A comparison of extinction risk in shallow versus deep water reefs

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Background

Often called the rainforests of the sea, coral reefs are one of the most diverse ecosystems on Earth, but this diversity is in trouble. Recently, coral reefs are thought to be experiencing a worldwide decline from increases in pollution and global temperatures, and certain coral reef ecosystems are more threatened than others (Jackson 2010). Coral reefs are considered to be one of the most resilient ecosystems throughout the history of life on Earth, but currently, more than sixty percent of remaining coral reefs are threatened with extinction (Bongaerts et al. 2010; Bridge et al. 2013). In particular, shallow coral reefs are currently facing a higher risk of extinction than deep coral reefs—this is largely due to more human contact and increased environmental variation in shallow reefs (Bak et al. 2005). However, it is important to consider that because of increased accessibility of shallow reefs, data on shallow coral reefs are typically more abundant than on deep coral reefs. Due to this shortcoming, extinction risk for deep coral reefs are likely underestimated (Menza et al. 2007a). While shallow reef conservation is typically prioritized, conservation of both shallow coral reefs and deep coral reefs is important to preserve the biodiversity of coral reefs.

Shallow coral reefs and deep coral reefs share some fundamental ecological qualities, but they are also characterized by distinct traits. Shallow reefs are typically characterized as existing in a 0-30 meters depth range with light penetration (Menza et al. 2007a). Due to relatively consistent light penetration, shallow reefs have the highest percent cover of photosynthetic organisms in comparison to other reefs (Slattery and Lesser 2012). Shallow reefs are the type of ecosystem that we usually think of when we think about coral reefs because they occupy warm, shallow, tropical waters. We have more contact with shallow reefs making them a much more studied and identifiable ecosystem. Deep coral reefs, on the other hand, are much less accessible because of their depth, and the costs associated with their exploration. Deep reefs are characterized as existing below 30 meters in depth and typically have little or no light penetration (Bongaerts et al. 2010). They are commonly found in deep water canyons or on continental slopes or shelves and have been known to reach depths of up to 3,000 meters (Hourigan et al. 2007). The majority of deep water corals have separate sexes, which is a contrast from shallow water corals, which are typically hermaphrodites (Roberts et al. 2006). In contrast to shallow reefs, deep reefs tend to have greater total coral cover, but with lower coral diversity (Menza et al. 2008b).

Cold-water reefs are a type of deep reef, which are particularly understudied, but recent research has provided some insight into the ecology of cold-water reefs including their reproductive ecology, biodiversity levels, and change over geological time (Roberts et al. 2006). Cold-water coral reefs are particularly diverse deep coral reef ecosystems, but little is known regarding the relationship between cold-water reef species (Roberts et al. 2006). Another classification of coral reefs called mesophotic coral reefs exist on a continuum from shallow to deep reefs and experience a gradient of light penetration. Mesophotic reefs are usually similar to near-by shallow reef communities demonstrating that site-specific variation is often a reflection of the regional history of the area (Slattery and Lesser 2012). Mesophototic reefs can exist anywhere from 30 to 1550 meters below the surface, often regarded as the gradient between shallow reefs and deep reefs (Slattery and Lesser 2012) Because mesophotic reefs are on a depth and light continuum, research on mesophotic reefs provides insight into both shallow water reefs and deep water reefs (Slattery and Lesser 2012).

Different patterns of coral reef extinctions in Earth's geologic history can shed light on current coral reef extinctions. Coral reefs have been exposed to a variety of environmental disturbances over the course of their history and have fallen victim to multiple mass extinction events (Budd 2000). For example, massive influxes of carbon at the end of the Paleocene epoch caused intense global warming, ocean acidification, mass extinction throughout the deep sea and the worldwide disappearance of coral reefs (Jackson 2010). Cold-water corals are particularly useful in studying coral reef establishment and extinction as well as past ocean conditions because they serve as "paleo-environmental archives" (Roberts et al. 2006). By studying the banded skeletal structure of cold-water corals, we can learn about past seawater temperatures and water chemistry (Roberts et al. 2006). This provides insight into ocean conditions that lead to coral reef decline in the past.

An instance when deep water reefs were noticeably impacted by ocean acidification and increased carbon dioxide levels was during the Paleocene-Eocene 55 million years ago, which was associated with a striking change in deep sea coral communities (Jackson 2010). During this Paleocene-Eocene thermal maximum (PETM), sharp increases in carbon in the atmosphere and ocean led to mass extinction and complete reorganization of associated trophic levels (Jackson 2010). Typically following intervals of increased diversity and origination rates, there is a concentration of extinction in coral reef ecosystems, and this has been demonstrated during the Cenozoic (Budd 2000). Phases of coral reef diversification and extinction are characterized by about 30-50 million years of high diversity followed by a mass extinction event and approximately 8-20 million years of lower diversity—these general intervals have been detected over the time period that coral reefs have existed on Earth. Over the course of time, coral reefs have historically suffered from climate changes and rises in sea-level, and while coral reef ecosystems are still surviving today, the recent effects of global climate change may be catastrophic to modern coral reef ecosystems (Budd 2000). In the past 10 million years, slight changes in ocean conditions were enough to alter coral reef ecosystem origination and dynamics (Jackson 2010). Modern Caribbean reefs are structured by large long-living colonies as a result of historical trends in species origination accelerating greater than extinction rates in historical Neogene reefs (Johnson 1995). We can see the influence on historical coral reefs on the structure of current coral reef ecosystems.

With rapidly increasing levels of carbon dioxide in our current atmosphere and ocean, similar results of the PETM could be observed in modern coral reef ecosystems. By studying past extinction events, we can examine how changes in the environment affect different coral reef ecosystems and learn how to protect the remaining diversity of coral reefs on earth. Both cold-water coral reefs and deep water coral reefs are threat-

*This author wrote the paper as a part of BIOL484: Senior Seminar: Biology of Extinction under the direction of Dr. Menke ened from the intensifying effects of pollution, climate change, and over-exploitation, however, based on recent research, shallow coral reefs are at a higher risk of extinction (Carpenter et al. 2008, Bak et al. 2005). This paper provides a comparison of threats to shallow coral reefs versus threats to deep coral reefs and an exploration of how shallow and deep coral reef ecosystems are connected. This investigation leads to a discussion of the relative risk of extinction to shallow coral reefs in comparison to deep coral reefs. Finally, shortcomings in the data and conservation implications of research on various coral reef ecosystems are explored.

Extinction Risk of Shallow and Deep Coral Reefs

General Threats to Coral Reefs

With increased globalization of the human race, ocean ecosystems have greatly suffered from overexploitation, increased carbon dioxide, and pollution (Jackson 2010). Global climate change, coral bleaching, overfishing, and ocean acidification threaten both shallow coral reefs and deep coral reefs across the globe. Based on the IUCN Red List, 32% of reef-building corals are at elevated risks of extinction (Carpenter et al. 2008). Exploitation, pollution, and the rise of carbon dioxide interact in complex ways to effect physical, chemical and biological changes in a synergistic manner (Jackson 2010). Natural disturbances such as major storms and diseases within coral populations also contribute to coral reef degradation (Porter et al. 1982). While it seems like deeper coral reefs would be in the clear of some of these threats, it appears that all coral reef ecosystems are suffering from the impact of human activity.

Extinction risk for corals has greatly increased since the advent mass bleaching events, and this could soon lead to large-scale global biodiversity loss of corals (Carpenter et al. 2008). Bleaching is largely the result of raised sea temperatures, and events have been recorded since the 1980s with the number of cases of coral bleaching having vastly increased since then (Baker et al 2008). Scleractinian (reef-building) corals have a symbiotic relationship with a sing-celled algae known as zooxanthellae, which gains a protective environment by living in the coral polyp tissues, and in turn, provides the coral with carbon molecules needed in coral growth and reproduction (Baker et al. 2008) . Coral bleaching occurs when zooxanthellae densities within the coral decline or when the photosynthetic pigment concentration decreases, and occasionally these effects combine (Baker et al. 2008). Coral bleaching gets its name because of the pigment loss, leaving only the white calcium carbonate skeleton of coral. Coral bleaching is one of the major threats to coral reef ecosystems around the globe, particularly to coral reefs that are shallower than 20 meters, but deep-water bleaching has also been an issue (Baker et al. 2008; Bak et al. 2005). Coral bleaching has varying effects at different depths as well as among different taxa (Marshall and Baird 2000). While shallow coral reefs and deep coral reefs face some common threats, each ecosystem has distinct threats that contribute to its relative risk of extinction.

Shallow Coral Reef Threats

Shallow coral reefs are particularly susceptible to human contact and are experiencing increased environmental variation. Shallow reefs are more often exposed to varying conditions of water quality and temperature, and they are more susceptible to degradation from human contact like unsustainable tourism and over-fishing (Bongaerts et al. 2010). Direct contact with shallow coral reefs is an easily observable threat, but the effects of more long-term threats such as climate change are becoming increasingly evident (Baker et al. 2008). Increases in temperature in shallow waters are correlated with the spread of white syndrome, a disease affecting Pacific shallow corals (Bruno et al 2007). Data show that following warmer years, outbreaks of white syndrome increased significantly on reefs with at least fifty percent cover (Bruno et al. 2007). Shallow water reefs are particularly susceptible to temperature stress experiencing a significant reduction in coral cover, species diversity, and species number, while these trends were not significant for deep water reefs (Porter et al. 1982).

Large-scale bleaching has had major effects on shallow corals, and varying responses among shallow water coral taxa are largely due to assemblage composition (Marshall and Baird 2000). Bleaching weakens corals, which can lead to the increased prevalence of disease and long term effects such as loss of frame-building coral and the resulting loss of habitat for other organisms (Baker et al. 2008). A 20 year survey of coral cover, number of coral colonies, and coral diversity in the Netherlands Antilles found that coral colonies, coral cover, and diversity significantly decreased in shallow reefs (Bak and Nieuwland, 1995). These trends (aside from diversity) later showed to be consistent for 30 total years (Bak et al. 2005). From 1973, when the survey began, coral colonies in shallow reefs decreased significantly from an average of just over 150 colonies per quadrant to around 50 colonies per quadrant in 2003 (Bak et al. 2005). Similarly, a significant decrease in coral cover was observed with a drop from 45 percent coral cover in 1973 to 25 percent coral cover in 2003 (Bak et al. 2005). Additional studies in the Caribbean show that coral cover in some shallow areas have experienced a 40 percent reduction in the past 30 years (Bak et al. 2005).

Shallow coral reef degradation is not limited to the Caribbean region. While less is known about the specifics of coral loss in the Indo-Pacific region, this region contains the majority of the world's coral reefs (Bruno and Selig 2007). Despite recent recovery in some areas of the Indo-Pacific, the rate and extent of coral loss in the Indo-Pacific is significant and much higher than previously projected (Bruno and Selig 2007). The study carried out by Bruno and Selig (2007) was the first long-term analysis of coral conditions in this region. The data show that the loss of coral cover began sooner than previous studies indicated and that this loss is mostly consistent throughout the region (Bruno and Selig 2007). This study only looked at shallow reefs, but it affirmed the assumption that coral cover decline is a world-wide occurrence (Bruno and Selig 2007). Knowing that coral cover decline is an issue across the globe is important when trying to come up with management techniques for coral reef conservation.

Overall, the major threats to shallow reefs include direct human contact, overexploitation by fisheries, and the effects of global climate change including increase in ocean water temperatures leading to coral bleaching, sea-level rise, and ocean acidification. Natural threats to shallow reefs include hurricanes and other natural disasters (Bak et al. 2005). Shallow reefs are more commonly studied than deep reefs, and therefore data on shallow reefs are much more prevalent. Human contact with shallow ecosystems include coastal development, increase in pollution, and increase in runoff (Bak et al. 2005). Some of these threats also have an effect on deep coral reefs, however deep coral reefs also have unique threats.

Deep Coral Reef Threats

Deep coral reef threats are not as well understood, but ocean acidification, deep-reef bleaching, sedimentation from storms, and deep-ocean trawling are threatening deep coral reef ecosystems (Bak et al. 2005, Roberts et al. 2006). A subset of deep water reefs, cold-water reefs are particularly threatened by deep-water trawling, seabed mining, and ocean acidification (Roberts et al. 2006). A study by Bak and colleagues found that the major threats to deep reefs include deep sea bleaching and storm generated sedimentation (2005). Other studies have discovered trends that have never before been documents. One such study by Meza and his colleagues (2007b) found that deep Caribbean reef had significantly more dead coral with algal turf than compared shallow reefs—this was an unexpected result of the study and demonstrates how deeper reefs may be even more at risk than we had previously anticipated. Despite little light penetration in deep reefs, reefs with zooxanthellae have been found at depths of up to 199 meters, and can suffer from deep bleaching (Menza et al. 2007b).

Compared to shallow reefs, deep reefs are less likely to suffer from environmental disturbances because they are not as exposed to environmental perturbations like shallow reefs are (Oppen et al. 2011). Unlike trends observed in shallow coral reefs, over time, deep reef diversity tends to decline more than coral cover (Bak et al. 2005). A twenty year survey of coral cover and number of coral colonies in the Netherlands Antilles found that coral colonies and coral cover did not significantly decrease in deep reefs, but diversity significantly decreased (Bak and Nieuwland, 1995). This trend was again demonstrated in a follow up survey 10 years after the initial study (Bak et al. 2005). In this region, deep coral reef species diversity decreased from eight species in 1973 to six species in 2003 (Bak et al. 2005). Overall, deep coral reefs, like shallow reefs are subjected to the effects of climatic changes, but are more susceptible to deep-water trawling (Roberts et al. 2006).

Shallow Reef and Deep Reef Connection

Shallow Reefs are connected to deep reefs in a way that may influence the extinction risk in each ecosystem. The 'deep reef refugia' hypothesis (DRRH) states that deep water reefs are largely protected from disturbances that commonly impact shallow water reefs, and deep water reefs can serve as a reproductive source for shallow water reefs when they are degraded by a disturbance (Bongaerts et al. 2010). Shallow reefs tend to experience distinct disturbances such as hurricanes and white band disease, and therefore, shallow reefs would benefit from deep water refuges that are not as impacted from these disturbances (Bongaerts et al. 2010). Larval connectivity between shallow and deep reefs is limited to 'depth-generalist' coral species, constituting only about a quarter of total coral biodiversity (Bongaerts et al. 2010). Depth-generalist species can occupy multiple depths, and are not limited to only shallow or deep coral reefs (Bongaerts et al. 2010). The most likely source for refuges to help with shallow reef recovery would be in the upper mesophotoic zone, which is around 30 to 60 meters below the ocean surface (Bongaerts et al. 2010).

Shallow water coral reefs may benefit from migration from deep water refuges. For example, in Scoot Reef in Australia, there is evidence of larval recruitment in shallow reefs that are deep water in origin (Oppen et al. 2011). In this study by Oppen and her colleagues (2011), migration from deeper depths to shallower depths was detected at all three locations in their study. While there is evidence for migration, the data show significant genetic differences in nearly the majority of the population tested, indicating that interbreeding of populations from the deep reefs to shallow reefs was unlikely (Oppen et al. 2011). Despite this genetic differentiation, migration between various depths indicate that deep water reefs have potential to serve as refuges for degraded shallow reefs, which depend on larval recruitment from outside coral reefs (Bridge et al. 2013). Aside from serving as refuges, the majority of shallow coral species and other coral reef biota extend into lower depths—in the Caribbean, over three quarters of shallow coral species occupy the mesophotic zone, and nearly half of those species extend to into deeper zones (Bridge et al. 2013). Because of this important connection between deep and shallow reefs and the potential of deep reefs to serve as refuges during disturbances, it is critical to consider both shallow reefs and deep reefs when protecting the coral reef ecosystem as a whole.

Discussion

Conclusion and Limitations

Based on data on both shallow reefs and deep reefs across the globe, shallow reefs are currently faced with a higher risk of extinction (Bak et al. 2005; Jackson 2010; Bruno and Selig 2007) . This is particularly due to increased human contact and environmental variation in shallow reefs—deep reefs are largely protected from many of these disturbances (Bongaerts et al. 2010; Porter el al. 1982). Additionally overexploitation of resources, pollution (especially runoff), and the rise of carbon dioxide all contribute to the degradation the physical and biological state of shallow reefs (Jackson 2010). While deep coral reefs suffer from exploitation from deep-water trawling and increased ocean acidification, deep coral reefs are largely protected from the numerous environmental perturbations that exist near the surface of the ocean (Roberts et al. 2006; Oppen et al. 2011). For example, long-term studies at multiple sites in the Caribbean show that shallow reefs have experienced significant declines in coral cover and number of coral colonies, but this trend was not observed in deep coral reefs (Bak and Nieuwland 1995; Bak et al. 2005).

However, there are limitations to comparing shallow and deep reefs because the literature is unbalanced. Largely due to accessibility, there are more data on shallow reefs than on deep reefs. There is a lack of research on major ecological dynamics of deep water coral reefs such as coral reproduction and species interactions within and among deep reefs (Bongaerts et al. 2009). Cold-water reefs are particularly understudied and would benefit from more surveys, though this research can be expensive and difficult to target (Roberts et al. 2008). Most of the data on coral reef ecosystems is limited to reefs shallower than 20 meters (Bak 2005). This is because researching deep reefs is costly and requires more advanced technology such as remotely operated vehicles, whereas research on shallow reefs can be easily achieved by SCUBA diving (Menza et al. 2007b). Also deep water reefs are not mapped as extensively as shallow reefs, making them more difficult to research (Menza et al. 2007a). The lack of mapped deep reefs is also a result of a lack of research.

Research concentrated on shallow reefs creates a bias in the view we have of coral reefs, and the risk of extinction to deep coral reefs is likely highly underestimated (Menza 2007a). A literature survey found that searching for peer-reviewed articles about various coral reef depths resulted in a exponential decline in the number of papers as the depth of the reefs increased indicating a skew in the primary literature (Menza et al. 2007). Aside from just comparing deep coral reefs to shallow coral reefs, there is also a regional bias in the literature for research on coral reefs in the Caribbean, despite the Indo-Pacific consisting of 75 percent of the coral reefs on the globe (Bruno and Selig 2007). This also creates biases in the research to a specific region of the globe, so assessment of coral degradation in the Indo-Pacific is likely underestimated (Bruno and Selig 2007). These biases should be considered when assessing coral reef extinction risk and establishing conservation efforts.

Conservation Implications

Coral reef extinction events in the geologic record can help us understand why corals are currently declining and assess if we can halt or reverse this degradation. For example, sudden increases of ocean acidification during the Paleocene-Eocene thermal maximum resulted in extreme changes in deep coral reef communities (Jackson 2010). Recent surges in ocean acidification in deep coral reefs could also lead to catastrophic changes in deep-sea communities (Jackson 2010). Deep coral reef conservation is necessary to attempt to avoid this outcome. Additionally, deep reefs can provide propagules for shallow reefs and therefore should also be prioritized (Bongaerts et al. 2009). An ecosystem-approach to conservation is important as deep reefs and shallow reefs are connected (Bridge et al. 2013).

We now require significant efforts to increase our knowledge of both deep and shallow coral reef ecosystems, how they are connected, and how to protect them. Shallow reefs are typically more susceptible to disturbances, and as shallow reefs continue to degrade, deep reefs will eventually become target to overexploitation (Bridge et al. 2013). Additionally, because shallow reefs experience degradation from surface threats that deep reefs do not, priority on deep reef conservation is necessary as deep reefs, especially those in the upper mesophotic zone, have been shown to serve as refuges for shallow coral communities (Bongaerts et al. 2010; Oppen et al. 2011). Furthermore, the majority of coral species and associated biota that occupy shallow reefs also occupy lower depths into the mesophotoic and deep coral reef range (Bridge et al. 2013).

Based on the available literature, shallow reefs face a greater extinction risk than deep reefs making them an obvious conservation priority (Bride et al. 2013; Bak et al. 2005; Porter el al. 1982). Significant declines in coral cover have been documented across the globe, and management plans for coral reef protection should reflect this finding (Jackson 2010). Coral reefs support some of the highest biodiversity of any ecosystem in the world, and corals provide a critical framework for other organisms in the ecosystem (Bruno and Selig 2007). In terms of human benefit, coral reefs serve as natural breakwaters to protect costal land, attract a great deal of tourism, which supports numerous economies, provide food and medicines, and provide important ecosystem services (Baker et al. 2008; Jackson 2010). Coral reefs have experienced significant degradation in recent years and require urgent protection—in China alone, eighty percent of coral cover has been lost over the past thirty years as a result of overfishing and shoreline destruction (Bridge et al. 2013). The effects of climate change are accumulating at faster rates than previously expected, and the majority of coral reef ecosystems are threatened (Jackson 2010). While we often prioritize shallow reef conservation, it is important to conserve both shallow reefs and deep reefs to preserve the biodiversity of the coral reef ecosystem as a whole.

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