

Oxygen: the universal currency on coral reefs

Hannah R. Nelson^{1,2}  · Andrew H. Altieri^{1,3}

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Abstract Coral reefs are suffering unprecedented declines worldwide. Most studies focus on stressors such as rising temperatures, nutrient pollution, overfishing, and ocean acidification as drivers of this degradation. However, recent mass mortality events associated with low oxygen on coral reefs indicate that oxygen is a critical factor that can be limiting in reef environments. Here, we present evidence that integrates across disciplines and perspectives to reveal how natural and anthropogenic factors drive variation in oxygen at multiple scales on coral reefs. This variation, in turn, limits essential processes such as productivity, respiration, and calcification on reefs and often plays a role in the outcome of interactions between corals and their competitors, pathogens, and mutualists. Moreover, the apparent effects of temperature, eutrophication, acidification, and other stressors on corals are commonly mediated by oxygen. As a consequence, the imprint of oxygen variation is evident in many patterns including reef biodiversity, coral bleaching, colony morphology, and fish

behavior. We suggest that the structure and dynamics of coral reefs can be fully understood only by considering the ubiquitous role of oxygen, and we identify critical areas of future oxygen research to guide the study and management of coral reefs in a changing world.

Keywords Bleaching · Calcification · Climate change · Dead zones · Hyperoxia · Hypoxia

Introduction

Coral reefs around the globe are suffering severe population declines and loss of diversity (Gardner et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007). To understand and counteract these trends, studies have focused primarily on the roles of warming oceans (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Munday et al. 2008), ocean acidification (Doney et al. 2009; Pandolfi et al. 2011; Andersson and Gledhill 2013), and overfishing (Hughes 1994; McManus 1997; Cinner et al. 2016). However, a recent awareness of mass mortalities of coral reef organisms due to hypoxia (Altieri et al. 2017), and the projected increase in the frequency and severity of dead zones due to climate change (Altieri and Gedan 2015), identify how dissolved oxygen can be a critically limiting factor on coral reefs and indicate that hypoxia may pose an increasingly significant threat to tropical coral reefs.

Oxygen is fundamental to many aspects of reef functioning and health. It serves as a universal currency; consumed by nearly all reef species, produced by corals, algae, and other photosynthetic organisms, exchanged between mutualists, and suppressed by competitors and disease. At the reef scale, dissolved oxygen concentrations typically range from 50% air saturation to upward of 200% air

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✉ Hannah R. Nelson
hnelson@ucdavis.edu

¹ Smithsonian Tropical Research Institute,
Apartado 0843-03092 Balboa, Ancon, Republic of Panama

² Center for Population Biology, University of California,
Davis, One Shields Avenue, Davis, CA 95616, USA

³ Department of Environmental Engineering Sciences,
Engineering School of Sustainable Infrastructure and
Environment, University of Florida, Gainesville, FL 32611,
USA

saturation (corresponding to 3.4–13.6 mg O₂ l⁻¹ at 27 °C), depending on location and time of day (Fig. 1d). However, values can fall to a level that is deficient (hypoxia) or completely lacking in oxygen (anoxia). Conventionally, 2.8 mg O₂ l⁻¹ (or 41% air saturation at 27 °C) has been used to designate waters as hypoxic, but this single universal threshold fails to capture the considerable variation in hypoxia tolerance among taxa, and is higher than the empirical sublethal and lethal oxygen thresholds for many benthic marine species (Vaquer-Sunyer and Duarte 2008). Hyperoxia refers to an excess of oxygen above 100% oxygen saturation (corresponding to 6.8 mg O₂ l⁻¹ at 27 °C). Normoxia refers to the range of oxygen conditions between hypoxia and hyperoxia. Both hypoxia and hyperoxia can act as stressors on reefs.

Oxygen directly and indirectly drives many key physiological processes in corals, including respiration (Yonge et al. 1932; Shick 1990; Dodds et al. 2007), photosynthesis (Gardella and Edmunds 1999; Finelli et al. 2006; Mass et al. 2010), and calcification (Rinkevich and Loya 1984; Al-Horani et al. 2007; Colombo-Pallotta et al. 2010; Wijgerde et al. 2012, 2014) (Fig. 2). Furthermore, emerging evidence has highlighted the importance of oxygen in mediating the dynamics and interactions of algae (Dinsdale and Rohwer 2011; Barott and Rohwer 2012; Gregg et al. 2013; Jorissen et al. 2016), fish (Nilsson et al. 2010; Pauly and Cheung 2018), disease (Dinsdale and Rohwer 2011;

Onton et al. 2011; Barott and Rohwer 2012; Glas et al. 2012), and bleaching (Lesser 1996; Lesser and Farrell 2004; Altieri et al. 2017) on coral reefs. The fundamental importance of oxygen to life has been used to develop important theoretical frameworks, such as the concept of oxygen- and capacity-limited thermal tolerance, which mechanistically links molecular to ecosystem levels of biological organization to understand the effects of various global change drivers on marine organisms (Pörtner 2012; Bozinovic and Pörtner 2015). Energy, whether it is gained by the production, consumption, or exchange of oxygen, is fundamental for the existence of all aerobic organisms, which is why oxygen acts as universal currency underlying many of the biological and physiological processes described in this review.

A body of knowledge is developing as to how oxygen is a driver and indicator of reef dynamics, but studies are typically limited to a single ecological scale (e.g., surface of colony, reef) or process (e.g., coral–algal competition, bleaching, calcification). Here, we synthesize this diverse literature to provide the first comprehensive review of the role of oxygen on coral reefs, and thereby develop an emergent perspective that suggests the dynamics of coral reefs cannot be understood without an understanding of oxygen on reefs. By integrating across scales of ecological organization, we show how processes at one scale can lead to stress at another, and demonstrate how small-scale

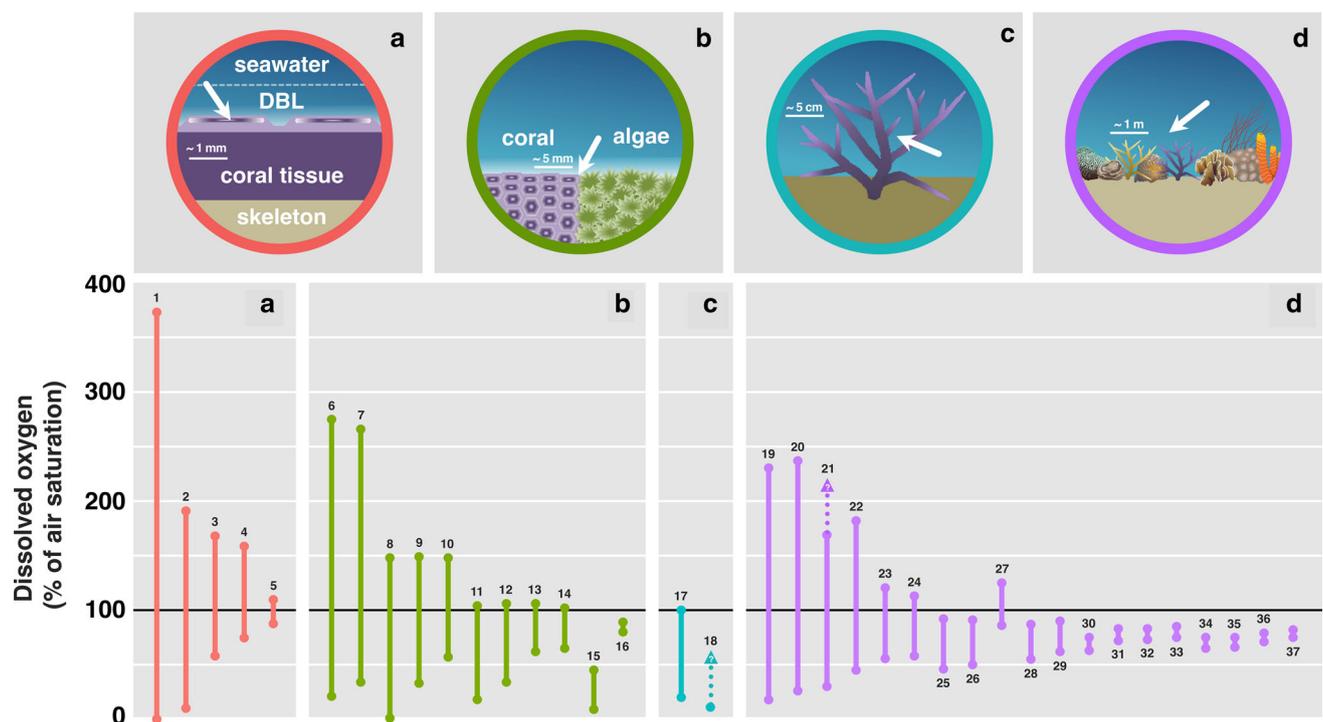


Fig. 1 Typical oxygen variation at the scale of the **a** surface of a coral colony, **b** coral–algal interface, **c** water between coral branches, and **d** reef scale (see ESM Table S1 for key)

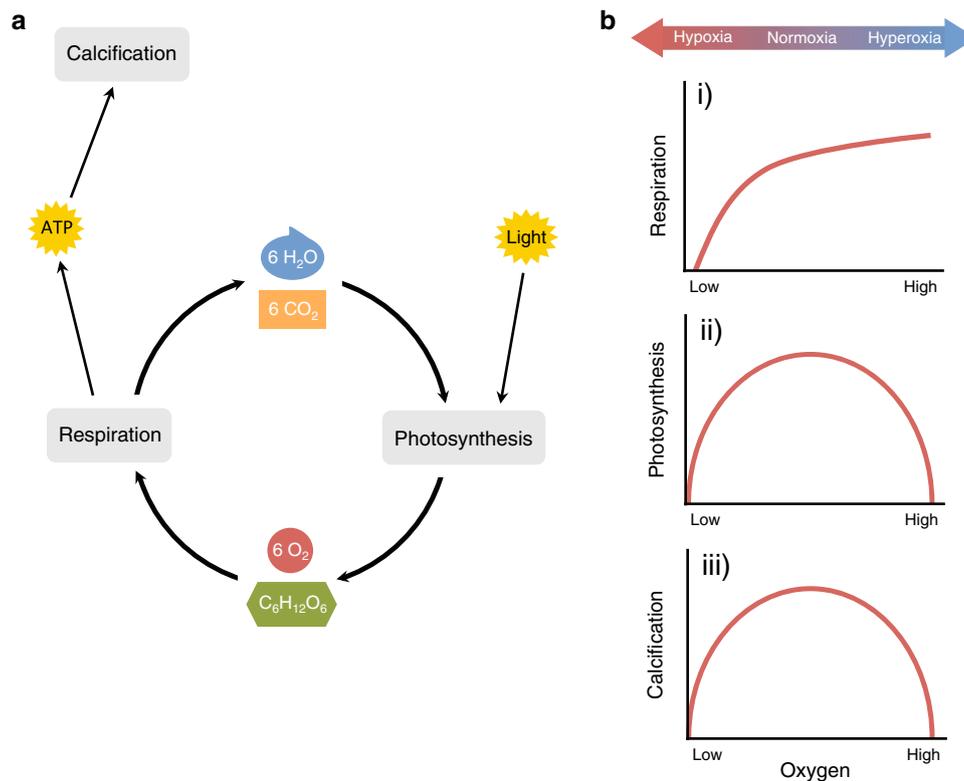


Fig. 2 a Relationship between respiration, photosynthesis, and calcification. The products of coral respiration (water, carbon dioxide) are used as substrates in zooxanthellae photosynthesis, and the products of photosynthesis (oxygen, glucose) are used as substrates in respiration. The energy required for coral calcification is generated by respiration. **b** Effects of oxygen on coral respiration, photosynthesis, and calcification. (i) At low oxygen concentrations, respiration is limited by oxygen availability. At high oxygen concentrations,

respiration is largely independent of oxygen availability. (ii) At low oxygen concentrations, limited respiration reduces photosynthesis. At high oxygen concentrations, reactive oxygen species (ROS) and photorespiration reduce photosynthesis. (iii) At low oxygen concentrations, limited photosynthesis and respiration reduce calcification. At high oxygen concentrations, ROS and reduced photosynthesis reduce calcification

experiments and organismal processes can be used to predict large-scale responses to changing oxygen regimes.

The objectives of this review are threefold. First, we examine the biological and physical processes driving spatiotemporal variation in oxygen on reefs, building up from the colony to the reef scale. Second, we evaluate the consequences of routine and extreme oxygen concentrations for the structure of function of coral reef ecosystems. Specifically, we consider how hypoxia and hyperoxia act as stressors on reefs and how oxygen mediates interactions between corals and other reef organisms. Finally, we characterize the factors driving the formation of dead zones and address directions for management and future work

Colony scale: the role of physiology, morphology, and flow

Oxygen as a physiological driver: respiration, photosynthesis, and calcification

All aerobic organisms consume oxygen during respiration, although patterns of oxygen consumption vary widely among taxa (Mangum and Van Winkle 1973). In respiratory physiology, organisms have traditionally been divided into two classes according to whether their rate of oxygen consumption varies with environmental oxygen partial pressure (i.e., oxyconformers) or is largely independent of environmental oxygen partial pressure (i.e., oxyregulators) (e.g., Yonge et al. 1932; Melzner et al. 2013; Lefevre et al. 2015). In reality, organisms rarely express perfect conformity or regulation, but generally exhibit some intermediate response (Mangum and Van Winkle 1973; Mueller and Seymour 2011). Understanding the shape of this response curve is important because it describes how an organism's respiration rate (i.e., oxygen consumption) will respond to

changes in their oxygen environment. Very few studies in corals have quantified oxygen consumption rates over a range of environmental oxygen partial pressures (Dodds et al. 2007), but through those few studies (Yonge et al. 1932; Shick 1990; Dodds et al. 2007), along with a number of studies on closely related anemones (Sassaman and Mangum 1972, 1973, 1974; Shumway 1978; Ellington 1982; Tytler and Davies 1984; Shick 1990; Harland and Davies 1995), some general trends have emerged.

Anthozoans (e.g., corals, anemones), like many other non-bilaterian metazoans, lack the ability to actively ventilate their external surfaces (Sassaman and Mangum 1974; Shick 1990; Patterson 1992a). Despite the absence of respiratory adaptations found in Bilateria (e.g., lungs, gills, tracheal systems), most anthozoans are not perfect conformers, but typically exhibit partial or imperfect metabolic regulation (Yonge et al. 1932; Sassaman and Mangum 1972, 1973; Ellington 1982; Tytler and Davies 1984; Shick 1990). In general, the rate of oxygen consumption in anthozoans tends to decline with decreasing environmental oxygen concentrations, with more pronounced declines in oxygen consumption rates at lower oxygen concentrations (Yonge et al. 1932; Sassaman and Mangum 1972, 1973; Ellington 1982; Tytler and Davies 1984; Shick 1990). However, some species are capable of maintaining oxygen consumption with decreasing oxygen availability until some critical oxygen pressure [usually between 30 and 50% air saturation (Yonge et al. 1932; Shumway 1978)], where their rate of oxygen consumption then begins to decrease steadily (Yonge et al. 1932; Shumway 1978; Dodds et al. 2007).

It is often assumed that oxygen consumption reaches a plateau at 100% air saturation, but experiments indicate that oxygen uptake in anthozoans can continue to increase beyond this point (Mangum and Van Winkle 1973; Shick 1990; Harland and Davies 1995). Similarly, zooxanthellae isolated from coral also show a significant elevation of aerobic respiration with hyperoxia (Gardella and Edmunds 1999). At low oxygen conditions, many anthozoans cease oxygen consumption before they have exhausted the supply of oxygen available to them (Mangum and Van Winkle 1973; Sassaman and Mangum 1973; Ellington 1982). This shutdown of aerobic respiration corresponds to a shift to anaerobic pathways, which is a less efficient method of converting energy, but does not require the use of oxygen (Mangum and Van Winkle 1973; Sassaman and Mangum 1973; Ellington 1982; Murphy and Richmond 2016).

Corals and their endosymbiotic algae are tightly coupled through the linked processes of respiration and photosynthesis. Aerobic respiration uses oxygen to break down glucose, creating energy as adenosine triphosphate (ATP), with water and carbon dioxide as by-products. Photosynthesis uses the energy from sunlight to produce glucose

from carbon dioxide and water, releasing oxygen as a by-product. Since the products of aerobic respiration in corals are used as substrates in zooxanthellae photosynthesis, and vice versa, there is a positive feedback loop between the two processes (Gardella and Edmunds 1999). Stable isotope analyses have demonstrated that carbon dioxide from coral metabolism represents the principal source of carbon dioxide for photosynthesis by zooxanthellae in shallow-water corals, and this metabolic carbon dioxide can be completely consumed by photosynthesis (Muscatine et al. 1989). Therefore, not only can the availability of oxygen limit coral respiration, but also it can indirectly limit photosynthesis by limiting the supply of carbon dioxide that coral respiration provides to zooxanthellae (Harland and Davies 1995). Oxygen availability can also limit zooxanthellae respiration (Gardella and Edmunds 1999). Experimental studies with both a symbiotic coral (Gardella and Edmunds 1999) and symbiotic anemone (Harland and Davies 1995) have shown that increased oxygen saturations can enhance zooxanthellae photosynthetic rates. Corals also show a significant increase in photosynthetic efficiency (i.e., effective quantum yield of photosystem II) with normoxia compared to anoxia (Ulstrup et al. 2005).

While increasing oxygen availability can support high respiratory rates, which in turn support high photosynthetic rates (by creating a CO₂ rich microenvironment), oxygen concentrations above a certain level can actually impede photosynthesis in corals. The accumulation of oxygen can inhibit photosynthesis in corals through two mechanisms, energetically costly photorespiration and the direct toxicity of reactive oxygen species (ROS) (Finelli et al. 2006; Mass et al. 2010). Photorespiration occurs when ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), a key enzyme in photosynthesis, uses oxygen as a substrate instead of carbon dioxide (Jordan and Ogren 1981). When RuBisCO binds to oxygen, rather than initiating the process of carbon fixation, the pathway results in a loss of fixed carbon and wastes energy (Jordan and Ogren 1981). Photorespiration may be especially problematic for corals because zooxanthellae possess a RuBisCO structure similar to the form possessed by anaerobic bacteria, which has a much lower specificity for carbon dioxide compared to the form possessed by eukaryotic algae and higher plants (Whitney et al. 1995). So while the RuBisCO system can consume oxygen and help prevent the production of toxic ROS (Apel and Hirt 2004), photorespiration can result in a reduction in photosynthesis at high oxygen concentrations (Finelli et al. 2006; Mass et al. 2010). ROS are produced through processes such as the photoreduction of O₂, which is known as the Mehler reaction and occurs in the chloroplasts of zooxanthellae (Mehler 1951; Roberty et al. 2014). ROS are known to directly damage RuBisCO and photosystem II (Lesser 1996). The addition of exogenous

antioxidants (that scavenge ROS) improves photosynthetic performance in cultured zooxanthellae and intact corals experiencing oxidative stress (Lesser 1996, 1997), confirming the role of ROS in decreased photosynthetic performance.

While some experimental studies have demonstrated that corals show a decrease in net photosynthesis (Mass et al. 2010) and photosynthetic efficiency (Finelli et al. 2006) when exposed to hyperoxia, other studies on zooxanthellae isolated from coral (Gardella and Edmunds 1999) and intact symbiotic sea anemones (Harland and Davies 1995) have shown gross photosynthetic rates increase with hyperoxia. This apparent discrepancy between studies demonstrating hyperoxia impedes photosynthesis, and those demonstrating hyperoxia enhances photosynthesis may be due to differences in the timescales of the experimental incubations (Gardella and Edmunds 1999) or differences among taxa. Alternatively, it is possible that the negative impacts of hyperoxia on photosynthesis only manifest over some critical oxygen threshold. The studies demonstrating that hyperoxia enhances photosynthesis used hyperoxic treatments of 150% air saturation (Harland and Davies 1995; Gardella and Edmunds 1999), while the studies demonstrating that hyperoxia impedes photosynthesis used hyperoxic treatments $\geq 200\%$ air saturation (Finelli et al. 2006; Mass et al. 2010). Overall, the above findings suggest that the relationship between photosynthetic rates and oxygen availability is unimodal. Initially, photosynthesis is enhanced by increasing oxygen (via enhanced respiratory products), but above a certain concentration, increasing oxygen decreases photosynthetic rates due to the effects of photorespiration and ROS. Further studies testing photosynthetic rates in corals over a wide range of oxygen concentrations are needed to discern the exact shape and threshold concentrations of this curve.

The relationship between calcification and oxygen availability is also unimodal (Wijgerde et al. 2012). Calcification is the process by which corals accrete their calcium carbonate skeleton. The deposition of calcium carbonate is metabolically demanding (e.g., 13–30% of total energy budget for coral; Cohen and Holcomb 2009; Allemand et al. 2010), which is generated by aerobic respiration (Colombo-Pallotta et al. 2010). Since the products of photosynthesis (e.g., photosynthates, oxygen) fuel aerobic respiration of corals in light, photosynthesis has a critical role in calcification; thus, calcification in zooxanthellate corals has been called a “photosynthesis-driven” process (Chalker and Taylor 1975; Colombo-Pallotta et al. 2010). Therefore, the availability of oxygen can limit the energy available for calcification by limiting photosynthesis and respiration (Colombo-Pallotta et al. 2010). Experimental studies have shown that oxygen can exert a strong control on both light (Wijgerde et al. 2012) and dark

(Rinkevich and Loya 1984; Al-Horani et al. 2007; Colombo-Pallotta et al. 2010; Wijgerde et al. 2012, 2014) calcification in corals.

Above a certain point, increasing oxygen concentrations can impede calcification in corals (Wijgerde et al. 2012, 2014). There are at least three possible pathways by which hyperoxia can inhibit calcification in corals. First, the accumulation of ROS under hyperoxic conditions may directly damage cellular components responsible for calcification (Wijgerde et al. 2012). Second, the formation of ROS may cause corals to invest metabolic energy in the production of antioxidants rather than calcification (Wijgerde et al. 2014). Third, hyperoxia may limit calcification indirectly by inhibiting photosynthesis, which acts as a major driver of coral calcification in light (Wijgerde et al. 2014). Similar to photosynthesis, the optimal oxygen saturation for calcification may be above 100% air saturation. For example, one study that measured calcification in the Pacific coral *Galaxea fascicularis* over a range of ambient oxygen saturations (13, 50, 80, 110, 150, and 280%) found that overall calcification rates were highest at 80, 110, and 150%, irrespective of light conditions and zooplankton feeding (Wijgerde et al. 2012). The effect of increasing oxygen saturations on light calcification in corals also depends on the pH of the surrounding water (Wijgerde et al. 2014). Given that oxygen simultaneously affects photosynthesis and respiration, both of which play a significant role in coral calcification, untangling the mechanisms underlying the relationship between oxygen and coral calcification will be complex, but this area of research warrants further investigation.

The DBL and diel oxygen cycle

During the day, the zooxanthellae that live within coral tissues produce oxygen as a by-product of photosynthesis (Yonge et al. 1932; Roffman 1968). Most of this oxygen (ca. 78–90%) is immediately consumed by coral respiration (Kühl et al. 1995; Al-Horani et al. 2003a, b). Since the rate of oxygen production by zooxanthellae photosynthesis exceeds the rate of oxygen consumption by coral respiration, excess oxygen is released from corals to the surrounding seawater throughout the day (Yonge et al. 1932; Finelli et al. 2006; Al-Horani et al. 2007; Mass et al. 2010). At night, photosynthesis ceases due to the lack of light, but coral respiration continues, albeit at a lower level (Kühl et al. 1995; Al-Horani et al. 2003a). Since the demand for oxygen is no longer supplied internally by zooxanthellae, corals must draw oxygen from their environment during the night (Al-Horani et al. 2007). Thus, corals are net producers of oxygen during the day and net consumers of oxygen at night (Al-Horani et al. 2007; Fig. 3).

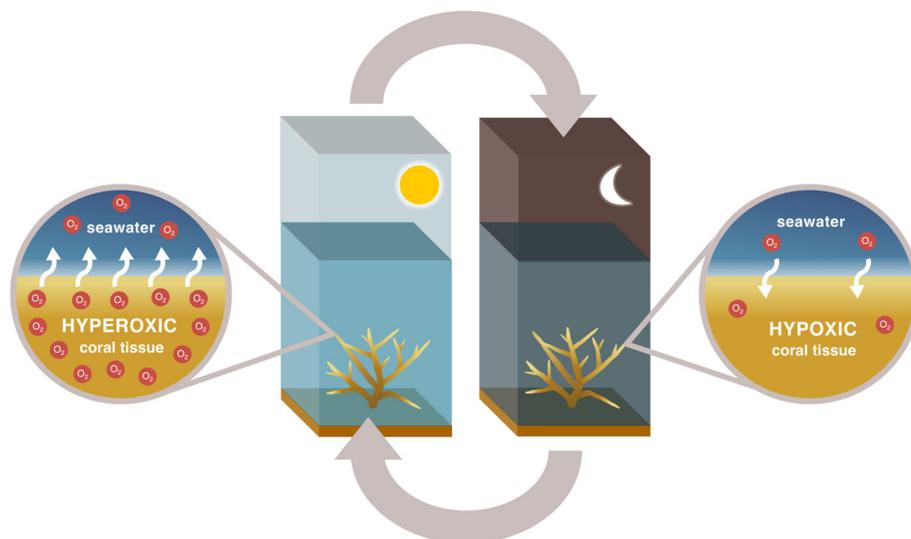


Fig. 3 Diel oxygen cycle. During the day, oxygen production by zooxanthellae photosynthesis exceeds oxygen consumption by coral respiration, so excess oxygen is released to the surrounding seawater. This efflux of oxygen is limited by diffusion, causing the coral tissues and water in the diffusive boundary layer (DBL) to be hyperoxic

throughout the day. At night, respiration continues but photosynthesis ceases, so corals must draw oxygen from their environment. The limited diffusive influx of oxygen causes coral tissues and their surrounding DBL to be hypoxic at night

The movement of oxygen between coral tissue and the surrounding seawater is modulated by the diffusive boundary layer (DBL) (Shashar et al. 1993; Kühl et al. 1995), a thin layer of stagnant water located adjacent to all aquatic organisms (Patterson 1992b). The DBL surrounding a coral is usually only a few millimeters thick, but it completely encompasses the colony (Shashar et al. 1993). As a consequence, the transfer of dissolved substances (e.g., oxygen) into or out of the coral must occur through passive diffusion (Dennison and Barnes 1988; Patterson et al. 1991). The rate of this diffusion is inversely proportional to the thickness of the DBL (Shashar et al. 1996). Increased water movement around the colony (Patterson et al. 1991; Shashar et al. 1993; Kühl et al. 1995) and increased water temperature (Jørgensen and Revsbech 1985) decrease the thickness of the DBL.

While thin DBLs allow for rapid solute exchange and thick DBLs impede the mass transfer of dissolved substances (Dennison and Barnes 1988; Patterson et al. 1991), in either case there is a microenvironment within the DBL adjacent to coral colonies in which oxygen levels are influenced by coral metabolism and differ from the surrounding water. A consequence of this diffusion limitation is that corals routinely experience both high and low oxygen extremes on a diel cycle (Yonge et al. 1932; Shashar et al. 1993; Kühl et al. 1995; Gardella and Edmunds 1999). During the day, the limited efflux of photosynthetically derived oxygen from coral tissues to the surrounding seawater causes coral tissues to experience an extreme supersaturation of oxygen, which can exceed 250% air

saturation (Shashar et al. 1993; Kühl et al. 1995; Gardella and Edmunds 1999). This accumulation of oxygen within coral tissues can limit photosynthesis (Rex et al. 1995; Finelli et al. 2006; Mass et al. 2010) and light calcification (Wijgerde et al. 2012, 2014). At night, the respiratory consumption of oxygen combined with the limited influx of oxygen from the surrounding seawater results in an extreme internal oxygen depletion (Shashar et al. 1993; Kühl et al. 1995; Gardella and Edmunds 1999) that can fall below 2% air saturation (Shashar et al. 1993; Kühl et al. 1995). This reduction in the availability of oxygen to corals can limit dark respiration (Shick 1990; Kühl et al. 1995; Rex et al. 1995) and dark calcification (Rinkevich and Loya 1984; Al-Horani et al. 2007; Colombo-Pallotta et al. 2010; Wijgerde et al. 2012, 2014). It is hypothesized that cnidarians, such as corals, extend their tentacles into the water column and inflate their polyps not only to feed, but also to reduce oxygen limitation by increasing the surface-to-volume ratio and exposed surface area of their tissues to enhance diffusion rates (Shashar et al. 1993; Dodds et al. 2007). In contrast to changes in CO₂ and pH following experimental changes in light conditions, which can take several minutes (de Beer et al. 2000), oxygen concentrations at the surface of coral tissue change in seconds (Shashar et al. 1993; Kühl et al. 1995; de Beer et al. 2000; Marshall and Clode 2003). Consequently, corals experience hyperoxia throughout the day and hypoxia during the night, with rapid transitions between both extremes (Shashar et al. 1993; Kühl et al. 1995; de Beer et al. 2000; Marshall and Clode 2003).

Effects of flow and morphology on oxygen environments at colony scale

The link between flow and coral health is well established. Decreased water movement can decrease the growth, survival, and fecundity of corals (Jokiel 1978). Corals inhabiting areas with low flows are also more likely to bleach (Nakamura and van Woessik 2001). This difference in bleaching vulnerability has been attributed to oxygen; corals that inhabit sheltered locations experience lower rates of solute exchange (due to thicker DBLs), leading to the accumulation of intracellular oxygen, which can increase oxidative stress and bleaching rates (Nakamura and van Woessik 2001). A similar phenomenon has been hypothesized to operate at smaller scales. The morphology and variable textures across a singly colony may create a mosaic of shear stress levels over the coral surface which could enhance or limit the rate of solute exchange on the scale of individual polyps (Finelli et al. 2006). Thus, oxidative stress contributes to both the variation in bleaching among colonies on a single reef and the patchy nature of coral bleaching within a single coral colony.

Colony morphology also has a large influence on the magnitude of hypoxia and hyperoxia experienced by corals. Branching coral colonies are especially vulnerable to developing extreme oxygen conditions relative to other morphologies (e.g., plating, mounding). As incoming water encounters branches, momentum transfers from the water to the colony, and this loss of energy causes the water in the interior of branching coral colonies to become increasingly stagnant (Chamberlain and Graus 1975). Due to this lack of water movement and coral respiration, the water between coral branches can develop intense hyperoxia during the day ($\sim 200\%$ air saturation; Nilsson et al. 2007b) and severe hypoxia at night ($< 20\%$ air saturation; Nilsson et al. 2004; Goldshmid et al. 2004). With increasing flow, water can penetrate further into the colony; however, even at very high flow speeds (e.g., 35 cm s^{-1}) internal stagnation does not completely disappear (Chamberlain and Graus 1975). Larger branched colonies with more open frameworks and regular branching patterns also permit more water exchange to the interior of their colonies (Chamberlain and Graus 1975).

Differences in the rate of oxygen diffusion due to colony morphology can have important consequences for coral physiology. For example, two ecomorphs of the smooth cauliflower coral *Stylophora pistillata* with variable branching morphologies exhibit different respiratory responses to experimental hyperoxic conditions (Shick 1990). The ecomorph with thin, widely spaced branches showed a slight decrease in dark respiration under hyperoxia, while the ecomorph with thick, closely spaced branches exhibited a significant enhancement of dark

respiration under hyperoxia (Shick 1990). These variable responses can be attributed to differences in diffusion between the two ecomorphs; only the ecomorph with thick, closely spaced branches had diffusion-limited oxygen concentrations and respiration rates alleviated by experimental hyperoxia (Shick 1990). The relationship between coral morphology and the diffusion of oxygen may also have consequences on longer, evolutionary timescales. Gas exchange has been hypothesized to act as a selective pressure on coral morphology, effectively limiting colony size (Chamberlain and Graus 1975) and promoting the evolution of upright morphologies that reduce diffusion gradients by forming turbulent water flows (Helmuth and Sebens 1993).

Reef scale: processes driving diel oxygen cycling on reef landscapes

Biological processes

A combination of biological and physical processes controls the concentration of oxygen in the water column above coral reefs (Kraines et al. 1996). At the reef scale, as at the colony scale, oxygen fluxes are dominated by photosynthesis during the day and respiration at night; consequently, the concentration of oxygen on reefs is higher during the day and lower at night (Kinsey and Kinsey 1967; Kraines et al. 1996; Ohde and van Woessik 1999; Niggel et al. 2010; Wild et al. 2010). Symbiotic anthozoans (e.g., coral, anemones), aquatic plants, algae, and photosynthetic eubacteria routinely photosynthesize on reefs (Kraines et al. 1996). Respiration occurs in all aerobic organisms (Best et al. 2007).

The amount of benthic algae cover on reefs can affect the magnitude of daily oxygen fluctuations. Studies on coral reefs in the Red Sea have demonstrated that algae-dominated sites show a larger range in diurnal variation than coral-dominated sites and that diurnal variations in oxygen concentrations on these reefs display a strong positive correlation with benthic algae cover, but not with coral cover (Niggel et al. 2010; Wild et al. 2010). In addition, the mean daily oxygen concentration directly above the reef was significantly lower at algae-dominated sites compared to adjacent coral-dominated sites, suggesting that the negative effects of algal respiration on dissolved oxygen concentration outweigh the positive effects of photosynthesis when averaged over a 24-h period (Niggel et al. 2010; Wild et al. 2010).

Physical processes

Biological processes alone do not account for net oxygen fluxes on reefs. An oxygen model developed for a coral reef system in Japan determined that gas exchange between the air and sea has a significant effect on the oxygen concentrations on reef flats and lagoons (Kraines et al. 1996). Mass transport of water by currents and tidal flow between lagoons, reef flats, and the open ocean also affects oxygen availability on reefs (Kraines et al. 1996). Shallow reef environments, such as reef flats, tend to have greater diel variations in oxygen compared to deeper reef environments, routinely becoming hyperoxic during the day and hypoxic at night (e.g., Kinsey and Kinsey 1967; Kraines et al. 1996; Ohde and van Woesik 1999; Fig. 1). Increasing temperature, increasing salinity, and decreasing pressure all decrease the solubility of oxygen in water (Best et al. 2007). Very few studies have quantified in situ oxygen availability in coral reef ecosystems (Wild et al. 2010), so our current understanding of the normal range of variability in oxygen at the reef scale, along with the relative importance of biological and physical processes in determining oxygen availability on reefs, is still quite limited.

Hypoxia and hyperoxia as stressors on reefs

Hypoxia as a stressor

Classically, hypoxic habitats have been defined as environments where the dissolved oxygen level is below a certain threshold, most commonly around 2 mg l^{-1} (Vaquer-Sunyer and Duarte 2008). However, the approach of a single, universal threshold fails to capture the considerable variation among organisms in both when and how they respond to low oxygen conditions. There is over an order of magnitude variation among marine benthic organisms in their lethal and sublethal thresholds of hypoxia (Vaquer-Sunyer and Duarte 2008). Crustaceans and fish are typically more sensitive to low oxygen conditions compared to other phyla, with cnidarians, molluscs, and priapulids among the most tolerant taxa (Vaquer-Sunyer and Duarte 2008). Differences in hypoxia tolerance between genera can also be immense. For example, during a hypoxic event caused by a dinoflagellate bloom on reefs around Caño Island, Costa Rica, some corals experienced 90–100% mortality (*Pocillopora* spp.), while other species experienced 0% mortality at the same sites and depths (*Porites lobata*, *Gardineroseris planulata*, *Pavona clavus*, *Pavona gigantea*) (Guzmán et al. 1990). Generally branching and solitary corals (e.g., *Acropora*, *Pocillopora*, *Stylophora*, *Fungia* spp.) suffer the highest mortality during severe

hypoxic events, whereas massive, submassive, and encrusting corals (e.g., *Porites*, *Favia* spp.) are the least affected (Guzmán et al. 1990; Simpson et al. 1993; Genin et al. 1995; Adjeroud et al. 2001; Laboy-Nieves et al. 2001). There are limited data available on the response of other coral reef invertebrates to hypoxia, but there is clearly considerable variation in susceptibility, with some species experiencing mass mortalities during severe hypoxic events while others are seemingly not affected at all (e.g., Adjeroud et al. 2001; Laboy-Nieves et al. 2001). Among coral reef fishes, genera that have an obligate association with living coral (e.g., *Gobiodon*, *Paragobiodon*, and *Caracanthus*) and thus inhabit the nocturnally hypoxic spaces within branching coral colonies, usually exhibit a greater hypoxia tolerance than other reef fish (Nilsson and Östlund-Nilsson 2004; Nilsson et al. 2004, 2007a).

Coral reef organisms display a wide variety of behavioral and physiological responses to hypoxia (Fig. 4). As discussed above, oxygen availability can directly or indirectly limit respiration, photosynthesis, and calcification in corals. In addition, many corals bleach when exposed to hypoxia (Yonge et al. 1932; Zhu et al. 2004; Altieri et al. 2017). Mobile reef animals often respond to hypoxia by moving upward to access more oxygenated water. For example, mobile reef invertebrates have been observed migrating out of crevices and burrows to the surface of the substratum during hypoxic events (Simpson et al. 1993; Laboy-Nieves et al. 2001; Altieri et al. 2017). Echinoderms and crabs that normally live among the branches of large arborescent coral colonies have been found on the outer, upper surfaces of colonies in severely hypoxic conditions (Simpson et al. 1993). Similarly, moray eels and other typically benthic fish have been seen swimming at the water surface during a hypoxic event (Simpson et al. 1993). Mouthbrooding significantly reduces the ability of fish to take up oxygen at low ambient oxygen levels, so male cardinalfish will spit out their eggs under hypoxic conditions (Östlund-Nilsson and Nilsson 2004). Some reef fish respond to severe hypoxia by entering a phase of metabolic and ventilatory depression (Routley et al. 2002). Little is known about the metabolic adaptations of reef invertebrates to hypoxia, but generally invertebrates are known to respond to low oxygen levels through depression of activity (Diehl et al. 1979), reduced feeding (Tamai 1993; Llanso and Diaz 1994; Bell et al. 2003), metabolic depression (Rutherford and Thuesen 2005), and/or altered heart rates (Harper and Reiber 1999).

One of the most common physiological responses to hypoxia that organisms exhibit is a switch from aerobic to anaerobic metabolic pathways (Vaquer-Sunyer and Duarte 2008), often before they have even exhausted their supply of available oxygen (Mangum and Van Winkle 1973;

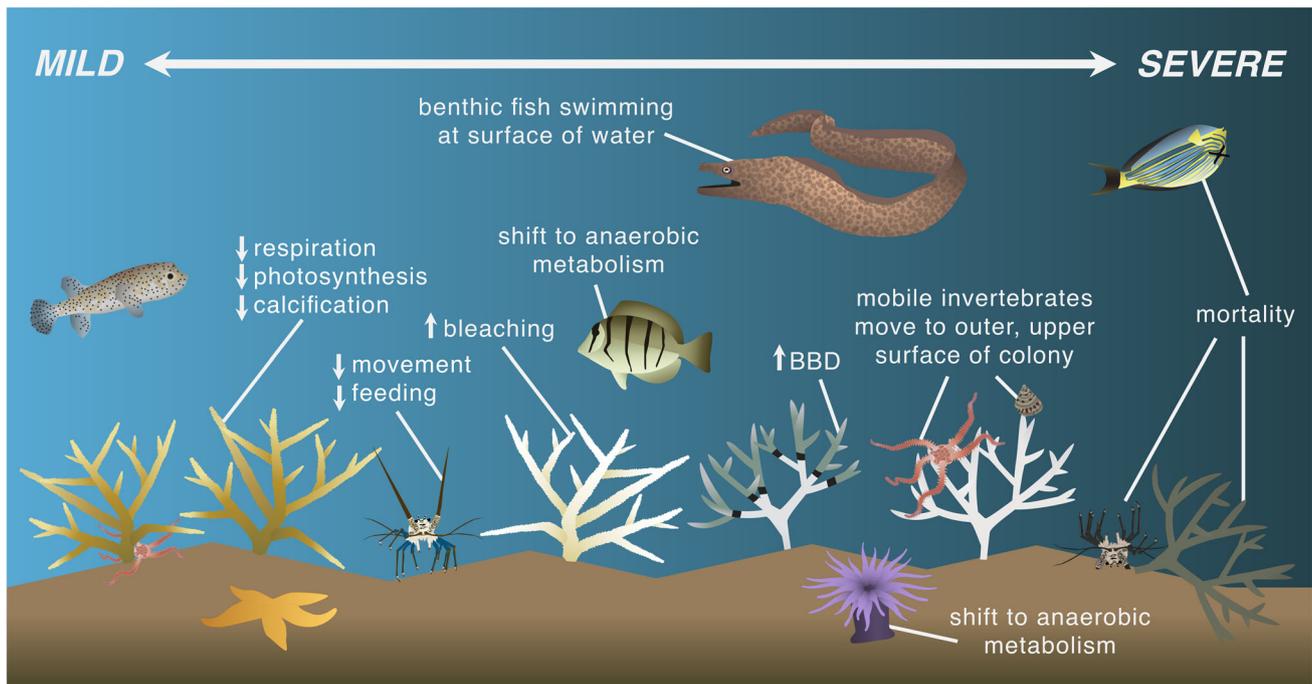


Fig. 4 Behavioral and physiological responses of reef organisms to hypoxia

Ellington 1982). A recent study of the metabolic response of the reef coral *Montipora capitata* to hypoxia found that corals exposed to prolonged hypoxic conditions (> 12 h) showed increased activity of alanine dehydrogenase (ADH) and strombine dehydrogenase (SDH), key enzymes in anaerobic respiration (Murphy and Richmond 2016). Coral reef fishes can have high anaerobic capacities (Nilsson and Östlund-Nilsson 2004; Nilsson et al. 2007a). However, the drawback of relying on anaerobic glycolysis for surviving hypoxia is the buildup of lactate, which has to be oxidized when oxygen levels increase again, causing an oxygen debt that slows recovery from hypoxia (Nilsson et al. 2007c). In addition, the buildup of lactate (i.e., acidosis) can be lethal to fish (Nilsson and Östlund-Nilsson 2008). There is evidence suggesting that acidosis caused by anaerobic metabolism, rather than an inability to produce enough ATP, is the cause of anoxic death in some fish (Nilsson and Östlund-Nilsson 2008). Consequently, it has been hypothesized that the most viable strategy for long-term hypoxic survival is to possess a critical oxygen pressure low enough to avoid reliance on anaerobic metabolism (Nilsson et al. 2007c; Nilsson and Östlund-Nilsson 2008).

In general, the response of organisms to hypoxia is dependent on both the concentration of dissolved oxygen and the duration of exposure to reduced oxygen levels (Best et al. 2007). Corals can survive severe hypoxic conditions (< 5% air saturation) in the laboratory for periods ranging from several hours to at least a week,

depending on the species (Mayer 1917; Yonge et al. 1932; Sassaman and Mangum 1973; Dodds et al. 2007; Weber et al. 2012; Haas et al. 2014; Altieri et al. 2017). However, these experiments rarely mimic natural flow or light conditions, so coral survival may differ in the field. Coral reef fishes can maintain their rate of oxygen consumption down to 13–34% air saturation and most appear unaffected by hypoxia (e.g., no signs of agitation or loss of balance) until oxygen levels fall below 10% air saturation (Nilsson and Östlund-Nilsson 2004; Nilsson et al. 2007a). The impacts of hypoxia on organisms depend not only on the magnitude and duration of low oxygen exposure, but also on their previous exposure to hypoxic conditions. For example, the shallow reef platforms where the epaulette shark (*Hemiscyllium ocellatum*) lives become progressively more hypoxic during subsequent nocturnal low tides, resulting in a natural hypoxic preconditioning regimen that enhances the physiological response of the shark to hypoxia (Routley et al. 2002; Nilsson and Renshaw 2004).

Climate change and multi-stressor interactions with hypoxia

Finally, it is important to note that the presence of additional stressors on reefs has profound implications for the hypoxia tolerance of reef organisms. Ocean waters are becoming increasingly warmer and more acidic due to anthropogenic carbon dioxide emissions (IPCC 2013). Marine organisms have reduced hypoxia survival times and

increased median lethal concentrations when exposed to warmer temperatures (Vaquer-Sunyer and Duarte 2011), as demonstrated in several coral reef fishes (Nilsson et al. 2010; Sørensen et al. 2014). Since metabolic rates increase exponentially with temperature (Brown et al. 2004), increased sea surface temperatures can result in a higher oxygen demand by both the microbes and algae that deplete oxygen, and by the macrofauna that are dependent on oxygen. A recent study investigating 11 hypoxia-driven mass mortality events in atoll lagoons in the Pacific determined that all but one event took place during or at the end of the warm season (Andréfouët et al. 2015). The majority of documented dead zones in marine ecosystems are in regions predicted to experience over 2 °C warming by the end of this century due to climate change (Altieri and Gedan 2015). The threat posed by increased seawater temperatures for hypoxia is twofold; increased temperatures result in less oxygen available not only because there is a higher demand for oxygen (Brown et al. 2004), but also because the solubility of oxygen is lower in warmer waters (Weiss 1970).

Much less is known about the effects of ocean acidification on hypoxia tolerance (Melzner et al. 2013), but emerging evidence suggests that reductions in the pH of seawater could reduce the hypoxia tolerance of reef organisms. Experimental work with the coral *Montipora peltiformis* has shown that these corals can survive separate exposures of anoxia and low pH for at least 4 d, but the combination of anoxia and low pH leads to colony death within 24 h (Weber et al. 2012). Low dissolved oxygen conditions are likely to occur in concert with acidification because the respiration of microbes and algal blooms that generates hypoxic conditions also creates an abundance of carbon dioxide, which lowers seawater pH levels (Altieri and Gedan 2015). The majority of experimental work on the hypoxia tolerance of marine organisms has been carried out without the simultaneous manipulation of pH or temperature (Vaquer-Sunyer and Duarte 2008), suggesting that the thresholds established by these laboratory manipulations likely overestimate the tolerance of reef organisms to conditions associated with hypoxia in their natural environments.

Hyperoxia as a stressor

Although aerobic organisms depend on oxygen to survive, and hypoxia is widely recognized as a stressor in aquatic ecosystems, hyperoxia can also have negative effects on coral reefs. During the day, the production of oxygen due to zooxanthellae photosynthesis and limited efflux of oxygen via diffusion causes an accumulation of oxygen within the tissues of symbiotic cnidarians, such as corals (Shashar et al. 1993; Kühl et al. 1995; Gardella and

Edmunds 1999). This excess oxygen is problematic because physiological hyperoxia, combined with exposure to thermal stress or UV radiation, causes an increased production of reactive oxygen species (Lesser and Shick 1989; Dykens and Shick 1982; Lesser et al. 1990; Dykens et al. 1992; Lesser 1996, 1997).

Organisms are continually under threat of attack by the toxic reactive oxygen species produced by their own metabolism (Fridovich 1977), which can accumulate when overall oxygen concentrations become elevated. Reactive oxygen species (ROS), often referred to as oxygen radicals or reactive oxygen intermediates (ROI), are partially reduced forms of atmospheric oxygen (O₂), such as the singlet oxygen (¹O₂), superoxide radical (O₂⁻), hydrogen peroxide (H₂O₂), and hydroxyl radical (OH[·]) (Fridovich 1977). In contrast to atmospheric oxygen, ROS are highly reactive and capable of causing serious cellular damage though the oxidation of various cellular components (Fridovich 1977). Because these toxic oxygen intermediates are inevitable by-products of respiration and photosynthesis, organisms have evolved elaborate defenses to inactivate and prevent the formation of these reactive species (see Mittler 2002; Lesser 2006 for reviews). These antioxidant defenses include active enzymatic antioxidants (e.g., superoxide dismutase, catalase, peroxidases), and passive second-line defenses in the form of non-enzymatic antioxidants (e.g., ascorbic acid, glutathione, carotenoids), that collectively scavenge ROS (Fridovich 1977, 1978; Lesser 2006). However, these defenses against oxygen toxicity can be overwhelmed when the degree of oxygen exposure is significantly increased (Fridovich 1977). Oxidative stress occurs when the production and accumulation of ROS occurs at a rate beyond the capacity of an organism to quench them which can damage lipids, proteins, and DNA (see Lesser 2006 for review).

Both corals and their algal symbionts produce increased levels of antioxidant defense enzymes under elevated light and temperature conditions (Dykens and Shick 1982; Dykens et al. 1992; Lesser 1996). However, high fluxes of ROS can overwhelm these defenses, subsequently causing cellular damage and expulsion of symbionts (Lesser 1996, 1997, 2006). The role of oxidative stress in coral bleaching has been thoroughly studied and is reviewed elsewhere by Lesser (2004, 2006). Oxidative stress has also been implicated in the reduced photosynthetic and calcification rates of corals under hyperoxia (Finelli et al. 2006; Mass et al. 2010; Wijgerde et al. 2012, 2014). To our knowledge, the genomic response of reef organisms to oxidative stress has not been investigated yet, but parallel work on the genomic response of reef corals (Barshis et al. 2013) and reef fish (Kassahn et al. 2007) to heat stress suggests that this approach yields promise in advancing our

understanding of the molecular pathways used by reef organisms in responding to environmental stress.

ROS are increasingly formed under hyperoxia, so exposure to hyperoxic environments on coral reefs likely leads to toxic effects dependent on the degree of hyperoxia and duration of the exposure (Jamieson et al. 1986). Fish that inhabit branching coral colonies and those that live in shallow reef environments, such as reef flats, routinely experience hyperoxia (Nilsson et al. 2007b). In contrast to the many studies on the tolerance of reef fish to hypoxia, there are no studies on how reef fish respond to hyperoxia (Nilsson et al. 2007b). In general, the glutathione system plays an important role in resisting oxygen-induced damage in fish (see Lushchak and Bagnyukova 2006 for review), but whether coral reef fishes have particularly well-developed mechanisms for counteracting oxidative stress remains to be explored (Nilsson et al. 2007b).

Community scale: interactions between corals and other reef organisms mediated by oxygen

Effects of benthic fish and invertebrates on coral oxygen environments

Many branching corals are host to zooplanktivorous fishes (Goldshmid et al. 2004) that retreat nightly to the pockets of water among coral branches (Goldshmid et al. 2004). In contrast to the stationary sleep exhibited by diurnal reef fishes that spend their night in non-living shelters (e.g., rock caves and crevices), these site-attached fishes exhibit a behavior called “sleep swimming” (Goldshmid et al. 2004). Throughout the night, these fish continuously move their fins, which actively enhance oxygen fluxes to the coral host by exchanging water between the coral branches and reducing the thickness of the DBL (Goldshmid et al. 2004). Because of this fanning behavior, along with other benefits that fish provide their coral hosts, corals that harbor fish have higher photosynthetic rates, grow faster, and have higher reproductive outputs than those without fish (Lieberman et al. 1995; Garcia-Herrera et al. 2017). This fish behavior is not unique to corals; anemonefish also oxygenate their hosts at night (Szczebak et al. 2013). However, the aquarium industry might present a threat to these beneficial mutualisms as two common species of coral-fanning reef fishes, the green chromis (*Chromis viridis*) and the humbug damselfish (*Dascyllus aruanus*), are among the top five most traded species of ornamental fish worldwide (Wabnitz et al. 2003).

The effect of benthic invertebrates on coral oxygen environments has not been quantified yet to our knowledge, but it is likely that some benthic invertebrates also enhance oxygen fluxes to coral colonies. Endolithic

macroorganisms, such as the boring bivalve *Lithophaga lessepsiana*, can create strong microcurrents (Shashar et al. 1993), which would reduce the effect of the boundary layer on its coral host. In addition, macrofauna that inhabit coral reef sediments, such as amphipods, anemones, and acorn worms, likely enhance oxidation of the surface sediment layers through bioturbation (Clavier et al. 2008).

The role of oxygen in coral–algal interactions

While corals routinely experience hypoxia at night (Shashar et al. 1993; Kühl et al. 1995; Gardella and Edmunds 1999; Goldshmid et al. 2004; Nilsson et al. 2004), corals in the presence of benthic algae may also experience hypoxia during the day (Smith et al. 2006; Barott et al. 2009, 2011; Haas et al. 2013). Two hypotheses have emerged to explain why hypoxic conditions can develop at coral–algal interfaces under light. First, in what is known as the “microbially mediated competition hypothesis,” dissolved organic carbon (DOC) released by benthic reef algae during photosynthesis stimulates rapid microbial growth and/or respiration near corals, creating localized regions of hypoxia (Smith et al. 2006; Brown and Carpenter 2013; Jorissen et al. 2016). In contrast to corals, which release organic matter primarily as mucus (Naumann et al. 2010), organic matter released by algae is generally dissolved (Haas et al. 2010a, b). Macroalgae, turf, and crustose coralline algae (CCA) all exude significant amounts of labile DOC into their surrounding environment during daylight hours (Haas et al. 2011). This primary producer-derived DOC is readily consumed by bacterioplankton, stimulating their growth and concomitant oxygen drawdown (Haas et al. 2011, 2016). The addition of antibiotics reduces or eliminates low oxygen conditions in coral–algal interaction zones in both the light (Smith et al. 2006; Brown and Carpenter 2013) and dark (Jorissen et al. 2016; but see Brown and Carpenter 2013), providing further evidence that microbial activity contributes to hypoxia at coral–algal interfaces.

Second, decreased zooxanthellae photosynthesis may result in hypoxia at the interface between coral and algae, if more oxygen is consumed via respiration than produced via photosynthesis in the coral–algal interaction zone. Decreased zooxanthellae photosynthesis at the interface between coral and algae can arise from several mechanisms, including: reduced symbiont densities along the growing edge of coral colonies (Oliver 1984), reduced water flow and increased DBL due to the presence of algae (Brown and Carpenter 2013; Jorissen et al. 2016), and/or the effects of algal abrasion, shading, and/or allelopathy on corals (Barott et al. 2011). For example, a study that investigated interactions between the coral *Montastrea annularis* and macroalga *Halimeda opuntia* suggested that

shading and allelopathy, rather than microbial activity, drive hypoxia at this coral–algal interface because the coral tissue bleached, with little change in the bacterial community, in the presence of the algae (Barott et al. 2011).

The presence and magnitude of hypoxia at a coral–algal interface vary widely among algal genera (Smith et al. 2006; Barott et al. 2009, 2011; Jorissen et al. 2016), with corals also exhibiting taxon-specific responses to algal treatments (Smith et al. 2006). For example, in contrast to the daytime hypoxia that generally develops in the interaction zone between most corals and algae (Smith et al. 2006; Barott et al. 2009, 2011; Haas et al. 2013), the interaction zone between the massive coral *Porites* spp. and various algae typically remains hyperoxic during the day (Wangpraseurt et al. 2012; Brown and Carpenter 2013; Jorissen et al. 2016). Similarly, while the interaction zones between macroalgae and coral (Smith et al. 2006; Barott et al. 2009, 2011; Haas et al. 2013) and between turf algae and coral (Barott et al. 2009, 2011) frequently exhibit daytime hypoxia, hypoxic conditions do not typically develop in the interaction zone between CCA and coral during the day (Barott et al. 2009, 2011; Wangpraseurt et al. 2012).

The mechanism and extent of hypoxia in coral–algal interactions are also highly dependent on the ambient flow regime. For example, one study found that hypoxic and hyperoxic conditions were present in coral–algal interactions only in low-flow (0 cm s^{-1}) and no-flow (7.7 cm s^{-1}) conditions, while in high flow (14.5 cm s^{-1}) the oxygen concentrations immediately above the zone of interaction were not different from ambient oxygen concentrations (Brown and Carpenter 2013). The thickness of the DBL and magnitude of hypoxia associated with coral–algal interfaces decrease with increasing flow speeds (Brown and Carpenter 2013; Jorissen et al. 2016). A thicker DBL is more likely to facilitate the development of hypoxia in the interaction zones between coral and algae by creating a diffusion-limited environment, which impedes the influx of oxygen and limits the removal of harmful metabolic waste products and microbes (Barott and Rohwer 2012; Jorissen et al. 2016).

Regardless of the mechanisms driving the low oxygen conditions that often develop in the interaction zones between coral and algae, these hypoxic interfaces can have severe negative consequences for coral. Hypoxic coral–algal interaction zones are accompanied by altered pigmentation and disruption of coral tissue (Barott et al. 2009; Smith et al. 2006), bleaching (Barott et al. 2009, 2011), and in some cases, even coral mortality (Smith et al. 2006). In contrast to corals, algae are significantly more tolerant to low oxygen conditions (Haas et al. 2014). This difference in susceptibility, and the prevalence of localized hypoxia at coral–algal interfaces, suggests that low oxygen stress is

one of the mechanisms underlying algal dominance in coral–algal interactions which could contribute to the positive feedback loop promoting algal dominance when natural and/or anthropogenic stressors increase algal biomass or productivity (Smith et al. 2006; Jorissen et al. 2016).

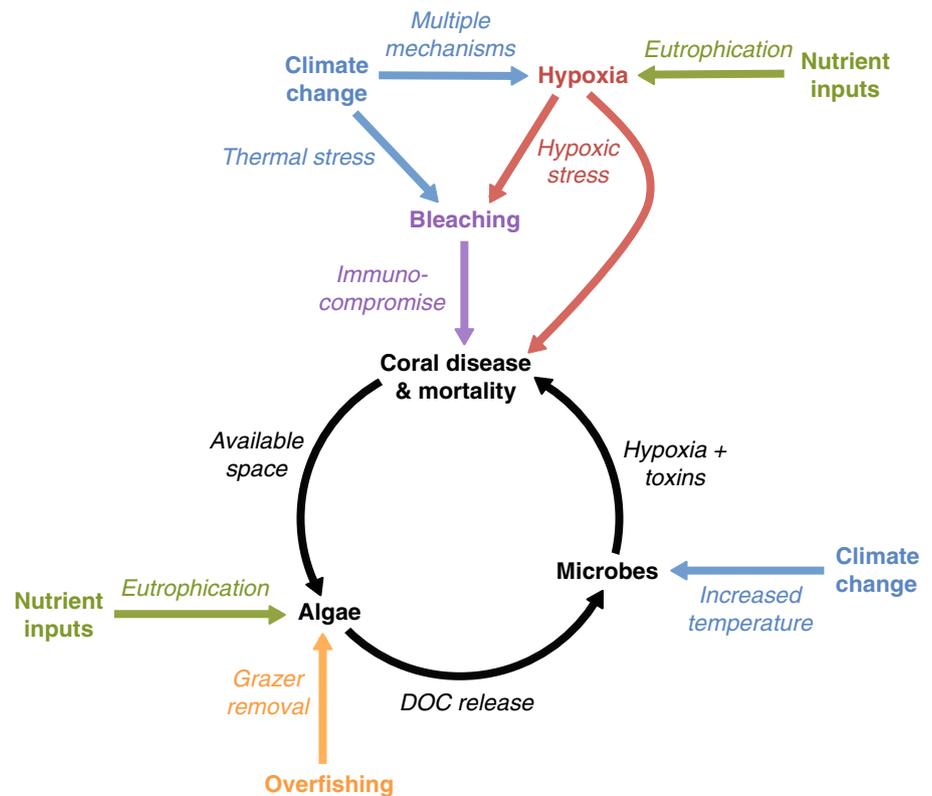
The role of oxygen in coral–disease interactions

Black band disease (BBD) is a highly virulent disease with a global distribution that affects a wide range of coral taxa (see Sato et al. 2016 for review). The disease manifests as a darkly pigmented $\sim 1\text{-mm}$ -thick microbial mat that migrates over the surface of coral, rapidly degrading coral tissue and leaving behind bare skeleton (Sato et al. 2016). The base of the BBD mat is consistently hypoxic or anoxic, depending on the light conditions (Glas et al. 2012). This oxygen depletion, along with the high concentrations of sulfide produced by the mat, is lethal to coral tissue (Carlton and Richardson 1995; Glas et al. 2012). The migration speed of BBD lesions is correlated with the level of oxygen depletion; in other words, the virulence of BBD appears driven, in part, by the extent of the hypoxic or anoxic conditions developed by the mat (Glas et al. 2012).

On a larger site scale, the prevalence of BBD on reefs has been correlated with the severity of anoxic events in the water column, suggesting that increased anoxia causes a loss of coral resilience, making colonies more susceptible to disease (Onton et al. 2011). Thus, not only does the hypoxia-tolerant BBD create localized zones of hypoxia that degrade coral, but also BBD is more common at sites repeatedly stressed by anoxic events. Although the disease typically affects only 1–10% of colonies on a reef at a given time (Green and Bruckner 2000), the predicted increase in coastal hypoxic conditions due to the ongoing effects of climate change (Altieri and Gedan 2015) suggests that the incidence of BBD disease is likely to increase in the future.

The dynamics of hypoxia, algae, and disease are hypothesized to be linked through the DDAM (DOC, Disease, Algae, Microbe) model (Dinsdale and Rohwer 2011; Barott and Rohwer 2012; Gregg et al. 2013; Haas et al. 2016; Fig. 5). In this proposed positive feedback loop, algae releases DOC, stimulating rapid microbial growth, which creates localized hypoxic zones, resulting in increased coral disease and mortality (Dinsdale and Rohwer 2011; Barott and Rohwer 2012; Gregg et al. 2013; Haas et al. 2016). Overfishing, eutrophication, and climate change act as catalysts in this model. The removal of grazers and increases in nutrients allow for higher algal cover on reefs, which feeds directly into the first part of the feedback loop (Dinsdale and Rohwer 2011). Climate change likely exacerbates multiple components of the

Fig. 5 The dissolved organic carbon (DOC), Disease, fleshy Algae, and Microbes (DDAM) model. In this positive feedback loop, algae releases DOC, stimulating rapid microbial growth, which creates localized hypoxic zones, resulting in increased coral disease and disease and mortality. Anthropogenic stressors, such as climate change, overfishing, and eutrophication-driven hypoxia, act as catalysts in this model



DDAM model because increasing sea surface temperatures: (a) directly cause coral bleaching, (b) stimulate microbial activity, and (c) enhance algae DOC release through increased photosynthesis (Dinsdale and Rohwer 2011).

Dead zones

Severe depletions of dissolved oxygen in coastal waters can cause the formation of dead zones, areas where severe hypoxia causes the mass mortality or migration of megafauna (e.g., fishes and large invertebrates). Although hypoxia can arise under entirely natural processes, anthropogenic threats, such as eutrophication and climate change, have significantly increased the frequency, spread, and severity of dead zones worldwide (Diaz and Rosenberg 2008; Rabalais et al. 2010; Altieri and Gedan 2015). The number of dead zones in marine ecosystems has approximately doubled each decade since the 1960s (Diaz and Rosenberg 2008). We identified over 25 events around the world in which hypoxia has been implicated in the mortality of tropical coral reef organisms (Table 1), with half of these events occurring in the last two decades. Relative to temperate habitats, dead zones on tropical reefs are likely severely underreported, reflecting a lack of research infrastructure in many tropical regions, a paucity of oxygen

monitoring on reefs, and the difficulty of identifying hypoxia-driven mortality after it has occurred (Altieri et al. 2017). In general, hypoxia tends to be overlooked until higher-level ecosystem effects are manifested, which are rarely the result of a single stressor, making it difficult to isolate the effects of hypoxia (Diaz and Rosenberg 2008).

Although dead zones are formed throughout the world's oceans and can arise through a variety of different pathways, they typically have two common features: (1) factor(s) that increase oxygen demand, reducing the oxygen available in the system, and (2) factor(s) that prevent the restoration of oxygen in the system (i.e., reoxygenation). There are several pathways that can lead to increased oxygen demand on coral reefs, including coral spawn slicks, excess organic matter and nutrients, and increased seawater temperatures.

Large coral spawn slicks sometimes form when calm weather coincides with coral mass spawning events (Simpson et al. 1993; Hobbs and Macrae 2012). The respiratory demand of the coral spawn causes a severe depletion of dissolved oxygen in the water column, resulting in extreme hypoxic conditions and mass mortalities of reef organisms (Simpson et al. 1993; Hobbs and Macrae 2012). This oxygen depletion is further maintained by subsequent decomposition of the spawn slicks and dead organisms (Simpson et al. 1993; Hobbs and Macrae 2012).

Table 1 Events in which hypoxia was implicated in mortality of coral reef organisms

Dead zone event			Factors that increase oxygen demand				Factors that prevent reoxygenation				References					
System	Country	Year(s)	Mortality	Increased temperature	Coral spawn slicks	Excess organic matter	Excess nutrients	Algal bloom	Poor flushing	Water column stratification	Calm seas	Low swell	Low current speeds	Light winds	Neap tides	References
Kaneohe Bay	USA	1965	Fish, corals, other invertebrates			×	×	×						×		Banner (1968)
Central West Florida Shelf (Gulf of Mexico)	USA	1971	Fish, corals, other invertebrates					×	×							Smith (1975)
Florida Keys	USA	1984–1989	Corals			×	×	×								Lapointe and Matzie (1996)
Caño Island	Costa Rica	1985	Fish, corals, other invertebrates					×								Guzmán et al. (1990)
Uva Island	Panama	1985	Corals					×								Guzmán et al. (1990)
Bills Bay	Australia	1989	Fish, corals, other invertebrates		×				×					×	×	Simpson et al. (1993)
Gulf of Eilat (Aqaba)	Israel	1992	Corals				×	×								Genin et al. (1995)
Hikueru Atoll	French Polynesia	1994	Fish, corals, other invertebrates	×				×	×	×				×		Harris and Fiechez (1995), Adjeroud et al. (2001) and Andréfouët et al. (2015)
Manihi Atoll	French Polynesia	1994, 1997, 1998	Oysters (farmed)	×					×	×				×		Andréfouët et al. (2015)
Morrocoy National Park	Venezuela	1996	Fish, corals, other invertebrates				×	×					×			Laboy-Nieves et al. (2001)
Mentawai Islands	Indonesia	1997	Fish, corals			×		×						×		Abram et al. (2003)
Takapoto Atoll	French Polynesia	1998	Oysters (farmed), benthos	×					×	×				×		Andréfouët et al. (2015)
Takarua Atoll	French Polynesia	2000, 2001	Oysters (farmed)	×					×	×				×		Andréfouët et al. (2015)
Fangatau Atoll	French Polynesia	2004	Giant clams	×					×	×				×		Andréfouët et al. (2015)
Passage between Santiago and Luzon Islands	Philippines	2004	Fish (farmed)			×			×					×		Villanueva et al. (2005)

Table 1 continued

System	Country	Year(s)	Mortality	Factors that increase oxygen demand				Factors that prevent reoxygenation				References			
				Increased temperature	Coral spawn slicks	Excess organic matter	Excess nutrients	Algal bloom	Poor flushing	Water column stratification	Calm seas		Low swell	Low current speeds	Light winds
Central West Florida Shelf (Gulf of Mexico)	USA	2005	Fish, corals, other invertebrates					×							Dupont et al. (2010)
Cocos (Keeling) Islands	Australia	2007–2008, 2009	Fish, invertebrates	×					×				×		Hobbs and McDonald (2010)
Tatakoto Atoll	French Polynesia	2009	Giant clams	×					×				×		Andréfouët et al. (2013, 2015)
Bahia Almirante	Panama	2010	Corals, other invertebrates	×	×								×		Altieri et al. (2017)
Marovo Lagoon	Solomon Islands	2011	Fish, invertebrates, turtles, dolphins, birds	×	×			×					×		Albert et al. (2011, 2012)
Ahe Atoll	French Polynesia	2012	Oysters (farmed)										×		Andréfouët et al. (2015)
Cocos (Keeling) Islands	Australia	2012	Fish, corals, other invertebrates		×								×		Hobbs and Macrae (2012)
Manihiki Atoll	Cook Islands	2012	Oysters (farmed)	×									×		Andréfouët et al. (2015)

One of the primary anthropogenic activities resulting in changes in dissolved oxygen concentrations in marine ecosystems is the addition of organic matter (Best et al. 2007). Microorganisms decompose organic matter, and the microbial respiration associated with this decomposition can reduce the amount of dissolved oxygen available in the reef waters down to lethal levels (Smith et al. 1981; Pastorok and Bilyard 1985; Jokiel et al. 1993; Loya 2004; Villanueva et al. 2005). Excess organic matter on coral reefs can come from several sources, including sewage pollution (Smith et al. 1981; Pastorok and Bilyard 1985; Jokiel et al. 1993; Genin et al. 1995), mariculture effluent (Loya 2004; Villanueva et al. 2005), and the presence of benthic algae (Gregg et al. 2013; Haas et al. 2010a, b, 2011). Mariculture, such as fish farms, can cause a substantial accumulation of organic matter on nearby reefs through the export of both fish feces and food waste (Loya 2004; Villanueva et al. 2005). For example, intensive net-pen fish farms in the northern most region of the Gulf of Eilat are fed over 4000 tons of protein-rich added food per year (Gordin 2000). The effluent produced by these farms, combined with the flow of Eilat's urban sewage into the sea (prior to 1995), has caused a continued mass killing of the gulf's corals (Loya 2004). While the presence of benthic algae has not been explicitly linked to hypoxic dead zones on reefs, turf algae, macroalgae, and benthic cyanobacterial mats are known to release significantly higher amounts of DOC on reefs compared to calcifying reef organisms such as coral and CCA (Haas et al. 2010a, b, Haas et al. 2011; Gregg et al. 2013; Brocke et al. 2015; Ford et al. 2018). Organic matter derived from benthic algae stimulates planktonic microbial oxygen consumption more than seagrass- or coral-derived organic matter (Haas et al. 2010b). Consequently, there are significantly lower oxygen concentrations, particularly during the night, at algae-dominated sites compared to other benthic lagoon environments (Haas et al. 2010b). In addition, the DOC released by ungrazed fleshy algae supports pathogenic bacterial communities that harm corals and maintain algal competitive dominance (Haas et al. 2016). The above evidence suggests that the presence of benthic algae may play an important role in the formation of dead zones on reefs through increased microbialization.

Excess nutrients increase oxygen demand through the process of eutrophication. When a body of water becomes enriched in dissolved nutrients (e.g., nitrates, phosphates), it can stimulate an explosive growth of planktonic algae or cyanobacteria (Diaz and Rosenberg 2008). When these organisms die and are decomposed by bacteria, the subsequent increase in microbial respiration depletes the water of oxygen, which can cause the formation of dead zones (Diaz and Rosenberg 2008). The most common agents of harmful algal blooms on coral reefs are dinoflagellates

(e.g., Smith 1975; Guzmán et al. 1990; Abram et al. 2003; Dupont et al. 2010), but blooms of green algae (e.g., Genin et al. 1995; Lapointe 1997; Lapointe et al. 2005; Smith et al. 2005) and cyanobacteria (e.g., Baas Becking 1951; Bowman and Lancaster 1965; Thacker and Paul 2001; Albert et al. 2005; see Charpy et al. 2012 for review) have also been noted.

There are several possible mechanisms for nutrient enrichment of coral reefs. Excess nutrients on reefs are often derived from anthropogenic land-based sources, such as agricultural runoff or untreated sewage (Pastorok and Bilyard 1985; Smith et al. 1981; Jokiel et al. 1993; Altieri et al. 2017). Because rains increase the amount of runoff from land, many eutrophication-driven dead zone events on reefs occur during periods of extraordinarily heavy rains (Banner 1968; Jokiel et al. 1993; Lapointe and Matzie 1996). Nutrients released by fish farms can also drive eutrophication on nearby reefs (Villanueva et al. 2005). Coral reefs can also become enriched in nutrients through natural processes. Coastal upwelling, which brings a surge of cold, nutrient-rich water to the surface, can cause extensive phytoplankton blooms associated with mass mortality of reef organisms (Genin et al. 1995; Laboy-Nieves et al. 2001). Regardless of the mechanisms underlying increased oxygen demand, the mortality of reef organisms due to hypoxia can produce a positive feedback cycle where the bacterial decomposition of these dead organisms accelerates oxygen depletion, prolonging hypoxic conditions and inducing further mortality (Smith 1975; Guzmán et al. 1990; Simpson et al. 1993; Hobbs and Macrae 2012).

In contrast to the mostly biologically driven increases in oxygen demand on reefs, the factors that prevent reoxygenation on reefs are predominately physical. Like other marine systems, hypoxia on reefs is often associated with a semi-enclosed or closed hydrogeomorphology that, combined with water-column stratification, restricts water exchange with more oxygenated waters at the surface or open ocean (Diaz and Rosenberg 2008; Andréfouët et al. 2015). Coral reefs located in semi-enclosed and closed basins and atolls frequently become stratified under periods of calm winds, leading to the formation of dead zones (Andréfouët et al. 2015; Altieri et al. 2017). Along with the hydrogeomorphology of the system, the weather has a large influence on the development and persistence of hypoxic conditions on coral reefs. Unusually light winds, low swell, and low current speeds are often implicated in reef dead zone events (e.g., Simpson et al. 1993; Harris and Fichez 1995; Adjeroud et al. 2001; Laboy-Nieves et al. 2001; Hobbs and McDonald 2010; Hobbs and Macrae 2012; Andréfouët et al. 2015; Altieri et al. 2017). The tidal cycle can also influence the development of dead zones due to reduced water movement or flushing during neap tides (Villanueva et al. 2005). Poor flushing of lagoons due to wind, wave, or tidal

conditions is a prerequisite for the formation of coral spawn slicks during mass spawning events, where the lack of water exchange retains coral spawn in a single area (where their decomposition rapidly depletes the water of oxygen) and prevents reoxygenation of the system (Simpson et al. 1993; Hobbs and Macrae 2012).

Although coral reef mortality was first attributed to dead zones several decades ago (e.g., Banner 1968; Smith 1975), the recovery of reefs following these events remains poorly understood (Altieri et al. 2017). The long-term effects of hypoxia on coral reefs are likely to be different and more severe than other disturbances on reefs because hypoxia simultaneously impacts a wide range of taxa including reef-builders, consumers, and microbes (Altieri et al. 2017). The mass mortality of coral reef organisms due to severe hypoxia is usually followed by some degree of recolonization with the return of normal oxygen conditions (Banner 1968; Smith 1975; Dupont et al. 2010). Given the slow-growing nature of corals and the variety of threats faced by modern reefs, however, recovery rates can be on the order of years (Dupont et al. 2010) to decades (Smith 1975). Regardless of the rate of recovery, the pattern of species that establish during recovery from severe hypoxia events does not usually mirror the pattern of species loss (Diaz and Rosenberg 2008; Nelson et al. 2016). On coral reefs recolonization by some taxa is relatively rapid (e.g., benthic algae, polychaetes, fishes) while others (e.g., corals, echinoderms, mollusks) is slow and may take several years (Banner 1968; Smith 1975; Dupont et al. 2010).

Directions for resource management and future work

Despite the fundamental role of oxygen in the dynamics of corals and other reef organisms, the study of oxygen dynamics on coral reefs is still in its infancy. Although the threat of hypoxia to reefs appears to be larger than estimated, and growing (Altieri et al. in review), very few reefs are monitored for oxygen, and so our knowledge of the relative importance of various biological and physical processes associated with the spatiotemporal variation in oxygen on reefs remains limited. In addition to increased monitoring, we stress the need for more research on the genomic response to oxygen stress and molecular basis for interspecific differences in tolerance. The relationship between oxygen saturation and coral physiology, along with lethal oxygen thresholds, has only been established for a few species and warrants further investigation. We need more studies considering the role of hypoxia and hyperoxia in reef dwelling organisms other than corals in order to predict how whole reef communities, including harvested species of fish and invertebrates, will respond to oxygen

stress. Finally, given the suite of challenges faced by current reefs, examining the short- and long-term effects of oxygen stress for reef resilience, along with investigating interactions between hypoxia and other stressors including warming, ocean acidification, algal overgrowth, and disease, demands further study.

Oxygen is created, consumed, and exchanged through many reef processes across a variety of scales. To untangle the complex dynamics of oxygen on reefs, we suggest that more studies need to integrate across scales, using a combination of laboratory and field techniques. This approach has already yielded some important insights, such as how hypoxia acts not only as a driver of coral disease and algal dominance at the reef scale, but also as a consequence of both disease and algae at smaller, millimeter scales. A multi-scale approach was integral to the discovery of these feedback loops, which can have devastating consequences for coral. Other potential feedbacks, for example, between the respiration of individual colonies and overall oxygen concentrations on reefs, are likely to emerge as more studies work across scales. Developing a more complete understanding of how oxygen acts as a currency that mediates reef functioning and health is essential to conserving reefs now and in the future.

Although our understanding of the processes and mechanisms that drive variation in oxygen on coral reefs is incomplete, there are some clear strategies that managers can implement to reduce the frequency and severity of dead zones. Preempting a shift to macroalgae dominance following a hypoxia-driven mass mortality of coral depends, in part, on the whether sufficient grazing pressure is present (Kuempel and Altieri 2017), so protecting herbivorous fish and invertebrate communities may be essential for maintaining reef functioning following extreme oxygen events. Like their temperate counterparts, dead zones on coral reefs are usually formed by the confluence of several factors that increase oxygen demand and prevent reoxygenation, rather than a single cause. For example, the extreme hypoxic event that occurred in Panama in 2010 occurred in a semi-enclosed basin with restricted exchange with the open ocean that suffers from seasonal periods of low winds and high temperatures and increasing influx of nutrients from agricultural runoff and untreated sewage (Altieri et al. 2017). Reducing anthropogenic sources of organic matter and nutrients, which contribute to increased oxygen demand, is likely to be essential to mitigating oxygen stress. In temperate marine systems, management of nutrients and carbon inputs has successfully eliminated dead zones from several systems (Diaz and Rosenberg 2008), suggesting that similar management strategies on a local scale could prevent or reverse the development of many dead zones on coral reefs.

Concluding remarks

Tropical coral reefs are characterized by extreme oxygen fluctuations. Both hypoxia and hyperoxia are routinely present on reefs across all scales of examination, from the surface and tissue of coral colonies up to the landscape scale. The discovery of this regularly occurring wide variation in oxygen concentrations has been taken as evidence that corals must be adapted to function in both high and low oxygen environments. Following their Great Barrier Reef expedition in the late 1920s, Yonge et al. (1932) concluded “There can be no doubt that reef-building corals are exceptionally well fitted for survival in water of very variable oxygen content.” This sentiment has been echoed throughout the literature by several other authors. After characterizing the extreme diel fluctuations of oxygen in coral boundary layers, Shashar et al. (1993) stated, “Corals and endolithic algae must be adapted to function at both very low and very high oxygen concentrations.” Similarly, Gardella and Edmunds (1999) have suggested “The routine occurrence of widely differing oxygen saturations within coral tissues makes it likely that both the host and the symbionts have constitutive mechanisms to deal with extreme concentrations of metabolite.” While corals have certainly evolved physiological mechanisms to deal with heterogeneous oxygen conditions and may function better than most taxa at high and low oxygen saturations, these statements overlook the consequences of living in extreme oxygen environments for these organisms.

Corals exhibit reduced photosynthetic and calcification rates when subject to hypoxia and hyperoxia. Emerging evidence suggests that hypoxia is both a driver and consequence of coral disease and increased algal dominance on reefs. Oxidative stress has been proposed as a unifying mechanism by which several environmental threats cause coral bleaching, and in recent decades, hypoxia has been implicated in a number of mass mortality events on coral reefs around the world. The unprecedented rise in coastal dead zones due to eutrophication and climate change suggests that oxygen offers crucial insights into severe bleaching and mass mortality events, in addition to being a major determinant of normal reef functioning and health. Given the integral role of oxygen in mediating reef dynamics across at all levels of biological organization, we suggest that developing a better understanding of the mechanisms and processes that drive variation in this universal “currency” across multiple scales is essential for conserving coral reefs.

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