

Bleaching of Coral Reefs Due to Ocean Acidification and Warming

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Abstract

Climate change is impacting marine ecosystems in a multitude of ways. Consequences of greenhouse gas emissions, due to anthropogenic factors, include acidification of the ocean and increased global temperature. Coral reefs and their ecosystems are under severe threat for extinction under continued warming conditions. Corals are experiencing a reduction in calcification, loss of productivity, and bleaching due to expulsion of their symbiotic zooxanthellae. Various reef fishes and invertebrates rely on corals for habitat and food sources; therefore, coral degradation can collapse the entire reef ecosystem. The loss of corals has implications for reduced coastal protection as well as economic losses associated with reef fisheries and tourism. Corals show variable responses and adaptation methods to bleaching based on biological or environmental factors. Some corals are naturally thermally sensitive while others are able to withstand more heat. Over the past decade there has been an increase in the sea surface temperature required to initiate bleaching which implies that corals are likely already in the process of adapting to global warming. However, a loss of diversity in coral reefs will be associated with the survival of only the thermally tolerant coral species. Reduction in coral coverage and diversity causes a subsequent loss of species richness, abundance, and diversity of reef fishes. These dynamic ecosystems could experience irreversible consequences if greenhouse gas emissions are not mitigated.

Introduction

Globally, oceans are experiencing adverse consequences due to anthropogenic induced climate change. Greenhouse gas emissions from the burning of fossil fuels are increasing the carbon dioxide in the atmosphere (Keeling and Heimann 1986). Emissions also impact other climactic variables such as temperature. Rising greenhouse gas concentrations in the atmosphere are associated with increased global temperature (Petit et al. 1999). Deglaciation associated with increased global temperature acts as a feedback loop with changes in albedo to continue to increase warming (Petit et al. 1999). Carbon dioxide concentrations in the atmosphere impact the ocean due to interactions of the global carbon cycle. The atmosphere and the ocean exchange carbon to reach equilibrium, therefore the ocean acts as a sink for the excess carbon dioxide from emissions (Feely et al. 2004).

Marine ecosystems may experience irreversible changes from increased carbon dioxide emissions. This is especially relevant for ecosystems in surface waters which are subject to more rapid fluctuations of oceanographic conditions (Feely et al. 2004). In particular, coral reefs and their local ecosystems are threatened from these climate change consequences (Carpenter et al. 2008). The conservation status of corals has been identified with the use of International Union for Conservation of Nature Red List Criteria, where species are considered threatened if they are categorized as vulnerable, endangered, or critically endangered (Carpenter et al. 2008). A Red List assessment showed that 32.8% of the 704 reef-building coral species analyzed for conservation status are at elevated risk for becoming extinct (Carpenter et al. 2008). Prior to 1998, only 1.85% of the 704 coral species would have been considered threatened (Carpenter et al. 2008). This demonstrates that coral extinction risk is rising. A recent study conducted in the Colombian Caribbean determined that 100% of the local coral ecosystems ranked as at risk for extinction (Uribe et al. 2021). 11.4% (92 km²) of total coral coverage ranked as vulnerable, 83.5% (673 km²) is endangered, and 5.1% (40.7 km²) ranked as critically endangered (Uribe et al. 2021). Without the mitigation of emissions, coral extinction risk can continue to rise.

Coral ecosystems are dynamic environments that provide essential habitat and food for other organisms. Coral reefs are one of the most highly diverse ecosystems on Earth, generally with several species of corals contributing to the reef formation (Hoegh-Guldberg et al. 2007). The distribution of reefs is vast, observed worldwide across tropical and semi-tropical environments as both continental and oceanic ecosystems (Uribe et al. 2021). Corals can live in

surface waters (<20 m deep), deep waters (>20 m deep), or some species can reside outside reef habitats (Carpenter et al. 2008). Reef-building corals are biological hotspots and are the key element to maintaining diversity in the ecosystem (Hoegh-Guldberg et al. 2007). The loss of coral poses a relentless problem for the sustainability of fishes and invertebrates that rely on the reefs' resources (Hoegh-Guldberg et al. 2007). Corals also provide important services to marine industries. The degradation of corals reduces coastal protection and causes severe economic losses for local fisheries and tourism (Hoegh-Guldberg et al. 2007). Therefore, the impact of corals extends beyond marine ecosystems to the livelihood of local human communities.

Carbonate chemistry of the ocean

Ocean chemistry is changing in response to carbon dioxide emissions and it has ecological consequences. The acidity of the ocean is measured by pH (the concentration of hydrogen ions), with normal seawater having a pH of 8.0-8.2 on a logarithmic scale of 0-14 (Kleypas et al. 1999). Excess carbon dioxide in the atmosphere adjusts the carbonate chemistry of the ocean, reducing pH in a process called ocean acidification (Kleypas et al. 1999). Over the 20th century an increase in atmospheric carbon dioxide concentration has led to the reduction of seawater pH by 0.1 (Hoegh-Guldberg et al. 2007). It is projected that, without mitigation of emissions, by the end of this century seawater pH will drop by 0.4 (Hoegh-Guldberg et al. 2007). The process of ocean acidification happens as the atmospheric carbon dioxide enters the ocean via air-sea interaction. When the carbon dioxide enters the ocean, it reacts with water and dissociates, creating hydrogen ions and reducing pH (Hoegh-Guldberg et al. 2007). These hydrogen ions react with carbonate via the ocean's carbonic acid-bicarbonate-carbonate buffering system (Figure 1, Hoegh-Guldberg et al. 2007). Essentially, this buffering system acts to uptake carbonate from the marine environment to form bicarbonate ions (Figure 1, Hoegh-Guldberg et al. 2007). Accordingly, bicarbonate ions increase while carbonate in the ocean decreases. A reduction of carbonate in the ocean influences which organisms can sustain their growth (Mollica et al. 2018). If some organisms cannot sustain growth, trophic structure of their ecosystem may collapse. Ocean acidification will therefore have irreversible consequences on biological interactions between species (Feely et al. 2004).

Ocean acidification impacts corals and other marine organisms that build their shells/skeletons out of calcium carbonate due to the lack of available carbonate ions (Mollica et

al. 2018). Reduction in pH decreases the calcification of corals and recovery is not possible under acidic conditions (Hoegh-Guldberg et al. 2007). In addition, approximately half of all calcium carbonate produced yearly is dissolved due to the acidifying ocean conditions (Feely et al. 2004). A lack of carbonate inhibits coral growth by impacting the densification of skeletons (Mollica et al. 2018). This has a direct effect on the structural integrity and strength of corals. A fragile coral skeleton is more susceptible to fragmentation due to physical, chemical, and biological disturbances such as storm waves, dissolution, or bioerosion (Hoegh-Guldberg et al. 2007). The structural complexity, defined as the ecosystem's physical framework (Graham and Nash 2013), of coral reefs will be reduced if calcification is exceeded by erosion (Hoegh-Guldberg et al. 2007). A reduction in structural complexity will diminish the habitat and coastal protection that corals provide (Hoegh-Guldberg et al. 2007). Therefore, corals and other calcifying organisms will suffer from increased threat as carbon dioxide concentrations continue to increase.

Coral bleaching

Corals have a very important symbiotic relationship with a type of photosynthetic dinoflagellate algae called zooxanthellae. Zooxanthellae are from the genus *Symbiodinium* (Berkelmans and van Oppen 2006). Coral polyps are densely packed with zooxanthellae, with greater than 10^6 individuals per cm^2 (Berkelmans and van Oppen 2006). In fact, 8 clades (A-H) of zooxanthellae are known to be associated with corals. Although corals generally associate with only one type of zooxanthellae there are some corals that house multiple symbionts concurrently (Berkelmans and van Oppen 2006). For example, most corals that are a part of the Great Barrier Reef, Australia, are observed to have a dominant symbiont and a secondary symbiont (Berkelmans and van Oppen 2006). Their symbiotic relationship allows for the exchange of nutrients between the coral host and the zooxanthellae (Berkelmans and van Oppen 2006). The production of photosynthetic nutrients is made possible due to reef-building corals living in sunlit surface waters. Zooxanthellae are responsible for maintaining the growth and calcification of corals as they use solar energy to provide photosynthetic products which fulfill greater than 95% of coral metabolic requirements (Hoegh-Guldberg et al. 2007).

Coral bleaching has devastating consequences for the relationship between zooxanthellae and their host. When average seawater temperature outstrips the average maximum summer

temperature by about 1-2 degrees Celsius (C) the bleaching of corals can occur (Jones et al. 2002). Coral bleaching describes the expulsion of the symbiotic zooxanthellae from the coral polyp (Berkelmans and van Oppen 2006). The expulsion is partly due to a reduction in functionality of the zooxanthellae. Heat damage inhibits the ability of zooxanthellae to perform carbon dioxide fixation, initiating their separation from the coral polyps (Jones et al. 2002). Zooxanthellae density within coral tissues decreases with increasing temperature (Figure 2, Jones et al. 2002). After 4 hours of exposure to 34 degrees C water the density of zooxanthellae in the stony coral, *Stylophora pistillata*, reduced to approximately 60% of its initial density observed in 28 degrees C (ambient) water (Figure 2, Jones et al. 2002). In addition, gross production of oxygen via the photosynthetic zooxanthellae drastically decreases with temperature (Jones et al. 2002). When exposed to 34 degree C water for 4 hours gross photosynthesis of zooxanthellae in *Stylophora pistillata* decreased to less than 10% of the photosynthetic production observed in 28 degree C water (Jones et al. 2002). Therefore, as temperature increases, zooxanthellae are reduced in both abundance and efficiency. Another study experimentally examined two coral species, *Acropora muricata* and *Acropora hyacinthus*, for bleaching over a 12-week period (Anderson et al. 2019). These corals were collected from Davies Reef on the Great Barrier Reef (Anderson et al. 2019). Regardless of simulated atmospheric carbon dioxide concentrations, when exposed to 31 degree C water (2.5 degrees C higher than the maximum summer temperature at Davies Reef) most of the *A. muricata* were bleached and survivorship was a mere 10% (Anderson et al. 2019). Under these same conditions less than 5% of the *A. hyacinthus* survived (Anderson et al. 2019). Therefore, heat stress (+ 2.5 degrees C) is the most significant factor for mortality of reef-building corals (Anderson et al. 2019). This is significant because it is predicted that by 2100 there will be an increase of 1-3 degrees C in the average temperature of tropical waters (Berkelmans and van Oppen 2006). For the remainder of this paper the heat tolerance of corals will be used to describe the tolerance of the symbiotic relationship between corals and zooxanthellae to temperature.

Ocean acidification also plays a role in coral bleaching. Some symbiont zooxanthellae can initially gain energy from excess dissolved carbon dioxide, providing some resistance to ocean acidification (Guillermic et al. 2021). However, *Pocillopora damicornis*, a species of stony coral, loses this resistance to ocean acidification upon bleaching (Guillermic et al. 2021). This highlights the importance of the symbiotic relationship between corals and zooxanthellae. A case

study from Heron Island, Great Barrier Reef, examined the synergy between pH and temperature on bleaching, calcification, and productivity of three important coral reef organisms over 8 weeks (Anthony et al. 2008). Three pH ranges (8.0-8.4, 7.85-7.95, and 7.60-7.70) and two temperature groups (25-26 and 28-29 degrees C) were studied (Anthony et al. 2008). The three organisms tested were *Acropora intermedia* (staghorn corals), *Porites lobata* (massive corals), and *Porolithon onkodes* (crustose coralline algae - CCA) (Anthony et al. 2008). CCA was included in this study because it functions as a settlement cue for corals and aids in reef building (Anthony et al. 2008). Overall, productivity and calcification decrease with a reduction in pH, while bleaching increases with decreasing pH (Anthony et al. 2008). Coral productivity is directly attributed to the symbiotic zooxanthellae living within the polyp tissue. Consequently, when bleaching expels the zooxanthellae from the coral polyps productivity is reduced (Anthony et al. 2008). Acidity had a more significant impact on bleaching than temperature for staghorn coral and CCA (Figure 3, Anthony et al. 2008). In these organisms, relative to the control state, bleaching increased by 20% under the high temperature condition whereas the low pH condition induced a 40-50% increase in bleaching (Figure 3, Anthony et al. 2008). Massive coral experienced less bleaching than the other organisms; under low pH and high temperature conditions bleaching increased 20% relative to the control (Figure 3, Anthony et al. 2008). However, bleaching was magnified by 50% due to temperature in massive coral as opposed to only 10-20% in staghorn coral and CCA (Figure 3, Anthony et al. 2008). Therefore, warming and ocean acidification act synergistically to reduce thermal thresholds for bleaching while the quantitative impact varies by species (Anthony et al. 2008).

Bleaching of corals impacts entire reef systems. When a single reef experiences coral bleaching this is considered a localized bleaching event (Jones et al. 2002). In contrast, if several reefs across a large area are bleached, this is called a mass bleaching event (Jones et al. 2002). Both of these bleaching events are related to seawater temperature anomalies (Jones et al. 2002). There have been three global-scale mass bleaching events (1998, 2002, and 2015/2016) since this phenomenon was first recorded in the 1980s (Hughes et al. 2017). These bleaching events have progressively caused more widespread and severe impacts on the local corals at the Great Barrier Reef (Hughes et al. 2017). Extreme bleaching of reefs was 4 times higher in 2016 than it was in 1998 or 2002 with bleaching occurring in more than 60% of corals (Hughes et al. 2017).

Adaptation to coral bleaching

Coral species are showing variable impacts and responses to coral bleaching events. There are both environmental and biological factors that influence which corals are resistant to bleaching. Species either residing in deeper reef slopes or those that do not rely on reef habitats are the only ones that are not considered threatened (Carpenter et al. 2008). This provides insight into the importance of the mutual relationship between corals and their reef ecosystems as well as the depth at which they live. The variability of the environment in which the corals live also affects their survival. With a 1 degree C wider range in daily temperature the probability of bleaching is decreased by a factor of 33 (Safaie et al. 2018). Therefore, regions with high-frequency temperature fluctuations host coral ecosystems that are more resistant to bleaching (Safaie et al. 2018). If corals that reside in stable temperature conditions are more susceptible to bleaching it highlights a possibility for reefs to become regionally limited in comparison to the current distribution of reefs. A biological factor that poses hope for the future of corals is changing their relationship with their symbiotic zooxanthellae. Some corals are able to acclimatize to high temperature anomalies by adjusting their dominant zooxanthellae symbiont type which could help their survival (Berkelmans and van Oppen 2006). These corals can obtain resistance to thermal stress by changing their dominant symbiont clade from C to D (Berkelmans and van Oppen 2006). Corals can tolerate approximately a 1-1.5 degree C increase in temperature with clade D, the most thermally tolerant type, dominating their tissue (Berkelmans and van Oppen 2006). It has been observed that clade D symbionts are more abundant than other clades in coral reefs that have experienced repeated bleaching events (Berkelmans and van Oppen 2006). This provides an advantage to corals that have various types of symbiotic algae residing in their tissues that they can shuffle (Berkelmans and van Oppen 2006). Despite this adaptation, corals may remain at risk if emissions are not mitigated.

Natural selection may be changing the traits of coral populations as the ocean becomes warmer and more acidic. There is evidence that major warming events that cause coral bleaching can lead to adaptation due to thermal stress (Guest et al. 2012). Observations in Singapore and Tioman Island found that regions that had bleached during the 1998 bleaching event experienced less severe bleaching during the 2010 bleaching event that impacted South East Asia (Guest et al. 2012). Adaptation due to natural selection results in the evolution of a population with the survivors consisting of those that confer higher fitness in their environment. Adaptation of corals

in response to warming has led to the loss of thermally sensitive corals and the increase of corals that are thermally resistant (Guest et al. 2012). There is reason to believe that this pattern may be applicable to corals globally. Coral communities likely have already started adapting to climate change as current bleaching frequency is lower than model predictions that are based on global sea surface temperature (Logan et al. 2014).

Over the past two decades the onset of coral bleaching has changed. Observations from 1998 to 2017 of 3351 coral bleaching sites across 81 countries were compared to determine patterns of bleaching (Figure 4, Sully et al. 2019). Results found that over the past decade the sea surface temperature that initiates coral bleaching has increased by approximately 0.6 degrees C despite bleaching becoming more severe and frequent (Figure 4, Sully et al. 2019). From 1998 to 2006 the average sea surface temperature observed during bleaching was 28.1 degrees C whereas from 2007 to 2017 it was 28.7 degrees C (Figure 4, Sully et al. 2019). This implies that genotype frequencies of the coral population may have changed, resulting in the new population being more thermally resistance to bleaching (Sully et al. 2019). This finding would also result in a decline of thermally sensitive corals as resistant species have a higher chance for survival. Thermally sensitive corals have already began experiencing local extinction (van der Zande et al. 2020). Another study examined the impact of business-as-usual emission rates of carbon dioxide on coral bleaching due to ocean acidification and warming (van der Zande et al. 2020). Results showed that by 2100 thermally sensitive corals will likely be eliminated from reefs while even thermally tolerant species will experience bleaching (van der Zande et al. 2020).

Although some species are able to acclimatize to major bleaching events, annual bleaching and continual warming may pose a different problem for corals. Further warming, even as little as an increase in temperature of 0.5 degrees C, will cause the loss of coral thermal tolerance (Ainsworth et al. 2016). Loss of this adaptive trait will escalate coral deterioration. Under repeated bleaching some species can no longer fully recover as they experience cumulative degradation (Schoepf et al. 2015). Impacts of repeated bleaching may be magnified when a species is already susceptible to warming. Heat-sensitive species will be threatened by extinction if their recovery capacity is continually limited (Schoepf et al. 2015). Annual bleaching can cause the loss of susceptible species resulting in a decrease of coral abundance and diversity in reef ecosystems (Grottoli et al. 2014). As natural selection acts on corals, diversity will be lost since some species will become extinct if their thermal tolerance threshold is exceeded. If

climate change continues at its current rate reefs will consist of only a few dominant species of corals that are most tolerant to bleaching (van der Zande et al. 2020).

Impacts of coral degradation of reef ecosystems

The loss of corals and the habitat they provide for other organisms has substantial implications for the reef ecosystem. Many fishes, such as parrotfish, reside in reef ecosystems for the natural habitat and opportunity for grazing that corals provide (Hoegh-Guldberg et al. 2007). Coral deterioration instigates a loss of food sources for the community. Reefs that had clear evidence of bleaching showed a reduction in coral coverage of approximately 60% and a resulting decrease in fish richness of about 10% (Stuart-Smith et al. 2018). These reef fishes are likely forced to move to a new environment or compete for limited space and resources. A compilation of 76 studies conducted on reefs worldwide showed that 62.1% coral loss resulted in a 6.7% decrease of reef fishes' species richness, indicating that diversity has been reduced (Figure 5, Pratchett et al. 2011). This study showed that coral loss in tandem with a reduction of the ecosystem's structural complexity, representing long-term physical impacts, plays a more substantial role in impacting reef fishes than short-term biological changes (Figure 5, Pratchett et al. 2011). Abundance of fishes also decreased in 60% (815 of 1360 cases) after greater than 10% coral loss (Pratchett et al. 2011). 499 of the 1360 cases experienced a disproportionate loss of abundance, up to five times larger than the reduction of coral coverage (Pratchett et al. 2011). A decline in abundance has been observed for various functional groups of fishes such as corallivores, planktivores, carnivores, and herbivores (Pratchett et al. 2011). This demonstrates that the natural structure of ecosystems can be disrupted by the loss of coral cover. Entire ecosystems also experience trophic restructuring, related to sea surface temperature, depending upon the thermal tolerance of community members such as fishes and invertebrates (Stuart-Smith et al. 2018). Previously observed patterns of diversity of reef fishes and invertebrates related to latitude were adjusted due to thermal stress (Stuart-Smith et al. 2018). At some sites on the Great Barrier Reef, herbivorous fishes that remove algae from corals via scraping decreased by about 6% in frequency after the 2016 mass bleaching event (Stuart-Smith et al. 2018). This is important because scraping fishes aid in the recovery process of reefs after coral bleaching (Stuart-Smith et al. 2018).

The structural complexity of reefs is important for the sustainability and functionality of their ecosystem. Structural complexity of reefs has a positive correlation with coral recovery, fish density, and fish biomass (Graham and Nash 2013). This is significant for corals under stress since it provides an opportunity for survival. It could also show that naturally more complex coral species have an advantage over other species under harsh conditions. Structural complexity exhibits a negative correlation with algal cover (Graham and Nash 2013). This negative correlation could be attributed to the increase in fishes as some feed on algae. Coral is replaced by macroalgae through reef degradation (Pratchett et al. 2011) which blocks the sunlight to the reef and the symbiotic zooxanthellae cannot successfully perform photosynthesis. Therefore, this result has important implications for the growth and productivity of corals. Additionally, corals' resilience and recovery are impeded by the growth of macroalgae (Pratchett et al. 2011). This shows that the degradation of corals has long-term, cascading impacts throughout the entire reef ecosystem.

Current uncertainties

Some questions that are still outstanding in the field of coral bleaching are based around what main factors are contributing most to bleaching and their relative importance. It is difficult to discern the relative impact of a given variable on the probability of coral bleaching as many factors influence one another and are species dependent (Anthony et al. 2008). Coral disease has recently sparked interest in the field of bleaching as much is still unknown about coral disease etiology, what species it impacts, and its relation to bleaching (Hoegh-Guldberg et al. 2007). There is still much debate in the field about the response of corals to bleaching events. Although there is evidence that corals are responding adaptively to bleaching it is not fully understood if adaptation processes have been underestimated previously (Guest et al. 2012). Currently there is a lack of knowledge on how long the adaptation to thermal tolerance will help corals survive (Berkelmans and van Oppen 2006). Recent findings have shown various regional differences in coral bleaching and ecosystem restructuring associated with frequent temperature fluctuations (Safaie et al. 2018). However, there are still uncertainties about what other factors may be contributing to variable responses of corals across regions.

Recommendations for future research are focused around enhancing current knowledge about what consequences corals are facing due to sustained climate change. It is important to

collect data on the sea surface temperature that initiates bleaching throughout generations of corals to determine if thermally sensitive species are likely to experience regional extinction (Sully et al. 2019). It would be beneficial to analyze historical bleaching temperature prior to the past two decades to determine how quickly corals adapt to warming under increasing threat from emissions (Sully et al. 2019). It is essential for local fisheries to gain additional knowledge about the adverse consequences reef fishes are experiencing due to a loss of coral (Pratchett et al. 2011). Future research on coral restoration may provide a viable option for sustaining the diversity of coral reefs until policies are enacted to reduce greenhouse gas emissions.

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Figures

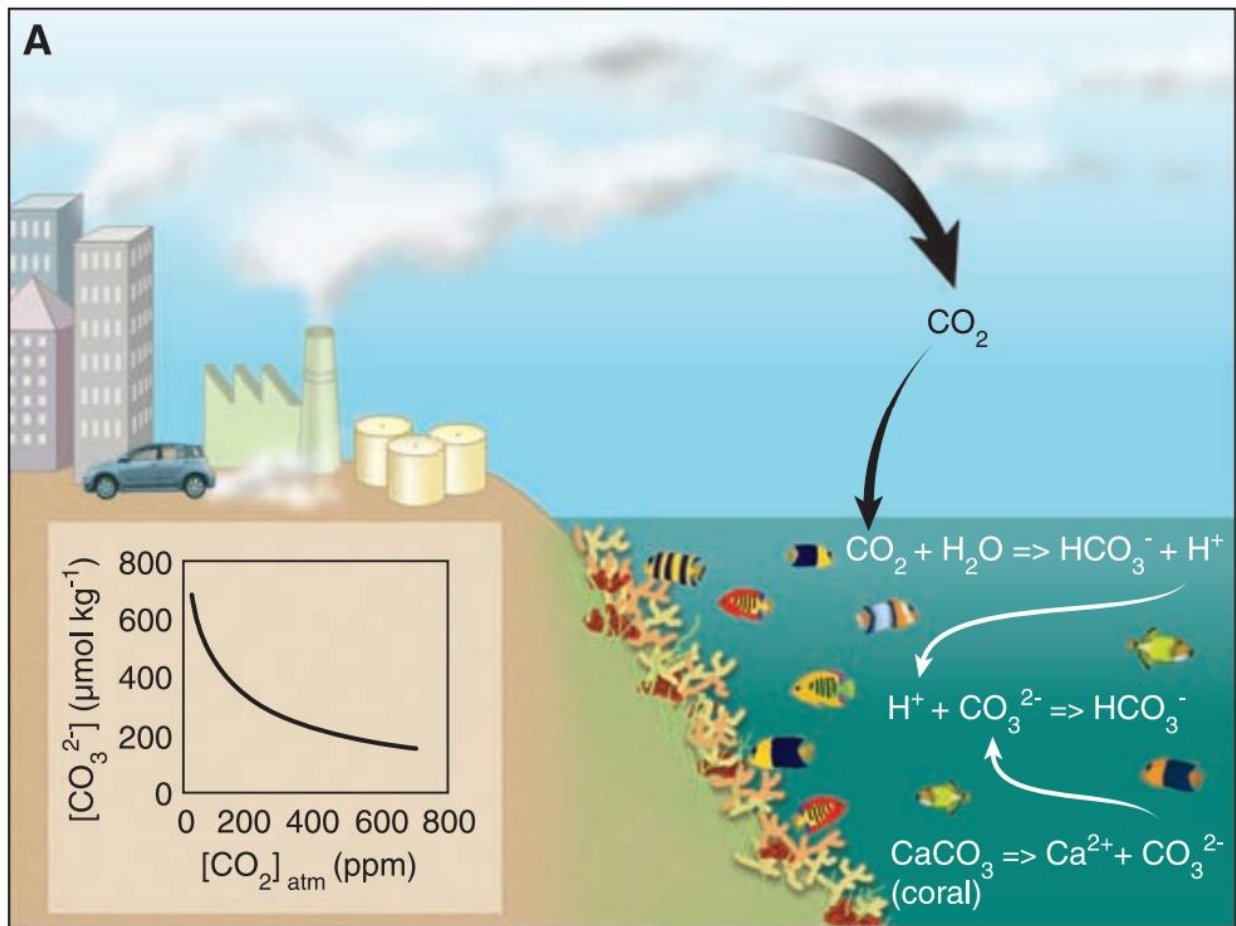


Figure 1: Relationship between carbon dioxide released via emissions and the reduction of carbonate available for calcifying organisms – from Hoegh-Guldberg et al. 2007.

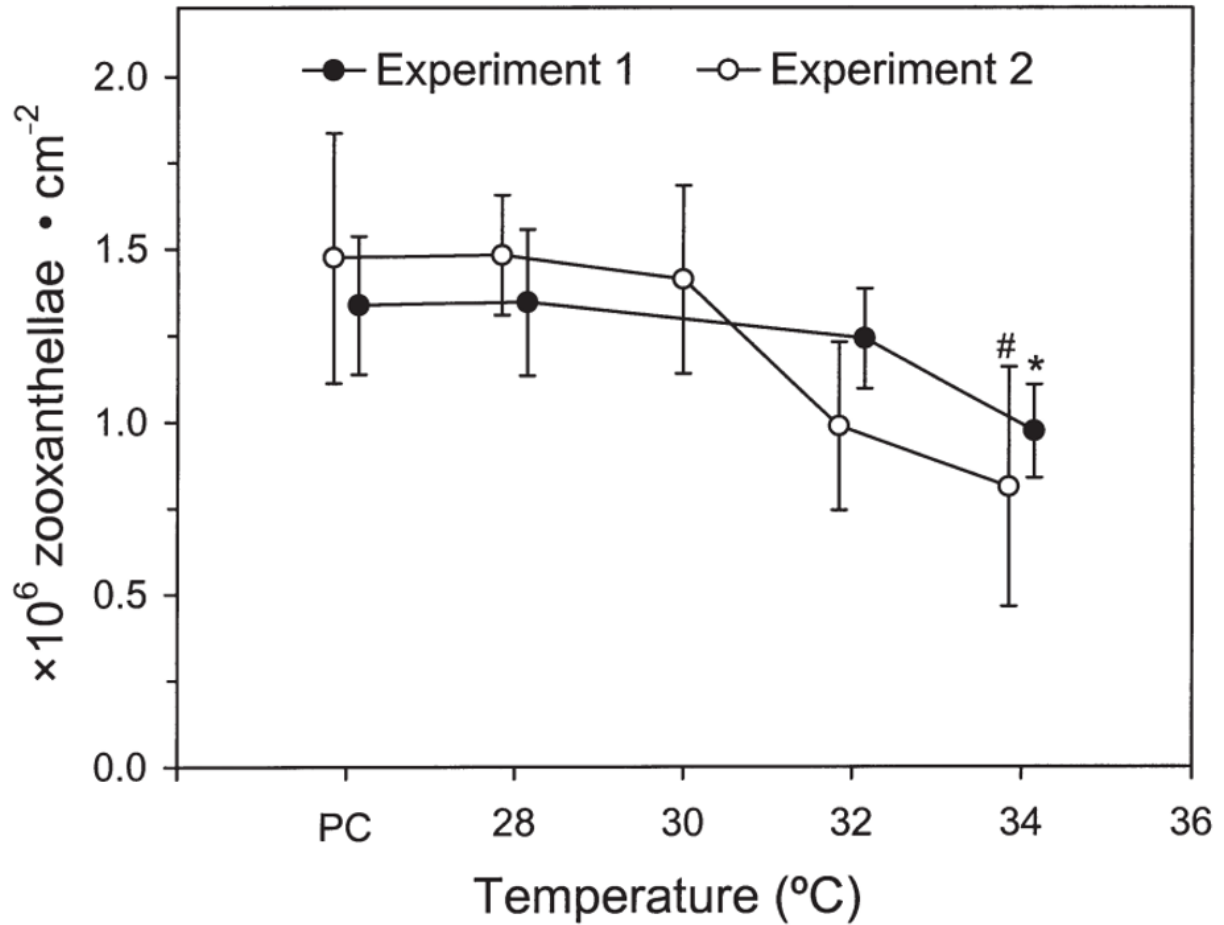


Figure 2: Mean values of zooxanthellae in the tissue of *Stylophora pistillata* under various temperature conditions. Data were collected for the duration of four hours at each temperature interval in degrees C: 28, 30, 32, and 34. Data points are shifted on the x-axis between experiments for clarity – adapted from Jones et al. 2002.

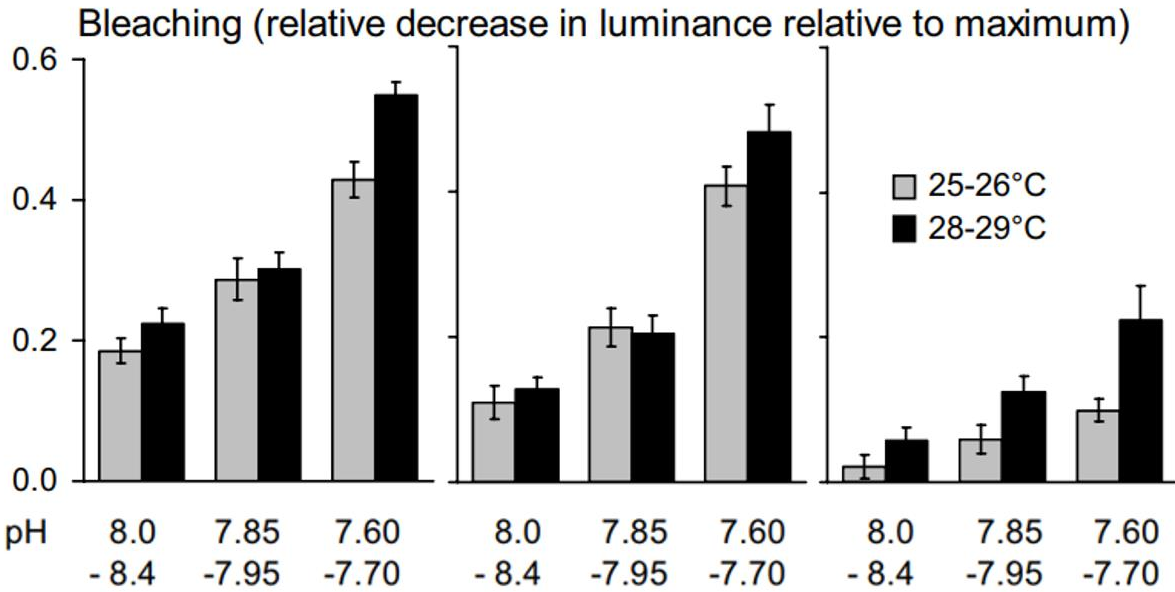
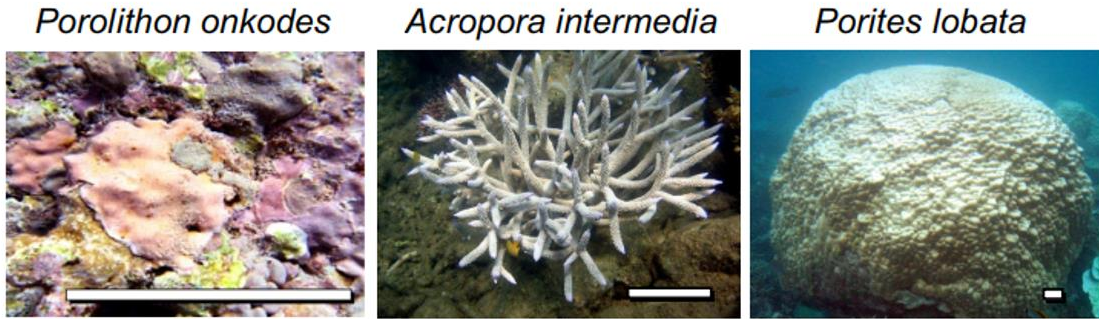


Figure 3: Bleaching of three coral reef organisms, *Acropora intermedia*, *Porites lobata*, and *Porolithon onkodes*, examined over an 8-week period. The study included three pH ranges (8.0-8.4, 7.85-7.95, and 7.60-7.70) and two temperature groups (25-26 and 28-29 degrees C) – adapted from Anthony et al. 2008.

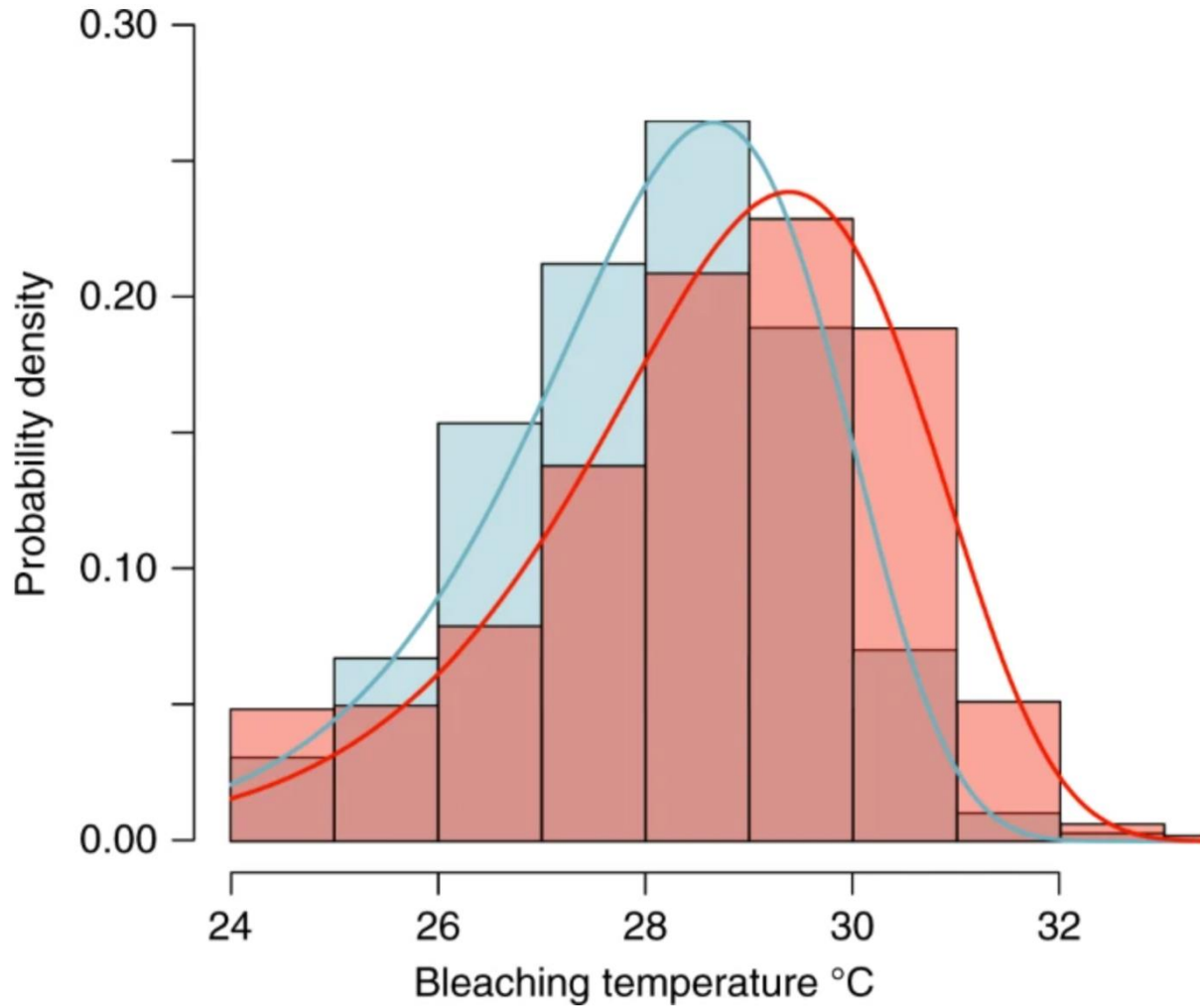


Figure 4: Probability of coral bleaching as a function of temperature. The blue curve represents 1998 to 2006 and the red curve represents 2007 to 2017 – from Sully et al. 2019.

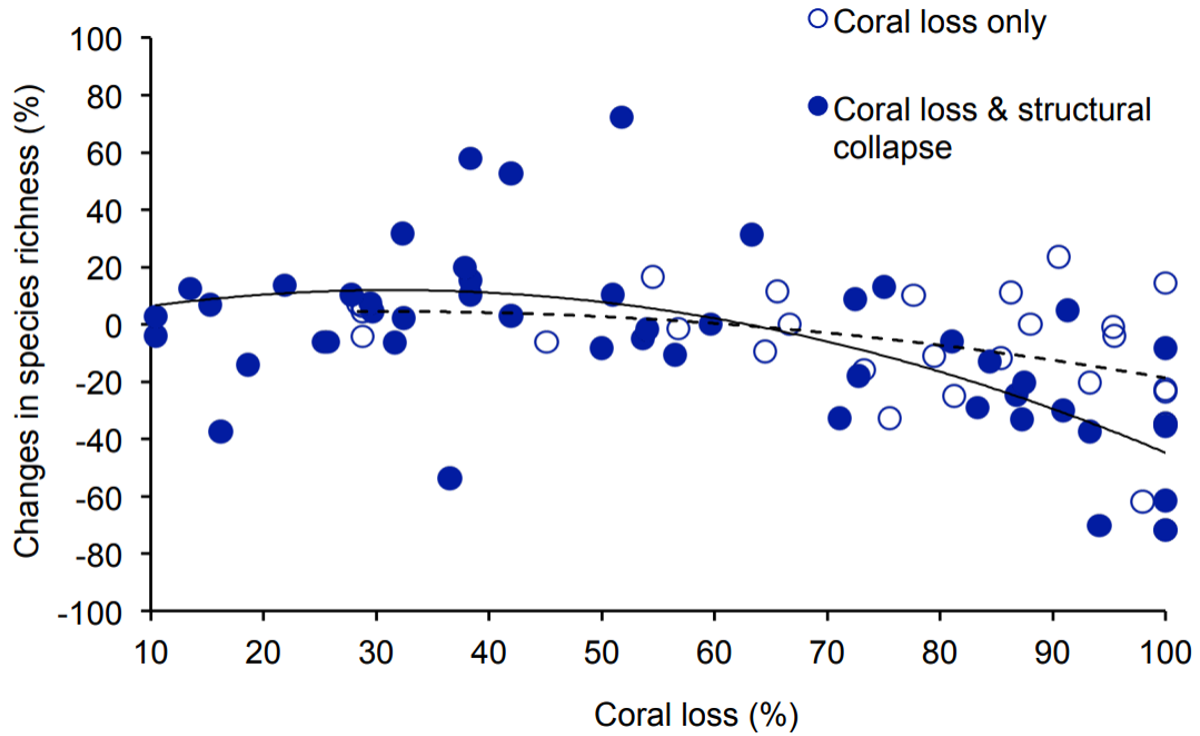


Figure 5: Correlation between percent coral loss and percent changes in reef fishes' species richness. Open circles indicate only coral loss with a dashed trendline (short-term biological impacts) whereas filled circles indicate both structural collapse and coral loss with a solid trendline (long-term physical impacts) – from Pratchett et al. 2011.