Ecological limitations to the resilience of coral reefs

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Abstract

The decline of coral reefs has been broadly attributed to human stressors being too strong and pervasive, whereas biological processes that may render coral reefs fragile have been sparsely considered. Here we review several ecological facets that can limit the ability of coral reefs to withstand disturbance. These include: *i*) many species lack the adaptive capacity to cope with the unprecedented disturbances they currently face; *ii*) human disturbances impact vulnerable life history stages, reducing reproductive output and the supply of recruits essential for recovery; *iii*) reefs can be vulnerable to the loss of few species, as niche specialization or temporal and spatial segregation makes each species unique (i.e., narrow ecological redundancy); in addition, many foundation species have similar sensitivity to disturbances suggesting that entire functions can be lost to single disturbances; *iv*) finally, feedback loops and extinction vortices may stabilize degraded states, or accelerate collapses even if stressors are removed. This review suggests that the degradation of coral reefs is due not only to the severity of human stressors but also the "fragility" of coral reefs. As such, appropriate governance is essential that aims to manage stressors while being inclusive of ecological process and human uses across trans-national scales. This is a considerable but necessary upgrade in current management if the integrity, and delivery of goods and services, of coral reefs is to be preserved.

Introduction

Coral reefs constitute one of the most diverse, socioeconomically important and threatened ecosystems in the world (Wilkinson 2002; Bellwood et al. 2004; Burke et al. 2011). Coral reefs harbor thousands of species (Reaka-Kudla 1997; Fisher et al. 2015) and provide food and livelihoods for millions of people, while safeguarding coastal populations from extreme weather disturbances (Wilkinson 2002; Adger et al. 2005; Burke et al. 2011). Unfortunately, the world's coral reefs are rapidly degrading (Wilkinson 2002; Bellwood et al. 2004; Burke et al. 2011), with ~19% of the total coral reef area effectively lost (Wilkinson 2002) and 60% to 75% under direct human pressures (Wilkinson 2002; Burke et al. 2011; Mora 2015). While some coral reefs have shown the capacity to recover from major disturbances (Gilmour et al. 2013; Graham et al. 2015), the majority of reefs are displaying a general decline in live coral cover (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012), and some have moved to "non-coral" states, for example dominated by macroalgae (Hughes 1994; Mumby et al. 2006; Graham et al. 2015). The economic and ecological value of coral reefs makes understanding the causes of their decline imperative.

The decline of coral reefs has been broadly attributed to threats emerging from climate change and widespread human expansion in coastal areas, which has facilitated exploitation of local resources, assisted colonization by invasive species, and led to the loss and degradation of habitats through fishing and runoff from agriculture and sewage systems (Wilkinson 2002; Gardner et al. 2003; Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007; Norström et al. 2009; Dudgeon et al. 2010; Burke et al. 2011; De'ath et al. 2012; Erftemeijer et al. 2012; Graham et al. 2015). While the magnitude of human stressors is an obvious and commonly cited reason for the decline of coral reefs, this could be compounded by the less commonly and sparsely considered limits of ecological resilience in coral reefs. Here we undertake a review of these factors. This review makes clear that the decline of coral reefs is likely a mixture of having not only strong and spatially pervasive stressors, but having ecosystems that are "fragile".

Limited adaptability

It is possible that the relative historical stability of tropical environments inhabited by coral reefs has led to organisms and ecosystems poorly adapted to environmental change (McClanahan et al. 2002). Consequently, contemporary human activities that change the intensity and spatial coverage of certain environmental variables (e.g., warming, acidification, etc), and/or introduce novel stressors (e.g. new species, fishing, pesticides, cyanide, heavy metals) can have profound impacts on coral reefs. Indeed physiological studies have revealed that many coral species have tolerances to temperature and pH very close to ambient temperature and pH (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg and Bruno 2010), although considerable variation exists among species and geographic locations in bleaching susceptibility (Pandolfi et al. 2011; Palumbi et al. 2014). Another well-known example of low resistance to human pressures is that of mega-fauna extinction due to exploitation [e.g., dugongs, sharks, etc, (Jackson 1997; Jackson et al. 2001; Pandolfi et al. 2003; Ward-Paige et al. 2010)]. These species typically experience limited natural mortality and thus have evolved life histories of slow growth and late sexual maturity, that make them highly vulnerable and prone to extinction due to even mild levels of human exploitation (Jackson 1997; Jackson et al. 2001; Pandolfi et al. 2003; Ward-Paige et al. 2010).

Many species on coral reefs appear to lack adaptations to withstand recent extreme and unprecedented stressors. Available data for vertebrate species suggest that rates of adaptation to cope with projected climate change over the next 100 years would need to be >10 000 times faster than rates typically observed (Quintero and Wiens 2013), although some evidence suggests that acclimatization and adaptation to thermal stress (Palumbi et al. 2014), and ocean acidification (McCulloch et al. 2012) can occur fairly quickly in some species of corals and reef fishes (Donelson et al. 2012; Miller et al. 2012). The capacity for acclimation and adaptation among species is currently poorly known, because much of this research is in its infancy and restricted to a handful of species. However, the observed declines of coral reefs so far indicates that coral reefs have and will modify their compositions and functioning based on the survivors to modern threats (Pandolfi et al. 2011; Graham et al. 2014).

Impaired meta-populations

Most species on coral reefs, including fishes and invertebrates, have a bi-partite life cycle, which includes a dispersive pelagic larval stage and a highly sedentary, benthic adult phase. These life history characteristics mean that the persistence, and hence functional roles, of most species on coral reefs inherently depend on meta-population dynamics (i.e., patches of habitats occupied by adults that are connected by larval dispersal). Unfortunately, coral reef meta-populations are highly vulnerable to human stressors.

Meta-population connectivity

Connectivity is an integral part of resilience in the face of chronic or stochastic disturbances, because it can maintain functions over broader scales and act as a store for replenishment, genetic supply, and adaptability potential (Nyström and Folke 2001; Nyström et al. 2008; Halford and Caley 2009). The interaction among human stressors on coral reefs can pose several double jeopardies to the dispersal and replenishment of reef fish population. For instance, habitat loss can increase isolation among reef patches, whereas warming can accelerate larval development and settlement (Bergenius et al. 2005; Levin 2006); as a result, larvae will have larger distances to travel but shorter times to do so (Munday et al. 2009; Hoegh-Guldberg and Bruno 2010; Mora and Sale 2011; Figueiredo et al. 2014). Likewise, chronic local human stressors (e.g., fishing, pollution) could shift the structure of local assemblages towards long-distance dispersers (given high mortality of self-recruiting species: Bellwood et al. 2004) and this could also be detrimental to recruitment because long-distance dispersers may face poor growing conditions (Swearer et al. 1999) and thus may face higher mortality upon recruitment (Bergenius et al. 2002). Pollutants can also prevent larvae from detecting settlement cues (Markey et al. 2007; Wenger et al. 2015) and can act as a barrier to larval recruitment (Richmond 1993).

Meta-population patches

Local adult populations in meta-population patches are fundamental to the supply of the propagules necessary for recovery, but are the prime direct and indirect targets of human activities. Coastal pollution (e.g. oil, heavy metals, pesticides), for instance, can interfere with chemical signals in corals leading to impaired reproductive synchrony among coral colonies (Peters et al. 1997) , possibly resulting in an Alleé effect despite a high density of colonies. Likewise, fishing directly removes individuals from local populations (Roberts 1995) preventing fish of reaching larger sizes and of producing more eggs [eggs are produced in proportion to a fish’s volume, which is proportional to the cube of its length (Lubchenco et al. 2003; Palumbi 2004)]. Eggs from larger or older mothers can also be of better quality and thus have higher chances of survival (Lubchenco et al. 2003; Palumbi 2004). Experimental studies have also demonstrated that intense fishing can reduce fish body size (Conover and Munch 2002) and lead to mal-adaptative strategies such as producing smaller and fewer eggs (Conover and Munch 2002; Walsh et al. 2006; Conover et al. 2009). Likewise, the ongoing loss (Gardner et al. 2003; Bruno and Selig 2007) and homogenization of coral reefs (Pratchett et al. 2008; Alvarez-Filip et al. 2009; Rogers et al. 2014) can lead to the intensification of ecological interactions, such as predation and competition, and thus a reduction of local populations and reproductive output (Pratchett et al. 2008; Forrester and Steele 2013; Rogers et al. 2014). This can occur for at least two reasons: 1) as reefs become architecturally simpler they provide fewer refuges from predation (Pratchett et al. 2008; Forrester and Steele 2013) and 2) because simpler reefs increase encounters among competitors thus increasing their exposure to predators (Hixon and Beets 1993; Hixon and Carr 1997; Pratchett et al. 2008). The diminishing complexity and supply of refuges in the context of ecological interactions suggests that reef populations will experience density-dependent mortality, even as populations get smaller (Hixon and Beets 1993; Hixon and Carr 1997; Loreau 2004; Forrester and Steele 2013).

Limited insurance in diverse systems

In diverse ecosystems numerous species are expected to have similar functional roles (so-called redundancy), different tolerances to one (so-called response diversity) or several (so-called co-tolerance) disturbances, such that the functional role of a lost species can be replaced by those that endure the disturbance (Nyström 2006; Nash et al. 2014). However, evidence for coral reefs often contrasts to those expected responses.

Limited functional redundancy

It is intuitive to imagine that in a large pool of species there will be numerous species with similar ecological functions (Bellwood et al. 2004). In coral reefs, the idea of functional redundancy is supported by the fact that the number of functional groups saturates as the number of species increases; in other words, there are many more species than functional groups indicating that multiple species play similar functional roles: they are redundant (Halpern and Floeter 2008; Mora et al. 2011). However, a saturating relationship between richness and functional diversity is not fully indicative of functional redundancy, as it fails to indicate the frequency of species within functional groups. For instance, exploration of the frequency distribution of species within functional groups has revealed strong right-skewed frequencies, with few functional groups having lots of species or large abundances, and most functional groups having a handful and at times single species or few individuals (Bellwood et al. 2004; Mouillot et al. 2013; Stuart-Smith et al. 2013). In the Caribbean, for instance, much of the historical rugosity of coral reefs was provided by *Acropora cervicornis* and *A. palmata* (Pandolfi and Jackson 2006), which have almost completely disappeared due to considerable damage by extreme hurricanes and disease outbreaks (Nyström et al. 2000). Likewise, the functional role of bioerosion on Indo-Pacific reefs is largely due to the giant humphead parrotfish (*Bolbometopon muricatum*), which is highly vulnerable to fishing due to its large size and life history (Bellwood et al. 2003).

The idea that diverse coral reefs have large redundancy of functional groups may also be ill-conceived, because of the gross classifications of functional groups. For instance, deeper exploration of morphological (Price et al. 2011) and dietary (Burkepile and Hay 2008) characteristics of species generally classified as herbivorous have revealed the existence of considerable differences among species. Such differences may result from niche specialization, and have non-trivial effects on resilience. For instance, variations in the palatability of algae (Littler et al. 1983) suggests that a broad portfolio of “herbivores” is required to keep algae in check [i.e. functional complementarity within a functional group, (Burkepile and Hay 2008; Rasher et al. 2013)] and that resilience could be highly dependent on a few species that specialize in the consumption of unpalatable algae (e.g., Bellwood et al. 2006a; Johansson et al. 2013). This suggests that it is not the total diversity that matters for resilience, but how diversity is apportioned across different functional groups.

Ecological redundancy can also be overestimated by the strong focus on single traits/characteristics (e.g., feeding behavior). When species within given functional groups are considered in the context of their home range, preferred feeding times and substrate, bite rates, reproductive rates, etc, the notion that species are redundant comes down significantly (Peterson et al. 1998; Isbell et al. 2011). Some species, for instance, can be classified as generalists based in their diet but be very specialized based on their foraging grounds (Brandl et al. 2015); the loss of such species may have critical effects on feeding functions in certain areas of the reefs. There is also evidence to show that even rare reef fish species often lack functional analogs, yet perform some key functions in ecosystems (Mouillot et al. 2013). Clearly, redundancy may not be as extensive in coral reefs as one would expect from their high diversity (Micheli and Halpern 2005; Stuart-Smith et al. 2013), suggesting that entire functions, and by default, ecosystem functioning, can be vulnerable to the loss of a handful of species (see also Jain et al. 2014). Functional redundancy has also been questioned because this could drive species to extinction mediated by competition (Loreau 2004).

If ecological specialization is pervasive in coral reefs, it will imply that the ecological roles of many species can be unique to the functioning of coral reefs and that ecosystem functioning should increase exponentially with the addition of new species because resource use optimization rather than loss due to competitive interactions is likely to prevail (Mora et al. 2014). Indeed, Mora et al. (2011) found that standing biomass (used as proxy of functioning) increased exponentially with the addition of new species, indicating the unique contributions of species to ecosystem functioning. They also found that given similar levels of disturbance, standing biomass was significantly more reduced in more diverse ecosystems, further highlighting the lack of redundancy and high vulnerability of diverse coral reef ecosystems. There are multiple pieces of evidence to suggest that many species in coral reefs play unique roles to the functioning of coral reefs (Bellwood et al. 2006a; Brandl and Bellwood 2014); even species that are rare can hold unique roles (Mouillot et al. 2013), and seemly “unimportant” species can become critically important under specific conditions (Bellwood et al. 2006a). The large spatial variations in species richness across geographical regions suggest that levels of ecological redundancy can vary greatly among places, which may help to explain observed spatial variations in the resilience of coral reefs to similar human stressors (Bellwood et al. 2004; Roff and Mumby 2012).

Our argument above is that the specialization that has been commonly argued to allow for the coexistence of many species in coral reefs (Sale 1977; Sale 1980; Wainwright and Bellwood 2002) can lead to reductions in functional redundancy. It should be acknowledged, however, that specialized morphological adaptations in other diverse ecosystems have not necessarily resulted in specialized habits [the so-called Liem’s paradox (Liem 1980)]. The flexibility to exploit resources beyond those to which species have specialized adaptations is possible if the specialized phenotype is still efficient in processing other resources, especially when preferred resources are low. In coral reef fishes, there is broad evidence of niche partitioning along food (Robertson et al. 1979; Robertson and Gaines 1986) and habitat (Robertson and Gaines 1986; Brandl and Bellwood 2014) resources, as well as considerable declines in abundance when specific habitat (Munday 2004; Pratchett et al. 2012) and food items (Pratchett et al. 2008) have declined, suggesting that specialization does exists among some reef fishes. However, there is also evidence that specialized phenotypes do not necessarily have specialized diets, supporting Liem’s paradox (Bellwood et al. 2006b). Further studies showed, however, that while species with specialized morphological adaptions may have generalized diets, they may have subtle partitioning of feeding microhabitats cautioning the use of morphological adaptions to assess specialization (Brandl et al. 2015). This is not to say that there are not ecological roles that can be played by many species but that the functioning of coral reefs is vulnerable to the loss of few species with specialized functions (Brandl and Bellwood 2014).

Limited response diversity and negative co-tolerance

Inherent in the idea that biodiversity confers resilience is that similar functional species will have differential sensitivity to stressors to ensure ecosystem recovery by the more resistant species within a given functional group (Elmqvist et al. 2003). However, high diversity may offer limited resilience if all species within a functional group respond equally to the same stressor, which may be common on coral reefs (Nyström et al. 2000; Bellwood et al. 2004; Nyström et al. 2008). Fishing, for instance, can impose a similar detrimental impact over many species of larger predators and large herbivores on coral reefs (Roberts 1995; Nyström et al. 2000; Bellwood et al. 2004; Micheli and Halpern 2005; Mora 2008; Mora et al. 2011). Similarly, branching and plating corals [e.g., Caribbean acropoids, (Nyström et al. 2000)], which provide most of the complexity of coral reefs, show comparable sensitivity to extreme hurricanes, warming and disease outbreaks (Nyström et al. 2000; Darling et al. 2013; Rogers et al. 2014).

Resilience to co-occurring stressors should be maximized by biodiversity if adaptation to one stressor increases resistance to, or the number of species expected to survive, other stressors (i.e., positive co-tolerance) (Vinebrooke et al. 2004). For coral reefs, Darling et al. (2013) found limited evidence of positive co-tolerance. Fishing and bleaching events have filtered (i.e., selected against) different sets of coral species, although some species were equally susceptible to both stressors, leading to reefs dominated by few coral species ("survivors") that are stress-tolerant (i.e., typically slow growing massive species) or have opportunistic "weedy" life histories that allow fast colonization. For reef fishes, Graham et al. (2011) showed that while fishing often targets large fishes, warming (via its effect on habitat loss) exerts greater effects on small bodied and more coral-specialized species, resulting in the fish community being greatly reduced when both stressors co-occur. Failing to gain resilience to one stressor after facing another stressor is a considerable concern for the stability of coral reefs worldwide, given the overlapping extent and variety of human disturbances (Fig. 1).

Feedback loops and extinction vortices

Resilience in coral reefs could be further compromised by numerous ecosystem, demographic and genetic feedback loops, operating independently of local diversity, that can stabilize degraded ecosystems or even accelerate the rate of decline (i.e., extinction vortices), even if stressors are subsequently removed.

Stabilizing ecosystem feedbacks

Several ecological processes can reinforce degraded ecosystem states (Hughes et al. 2010; Nyström et al. 2012; Shephard et al. 2012; Fung et al. 2013). For instance, a considerable loss of live coral cover (e.g. following hurricanes, coral bleaching episodes, disease) opens-up space, and if conditions are right, opportunistic fast-growing algae can reach an abundance beyond the grazing capacity of the standing stock of herbivores (Williams et al. 2001; Mumby et al. 2007a). Increasing algal abundance can enhance coral mortality and prevent coral recruitment and survival (Mumby et al. 2007b), directly by reducing suitable substratum for settlement, causing shadowing, overgrowing, causing chemically driven allopathic exclusions (Nyström et al. 2012), or indirectly by enhancing microbial communities and diseases (Smith et al. 2006). Some herbivorous fish species avoid patches of high algal density (Hoey and Bellwood 2011), further aggravating the challenge of maintaining cropped macroalgae (Williams et al. 2001). A similar stabilizing mechanism has been suggested for fish communities facing intense exploitation (Shephard et al. 2012; Fung et al. 2013). That is, juveniles of large fishes can face excessive competition and predation by more abundant smaller species whose abundances are “relaxed” from competition and/or predation due to the loss of larger fishes (Fung et al. 2013). In the longer term, the loss of corals can reduce structural complexity, potentially reducing the populations of herbivores (Graham et al. 2006). Stabilizing feedback loops suggest that reversal of an ecosystem shift can be significantly impeded even after a stressor has been completely removed (Nyström et al. 2012; Shephard et al. 2012).

Extinction vortices due to demographic feedback loops

Extinction vortices can be triggered by demographic processes if low abundance results in individuals failing to find mates, leading to a reproduction shortfall as part of a process variously known as depensation, the Allee effect, and inverse density-dependence (Myers et al. 1995; Gascoigne and Lipcius 2004). For instance, in large broadcasting corals, which contribute substantially to reef structure, fertilization can drop considerably just three hours after the peak of spawning suggesting that isolated colonies may fail to mix gametes increasing the risk of recruitment failure (Oliver and Babcock 1992). Allee effects at reproduction, combined with heavy exploitation, may have been responsible for the extinction of giant clams (*Tridacna gigas*) from Fiji, Guam, New Caledonia and the Northern Marianas (Wells 1997). Deleterious effects of small population size on species also facing extensive exploitation should be more pronounced among sedentary species like *Tridacna* (Wells 1997), or species that already occur in low densities, such as sharks (Ward-Paige et al. 2010). Human impacts may also reverse naturally occurring Allee effects with detrimental effects on coral reef resilience. For instance, populations of the coral-eating crown-of-thorns starfish (*Achantaster planci*) are thought to be naturally low due to Allee effects (Dulvy et al. 2004). However, fishing of starfish predators (Dulvy et al. 2004), in combination with greater nutrient loads that greatly increase growth and survival of starfish larvae (Brodie et al. 2005), have been implicated in preventing Allee effects and may cause outbreaks of the crown-of-thorns, which in turn cause considerable reductions in live-coral cover.

Extinction vortices due to genetic loss and “maladaptations”

If populations are reduced considerably, genetic variation may be reduced, which can completely truncate (Swain et al. 2007) or significantly delay (Allendorf and Hard 2009) recovery, even if stressors are removed. This occurs because genes are lost through adaptation by means of anthropogenic selection, and can be hard if not impossible to replace (Swain et al. 2007). Reduced genetic diversity can also decrease populations’ adaptive potential to natural environmental variability, leading to higher genetic drift, or the random loss of important alleles, and cause inbreeding depression or increasing expression of recessive deleterious genes and over-dominant genes (Soulé and Mills 1998; Tanaka 1998; Amos and Balmford 2001).

If population declines are caused by selective stressors, this could lead to directional selection and “maladaptations” that impair demographic processes and potentially cause extinction in what has been defined as “evolutionary suicide” (Rankin and Lopez-Sepulcre 2005). Evidence of such “maladaptations”, or changes in life history traits induced by human stressors is diverse. For example, size-selective fishing can induce substantial declines in fish mean body size, fecundity, larval viability, and sex-ratios, which in turn detrimentally affect recruitment, yield, and biomass (Warner 2002; Walsh et al. 2006). Likewise, increasing warming has been related to reductions in body size, clutch size and accelerated early development in several marine organisms (reviewed by Hoegh-Guldberg and Bruno 2010). Although the extent to which such “maladaptations” occur in nature is largely unknown, this is likely to change as new advances in genome-wide scanning improve our understanding of the genetic responses of organisms to anthropogenic stressors.

Paving a future for coral reefs

Evidence of the decline of coral reefs worldwide is relatively well documented (Wilkinson 2002). While there are obvious stressors to coral reefs (e.g., fishing, coastal pollution, climate change, invasive species, diseases, etc.), our review shows that there are also many ecological mechanisms that considerably limit the capacity of coral reefs to cope with such stressors. Coral reefs currently face a dangerous situation by being “fragile” while dealing with stressors that are not only intense but spatially pervasive (Nyström et al. 2000). There is also evidence to suggest that the more degraded a coral reef is, the harder it is to reverse the degradation. For instance, Mumby et al (2007a) modeled how reversing coral-algae phase shifts through the restoration of herbivorous fishes would require a fourfold increase of herbivores at coral covers of ~5%, but only a two- to three-fold increase at a coral cover of ~30%.

Having ecosystems that are fragile poses a major challenge for conservation because it suggests that the intensity of disturbances have to be reduced considerably. This calls for governance initiatives that are regional in scope and integral in their assessment of stressors and ecosystem limits while balancing human uses. These strategies should better account for drivers of change (e.g. climate change, migration, fishing, trade), ecosystem processes (e.g. dispersal and connectivity), policies (e.g. fisheries management), and actors (e.g. fishers, coastal developers) and should transgress borders of individual nations. The Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI) is an example of one such attempt. The intergovernmental agreement covers six nations (i.e. Indonesia, Malaysia, the Philippines, Timor Leste, Papua New Guinea and the Solomon Islands) with a mission to govern common pool resources, and strategically coordinate marine protected areas and climate adaptation actions (Fidelman et al. 2012). Strengthening similar stewardship over larger scales will be necessary for coral reefs to maintain their integrity and to continue delivering the many goods and services we obtain from them.

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Fig. 1. Modification of coral reefs. Coral reefs are typified by high biological diversity and habitat complexity, largely provided by reef building corals (A). However, due to a plethora of anthropogenic stressors, such as fishing (B), climate change (C), nutrient and sediment inputs (D), and introduced species (E), many reefs around the world are in decline, and some have shifted to a new ecosystem state, such as one dominated by macroalgae (F). These shifts can become permanent due to several stabilizing feedback loops and even accelerate to more degraded systems by extinctions vortices. Photo credits: A and F - Nick Graham, E - Emily Darling, B and C – Wiki-commons, D - MODIS-Aqua satellite image, NASA OceanColor website.