Eutrophication on Coral Reefs: What Is the Evidence for Phase Shifts, Nutrient Limitation and Coral Bleaching

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Coral reefs continue to experience extreme environmental pressure from climate change stressors, but many coral reefs are also exposed to eutrophication. It has been proposed that changes in the stoichiometry of ambient nutrients increase the mortality of corals, whereas eutrophication may facilitate phase shifts to macroalgae-dominated coral reefs when herbivory is low or absent. But are corals ever nutrient limited, and can eutrophication destabilize the coral symbiosis making it more sensitive to environmental stress because of climate change? The effects of eutrophication are confounded not just by the effects of climate change but by the presence of chemical pollutants in industrial, urban, and agricultural wastes. Because of these confounding effects, the increases in nutrients or changes in their stoichiometry in coastal environments, although they are important at the organismal and community level, cannot currently be disentangled from each other or from the more significant effects of climate change stressors on coral reefs.

Keywords: corals, eutrophication, nitrogen, coral bleaching, climate change

Coral reefs are highly productive and biodiverse ecosystems in otherwise oligotrophic waters, which is also known as *Darwin's paradox* (Darwin 1842). The evolutionary success of modern scleractinian corals, one of the primary builders of coral reefs (figure 1), is closely linked to the acquisition of their primary dinoflagellate endosymbionts (box 1) in the family Symbiodiniaceae within high-light, oligotrophic environments (Stanley 2006, Frankowiak et al. 2016, LaJeunesse et al. 2018). The molecular taxonomy of the algal symbionts had previously identified nine clades (clades A–I) and many phylotypes within each clade for the genus *Symbiodinium* (Thornhill et al. 2014). This taxonomic structure has now been replaced with a robust phylogeny of multiple genera in the family Symbiodiniaceae on the basis of both morphological and molecular characters (LaJeunesse et al. 2018). In addition, the proposed phylogeny reveals an ancient origin of the Symbiodiniaceae, beginning in the Mesozoic (approximately 140–200 million years ago), that is congruent with the radiation of scleractinian corals (LaJeunesse et al. 2018). These largely mutualistic associations (but see Wooldridge 2010, Lesser et al. 2013, Baker et al. 2018 for perspectives on the parasitic to mutualistic continuum) thrive in tropical and subtropical seas in which their intracellular, symbiotic dinoflagellates provide a major portion of their photosynthetically fixed carbon to the host. Although the organic carbon respired can almost fully satisfy daily energetic costs of the host, the *in hospite* recycling or conservation of inorganic nutrients such as nitrogen is essential for growth and survival of the holobiont (Lesser 2004, Yellowlees et al. 2008, Stambler 2011, Davy et al. 2012).

Currently, coral reef ecosystems are threatened worldwide by multiple stressors including thermal stress, ocean acidification, and coastal development with its secondary effects on sedimentation, nutrient loading, salinity, hypoxia, and chemical pollution (Fabricius 2005, Hoegh-Guldberg et al. 2007, D'Angelo and Wiedenmann 2014, Anthony 2016). These stressors, alone or in combination, can disrupt multiple cellular pathways, leading to cell death (i.e., apoptosis) and the phenomenon known as coral bleaching, whose endpoint is the mass expulsion of the symbiotic Symbiodiniaceae from their hosts, leading to significant levels of mortality (Lesser 2006, 2011). Studies on coral bleaching have shown that dysfunction of photosystem II (PSII) in the endosymbiotic Symbiodiniaceae is the primary target of both thermal and light stress and often occurs before visible signs of bleaching, measured using active chlorophyll fluorescence (Lesser 2004, Warner et al. 2010). Simultaneously, the production of reactive oxygen species (ROS) occurs and

BioScience 71: 1216–1233.
https://doi.org/10.1093/biosci/biab101

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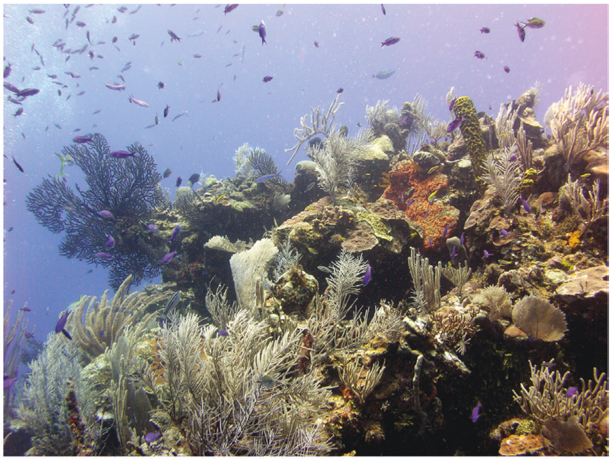

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Figure 1. Examples of diverse and healthy coral reefs from (a) Carrie Bow Cay, Belize on outer ridge at approximately 20 meter depth and (b) Komodo Island, Indonesia at approximately 15 meter depth. Photographs: Michael P. Lesser.

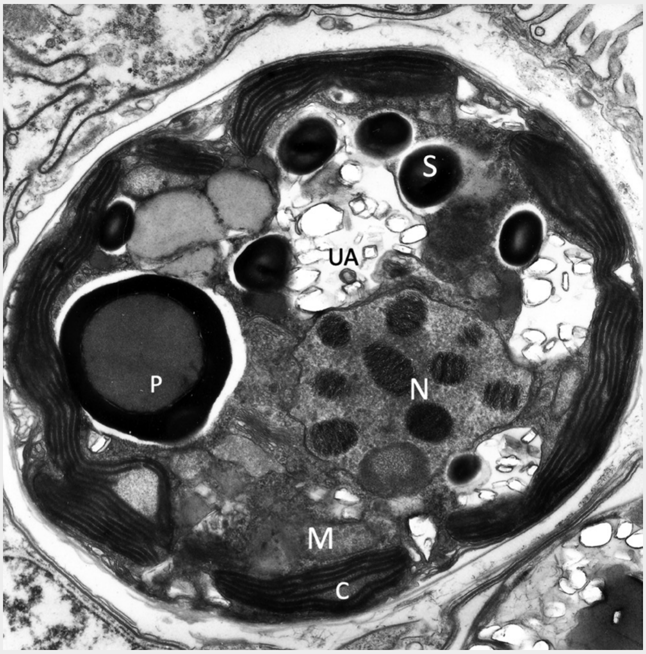
overwhelms antioxidant defenses (box 2) with damage to multiple cellular compartments, apoptosis, and expulsion of damaged Symbiodiniaceae (Lesser 2011). The generation of ROS, primarily in the chloroplast of the symbionts (figure 2), is proportional to the partial pressure of oxygen, and therefore irradiance, which is further exacerbated by photodynamic production of ROS due to exposure to ultraviolet radiation under hyperoxic conditions (Lesser 2006). Coral bleaching occurs on timeframes from days to months, is affected by variability in habitat characteristics (i.e., low light versus high light), and is affected by the intensity and duration of the environmental insults. In addition to large-scale climate change effects, there is increasing evidence that local effects such as eutrophication cause stress on coral reefs and potentially decrease resilience to climate change stressors. Land-based pollution of coastal waters can lead to not only eutrophication but multiple secondary effects, such as hypoxia, sedimentation, organic loading, exposure to pesticides, and the introduction of opportunistic pathogens (Szmant 2002). Of these, eutrophication has received the most attention where excess nutrients are believed to lead to significant changes in the benthic communities of coral reefs. In the present article, I review and evaluate examples of the historical and current literature on eutrophication effects on coral reefs and scleractinian corals. The goals are to identify whether current data and their interpretation can adequately identify a role for eutrophication in phase shifts to an algae-dominated state on coral reefs, whether corals are nutrient limited, and whether nutrient excess and altered stoichiometry increase the sensitivity of scleractinian corals to climate stressors.

Eutrophication and phase shifts on coral reefs

Most coral reefs develop and persist in tropical and subtropical oligotrophic waters very low in ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-), known as dissolved inorganic nitrogen (DIN). Concentrations of DIN on coral reefs are typically less than 1.0 micromole (μmol) per liter and less than 0.3 μmol per liter of phosphate (PO_4^{3-}) but as high as 10.0 μmol per liter of DIN and 0.6 μmol per liter of PO_4^{3-} (D'Elia and Wiebe 1990, Atkinson and Falter 2003, O'Neil and Capone 2008), especially in near-shore environments with riverine inputs (Fabricius 2005). Additionally, localized nutrient increases also occur consistently on many reefs because of upwelling or internal waves (Leichter et al. 2003, Wolanski et al. 2004), excretion by fish (Meyer et al. 1983), seabird guano (Graham et al. 2018), and pore (Atkinson and Falter 2003) or cave (Slattery et al. 2013) water efflux of DIN onto reefs. Almost 20 years ago, Szmant (2002) asked whether eutrophication was a major cause of coral reef decline. The conclusions from that review were that increases in anthropogenic nutrient enrichment alone were insufficient to explain community changes on most coral reefs and that ocean warming on reefs, leading to coral bleaching and mortality, was the primary cause of coral mortality, coral reef degradation, and the subsequent phase shifts to macroalgal dominance. Several studies had reported, especially throughout the Caribbean basin, that after extreme bleaching events, both direct and indirect (i.e., disease *sensu* Lesser et al. 2007a) coral mortality were high and resulted in a phase shift to macroalgae-dominated (i.e., fleshy frondose species) reefs in the Caribbean. This was facilitated by multiple disturbance events, including hurricanes, the loss of a major herbivore to disease (i.e., the sea urchin *Diadema antillarum*), and overfishing of herbivorous fish (Hughes 1994, Hughes et al. 2000). This top-down perspective on phase shifts was countered by bottom-up arguments that anthropogenic increases in nutrients (i.e., DIN) primarily controlled the proliferation of macroalgal communities on Caribbean coral reefs on the basis of the nutrient threshold hypothesis, by which increases in nutrients above 1.0 μmol per liter of DIN and 0.1 μmol per liter of PO_4^{3-} allow nutrient limited macroalgae to increase in disturbed habitats (Lapointe 1997, 1999). Lapointe (1999)

Box 1. General biology of Symbiodiniaceae.

Dinoflagellates are eukaryotic protists exhibiting mutualistic, commensal, parasitic, and free-living life histories that are taxonomically grouped with ciliates and apicomplexans in the superphylum Alveolata (Lesser et al. 2013). Of those dinoflagellates that are photosynthetic the Symbiodiniaceae, colloquially known as zooxanthellae, are extremely diverse and found as endosymbionts in corals, sponges, sea anemones, jellyfish, clams, nudibranchs, flatworms, ciliates and foraminifera (LaJeunesse et al. 2018). In scleractinian corals these endosymbionts are found intracellularly within vacuoles, known as symbiosomes, of host gastrodermal cells at high densities (~1×10^6 cells cm^2) where they are found as a slow-growing (1-3 divisions d^{-1}) stage morphologically resembling a cyst (see below). Here the term cyst is used, versus coccoid cell, consistent with previous descriptions of Symbiodiniaceae life cycles (Freudenthal et al. 1962, Yonge 1963), because it is the accepted terminology used for descriptions of dinoflagellate life cycles (Kremp 2013). The term coccoid cell, which simply refers to a round morphology, was assigned (e.g., Trench 1981) based on the assumption that Symbiodiniaceae cysts exhibiting metabolic activity are not, in fact, cysts. But it is well-known that dinoflagellate cysts have varying degrees of metabolic activity based on their function (Bravo and Figueroa 2014, Liu et al. 2020), and the occurrence of metabolic activity (i.e., photosynthesis) in Symbiodiniaceae cysts does not exclude them from being homologous to the cysts observed during the life cycle of other dinoflagellates (Kremp 2013). In fact, dinoflagellates are well known to encyst when nitrogen limitation occurs (Dagenais-Bellefeuille and Morse 2013), and it would be interesting to know if this occurs in the Symbiodiniaceae. The other major stage of Symbiodiniaceae life cycle is the motile zoospore, or gymnodinioid, stage resembling a free-living dinoflagellate and described from the light phase of the photoperiod in cultures where they release their "flagella" and encyst as the dark phase resumes. Here, the use of the term flagellum is a remnant from the early days of light microscopy prior to when any structural analysis was possible. The prokaryotic flagellum (made of the protein flagellin) is not homologous with the eukaryotic cilium (a 9+2 microtubule structure). Cladistically, they are not shared-derived characters, or synapomorphic (Margulis 1980). The zoospore stage of Symbiodiniaceae have two cilia, one associated with the sulcus and one with the cingulum, and all structures used for motility such as the eukaryotic cilium, bacterial flagellum and the archaellum of the archaea are examples of convergent evolution (Kahn and Scholey 2018). Corals acquire their Symbiodiniaceae either vertically (i.e., from the parent), or horizontally (i.e., from the environment) where they serve as primary producers and supply their coral host with up to 95% of carbon requirements as sugars, amino acids, carbohydrates and small peptides (Muscatine 1990, Lesser 2004). These compounds provide the coral with energy for respiration, growth, and the deposition of its CaCO3 skeleton (Muscatine 1990, Lesser 2004). Heterotrophy in corals, the consumption of zooplankton and other sources of particulate organic matter, however, is essential for providing nitrogen, phosphorus, and other nutrients that are needed to use the available carbon skeletons for protein synthesis and other essential biosynthetic requirements.



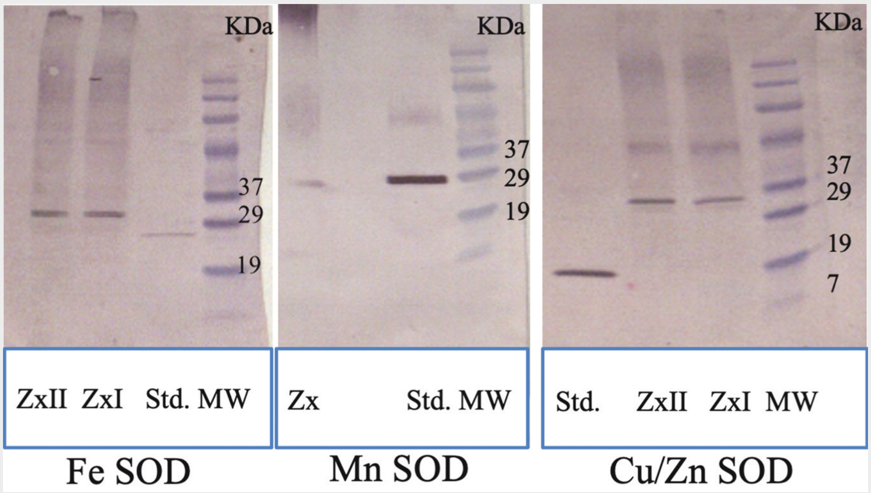
Transmission electron micrograph of Symbiodiniaceae cyst in host symbiosome from **Exaptasia pallida.** *Sample is from control treatment described in Lesser and Shick (1990). Note the presence of starch granules (S), chloroplasts (C) with normal thylakoid membranes, nucleus (N) with condensed chromatin material, mitochondria (M), pyrenoid (P) and what are putative uric acid (UA) crystals (*sensu *Clode et al. 2009).*

stated that growth rates for macroalgae become maximal at 0.5–1.0 μmol per liter of DIN, which would include most coral reefs today. If macroalgae are already at their maximum growth rates at these low nutrient concentrations then factors other than DIN concentration, such as substrate availability, irradiance, or herbivory, control macroalgal growth and biomass accumulation on many coral reefs.

Multifactorial and natural experiments have repeatedly demonstrated the primary role of herbivore loss in facilitating phase shifts when compared with eutrophication

Box 2. Reactive Oxygen Species in Corals.

Deviations in nutrient stoichiometry are believed to cause changes in the uncoupling of host control on symbiont growth rates leading to destabilization and large increases in the number of intracellular symbionts (Wiedenmann et al. 2013).Each additional symbiont cell represents an increase in the flux of ROS when exposed to thermal and light stress which needs to be quenched (Cunning and Baker 2013). Under normal conditions endosymbiotic Symbiodiniaceae produce photogenerated superoxide radicals (O_2^-), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and hydroxyl radicals (HO•) (Fig. 2) which increases under thermal and light stress leading to oxidative stress (Dykens et al. 1992, Lesser 1996, 2006, 2019, Suggett et al. 2008, Saragosti et al. 2010).Corals can mount antioxidant defenses against ROS, and two genera of Symbiodiniaceae (*Cladocopium* sp. and *Durisdinium* sp.) express the highest activities of the antioxidant enzyme superoxide dismutase (SOD) prior to exposure to thermal and light stress and this may have an advantage in the early stages of exposure to thermal and light stress (Lesser 2011, 2019).A unique evolutionary feature of the antioxidant defense against O_2^-, the principal ROS in many pathways that determines the level of oxidative stress, is that Symbiodiniaceae express all three metalloproteins of SOD. Cu/Zn SOD is principally a cytosolic enzyme in eukaryotes but is also found in plant chloroplasts, Fe SOD is found in the chloroplast, and Mn SOD is principally found in mitochondria (Halliwell and Gutteridge 1999, Asada 2000).The presence of various metalloproteins of SOD has been identified in several cnidarians and their Symbiodiniaceae symbionts (Lesser and Shick 1989, Matta et al. 1992, Richier et al. 2003, Lesser and Farrell 2004, Krueger et al. 2015). The presence of all three metalloproteins is hypothesized to be the result of the multiple symbiotic events that dinoflagellates have undergone since their rapid radiation during the late-Jurassic (Mesozoic era) ~ 150 mya (Falkowski et al. 2004).Additionally, both host cells (Perez and Weis 2006) and symbiotic dinoflagellates produce nitric oxide (NO•) (Bouchard and Yamasaki 2008).Nitric oxide synthase (NOS) activity in corals and sea anemones (Trapido-Rosenthal et al. 2005, Morrall et al. 2000) suggest that NO•production is followed by the production of highly reactive nitrogen species (RNS) such as peroxynitrite (ONOO-), an important contributor to redox stress and the initiation of coral bleaching (Lesser 2006, 2011, Weis, 2008, Hawkins and Davy 2013). Targets for ROS include the D1 protein of photosystem II, DNA, and ribulose 1, 5-bisphosphate decarboxylase/oxygenase (Rubisco) (Lesser 1996, Lesser and Farrell 2004).Photo-oxidative stress, both ROS and RNS production, has been proposed as a mechanism by which multiple environmental stressors, either independently or interactively, cause photosynthetic dysfunction and subsequently apoptosis that eventually manifests itself as coral bleaching (Lesser 2006, 2011, Weis 2008).



Western blots using polyclonal antibodies (Fe and Mn SOD Dr. John G. Scandalios, Cu/Zn Ab Sigma) against different SOD metalloproteins in* Breviolum minutum *(Symbiodiniaceae) done as described in Lesser and Kruse 2004 by Daniel Merselis. Lanes ZxI and ZxII are protein extractions with and without protease inhibitors. A standard lane for each metalloprotein (Sigma Inc.) is included as well as molecular weight standards (Bio-Rad Inc.). One result of the analysis is the molecular weight (32 KDa versus 16 KDa) of the Cu/Zn metalloprotein which suggests a dimer that cannot be separated under the reducing conditions of the gel (Lesser unpublished data).

(Carpenter 1996, Miller et al. 1999, Aronson and Precht 2000, Ostrander et al. 2000, Jompa and McCook 2002, Hughes et al. 2007, Burkepile and Hay 2009, Sotka and Hay 2009, Rasher et al. 2012, Jessen et al. 2013). From a physiological perspective, macrophytes in low-nutrient environments can respond positively to pulses of nutrients such as DIN and exhibit uptake kinetics that are concentration dependent (den Haan et al. 2016). The initial surge in uptake likely represents the replenishment of depleted, intracellular nitrogen pools and, depending on the elemental content (i.e., the ratio of carbon to nitrogen to phosphorus, C:N:P) of the algal tissues and the stoichiometry of the ambient nutrients, may not result in any increase in growth rate or biomass accumulation given that the C:N:P ratios of macrophytes more often suggests phosphorus rather than nitrogen limitation (Atkinson and Smith 1983). In fact, although

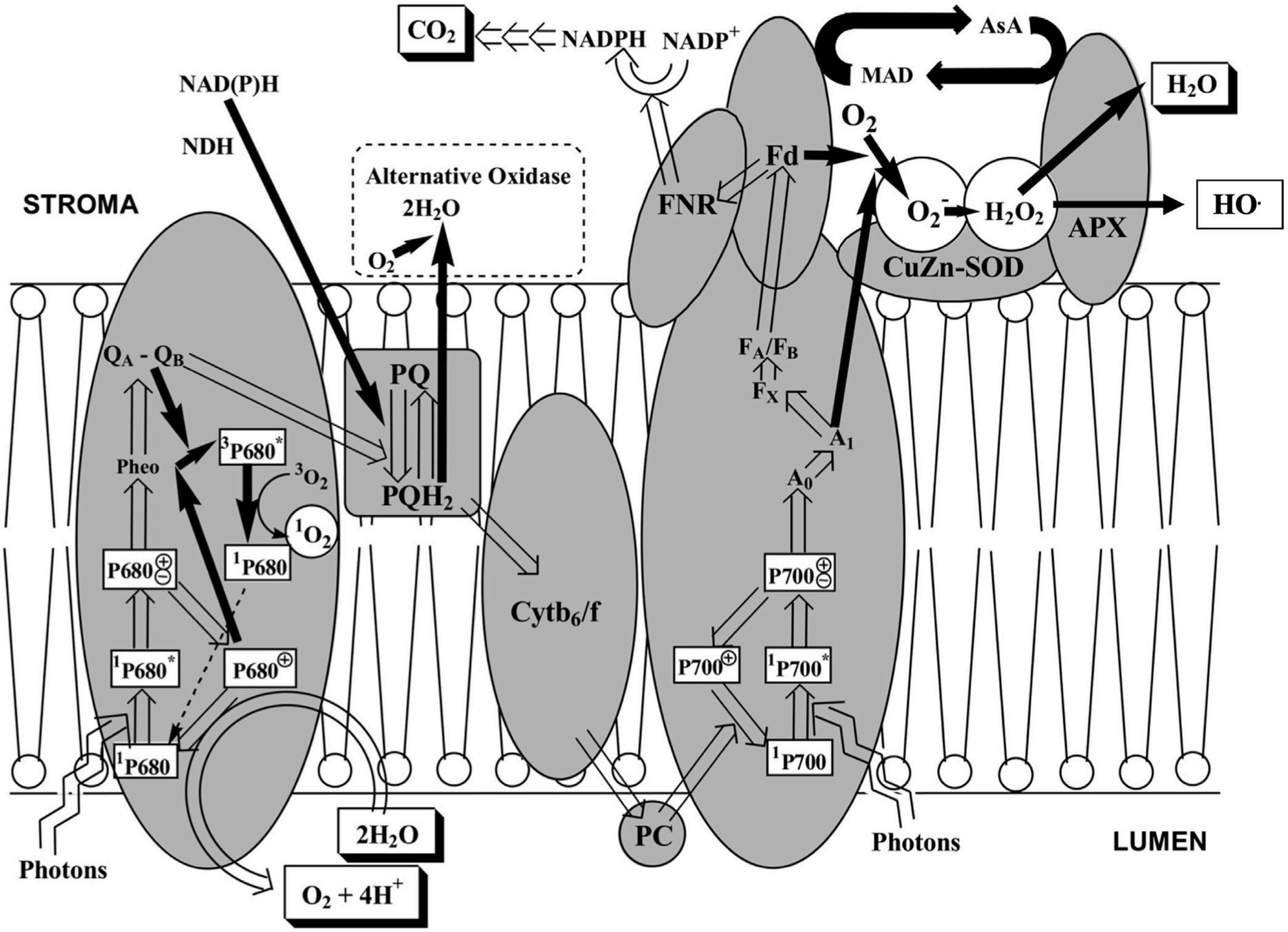


Figure 2. Production of singlet oxygen ($^1O_2$) in PSII and hydrogen peroxide (H_2O_2) and superoxide O_2^- radicals in PSI of the chloroplast thylakoids (Mehler reaction). Hydroxyl radicals ($HO^\cdot$) can be formed by H_2O_2 in the presence of transition metals (e.g., Fe^{2+}) by the Fenton or Haber–Weis reaction. Arrows within and between embedded PSII proteins represent the photoexcitation of reaction center chlorophylls and the electron flow under the saturating irradiances where all of the electrons generated are used for carbon dioxide fixation. Black arrows result from irradiances that exceed the capacity of the electron transport system and carbon dioxide fixation. Alternative oxidase, or plastid terminal oxidase, is a four-electron oxidase using plastoquinol as the electron donor without releasing ROS, as a component of chlororespiration in the dark. Abbreviations: NDH, nicotinamide adenine dinucleotide phosphate dehydrogenase complex; PQ, plastoquinone; PQH_2, plastoquinol. Source: Redrawn from Asada (2006).

nutrient addition does increase uptake rates dramatically in many cases for nutrient depleted macrophytes, it is not necessarily coupled with an increase in growth which is largely dependent on tissue nutrient status and other factors such as irradiance (Fong et al. 2003, Reef et al. 2012). In other words, ambient nutrient concentrations in the water column are not in steady state with, or coupled to, macroalgal growth rates and biomass accumulation.

One of the best-known long-term experiments carried out to understand the effects of eutrophication was the Enrichment of Nutrients on Coral Reefs Experiment (ENCORE) on the Great Barrier Reef (GBR), in the lagoon of One Tree Island. This 2-year experiment explicitly examined the effects of nutrient increases on multiple independent reefs previously considered to be pristine (Koop et al. 2001). During the first year the experimental nutrient loading resulted in final concentrations of 0.91 μmol per liter of NH_4^+ (standard deviation [SD] = 0.79) and 0.52 μmol per liter of PO_4^{3-} (SD = 0.32); with a molar nitrogen to phosphorus ratio [N:P] of 7.4. The percentage cover of frondose macroalgae was reported as approximately 2% at the beginning of the experiment and does not appear to have been quantified during or at the end of the experiment. Because there were no measurable effects in year 1, including the lack of any increase in growth or biomass of epilithic algal communities (i.e., turf algae), the concentrations of nutrients were increased in year 2, resulting in final concentrations of 11.3 μmol per liter of NH_4^+ (SD = 10.20) and 2.40 μmol per liter of PO_4^{3-} (SD = 1.61); with a N:P of 5.93 (Koop et al. 2001). Both years of nutrient addition were carried out with a background concentration of approximately 2.94 μmol per liter of NO_3^-, creating DIN concentrations that far exceed the limits defined by the nutrient threshold hypothesis (Lapointe 1997). Bell and colleagues (2007) argued that the lack of any growth in the epilithic algal communities was because the nutrient control and treatment atolls of the ENCORE experiment were saturated with respect to nutrient uptake kinetics, and growth only occurs when nutrients are introduced under limiting conditions if it occurs at all. Szmant (2002) and McCook (1999) also attributed the lack of any effects on epilithic algal community biomass during ENCORE as a confounding effect of the naturally high NO_3^- concentrations, with additional effects attributed to the differences in the sizes of the microatolls, as well as the tidally driven circulation in the lagoon, which, at low tide, may accentuate boundary layer effects and limit the diffusion of nutrients into turf or frondose macroalgae (Atkinson and Falter 2003). Finally, Bell and colleagues (2007) also argued that significant stands of macroalgae were already present at One Tree Island prior to ENCORE. Koop and colleagues (2001), however, reported a significant uptake of $^{15}NH_4$ in at least one species of macrophyte (i.e., the filamentous alga *Laurencia intricata*), but no growth occurred in response to nutrient addition (table 13 in Koop et al. 2001). As a point of comparison, biomass-normalized rates of maximum nutrient uptake in corals are significantly lower than those of macroalgae when they are exposed to large pulses of nutrients, such as a freshwater pulse event resulting in a 75-fold increase in NO_3^- and 31-fold increase in PO_4^{3-} (den Haan et al. 2016), and are transient events in most cases that do not necessarily result in an increase in growth.

Because community-wide changes in the frondose macroalgal communities were not quantified during ENCORE and no changes in the epilithic algal communities were detected, it is difficult to determine the effects of nutrient additions, if any, on macroalgae during ENCORE (*sensu* Szmant 2002). It should be noted that many coastal reefs on the GBR develop and persist without macroalgal overgrowth under a variety of nutrient levels that would not be considered oligotrophic (McCook 1999, Szmant 2002, Fabricius 2005). A recent analysis of coral cover on the GBR has also shown that poor water quality (i.e., high nutrients, sediments, and turbidity) is a proximate cause of long-term increases in coral resilience to thermal stress resulting in coral bleaching (MacNeil et al. 2019).

Another study monitored coral reef communities and ambient nutrient concentrations at Looe Key, in the Florida Keys, reportedly one of the most heavily affected coral reef systems in the world, for over 30 years (Lapointe et al. 2019). The authors interpreted their data as having demonstrated an increase in DIN concentrations and altered nutrient stoichiometry, which resulted in both algal blooms and ecosystem level stress leading to the decline of scleractinian corals on Looe Key and throughout the Florida Keys. Both sewage and agricultural runoff are identified as point sources for the eutrophication effects described in Lapointe and colleagues (2019). During the study, both positive and negative changes in nutrient concentrations and their ratios occur at Looe Key, but the relationship between individual nutrients and time predicts a small proportion of the variability in nutrient concentration (Lapointe et al. 2019). This observation and issues regarding the suitability of the data analyses used bring into question the veracity of the conclusions made for the effects on the benthic community (Julian et al. 2020). Even in the absence of these concerns, most of the measurements of DIN and PO_4^{3-} are at, or below, the 1.0 μmol per liter of DIN and 0.1 μmol per liter of PO_4^{3-} thresholds for the phase shift from coral to macroalgae-dominated coral reefs (Lapointe 1997) and are generally at, or above, those concentrations where the maximum growth rates of macroalgae reportedly occur (Bell et al. 2007). Finally, the average N:P ratio for the ambient water nutrients was predominately less than 20 suggesting marginal PO_4^{3-} limitation, given that an N:P ratio of approximately 16 indicates nutrient sufficiency, for the entire duration of the study. The only exceptions were those years during which significantly increased freshwater discharges from the Everglades occurred and N:P ratios as high as approximately 30 were observed (Lapointe et al. 2019). Only during those periods with the highest N:P ratios in the Florida Keys (1996–2000; Lapointe et al. 2019) are there sufficient benthic data to show an increase in macroalgal cover to around 16.5% (Mailo et al. 2008), whereas macroalgal cover on Looe Key was approximately 5% by the year 2000.

In fact, calculations for the role of the Everglades in nutrient loading across the Florida Keys suggest that it is minor compared with offshore inputs, such as those from internal waves, on an annual basis (Lamb and Swart 2008, Gibson et al. 2008). Despite a strong relationship between coral cover decline and DIN concentrations that explains 60% of the variance (figure 5a in Lapointe et al. 2019), there have been no significant differences in DIN concentrations since the 1990s and the 2000s for PO_4^{3-} concentrations. All mean values are at or barely greater than the threshold values at Looe Key (table 2 in Lapointe et al. 2019), and the N:P ratios are well below those used by Wiedenmann and colleagues (2013), in most years, to experimentally show increased sensitivity to thermal and light stress, causing coral bleaching. It is difficult to envision how these marginally elevated nitrogen levels led directly to the decline of scleractinian corals, whereas the confounding effects of ocean warming on coral mortality, which increases substrate availability for space-limited turf and frondose macroalgae, occurred over the same timeframe (Kuffner et al. 2015). Nutrient addition experiments in the Florida Keys reported an enrichment rate of DIN three times greater than the ambient values for 3 years, which resulted in *experimental* exposures with an average N:P ratio of approximately 15, suggesting nutrient sufficiency, and *control* plots with an average N:P ratio of approximately 33, indicating a transition to PO_4^{3-} deficiency

(Vega Thurber et al. 2014). Nutrient addition plots only showed increased coral bleaching in one bleaching sensitive species (i.e., *Agaricia* sp.), and the authors suggest that the thermal threshold for this species was lowered in the nutrient addition plots despite the fact that these plots do not appear to represent eutrophic conditions. Additionally, bleaching in these plots likely did not occur as was described by Wiedenmann and colleagues (2013), where increased bleaching susceptibility reportedly occurs from changes in nutrient stoichiometry, not higher nutrient concentrations.

Using the same plots in the Florida Keys as Vega Thurber and colleagues (2014) and including herbivore exclusion cages, Zaneveld and colleagues (2016) clearly showed that overfishing of herbivores causes a shift to algal dominance with little effect of nutrient addition on macroalgae. Other well controlled experiments conducted in the Florida Keys also show the importance of herbivores (i.e., top-down effects) in controlling macroalgal biomass and percentage cover (e.g., Sotka and Hay 2009). On the basis of our current knowledge, severe deviations in nutrient stoichiometry or elevated nutrient concentrations far greater than those observed in the Looe Key study and similar to other long-term nutrient data for the Florida Keys (e.g., Lamb and Swart 2008) would be required to disrupt coral physiology and to lead to significant coral mortality (e.g., Wiedenmann et al. 2013, Duprey et al. 2016). Any such effects would need to be separated from the confounding effects of ocean warming, freshwater events, and chemical pollutants for the corals and coral reefs of the Florida Keys.

Finally, bimonthly inorganic nutrient measurements and tissue carbon and nitrogen content of the macrophyte *Turbinaria ornata* from the National Science Foundation Long Term Ecological Research station in Moorea (http://mcr.lternet.edu/research-areas/inorganic-nutrients) for the years 2005–2018 collected from fringing reef, backreef, and forereef habitats show that of over 426 measurements taken at the LTER 1 site, presumed to be the most affected by anthropogenic eutrophication across all reef habitats, only six had NO_x (NO_3^- and NO_2^-) greater than 1.0 μmol per liter. In addition, 42 measurements were greater then 0.2 μmol per liter of PO_4^{3-}, and only two measurements were greater than 0.3 μmol per liter of PO_4^{3-}, typical for oligotrophic coral reef waters (Atkinson and Falter 2003). If these data are reflective of nutrient concentrations around the island, then they represent pervasively low nutrient concentrations for extended periods of time on the reefs of Moorea. In Moorea, the community dynamics of the lagoonal reef system are significantly different from those on the outer forereef (Schmitt et al. 2019). After disturbance events causing coral mortality, forereef communities always returned to high coral cover, whereas disturbed lagoonal reef communities could return to high macroalgal cover, dominated by *T. ornata,* a robustly defended alga both physically and chemically as an adult plant (Bittick et al. 2010) or high coral cover, depending on the starting condition (i.e., turf versus macroalgal dominance) at the time of the disturbance (Schmitt et al. 2019). *Turbinaria ornata* increased in abundance on many lagoon reefs of Moorea during the 1980s when it established itself after severe coral mortality due to several cyclones and crown of thorns starfish outbreaks. On the forereef, sufficient herbivory pressure exists to remove young recruits of *T. ornata*, which are poorly defended against herbivory compared with adult plants (Han et al. 2016, Schmitt et al. 2019). In the lagoon and despite the greater abundance (i.e., twice as many) and biomass (i.e., 1.5 times as much) of herbivorous fish (see supplemental table S2 in Schmitt et al. 2019), macroalgal-dominated reefs exposed to any degree of herbivory were unable to remove adult *T. ornata*, and for reefs beginning with turf algae, there were lower but sufficient levels of herbivory to maintain reefs in a macroalgal-free state.

Given the low nutrient concentrations across reef habitats on Moorea, herbivory and reef history (i.e., disturbance events) appear to be the primary process controlling algal cover on forereefs, whereas the persistent algal cover of some lagoon reefs appears to be a permanent ecological state (Schmitt et al. 2019). Despite the low nutrient concentrations consistently observed on Moorea, Donovan and colleagues (2020) suggested that anthropogenically derived NO_3^- facilitated coral bleaching on Moorea in 2019 on the basis of the percentage nitrogen content in macroalgae, believed to be a long-term integrator of ambient nutrient concentrations. In addition, Adam and colleagues (2021), also using algal tissue nitrogen content as a proxy for eutrophication, conducted a multivariate analysis and concluded that the high percentage cover of macroalgae on lagoon patch reefs was a result of eutrophication, in the presence of an overall increase in herbivores in the lagoon (Han et al. 2016, Schmitt et al. 2019). The change in concentration of DIN reported for the lagoon reefs (see supplemental figure S12 for LTER 1 in Adam et al. 2021) is biologically inconsequential (but see Lapointe 1999). The mean concentration for all reef habitats was less than 1.0 μmol per liter, and the relationship between the nitrogen content of *T. ornata* and coral cover was insignificant (see supplemental figure S13 in Adam et al. 2021). In addition, although using the tissue nitrogen content of tropical macroalgae as an indicator of increased availability of nitrogen may be feasible, nutrient availability is not *a priori* coupled to growth, given that macrophytes are just as likely to be phosphorus rather than nitrogen limited (Atkinson and Smith 1983). The tissue concentrations of nutrients in macroalgae are also dependent on growth rates and other physiological processes (e.g., light and photosynthesis), in addition to the availability of nutrients (McCook 1999). All tissue nitrogen concentrations for *T. ornata* from Donovan and colleagues (2020) and Adam and colleagues (2021) are also below 1.5%, a critical minimum nitrogen level required for growth in macroalgae (Fujita et al. 1989, Duarte 1992). In fact, the carbon to nitrogen (C:N) ratio of *T. ornata* tissue from Moorea varies from approximately 34 to 40 on an annual basis, from approximately 35 to 41 on the basis of the site, and from 34 to 42 on the basis of the reef habitat, and these values overlap significantly and represent a similar degree of nitrogen limitation. Given that the half-saturation constant (K_s) for nutrient uptake is often greater than the ambient nutrient concentrations, the specific growth rates of macroalgae should be low (Atkinson and Smith 1983). The most parsimonious interpretation of all these data is that differential rates of algal removal by herbivory between reef habitats, not differential rates of algal growth based on nutrient supply, are most likely the cause of the observed changes in reef communities as it relates to phase shifts.

Donovan and colleagues (2020) cited the experiments of Burkepile and colleagues (2019) as support for their interpretation of the interactive effects of nutrients with thermal stress relative to their modeling outputs using the nitrogen content data from *T. ornata*. But Burkepile and colleagues (2019) conducted studies on corals in Moorea using slow-release nitrogen additions without PO_4^3, resulting in DIN concentrations between three and seven times above ambient levels which likely resulted in PO_4^{3-} limitation as well. Burkepile and colleagues (2019) quoted Wiedenmann and colleagues (2013) as evidence for eutrophication facilitated coral bleaching, and, in this scenario, the altered stoichiometry of the experimental nutrient regime is a reasonable interpretation for the data.

Are Scleractinian corals nutrient limited?

Scleractinian corals have traditionally been described as very efficient recyclers of nutrients between the coral host and their symbiotic Symbiodiniaceae (Fiore et al. 2010). On coral reefs, high fluxes of solar radiation drive symbiont photosynthesis, and, in combination with low concentrations of DIN in the ambient seawater, play a regulatory role in controlling the growth rates of Symbiodiniaceae *in hospite* (Falkowski et al. 1993, Dubinsky and Jokiel 1994), an essential aspect for maintaining the stability of the symbiosis.

For scleractinian corals, *in hospite* inorganic nitrogen concentrations (i.e., NH_4^+) have been reported to be over an order of magnitude greater than those in the ambient water column (Wilkerson and Muscatine 1984). Both the host and algal symbionts have NH_4^+ transporters and kinetically efficient enzymatic pathways (i.e., glutamine synthetase or glutamate dehydrogenase in the host and glutamate synthase in the symbiont) for assimilating NH_4^+ that were initially believed to be light dependent (Yellowlees et al. 2008). In the dark, however, host uptake of NH_4^+ in the presence of added organic carbon proceeds at rates comparable with those observed in the light, suggesting that *in hospite* nitrogen conservation by the host provides an important regulatory control on symbiont populations (Wang and Douglas 1998). The use of fixed carbon sources by the host to assimilate NH_4^+ has recently been supported by a combined meta-analysis and metabolomic study in which a host-dependent negative feedback mechanism that regulates nitrogen availability to symbionts was shown to be driven by symbiont-derived sources of carbon (Cui et al. 2019). Recent experiments have also shown that the capacity for NH_4^+ uptake is as much as 14 times lower in the host tissue than in that of symbiotic Symbiodiniaceae (Pernice et al. 2016). Unlike the coral host, Symbiodiniaceae also expresses nitrate reductase so these algal symbionts can take up ambient NO_3^-, which is found in submicromolar concentrations in seawater but generally in greater concentrations than NH_4^+, making its use a viable alternative when NH_4^+ is low or limiting (Miller and Yellowlees 1989, Badgley et al. 2006, Yellowlees et al. 2008). In a study on *Acropora palmata*, the simultaneous uptake of both NO_3^- and NH_4^+ from ambient seawater was observed, as was its incorporation into dissolved organic nitrogen (DON) and its subsequent release by the coral (Bythell 1990). A similar study on *Pocillopora damicornis* showed that both NO_3^- and NH_4^+ were taken up by the coral and incorporated into uric acid in the symbionts, where it was then mobilized for translocation to the host as DON (Kopp et al. 2013). DON, as urea or dissolved free amino acids, is also available to corals from the ambient seawater (Grover et al. 2006, 2008). However, NH_4^+, not NO_3^-, is the preferred source of inorganic nitrogen for Symbiodiniaceae on the basis of energetic costs, *in hospite* nutrient concentrations and enzyme kinetics (Miller and Yellowlees 1989, Badgley et al. 2006). In addition, heterotrophic subsidies supply an order of magnitude more nitrogen for the holobiont than DIN uptake by the symbionts from the ambient seawater when feeding for only 2 hours per day, and the symbionts retain DIN, whereas the host retains heterotrophically acquired organic nitrogen (Tremblay et al. 2015). Finally, many scleractinian corals also have the capability to fix molecular nitrogen (N_2), facilitated by several groups of diazotrophic symbionts (e.g., Lesser et al. 2004), and most of this fixed nitrogen is found in the symbiotic Symbiodiniaceae (Lesser et al. 2007b, 2019). Under normal, unstressed, environmental conditions, the amount of nitrogen supplied to the holobiont by N_2 fixation can be as high as 15% (Cardini et al. 2015, Bednarz et al. 2017, Lesser et al. 2019).

As with other inorganic nutrients, the concentration of PO_4^{3-} is very low in reef waters (ranging from undetectable to 0.3 μmol per liter), and the uptake from the environment requires the presence of endosymbiotic Symbiodiniaceae, suggesting some level of light dependence (Godinot et al. 2009, Ferrier-Pagés et al. 2016). Although PO_4^{3-} concentrations in seawater are extremely low, uptake occurs primarily by active transport, facilitated by membrane-bound phosphatases (Fitt and Trench 1983, Rands et al. 1993). PO_4^{3-} uptake is affected by light, temperature, and recent history of nutrient exposure, which affects PO_4^{3-} reserves *in hospite* and nutrient status as it relates specifically to nitrogen (i.e., N:P ratio; Ferrier-Pagés et al. 2016). In addition, the rates of PO_4^{3-} uptake in the presence of NO_3^- do not suggest that symbiotic Symbiodiniaceae are nitrogen limited (Godinot et al. 2011). Furthermore, complicating this picture is the hydrodynamically driven mass transfer effects on nutrient uptake for corals (e.g., Badgley et al. 2006) and coral reefs (Atkinson and Falter 2003, Falter et al. 2004), as well as heterotrophic inputs (Houlbréque and Ferrier-Pagés 2009), where it has been shown to supply the majority of PO_4^{3-} requirements (Muller-Parker et al. 1990).

Even though there are high concentrations of all nutrients *in hospite*, the acidic environment of the symbiosome (pH of approximately 4.0; Barott et al. 2015) dictates the form transported and its availability, on the basis of each nutrient's pKa, to the symbiotic Symbiodiniaceae (Miller and Yellowlees 1989). Subsequently, uptake occurs and is not directly affected by diffusion-depletion kinetics, the support of which has been derived primarily from studies on isolated Symbiodiniaceae (e.g., D'Elia et al. 1983). In fact, in the presence of strong regulatory control of nutrient uptake at the symbiosome versus diffusion depletion kinetics and the wide range of inorganic nutrient concentrations to which coral reefs are exposed (Szmant 2002, Atkinson and Falter 2003, Frabricius 2005), there remains to be answered the central question in coral biology: Are the symbionts of corals ever nutrient limited (*sensu* Cook and D'Elia 1987)? The population growth dynamics of symbiotic Symbiodiniaceae have historically been described as a chemostat that maintains a quasi steady state cell density (i.e., biomass). In response to a range of nutrient concentrations and as a function of irradiance, the delivery of nutrients into the symbiosome and the rate of symbiont loss then provide the required feedback that regulates cell division rates and biomass (Cook and D'Elia 1987, Muscatine et al. 1989, Falkowski et al. 1993). Although the concentration of available nutrients for the algal symbionts is sufficient to support their biomass and all functions of the cell, albeit at lower rates of growth for a given irradiance, the symbionts produce excess amounts of carbohydrates that are released to the host to support respiration, indicating that these symbionts are in a condition of unbalanced growth caused by nutrient limitation (Falkowski et al. 1993).

Nutrient limitation causes unbalanced growth and significant deviations from elemental ratios (e.g., C:N ratios) as one element becomes limiting. Historical (Miller and Yellowlees 1989) and recent data (Tanaka et al. 2018), however, suggest that Symbiodiniaceae populations *in hospite* may, in fact, not be nitrogen limited, despite the fact that nitrogen limitation is a central tenant of symbiosis stability in corals (for a review, see Rädecker et al. 2015). In Tanaka and colleagues (2018), the case for the lack of nutrient limitation in corals is the long turnover times of organic nitrogen and a double translocation system, such as that described by Tremblay and colleagues (2015). The notable difference between these studies is that Tanaka and colleagues (2018) did not consider heterotrophic inputs in their calculations. Similarly, recent experiments and reviews (Cui et al. 2019, Morris et al. 2019, Rädecker et al. 2021) have shown that NH_4^+ access for symbionts occurs only when photosynthetically derived carbon is made available to the host. If symbiont photosynthesis is inhibited, such as occurs during thermal and light stress, then less waste NH_4^+ is used by the host for amino acid biosynthesis and is available for assimilation by the symbionts leading to increases in symbiont growth and biomass (Dubinsky and Jokiel 1994, Wang and Douglas 1998, Rädecker et al. 2021), which is also supported by modeling studies (Cunning and Baker 2013, Cunning et al. 2017). Under these conditions subsequent exposure to thermal and light stress leads to an increase in ROS production and damage to the coral–algal symbiosis prior to visible bleaching (Rädecker et al. 2021) consistent with previously described timelines (Lesser 2011).

The support for nitrogen limitation is usually made with experiments incorporating extremely high nutrient concentrations (20–50 μmol of NH_4^+ or 2.0 μmol of PO_4^{3-} individually or together) that eventually cause a significant increase in the growth rates and more than a doubling of symbiont populations on an aerial basis, often without any signs of the symbiosis being destabilized (e.g., Hoegh-Guldberg 1994, Muller-Parker et al. 1994a). Long-term experiments have also shown that, under high irradiances and high nutrient conditions, the rates of cell division and biomass accumulation of symbionts increase and are released from regulatory growth control but did not bleach under 80% of ambient irradiance in Hawaii (Hoegh-Guldberg 1994, Muller-Parker et al. 1994a), despite N:P ratios of approximately 30 (Muller-Parker et al. 1994b). These results support the hypothesis that light intensity determines the onset of nutrient limitation, whereas the need for heterotrophic sources of nitrogen increases as the C:N ratio of the symbionts increases (Dubinsky and Jokiel 1994).

Predicting nutrient limitation and the specific limiting nutrient (*sensu* Liebig's law of the minimum) is historically based on the work of Redfield (1958), where the elemental composition and ratios of phytoplankton were described. Redfield (1958) posited that, on average, phytoplankton assimilate carbon, nitrogen, and phosphorus in a molar ratio of 106:16:1 with elevated C:N or lowered N:P ratios indicating nitrogen limitation. Therefore, a molar C:N ratio of approximately 6.6 and a molar N:P ratio of approximately 16 would indicate nutrient replete algae, although Geider and LaRoche (2002) pointed out that these values vary with different taxonomic groups of microalgae. Dinoflagellates generally have higher C:N ratios, between 8 and 10 (Falkowski and Raven 2007). In experiments in which corals were maintained under conditions of elevated DIN, C:N values of the symbionts decreased over unenriched controls (e.g., Muscatine et al. 1989, Muller-Parker et al. 1994a), and the symbionts of scleractinian corals collected from the field exhibited C:N ratios around 10 (Hawaii: Muller-Parker et al. 1994b, GBR: Blanckaert et al. 2020). Symbiodiniaceae from field-collected corals in other studies (Lesser et al. 2018, 2019) also had C:N values indicative of either nitrogen sufficiency or marginal nitrogen limitation (for Curaçao, mean = 13.63, standard error [SE] = 0.60; for Hawaii, mean = 11.49, SE = 0.56; for Australia, mean = 8.77, SE = 0.20). Symbiodiniaceae from *Orbicella faveolata* in the Florida Keys had C:N values between 6.5 and 6.8 (Cook et al. 2002), which appear to be the lowest reported to date.

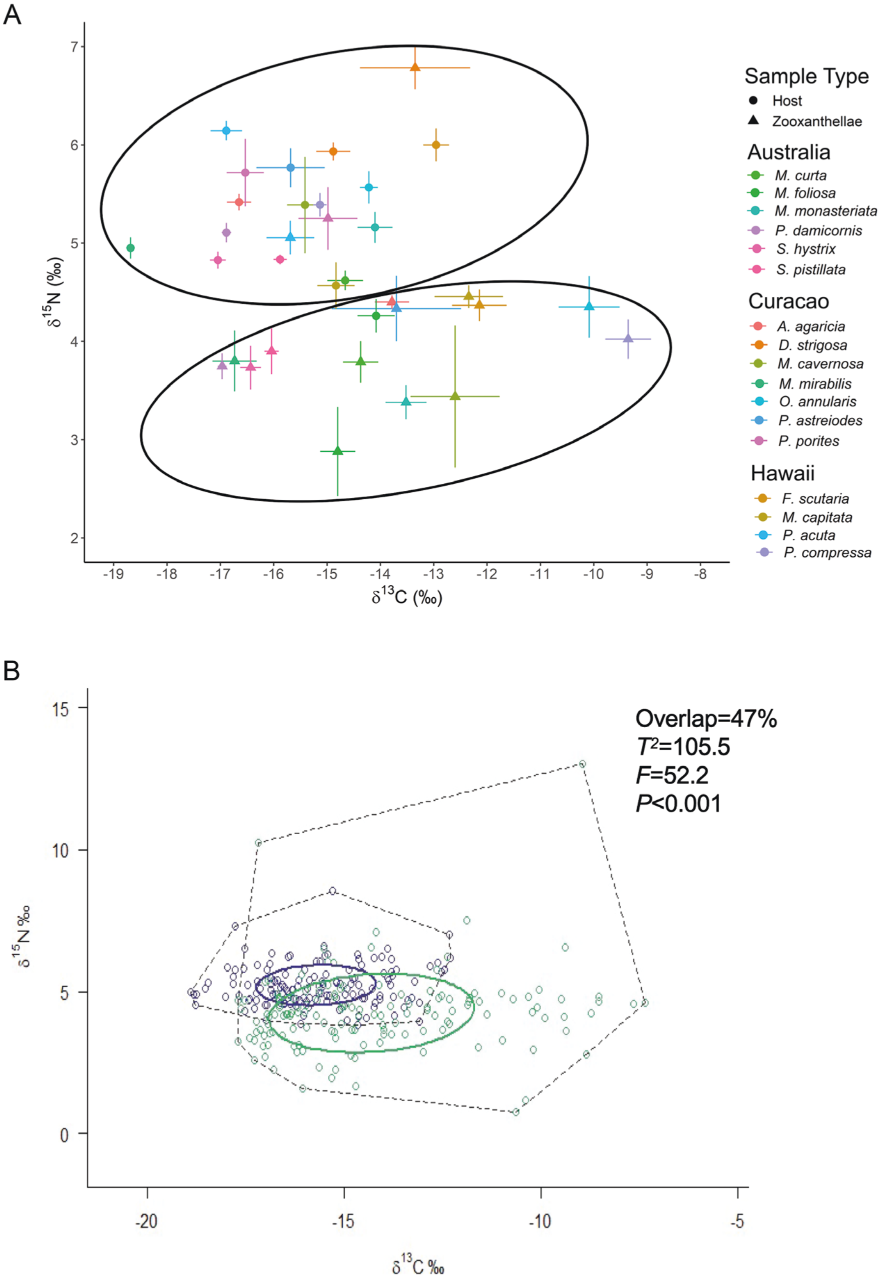


Figure 3. (a) Bivariate plot of the mean (n = 6 for Hawaii and Curacao, and n = 5–15 for Australia corals for both host and symbionts) of the natural abundance of δ^{13}C and δ^{15}N in the host tissues and Symbiodiniaceae of corals from Australia (Heron Island), Curaçao (buoy 1) and Hawaii (Kaneohe Bay). Both the coral tissue fraction (ANOVA, F(2,143) = 6.432, p = 0.0021), and the Symbiodiniaceae fraction (F(2,143) = 34.16, p < 0.0001) exhibited differences in their δ^{13}C signature on the basis of location. Post hoc multiple comparison testing revealed that corals from Hawaii had significantly less depleted δ^{13}C host signatures than Australia or Curaçao, whereas differences between all sites were observed for the Symbiodiniaceae δ^{13}C signatures (Tukey's HSD, p < 0.05). For the δ^{15}N signature of host tissues (F(2,143) = 21.24, p < 0.0001) and Symbiodiniaceae (F(2,143) = 11.28, p < 0.0001) significant effects of location were also detected. Post hoc multiple comparison testing revealed that corals from Hawaii and Curaçao had significantly enriched δ^{15}N for both host and Symbiodiniaceae signatures (Tukey's HSD, p < 0.05). Areas outlined by ellipses indicate host versus zooxanthellae isotopic signatures. (b) Stable Isotope Bayesian Ellipses in R analysis for corals described above to assess isotopic niche width. The blue dots represent coral host tissues, whereas the green dots represent symbionts. The dotted lines represent convex hulls that are highly sensitive to sample size, and the solid lines represent standard ellipse areas of overlap. The significant p values generated from a residual permutation procedure and Hotelling's T^2 test using the standard ellipse area data show that host and symbiont isotopic niches have a significant 47% overlap.

Transition to PO_4^{3-} limitation generally occurs at N:P ratios from 20 to 50. In a nitrogen supplement experiment, using *Pocillopora damicornis* (now known to be *Pocillopora acuta*) from Hawaii, declining C:N ratios were accompanied by an increase in N:P ratios to approximately 40, suggesting PO_4^{3-} limitation (Muller-Parker et al. 1994b). In symbiotic Symbiodiniaceae from corals on the GBR, N:P ratios were generally greater than 40, and as high as approximately 125, suggesting PO_4^{3-} limitation (Blanckaert et al. 2020). Cook and colleagues (2002) reported N:P values of 28.71 (SD = 5.58) inshore and 33.51 (SD = 4.75) offshore for symbionts from *O. faveolata* in the Florida Keys, again suggesting PO_4^{3-} limitation. These data suggest that PO_4^{3-} limitation, rather than nitrogen limitation, may be the general situation for Symbiodiniaceae *in hospite*.

Another important source of nutrients for corals is organic matter obtained via heterotrophy. Natural stable isotope abundances of carbon and nitrogen are an indication of the ecological sources of a given element. $\delta^{13}C$ values of approximately –12‰ to –13‰ indicate autotrophy, whereas $\delta^{13}C$ values of –17‰ to –18‰ indicate heterotrophy and the consumption of particulate organic matter (e.g., zooplankton). For the stable isotope data from the samples above (Lesser et al. 2018, 2019), the natural abundance of $\delta^{13}C$ for the host tissues show mean values for corals by region ranging from –14.92‰ to –15.99‰, whereas the Symbiodiniaceae ranged from –12.38‰ to –15.79‰ (figure 3a). These values suggest that the carbon requirements of these corals were obtained via mixotrophy. The $\delta^{15}N$ of host tissues ranged from 4.84‰ to 5.53‰, whereas the $\delta^{15}N$ of the symbiotic Symbiodiniaceae ranged from 3.69‰ to 4.82‰. These differences in $\delta^{15}N$ between host and symbiont suggest a modest dependence on heterotrophy (Swart et al. 2005). With these same samples, a quantitative isotopic niche overlap analysis using the Stable Isotope Bayesian Ellipses (SIBER) package in the R statistical software environment (Jackson et al. 2011), and the cutoffs described in Conti-Jerpe and colleagues (2020) where a niche overlap of greater than 70% indicates autotrophy and an overlap of less than 10% indicates heterotrophy was determined for each coral species. The trophic strategy in only two species is based on autotrophy (i.e., *Pseudodiploria strigosa* and *Porites porites* from Curaçao), with *Stylophora pistillata* from Australia is classified as mixotrophic and the remaining species classified as heterotrophs. Regional differences show that all corals from Australia and Hawaii are primarily heterotrophic, whereas the corals from Curaçao are mixotrophic, and one coral (*P. strigosa*) strongly influences the change from heterotrophy to mixotrophy in this group. Using the more accurate standard ellipse analysis on the combined data, however, shows that there is a very strong and significant signal of 47% niche overlap between the host and symbionts (figure 3b) with the net effect being mixotrophy for all holobionts.

Given that either mixotrophy or heterotrophy can supply large amounts of carbon, nitrogen, and phosphorus and trace nutrients such as manganese and iron, it suggests that the holobiont may rarely be nutrient limited and more dependent on the ability to feed heterotrophically, compared with using the available nutrients in the ambient water column (Houlbréque and Ferrier-Pagés 2009). It has also been observed that corals dependent primarily on a heterotrophic strategy were significantly more resistant to coral bleaching (Conti-Jerpe et al. 2020).

Impacts of elevated nutrients on stability of the coral–algae symbiosis

Eutrophication has been a topic of interest in the coral reef community for some time (Szmant 2002) and especially since Woolridge (2009a) published a modeling study using proxies for eutrophication suggesting that elevated DIN concentrations are correlated with sensitivity to thermal bleaching. The link with terrestrially sourced nitrogen was based on the availability and delivery of dissolved inorganic carbon (i.e., carbon dioxide limitation) and the role of DIN in controlling symbiont rates of division (Wooldridge 2009b). There was no discussion, however, of the role of PO_4^{3-} as a limiting nutrient that would have an important mechanistic effect on the sensitivity of symbionts to heat or light stress. Subsequently, Wiedenmann and colleagues (2013) examined the effects of eutrophication and deviations from Redfield ratios on the sensitivity of Symbiodiniaceae to thermal and light stress under controlled laboratory conditions. This destabilization has been shown to lead to increases in symbiont density, and when combined with environmental stress (e.g., increased thermal and light stress), an increase in ROS fluxes (box 2) leads to oxidative stress and the coral bleaching response, which includes the expulsion of symbionts from the host (Wiedenmann et al. 2013, Cunning and Baker 2013, Rädecker et al. 2021). For the Symbiodiniaceae of corals, PO_4^{3-} limitation appears to be common (Krueger et al. 2020). Here again, the host controls the amount of PO_4^{3-} reaching the symbionts because of the favorable pKa for PO_4^{3-} at the lower pH of the symbiosome (Miller and Yellowlees 1989). Given this, the N:P ratios of the nutrient additions for the altered nutrient stoichiometry experiments on *Acropora polystoma* were approximately 43 compared with controls with N:P ratios of approximately 22, which is in the lower part of the range defining PO_4^{3-} limitation (Wiedenmann et al. 2013). For corals experiencing the altered nutrient stoichiometry, exposure to irradiances of 90 or 160 μmol quanta per square meter (m^2) per second, at temperatures of 24 degrees Celsius (°C) showed no significant increase in their sensitivity to PSII function (i.e., decrease in quantum yields of PSII measured as the maximum ratio of variable fluorescence and maximum fluorescence). Only when irradiances were 160 μmol quanta per m^2 per second, and the temperature was increased to 30°C or 31°C were significant decreases in PSII photochemistry observed (Wiedenmann et al. 2013). These values represent midday irradiances between 23 and 30 meters on many coral reefs, but they are not typical for shallow coral reefs (Lesser 2000) so we might expect more severe effects at more realistic irradiances for shallow reefs (Lesser 2006, 2011).

The ecological ramifications of the experimental nutrient conditions used in Wiedenmann and colleagues (2013), which were not supported by an elemental analysis of the corals, are dependent on the nature of anthropogenically sourced nutrient load (Szmant 2002, Fabricius 2005). Subsequently, several studies described PO_4^{3-} limitation as the Achilles's heel of corals during thermal stress (e.g., Ezzatt et al. 2016) or indicated that the form of nitrogen, which can reflect its anthropogenic origin, is important and has differential impacts on corals, both positive and negative (Silbiger et al. 2018, Burkepile et al. 2019, Marangoni et al. 2020). Supporting these conclusions, a meta-analysis showed that coral species and morphology, nutrient source, and nutrient identity differentially affect the photobiology and calcification of scleractinian corals (Shantz and Burkepile 2014). In fact, Allgeier and colleagues (2020) showed that even those corals showing resilience in the face of eutrophication demonstrated subtle changes in the algal–host relationship poising the holobiont for a transition from mutualism to parasitism (*sensu* Lesser et al. 2013). And Tisthammer and colleagues (2021) showed that nearshore corals acclimatized to long-term anthropogenic stressors express a range of local adaptations, at the physiological and molecular levels, indicating they are more stress resilient.

One of the central roles of PO_4^{3-} is structural; phospholipids are a major component of membrane lipids and may constitute 25%–40% of total lipids in corals (Ferrier-Pagés et al. 2016). The underlying mechanism explaining PO_4^{3-} limitation effects on Symbiodiniaceae in Wiedenmann and colleagues (2013) was a change in the composition of thylakoid membrane lipids from phospholipids to sulfolipids and specifically to higher concentrations of sulfoquinovosyldiacylglycerol (SQDG) known to occur in dinoflagellates (Leblonde and Chapman 2000). SQDG is an acidic glycolipid normally found in small amounts in thylakoid membranes and associated with PSII in higher plants, where it is functionally similar to phosphatidylglycerol (PG; Mizusawa and Wada 2012). Despite SQDG being a minor component of thylakoid membrane composition, from an environmental stress perspective SQDG is essential for the protection of PSII in response to high temperature and light stress (Sato 2004). The response to nutrient stress, specifically PO_4^{3-} limitation, is to substitute affected phospholipids (i.e., PG) in the thylakoid membranes with sulfolipids, such as SQDG (Sato 2004). Because of the differences between PG and SQDG as it relates to the placement within and the structural integrity of thylakoid membranes, it has been difficult to ascertain the potential role or roles of SQDG during PO_4^{3-} limitation, but maintaining the anionic character of the membrane appears to be essential for the proper conformation of PSII reaction center proteins (Frentzen 2004). For many photoautotrophic organisms, however, SQDG biosynthesis during PO_4^{3-} limitation enables survival by maintaining lower rates of photosynthesis (Frentzen 2004, Sato 2004, Mizusawa and Wada 2012, Nakajima et al. 2018). But during PO_4^{3-} limitation (i.e., N:P ratios over 40), Wiedenmann and colleagues (2013) observed that SQDG increases, and tolerance to thermal and light stress decreases on the basis of the number of functional PSII units (i.e., lower quantum yields of PSII fluorescence) resulting in increased mortality.

For corals, the thylakoid membranes of symbiotic Symbiodiniaceae have been identified as a primary target of thermal and light stress, leading to PSII dysfunction and oxidative stress (e.g., Tchernov et al. 2004, Downs et al. 2013). There is good evidence that thermal stress induces changes in the saturation state (i.e., the number of double bonds in a hydrocarbon chain) in the fatty acids of thylakoid membranes for both higher plants (Schreiber and Berry 1977) and Symbiodiniaceae (Hill et al. 2009), but the degree of membrane stability is not only dependent on thermal stress, but it is also reliant on ambient irradiances during thermal stress (Schreiber and Berry 1977, Hill et al. 2009). Specifically, symbiotic dinoflagellates from corals exposed to high irradiances and thermal stress demonstrate an upward shift in the critical temperature in which the phase transitions of membrane lipids occur and results in an increase in membrane fluidity and photosynthetic dysfunction (Hill et al. 2009). There are, however, conflicting studies on the role of thylakoid membrane fluidity during thermal stress and coral bleaching. Tchernov and colleagues (2004) found that a lower ratio of C18:1 (saturated) to C18:4 (unsaturated) fatty acids in the thylakoid membrane indicated higher sensitivity to thermal stress as was shown by changes in variable chlorophyll fluorescence. This was interpreted as an uncoupling of PSII to photosynthetic electron transport, where PSII still was still able to split water and evolve oxygen creating hyperoxic conditions which results in the production of ROS (Lesser 2006, 2011). Díaz-Almeyda and colleagues (2011), however, did not find that the degree of unsaturation in thylakoid lipids was an indicator of sensitivity to thermal stress in Symbiodiniaceae but did acknowledge that adjustments in the thermal stability of thylakoid membranes appears to play an important role during acclimatization to changing temperatures. The importance of SQDG and its degree of unsaturation was recently demonstrated for both thermosensitive and thermotolerant Symbiodiniaceae under nutrient replete conditions (Rossett et al. 2019). Thermotolerant *Durusdinium trenchii* have lower concentrations of SQDG in their thylakoid membranes with increasing unsaturation, which imparts significant protection against the effects of temperature and light stress and results in decreased reactive oxygen species or reactive nitrogen species production (Lesser 2019, Rossett et al. 2019). The respective roles of thylakoid lipid saturation state and SQDG concentrations in the resilience of coral holobionts to thermal and light stress under nutrient replete or PO_4^{3-} limited conditions requires additional study.

Coral bleaching mediated by altered nutrient stoichiometry: Where might it occur?

The nutrient levels used in many of the studies described above (e.g., Wiedenmann et al. 2013) represent those observed on coastal coral reefs significantly affected by terrestrial and riverine influence. Where coastal reefs occur, one must consider that natural terrestrial influences from rivers with large watersheds discharge nitrogen primarily as dissolved organic nitrogen, whereas anthropogenic influences such as sewage and agricultural (i.e., both animal wastes and fertilizers) and nonpoint sources (e.g., urban surface runoff) consist of particulate nitrogen and DIN (Richmond et al. 2007, Brodie et al. 2011). A recent review of land-use impacts shows that forested terrestrial land use has net positive effects on coral reefs, whereas urban development and agriculture are associated with negative impacts (Carlson et al. 2019). These negative impacts include microalgal blooms, reduced downwelling irradiances (but see below), erosion and sedimentation, organic loading and hypoxia or anoxia, all of which can cause significant morbidity and mortality of corals (Szmant 2002, Fabricius 2005, Fabricius et al. 2014, Anthony 2016, Altieri et al. 2017, Brown et al. 2017).

Recent studies also show quite clearly that moderate increases in nutrients do not interact with other climate change stressors to destabilize the host–symbiont relationship (Becker et al. 2021, Dobson et al. 2021) or that pulses versus continuous exposure of nutrients, better simulating natural conditions, enhance the physiological performance of corals (van der Zande et al. 2021). Whenever significant eutrophication effects are observed, they usually occur under the highest concentrations of dissolved nutrients, concentrations not normally observed except in the most polluted sites in coastal environments, whose effects are confounded by the presence of multiple industrial and agricultural pollutants (Szmant 2002, Fabricius and De'ath 2004. Brodie et al. 2011). Also, many of these same experiments correlating changes in nutrient concentrations with coral bleaching are confounded by ecologically relevant changes in other water quality traits, such as the attenuation of light from either changes in water column optics (López-Londoño et al. 2021). Hypoxia, sedimentation, and the effects of other constituents of terrestrial or agricultural inputs into coastal waters, such as industrial chemicals and pesticides are also largely ignored. Sewage and agricultural pollution co-occur with the significant deviations in Redfield ratios reported to make corals more susceptible to coral bleaching (e.g., Wiedenmann et al. 2013). In addition to nutrients, these effluents contain heavy metals, endocrine disruptors, multiple pathogens, and pharmaceuticals any of which could significantly affect the biology of corals and the ecology of coral reefs long before or simultaneously with eutrophication (Wear and Vega Thurber 2015, Wear 2019). Wherever eutrophication occurs on coral reefs on large scales these other contaminants likely occur, but the confounding effects are almost never considered. Mechanistically, deviations from Redfield ratios may, in fact, lead to increased sensitivity to thermal and light stress (*sensu* Wiedenmann et al. 2013), but the confounding effects of other stressors may be negative or positive. For instance, in some cases an increase in turbidity as a result of coastal pollution may result in moderation of the effects of irradiance on thermal stress in corals (Sully and van Woesik 2019), but the causes of turbidity (e.g., flocculent organic material) may have negative effects as it settles onto corals (Brown et al. 2017). Such organic loading can have severe consequences, including hypoxia or anoxia related mortality (Altieri et al. 2017, Hughes et al. 2020). In the future climate change may also put its fingerprint on the severity of these potential effects as predicted changes in tropical precipitation (e.g., drying in large areas of the Caribbean and coastal Australia) could significantly affect discharge from watersheds in coastal environments (Neelin et al. 2006, Xie et al. 2010, Putnam and Broeker 2017).

Conclusions

What do these results suggest for reefs worldwide? On the basis of current studies exposure to excess nutrients can affect coral reefs and corals in negative ways that are very much context dependent. At the scale of entire reefs, the case for nutrients affecting ecological processes that lead to phase shifts is weak but not absent in the face of overwhelming support for top-down processes. At the organismal level there is good evidence that scleractinian corals may or may not be nutrient limited. The reality is that both conditions are likely to be true on the basis of ambient conditions and species-specific differences in their trophic ecology. Knowing the nutrient status of the coral–algae symbiosis, and other important reef taxa (e.g., macrophytes) is a critical feature of understanding the effects of excess nutrients on corals and coral reefs. Diminished coral health, caused by exposure to thermal and light stress, may also be exacerbated by opportunistic pathogens (*sensu* Lesser et al. 2007) when exposed to elevated nutrients (e.g., Zaneveld et al. 2016). In addition, ecologically realistic nutrient conditions (e.g., pulse versus press) must be used for any manipulative experiments, along with measurements of ambient nutrient levels and markers of nutrient status in the experimental organisms. Finally, if eutrophication, and subsequent deviations from Redfield ratios (i.e., PO_4^{3-} limitation) are causing a destabilization of the coral–Symbiodiniaceae symbiosis, we should then ask the following. What concentrations or stoichiometry of nutrients are sufficient to elicit the proposed changes (i.e., thylakoid membrane composition) at the cellular level in the endosymbionts of scleractinian corals that result in destabilization of the symbiosis and increased susceptibility to climate change stressors? Do current data or their interpretation support the widespread occurrence of the nutrient destabilization hypothesis (*sensu* Morris et al. 2019) on the basis of what we know about the nutrient dynamics of these symbioses and the observed DIN and PO_4^{3-} concentrations on coral reefs? And most important, from an ecological perspective, what are the potential confounding effects of eutrophication and other pollutants that co-occur in industrial, urban, and agricultural runoff that may contribute to or cause the increased susceptibility to coral bleaching in coastal environments relative to observed changes in the ecological structure of coral reefs?

Acknowledgments

The manuscript was greatly improved by comments from Clay Cook and Marc Slattery, for which I am very grateful. The data used in this publication are available on request to the author. Coral collection in Curaçao was assisted by Elizabeth Kintzing and Abbey Tedford. A special thank you to Keir Macartney for providing the analysis and figure for the stable isotopic niche separation (figure 3) and Daniel Merselis for the SOD western blots (box 2). Coral collections at Heron Island Research Station were made with the permission of the Great Barrier Reef Marine Park Authority (GBRMPA collecting permit no. G15/374471.1), in Curaçao collections were made under research permit (no. 2012/48584) issued by the Curaçao Ministry of Health, Environment, and Nature to the Caribbean Marine Biological Institute, and at the Hawaii institute of Marine Biology coral collections were permitted under Division of Aquatic Resources Special Activity permit no. 2015-17. The National Science Foundation (Biological Oceanography grant no. OCE-1632348 and Dimensions of Biodiversity grant no. OCE-1638296) supported this research.

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