water hypoxia and mass mortality on a Caribbean coral reef. *Bulletin of Marine Science, 94,* 143-144. https://doi.org/10.5343/bms.2017.1163

Johnston, D., Lourey, M., Van Tien, D., Luu, T.T., & Xuan, T.T. (2002). Water quality and plankton densities in mixed shrimp-mangrove forestry farming systems in Vietnam. *Aquaculture Research, 33,* 785-798. https://doi.org/10.1046/j.1365-2109.2002.00722.x

Jokiel, P.L., Hunter, C.L., Taguchi, S., & Watarai, L. (1993). Ecological impact of a fresh-water reef kill in Kanehohe Bay, Oahu, Hawaii. *Coral Reefs, 12,* 177-184. https://doi.org/10.1007/BF00334477

Kemp, W.M., Testa, J.M., Conley, D.J., Gilbert, D., & Hagy, J.D. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences, 6,* 2985-3008. https://doi.org/10.5194/bg-6-2985-2009

Kinsey, D.W., & Kinsey, B.E. (1967). Diurnal changes in oxygen content of water over coral reef platform at Heron 1. *Australian Journal of Marine and Freshwater Research, 18,* 23-34. https://doi.org/10.1071/MF9670023

Klein, S.G., Pitt, K.A., Nitschke, M.R., Goyen, S., Welsh, D.T., Suggett, D.J., & Carroll, A.J. (2017). *Symbiodinium* mitigate the combined effects of hypoxia and acidification on a noncalcifying cnidarian.

Global Change Biology, 23, 3690-3703. https://doi.org/10.1111/gcb.13718

Knight, J.M., Griffin, L., Dale, P.E.R., & Sheaves, M. (2013). Short-term dissolved oxygen patterns in sub-tropical mangroves. *Estuarine Coastal and Shelf Science, 131,* 290-296. https://doi.org/10.1016/j.ecss.2013.06.024

Koch, M., Bowes, G., Ross, C., & Zhang, X.H. (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology, 19*, 103-132. https://doi.org/10.1111/j.1365-2486.2012.02791.x

Koch, M.S., & Erskine, J.M. (2001). Sulfide as a phytotoxin to the tropical seagrass *Thalassia testudinum*: interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology, 266,* 81-95. https://doi.org/10.1016/S0022-0981(01)00339-2

Koch, M.S., Schopmeyer, S., Kyhn-Hansen, C., & Madden, C.J. (2007a). Synergistic effects of high temperature and sulfide on tropical seagrass. *Journal of Experimental Marine Biology and Ecology, 341,* 91-101. https://doi.org/10.1016/j.jembe.2006.10.004

Koch, M.S., Schopmeyer, S.A., Holmer, M., Madden, C.J., & Kyhn-Hansen, C. (2007b). *Thalassia testudinum* response to the interactive stressors hypersalinity, sulfide and hypoxia. *Aquatic Botany, 87,* 104-110. https://doi.org/10.1016/j.aquabot.2007.03.004

Krebs, J.M., McIvor, C.C., & Bell, S.S. (2014). Nekton community structure varies in response to coastal urbanization near mangrove tidal tributaries. *Estuaries and Coasts, 37,* 815-831. https://doi.org/10.1007/s12237-013-9726-9

Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., … Gattuso, J.-P. (2013). Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology, 19,* 1884-1896. https://doi.org/10.1111/gcb.12179

Kuempel, C.D., & Altieri, A.H. (2017). The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific Reports, 7*, 39670. https://doi.org/10.1038/srep39670

Kuhl, M., Cohen, Y., Dalsgaard, T., Jorgensen, B.B., & Revsbech, N.P. (1995). Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O_2, pH and light. *Marine Ecology Progress Series, 117,* 159-172. https://doi.org/10.3354/meps117159

Laboy-Nieves, E.N., Klein, E., Conde, J.E., Losada, F., Cruz, J.J., & Bone, D. (2001). Mass mortality of tropical marine communities in Morrocoy, Venezuela. *Bulletin of Marine Science, 68,* 163-179.

Lapointe, B.E., & Clark, M.W. (1992). Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries, 15,* 465-476. https://doi.org/10.2307/1352391

Lee, S.Y. (2016). From blue to black: Anthropogenic forcing of carbon and nitrogen influx to mangrove-lined estuaries in the South China Sea. *Marine Pollution Bulletin, 109*, 682-690. https://doi.org/10.1016/j.marpolbul.2016.01.008

Lenihan, H.S. (1999). Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecological Monographs, 69,* 251-275. https://doi.org/10.1890/0012-9615(1999)069[0251:PBCOOR]2.0.CO;2

Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., … Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences, 6,* 2063-2098. https://doi.org/10.5194/bg-6-2063-2009

Llanso, R.J., & Diaz, R.J. (1994). Tolerance to low dissolved oxygen by the tubicolous polychaete *Loimia medusa*. *Journal of the Marine Biological Association of the United Kingdom, 74*, 143-148. https://doi.org/10.1017/S0025315400035724

Loya, Y. (2004). The coral reefs of Eilat - past, present, and future: three decades of coral community structure studies. In E. Rosenberg & Y. Loya (Eds.). Coral Health and Disease. Springer-Verlag, Berlin, pp. 1-34. https://doi.org/10.1007/978-3-662-06414-6_1

Lu, C.Q., & Tian, H.Q. (2017). Global nitrogen and phosphorus fertilizer use for agriculture production in the past half century: shifted hot spots and nutrient imbalance. *Earth System Science Data, 9,* 181-192. https://doi.org/10.5194/essd-9-181-2017

Marsh, J.A., Dennison, W.C., & Alberte, R.S. (1986). Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *Journal of Experimental Marine Biology and Ecology, 101*, 257-267. https://doi.org/10.1016/0022-0981(86)90267-4

Mattone, C., & Sheaves, M. (2017). Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests. *Estuarine, Coastal and Shelf Science, 197*, 205-213. https://doi.org/10.1016/j.ecss.2017.08.028

Mayer, A.G. (1917). Is death from high temperature due to the accumulation of acid in the tissues? *American Journal of Physiology, 44,* 581-585. https://doi.org/10.1152/ajplegacy.1917.44.4.581

McKee, K.L. (1993). Soil physicochemical patterns and mangrove species distribution: reciprocal effects. *Journal of Ecology, 81,* 477-487. https://doi.org/10.2307/2261526

McKee, K.L. (1996). Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. *Tree Physiology, 16,* 883-889. https://doi.org/10.1093/treephys/16.11-12.883

McKee, K.L., Mendelssohn, I.A., & Hester, M.W. (1988). Reexamination of pore water sulfide concentrations and redox potential near the aerial roots of *Rhizophora mangle* and *Avecennia germinans*. *American Journal of Botany, 75*, 1352-1359. https://doi.org/10.1002/j.1537-2197.1988.tb14196.x

McLeod, E., & Salm, R.V. (2006). *Managing mangroves for resilience to climate change.* Gland, Switzerland.

MEA. (2005a). Millennium Ecosystem Assessment (MEA). Ecosystems and Human Well-being: Coastal Ecosystems. World Resources Institute, Washington, D.C.

MEA. (2005b). Millennium Ecosystem Assessment (MEA). Ecosystems and Human Well-being: Wetlands and Water., World Resources Institute, Washington, D.C.

Mialhe, F., Gunnell, Y., & Mering, C. (2013). The impacts of shrimp farming on land use, employment and migration in Tumbes, northern Peru. *Ocean & Coastal Management, 73,* 1-12. https://doi.org/10.1016/j.ocecoaman.2012.12.014

Middelburg, J.J., & Levin, L.A. (2009). Coastal hypoxia and sediment biogeochemistry. *Biogeosciences, 6,* 1273-1293. https://doi.org/10.5194/bg-6-1273-2009

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics, 29,* 215-233. https://doi.org/10.1016/S0921-8009(99)00009-9

Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A.,. … Llewellyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature, 427*, 533-536. https://doi.org/10.1038/nature02286

Munday, P.L., Jones, G.P., Pratchett, M.S., & Williams, A.J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries, 9,* 261-285. https://doi.org/10.1111/j.1467-2979.2008.00281.x

Nelson, H.R., & Altieri, A.H. (2019). Oxygen: The universal currency on coral reefs. *Coral Reefs, 38,* 177-198. https://doi.org/10.1007/s00338-019-01765-0

Nelson, H.R., Kuempel, C.D., & Altieri, A.H. (2016). The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere, 7*, e1399. https://doi.org/10.1002/ecs2.1399

Niggl, W., Naumann, M.S., Struck, U., Manasrah, R., & Wild, C. (2010). Organic matter release by the benthic upside-down jellyfish Cassiopea sp fuels pelagic food webs in coral reefs. *Journal of Experimental Marine Biology and Ecology, 384,* 99-106. https://doi.org/10.1016/j.jembe.2010.01.011

Nilsson, G.E., Hobbs, J.P., Munday,P.L., & Ostlund-Nilsson, S. (2004). Coward or braveheart: extreme habitat fidelity through hypoxia tolerance in a coral-dwelling goby. *Journal of Experimental Biology, 207,* 33-39. https://doi.org/10.1242/jeb.00713

Nilsson, G.E., Hobbs, J.P.A., Ostlund-Nilsson, S., & Munday, P.L. (2007). Hypoxia tolerance and air-breathing ability correlate with habitat preference in coral-dwelling fishes. *Coral Reefs, 26*, 241-248. https://doi.org/10.1007/s00338-006-0167-9

Nixon, S.W., & Oviatt, C.A. (1973). Ecology of a New England salt marsh. *Ecological Monographs, 43,* 463-498. https://doi.org/10.2307/1942303

Ohde, S., & van Woesik, R. (1999). Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bulletin of Marine Science, 65*, 559-576.

Okamura, K., Tanaka, K., Siow, R., Man, A., Kodama, M., & Ichikawa, T. (2010). Spring tide hypoxia with relation to chemical properties of the sediments in the Matang mangrove estuary, Malaysia. *Jarq-Japan Agricultural Research Quarterly, 44,* 325-333. https://doi.org/10.6090/jarq.44.325

Onton, K., Page, C.A., Wilson, S.K., Neale, S., & Armstrong, S. (2011). Distribution and drivers of coral disease at Ningaloo reef, Indian Ocean. *Marine Ecology Progress Series, 433,* 75-84. https://doi.org/10.3354/meps09156

Orr, A.P., & Moorhouse, F.W. (1933). a. Variations in some chemical and physical conditions on a near Low Isles reef. b. The temperature of the water in the Anchorage, Low Isles. c. Physical and chemical conditions in the mangrove swamps. *Scientific Report / Great Barrier Reef Expedition, 2,* 87-110.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., … Williams, S.L. (2006). A global crisis for seagrass ecosystems. *Bioscience, 56,* 987-996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Pastorok, R.A., & Bilyard, G.R. (1985). Effects of sewage pollution on coral reef communities. *Marine Ecology Progress Series, 21,* 175-189. https://doi.org/10.3354/meps021175

Paul, B.G., & Vogl, C.R. (2011). Impacts of shrimp farming in Bangladesh: Challenges and alternatives. *Ocean & Coastal Management, 54,* 201-211. https://doi.org/10.1016/j.ocecoaman.2010.12.001

Pedersen, O., Binzer, T., & Borum, J. (2004). Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant Cell and Environment, 27,* 595-602. https://doi.org/10.1111/j.1365-3040.2004.01173.x

Pedersen, O., Borum, J., Duarte, C.M., &. Fortes, M.D. (1998). Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. *Marine Ecology Progress Series, 169,* 283-288. https://doi.org/10.3354/meps169283

Pedersen, O., Colmer, T.D., Borum, J., Zavala-Perez, A., & Kendrick, G.A. (2016). Heat stress of two tropical seagrass species during low tides - impact on underwater net photosynthesis, dark respiration and diel in situ internal aeration. *New Phytologist, 210*, 1207-1218. https://doi.org/10.1111/nph.13900

Perez, M., Garcia, T., Invers, O., & Ruiz, J.M. (2008). Physiological responses of the seagrass *Posidonia oceanica* as indicators of fish farm impact. *Marine Pollution Bulletin, 56,* 869-879. https://doi.org/10.1016/j.marpolbul.2008.02.001

Peterson, M.S. (1990). Hypoxia-induced physiological changes in two mangrove swamp fishes: sheepshead minnow, *Cyprinodon variegatus* Lacepede and Sailfin Molly, *Poecilia latipinna* (Lesueur). *Comparative Biochemistry And Physiology A-Physiology, 97*, 17-21. https://doi.org/10.1016/0300-9629(90)90715-5

Plaisance, L., Caley, M.J., Brainard, R.E., & Knowlton, N. (2011). The Diversity of Coral Reefs: What Are We Missing? *PLoS ONE, 6,* e25026. https://doi.org/10.1371/journal.pone.0025026

Plus, M., Deslous-Paoli, J.M., & Dagault, F. (2003). Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany, 77,* 121-134. https://doi.org/10.1016/S0304-3770(03)00089-5

Pörtner, H.-O. (2010). Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology, 213,* 881-893. https://doi.org/10.1242/jeb.037523

Pregnall, A.M., Smith, R.D., Kursar, T.A., & Alberte, R.S. (1984). Metabolic adaptation of *Zostera marina* (eelgrass) to diurnal periods of root anoxia. *Marine Biology, 83*, 141-147. https://doi.org/10.1007/BF00394721

Rabalais, N.N., Diaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., & Zhang, J. (2010). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences, 7,* 585-619. https://doi.org/10.5194/bg-7-585-2010

Ralph, P.J., Tomasko, D.A., Moore, K., Seddon, S., & Macinnis-Ng, C.M. (2007). Human impacts on seagrasses: eutrophication, sedimentation, and contamination. In A.W.D. Larkum, R.J. Orth, & C.M. Duarte (Eds.). *Seagrasses: biology, ecology and conservation.* Springer, Dordrecht, pp. 567-593. https://doi.org/10.1007/1-4020-2983-7_24

Reaka-Kudla, M.L. (1997). The global biodiversity of coral reefs: A comparison with rain forests. In M.L. Reaka-Kudla, D.E. Wilson, & E.O. Wilson (Eds.). *Biodiversity II*. Joseph Henry Press, Washington, D.C, pp. 83-108.

Robblee, M.B., Barber, T.R., Carlson, P.R., Durako, M.J., Fourqurean, J.W., Muehlstein, L.K., ... Zieman, J.C. (1991). Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series, 71,* 297-299. https://doi.org/10.3354/meps071297

Rogers, C.S., Miller, J., Muller, E.M., Edmunds, P., Nemeth, R.S., Beets, J.P., … Voss, J.D. (2008). Ecology of coral reefs in the US Virgin Islands. In B.M. Riegl & R.E. Dodge (Eds.). *Coral Reefs of the USA.* Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-6847-8_8

Ronnback, P. (1999). The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics, 29,* 235-252. https://doi.org/10.1016/S0921-8009(99)00016-6

Routley, M.H., Nilsson, G.E., & Renshaw, G.M.C. (2002). Exposure to hypoxia primes the respiratory and metabolic responses of the epaulette shark to progressive hypoxia. *Comparative Biochemistry and Physiology A-Molecular and Integrative Physiology, 131*, 313-321. https://doi.org/10.1016/S1095-6433(01)00484-6

Rutherford, L.D., & Thuesen, E.V. (2005). Metabolic performance and survival of medusae in estuarine hypoxia. *Marine Ecology Progress Series, 294,* 189-200. https://doi.org/10.3354/meps294189

Samonte-Tan, G.P.B., White, A.T., Tercero, M.A., Diviva, J., Tabara, E., & Caballes, C. (2007). Economic valuation of coastal and marine resources: Bohol Marine Triangle, Philippines. *Coastal Management, 35,* 319-338. https://doi.org/10.1080/08920750601169634

Sassaman, C., & Mangum, C.P. (1973). Relationship between aerobic and anaerobic metabolism in estuarine anemones. *Comparative Biochemistry and Physiology, 44,* 1313-1319. https://doi.org/10.1016/0300-9629(73)90270-3

Seddon, S., Connolly, R.M., & Edyvane, K.S. (2000). Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany, 66*, 297-310. https://doi.org/10.1016/S0304-3770(99)00080-7

Shashar, N., Cohen, Y., & Loya, Y. (1993). Extreme diel fluctuations of oxygen in diffusive boundary layers surrounding stony corals. *Biological Bulletin, 185*, 455-461. https://doi.org/10.2307/1542485

Short, F.T., Davis, M.W., Gibson, R.A., & Zimmermann, C.F. (1985). Evidence for phosphorous limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine Coastal and Shelf Science, 20,* 419-430. https://doi.org/10.1016/0272-7714(85)90086-1

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., … Zieman, J.C. (2011). Extinction risk assessment of the world's seagrass species. *Biological Conservation, 144,* 1961-1971. https://doi.org/10.1016/j.biocon.2011.04.010

Short, F.T., & Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation, 23,* 17-27. https://doi.org/10.1017/S0376892900038212

Simpson, C.J., Cary, J.L., & Masini, R.J. (1993). Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs, 12,* 185-191. https://doi.org/10.1007/BF00334478

Smith, G.B. (1975). 1971 red tide and its impacts on certain reef communities in mid-eastern Gulf of Mexico. *Environmental Letters, 9,* 141-152. https://doi.org/10.1080/00139307509435843

Smith, J., Burford, M.A., Revill, A.T., Haese, R.R., & Fortune, J. (2012). Effect of nutrient loading on biogeochemical processes in tropical tidal creeks. *Biogeochemistry, 108*, 359-380. https://doi.org/10.1007/s10533-011-9605-z

Smith, J.E., Shaw, M., Edwards, R.A., Obura, D., Pantos, O., Sala, E., … Rohwer, F.L. (2006). Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters, 9,* 835-845. https://doi.org/10.1111/j.1461-0248.2006.00937.x

Smith, S.V., Kimmerer, W.J., Laws, E.A., Brock, R.E., & Walsh, T.W. (1981). Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. *Pacific Science, 35*, 279-402.

Spalding, M., Kainuma, M., & Collins, L. (2010). *World Atlas of Mangroves.* Earthscan, London, UK. https://doi.org/10.4324/9781849776608

Stram, D.L., Kincaid, C.R., & Campbell, D.E. (2005). Water quality modeling in the Rio Chone estuary. *Journal of Coastal Research, 21*, 797-810. https://doi.org/10.2112/011-NIS.1

Tamai, K. (1993). Tolerance of *Theora fragilis* (Bivalvia, Semelidae) to low concentrations of dissolved oxygen. *Nippon Suisan Gakkaishi, 59,* 615-620. https://doi.org/10.2331/suisan.59.615

Teh, L.S.L., Teh, L.C.L., & Sumaila, U.R. (2013). A global estimate of the number of coral reef fishers. *PLoS ONE, 8,* e65397. https://doi.org/10.1371/journal.pone.0065397

Terrados, J., Agawin, N.S.R., Duarte, C.M., Fortes, M.D., Kamp-Nielsen,L., & Burum, J. (1999). Nutrient limitation of the tropical seagrass *Enhalus acoroides* (L.) Royle in Cape Bolinao, NW Philippines. *Aquatic Botany, 65*, 123-139. https://doi.org/10.1016/S0304-3770(99)00036-4

Tomasko, D.A., Corbett, C.A., Greening, H.S., & Raulerson, G.E. (2005). Spatial and temporal variation in seagrass coverage in Southwest Florida: assessing the relative effects of anthropogenic nutrient load reductions and rainfall in four contiguous estuaries. *Marine Pollution Bulletin, 50,* 797-805. https://doi.org/10.1016/j.marpolbul.2005.02.010

Turko, A.J., & Wright, P.A. (2015). Evolution, ecology and physiology of amphibious killifishes (Cyprinodontiformes). *Journal of Fish Biology, 87,* 815-835. https://doi.org/10.1111/jfb.12758

Unsworth, R.K.F., & Cullen, L.C. (2010). Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters, 3,* 63-73. https://doi.org/10.1111/j.1755-263X.2010.00101.x

van de Koppel, J., van der Heide, T., Altieri, A.H., Eriksson, B.K., Bouma, T.J., Olff, H., & Silliman, B.R. (2015). Long-distance interactions regulate the structure and resilience of coastal ecosystems. *Annual Review of Marine Science, 7,* 139-158. https://doi.org/10.1146/annurev-marine-010814-015805

van der Heide, T., Govers, L.L., De Fouw, J., Olff, H., van der Geest, M., van Katwijk, M.M., … van Gils, J.A. (2012). A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science, 336*, 1432-1434. https://doi.org/10.1126/science.1219973

Vaquer-Sunyer, R., & Duarte, C.M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of*

Sciences of the United States of America, 105, 15452-15457. https://doi.org/10.1073/pnas.0803833105

Vaquer-Sunyer, R., & Duarte, C.M. (2011). Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Global Change Biology, 17,* 1788-1797. https://doi.org/10.1111/j.1365-2486.2010.02343.x

Villanueva, R.D., Yap, H.T., & Montano, M.N.E. (2005). Survivorship of coral juveniles in a fish farm environment. *Marine Pollution Bulletin, 51,* 580-589. https://doi.org/10.1016/j.marpolbul.2005.04.033

Vonk, J.A., Middelburg, J.J., Stapel, J., & Bouma, T.J. (2008). Dissolved organic nitrogen uptake by seagrasses. *Limnology and Oceanography, 53,* 542-548. https://doi.org/10.4319/lo.2008.53.2.0542

Walker, D.I., Kendrick, G.A., & McComb, A.J. (2007). Decline and recovery of seagrass ecosystems-dynamics of change. In A.W.D. Larkum, R.J. Orth, & C.M. Duarte (Eds.). *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, pp. 551-565. https://doi.org/10.1007/1-4020-2983-7_23

Watson, R.A., Coles, R.G., & Long, W.J.L. (1993). Simulation estimates of annual yield and landed value for commercial penaeid prawns from a tropical seagrass habitat, Northern Queensland, Australia. *Australian Journal of Marine and Freshwater Research, 44,* 211-219. https://doi.org/10.1071/MF9930211

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., … Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 12377-12381. https://doi.org/10.1073/pnas.0905620106

Weber, M., de Beer, D., Lott, C., Polerecky, L., Kohls, K., Abed, R.M.M., … Fabricius, K.E. (2012). Mechanisms of damage to corals exposed to sedimentation. *Proceedings of the National Academy of Sciences of the United States of America, 109,* E1558-E1567. https://doi.org/10.1073/pnas.1100715109

Wijgerde, T., Jurriaans, S., Hoofd, M., Verreth, J.A.J., & Osinga, R. (2012). Oxygen and Heterotrophy Affect Calcification of the Scleractinian Coral *Galaxea fascicularis*. *PLoS ONE, 7,* e52702. https://doi.org/10.1371/journal.pone.0052702

Wijgerde, T., Silva, C.I.F., Scherders, V., van Bleijswijk, J., Osinga, R. (2014). Coral calcification under daily oxygen saturation and pH dynamics reveals the important role of oxygen. *Biology Open, 3,* 489-493. https://doi.org/10.1242/bio.20147922

Wild, C., Jantzen, C., Struck, U., Hoegh-Guldberg, O., & Huettel, M. (2008). Biogeochemical responses following coral mass spawning on the Great Barrier Reef: pelagic-benthic coupling. *Coral Reefs, 27,* 123-132. https://doi.org/10.1007/s00338-007-0298-7

Yonge, S.C.M., Nicholls, A.G., & Yonge, M.J. (1932). The relationship between respiration in corals and the production of oxygen by their zooxanthellae. *Scientific Reports, Great Barrier Reef Expedition 1928-1929, 1,* 13-251.

Zieman, J.C., Fourqurean, J.W., & Frankovich, T.A. (1999). Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of turtle grass, *Thalassia testudinum*. *Estuaries, 22,* 460-470. https://doi.org/10.2307/1353211

Zimmerman, R.C., Smith, R.D., & Alberte, R.S. (1989). Thermal acclimation and whole-plant carbon balance in *Zostera marina* L. (eelgrass). *Journal of Experimental Marine Biology and Ecology*, *130,* 93-109. https://doi.org/10.1016/0022-0981(89)90197-4