

Ecological limitations to the resilience of coral reefs

Camilo Mora¹ · Nicholas A. J. Graham^{2,3} · Magnus Nyström⁴

Received: 22 June 2015 / Accepted: 27 June 2016 / Published online: 7 July 2016
© Springer-Verlag Berlin Heidelberg 2016

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 factors that can limit the ability of coral reefs to withstand disturbance. These include: (1) Many species lack the adaptive capacity to cope with the unprecedented disturbances they currently face; (2) human disturbances impact vulnerable life history stages, reducing reproductive output and the supply of recruits essential for recovery; (3) 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; and (4) 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 to not only the severity of human stressors but also the “fragility” of coral reefs. As such, appropriate

governance is essential to manage stressors while being inclusive of ecological process and human uses across transnational 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.

Keywords Diversity · Ecosystem function · Biodiversity loss · Conservation · Stability · Coral reef ecology

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 60–75% 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 or, at times, bivalves, sponges, tunicates, zoanths, or octocorals (Hughes 1994; Wilkinson 2002; Mumby et al. 2006; Bruno et al. 2009; Dudgeon et al. 2010; Graham

Communicated by Ecology Editor Dr. Stuart Sandin

✉ Camilo Mora
cmora@hawaii.edu

¹ Department of Geography, University of Hawaii, Honolulu, HI 96822, USA

² ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

³ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

⁴ Stockholm Resilience Centre, Stockholm University, 114 19 Stockholm, Sweden

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). These disturbances vary from global (e.g., warming, acidification) to local but occurring over vast geographical areas (e.g., fishing, pollution) (Knowlton 2001; Mora 2008; Mora et al. 2011), vary in their effects from antagonistic to additive to synergistic (Knowlton 2001; Darling and Côté 2008; Darling et al. 2010), from having direct to indirect effects over species (Hughes et al. 2003; Bellwood et al. 2004; Côté and Darling 2010), and some can be chronic and slow, but may interact with pulse and fast disturbances increasing susceptibility to community shifts (Nyström et al. 2000).

The magnitude of human stressors is an obvious and commonly cited reason for the decline of coral reefs. This decline, however, 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 and show that coral reefs have several ecological “weaknesses” to disturbances. The reduced ecological resilience of coral reefs combined with the severe and widespread distribution of stressors imposed by human activities raises considerable concerns for the long-term viability of coral reefs and the goods and services they provide while highlighting the urgent need for effective governance. Although at times we have drawn ecological knowledge from other marine ecosystems, our review is not intended to provide a contrast of the resilience of coral reefs to other ecosystems.

Limited adaptability

It is possible that the relative historical stability of tropical environments inhabited by coral reefs has led 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) 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; 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 yr 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 indicate that coral reefs have and will modify their compositions and functioning based on the survivors of modern threats (Pandolfi et al. 2011; Graham et al. 2014).

Impaired meta-populations

Most species on coral reefs, including fishes and invertebrates, have a bipartite life cycle, with 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 depends 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 (Bergenijs 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 toward long-distance dispersers (given high mortality of self-recruiting species: Bellwood et al. 2004). 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 (Bergenijs 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 Allee 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 maladaptive 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 in 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 (“redundancy”), different tolerances to one (“response diversity”) or several (“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). On 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 played by the giant humphead parrotfish (*Bolbometopon muricatum*), which is highly

vulnerable to fishing due to its large size and life history (Bellwood et al. 2003). Even rare species have been known to lack functional analogs for performing key functions in coral reef ecosystems (Mouillot et al. 2013).

The idea that diverse coral reefs have large redundancy within 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) suggest that a broad portfolio of “herbivores” are 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.

The assumption that coral reefs have high ecological redundancy can also be misleading by the strong focus on single traits/characteristics. For example, a diverse assemblage characterized solely on the feeding behaviors of the constituent species may give a sense of high ecological redundancy because many species are likely to be part of the same feeding groups. However, when species are further considered in the context of their home range, preferred feeding times and substrate, bite rates, and reproductive rates, the notion of high species redundancy is reduced (Peterson et al. 1998; Isbell et al. 2011). Petchey and Gaston (2007) demonstrated that the levels of functional redundancy decrease if many functional dimensions are used, and increases if fewer dimensions are used. Likewise, some species classified as generalists based on their diet can be very specialized with regard to foraging grounds (Brandl et al. 2015); the loss of such species may have critical effects on feeding functions in certain areas of reefs. 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 in ecological systems has also been questioned from a theoretical perspective because this should drive species to extinction mediated by competition (Loreau 2004); in other words, functional redundancy implies that species share many similar habits, which can trigger competition and a reduction in species fitness.

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 reduced in more diverse ecosystems, further highlighting the lack of redundancy and high vulnerability of diverse coral reef ecosystems. 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, 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 a 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 exist 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 adaptations may have generalized diets, they may have subtle partitioning of feeding microhabitats cautioning the use of morphological adaptations 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 acroporids; 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 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 broadcast-casting corals, which contribute substantially to reef structure, fertilization can drop considerably just 3 h 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

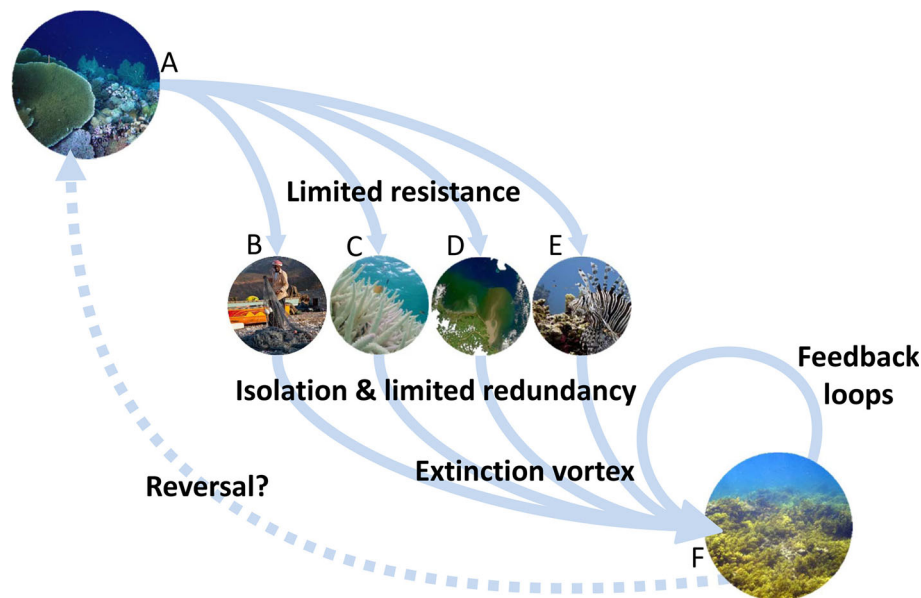


Fig. 1 General process of coral reef modification. Coral reefs are typified by high biological diversity and habitat complexity, largely provided by reef building corals (A). However, due to a plethora of anthropogenic stressors, such as fishing (B), climate change (C), nutrient and sediment inputs (D), and introduced species (E), many reefs around the world are in decline, and some have shifted to a new

ecosystem state, such as the 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. Photograph credits: A and F, Nick Graham; E, Emily Darling; B and C, Wikimedia Commons; D, MODIS Aqua satellite image, NASA OceanColor Web site (oceancolor.gsfc.nasa.gov/)

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 (*Acanthaster 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), has 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 overdominant 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 (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; Gardner et al. 2003; Bellwood et al. 2004; Bruno and Selig 2007;

Paddack et al. 2009). While there are obvious stressors to coral reefs (e.g., fishing, coastal pollution, climate change, invasive species, diseases), 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 in herbivores at coral cover of ~5%, but only a twofold to threefold 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 has 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 (Indonesia, Malaysia, the Philippines, Timor Leste, Papua New Guinea, and the Solomon Islands) with a mission to govern common 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.

References

- Adger WN, Hughes TP, Folke C, Carpenter SR, Rockström J (2005) Social-ecological resilience to coastal disasters. *Science* 309:1036–1039
- Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc Natl Acad Sci U S A* 106:9987–9994
- Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc Lond B Biol Sci* 276:3019–3025
- Amos W, Balmford A (2001) When does conservation genetics matter? *Heredity* 87:257–265
- Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol Lett* 6:281–285
- Bellwood DR, Hughes TP, Hoey AS (2006a) Sleeping functional group drives coral-reef recovery. *Curr Biol* 16:2434–2439
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2006b) Functional versatility supports coral reef biodiversity. *Proc R Soc Lond B Biol Sci* 273:101–107
- Bergenius MAJ, Meekan MG, Robertson DR, McCormick MI (2002) Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* 131:521–525
- Bergenius MAJ, McCormick MI, Meekan MG, Robertson DR (2005) Environmental influences on larval duration, growth and magnitude of settlement of a coral reef fish. *Mar Biol* 147:291–300
- Brandl SJ, Bellwood DR (2014) Individual-based analyses reveal limited functional overlap in a coral reef fish community. *J Anim Ecol* 83:661–670
- Brandl SJ, Robbins WD, Bellwood DR (2015) Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. *Proc R Soc Lond B Biol Sci* 282:20151147
- Brodie J, Fabricius K, De'ath G, Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Mar Pollut Bull* 51:266–278
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2:e711
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484
- Burke L, Reynter K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, D.C.
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc Natl Acad Sci U S A* 105:16201–16206
- Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96
- Conover DO, Munch SB, Arnott SA (2009) Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proc R Soc Lond B Biol Sci* 276:2015–2020
- Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. *PLoS Biol* 8:e1000438
- Darling ES, Côté IM (2008) Quantifying the evidence for ecological synergies. *Ecol Lett* 11:1278–1286
- Darling ES, McClanahan TR, Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conserv Lett* 3:122–130
- Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. *Glob Chang Biol* 19:1930–1940
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci U S A* 109:17995–17999
- Donelson JM, Munday PL, McCormick MI, Pitcher CR (2012) Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat Clim Chang* 2:30–32
- Dudgeon SR, Aronson RB, Bruno JF, Precht WF (2010) Phase shifts and stable states on coral reefs. *Mar Ecol Prog Ser* 413:201–216
- Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol Lett* 7:410–416

- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–494
- Erftemeijer PLA, Rieglc B, Hoeksemad BW, Todde PA (2012) Environmental impacts of dredging and other sediment disturbances on corals: a review. *Mar Pollut Bull* 64:1737–1765
- Fidelman P, Evans L, Fabinyi M, Foale S, Cinner J, Rosen F (2012) Governing large-scale marine commons: contextual challenges in the Coral Triangle. *Mar Policy* 36:42–53
- Figueiredo J, Baird AH, Harii S, Connolly SR (2014) Increased local retention of reef coral larvae as a result of ocean warming. *Nat Clim Chang* 4:498–502
- Fisher R, O’Leary Rebecca A, Low-Choy S, Mengersen K, Knowlton N, Brainard RE, Caley MJ (2015) Species richness on coral reefs and the pursuit of convergent global estimates. *Curr Biol* 25:500–505
- Forrester GE, Steele MA (2013) Reef fishes: density dependence and equilibrium in populations? In: Röhde K (ed) *The balance of nature and human impact*. Cambridge University Press, Cambridge, pp 7–20
- Fung T, Farnsworth KD, Shephard S, Reid DG, Rossberg AG (2013) Why the size structure of marine communities can require decades to recover from fishing. *Mar Ecol Prog Ser* 484:155–171
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. *Mar Ecol Prog Ser* 269:49–59
- Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69–71
- Graham NA, Cinner JE, Norström AV, Nyström M (2014) Coral reefs as novel ecosystems: embracing new futures. *Curr Opin Environ Sustain* 7:9–14
- Graham N, Jennings S, MacNeil M, Mouillot D, Wilson S (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci U S A* 103:8425–8429
- Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, Aaron MacNeil M, McClanahan TR, Öhman MC, Polunin NVC, Wilson SK (2011) Extinction vulnerability of coral reef fishes. *Ecol Lett* 14:341–348
- Halford AR, Caley MJ (2009) Towards an understanding of resilience in isolated coral reefs. *Glob Chang Biol* 15:3031–3045
- Halpern BS, Floeter SR (2008) Functional diversity responses to changing species richness in reef fish communities. *Mar Ecol Prog Ser* 364:147–156
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63:77–101
- Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world’s marine ecosystems. *Science* 328:1523–1528
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzilios ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecol Lett* 14:267–273
- Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. *Science* 265:1547–1551
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol* 25:633–642
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16:S23–S32
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jain M, Flynn DF, Prager CM, Hart GM, DeVan CM, Ahrestani FS, Palmer MI, Bunker DE, Knops JM, Jouseau CF (2014) The importance of rare species: a trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecol Evol* 4:104–112
- Johansson C, van de Leemput I, Depczynski M, Hoey A, Bellwood D (2013) Key herbivores reveal limited functional redundancy on inshore coral reefs. *Coral Reefs* 32:963–972
- Knowlton N (2001) The future of coral reefs. *Proc Natl Acad Sci U S A* 98:5419–5425
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282–297
- Liem KF (1980) Adaptive significance of intraspecific and interspecific differences in the feeding repertoires of cichlid fishes. *Amer Zool* 20:295–314
- Littler MM, Taylor PR, Littler DS (1983) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111–118
- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol Appl* 13:3–7
- Markey KL, Baird AH, Humphrey C, Negri AP (2007) Insecticides and a fungicide affect multiple coral life stages. *Mar Ecol Prog Ser* 330:127–137
- McClanahan TR, Polunin NV, Done TJ (2002) Ecological states and the resilience of coral reefs. *Conservation Ecology* 6:18
- McCulloch M, Falter J, Trotter J, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. *Nat Clim Chang* 2:623–627
- Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. *Ecol Lett* 8:391–400
- Miller GM, Watson S-A, Donelson JM, McCormick MI, Munday PL (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nat Clim Chang* 2:858–861
- Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proc R Soc Lond B Biol Sci* 275:767–773
- Mora C (2015) Perpetual struggle for conservation in a crowded world and the needed paradigm shift for easing ultimate burdens. In: Mora C (ed) *Ecology of fishes on coral reefs*. Cambridge University Press, Cambridge, pp 289–296
- Mora C, Sale P (2011) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Mar Ecol Prog Ser* 434:251–266
- Mora C, Danovaro R, Loreau M (2014) Alternative hypotheses to explain why biodiversity–ecosystem functioning relationships

- are concave-up in some natural ecosystems but concave-down in manipulative experiments. *Sci Rep* 4:5427
- Mora C, Aburto-Oropeza O, Ayala Bocos A, Ayotte PM, Banks S, Bauman AG, Beger M, Bessudo S, Booth DJ, Brokovich E, Brooks A, Chabanet P, Cinner JE, Cortés J, Cruz-Motta JJ, Cupul Magaña A, DeMartini EE, Edgar GJ, Feary DA, Ferse SCA, Friedlander AM, Gaston KJ, Gough C, Graham NAJ, Green A, Guzman H, Hardt M, Kulbicki M, Letourneur Y, López Pérez A, Loreau M, Loya Y, Martínez C, Mascareñas-Osorio I, Morove T, Nadon M-O, Nakamura Y, Paredes G, Polunin NVC, Pratchett MS, Reyes Bonilla H, Rivera F, Sala E, Sandin SA, Soler G, Stuart-Smith R, Tessier E, Tittensor DP, Tupper M, Usseglio P, Vigliola L, Wantiez L, Williams I, Wilson SK, Zapata FA (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol* 9:e1000606
- Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol* 11:e1001569
- Mumby PJ, Hastings A, Edwards HJ (2007a) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101
- Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007b) Trophic cascade facilitates coral recruitment in a marine reserve. *Proc Natl Acad Sci U S A* 104:8362–8367
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Glob Chang Biol* 10:1642–1647
- Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. *Coral Reefs* 28:379–395
- Myers RA, Barrowman NJ, Hutchings JA, Rosenberg AA (1995) Population dynamics of exploited fish stocks at low population levels. *Science* 269:1106–1108
- Nash K, Allen C, Angeler D, Barichievy C, Eason T, Garmestani A, Graham N, Granholm D, Knutson M, Nelson R, Nyström M, Stow C, Sundstrom S (2014) Discontinuities, cross-scale patterns and the organization of ecosystems. *Ecology* 95:654–667
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Mar Ecol Prog Ser* 376:295–306
- Nyström M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* 35:30–35
- Nyström M, Folke C (2001) Spatial resilience of coral reefs. *Ecosystems* 4:406–417
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Nyström M, Graham NAJ, Lokrantz J, Norstrom AV (2008) Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs* 27:795–809
- Nyström M, Norstrom AV, Blenckner T, de la Torre-Castro M, Eklof JS, Folke C, Osterblom H, Steneck RS, Thyresson M, Troell M (2012) Confronting feedbacks of degraded marine ecosystems. *Ecosystems* 15:695–710
- Oliver J, Babcock R (1992) Aspects of the fertilization ecology of broadcast spawning corals: sperm dilution effects and in situ measurements of fertilization. *Biol Bull* 183:409–417
- Paddock MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, Forrester GE, Friedlander AM, Garcia-Sais J, Gonzalez-Sanson G, Jordan LKB, McClellan DB, Miller MW, Molloy PP, Mumby PJ, Nagelkerken I, Nemeth M, Navas-Camacho R, Pitt J, Polunin NVC, Reyes-Nivia MC, Robertson DR, Rodriguez-Ramirez A, Salas E, Smith SR, Spieler RE, Steele MA, Williams ID, Wormald CL, Watkinson AR, Côté IM (2009) Recent region-wide declines in caribbean reef fish abundance. *Curr Biol* 19:590–595
- Palumbi SR (2004) Why mothers matter. *Nature* 430:621–622
- Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. *Science* 344:895–898
- Pandolfi JM, Jackson JBC (2006) Ecological persistence interrupted in Caribbean coral reefs. *Ecol Lett* 9:818–826
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333:418–422
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Petchey O, Gaston J (2007) Functional diversity (FD), species richness and community composition. *Ecol Lett* 5:402–411
- Peters EC, Gassman NJ, Firman JC, Richmond RH, Power EA (1997) Ecotoxicology of tropical marine ecosystems. *Environ Toxicol Chem* 16:12–40
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18
- Pratchett M, Munday P, Wilson S, Graham N, Cinner J, Bellwood D (2008) Effects of climate-induced coral bleaching on coral-reef fishes, ecological and economic consequences. *Oceanogr Mar Biol Annu Rev* 46:251–296
- Pratchett MS, Coker DJ, Jones GP, Munday PL (2012) Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. *Ecol Evol* 2:2168–2180
- Price SA, Holzman R, Near TJ, Wainwright PC (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol Lett* 14:462–469
- Quintero I, Wiens JJ (2013) Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol Lett* 16:1516–1516
- Rankin DJ, Lopez-Sepulcre A (2005) Can adaptation lead to extinction? *Oikos* 111:616–619
- Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94:1347–1358
- Reaka-Kudla ML (1997) The global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) *Biodiversity II: understanding and protecting our biological resources*. Joseph Henry Press, Washington, DC, USA, pp 83–108
- Richmond RH (1993) Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Am Zool* 33:524–536
- Roberts CM (1995) Effects of fishing on the ecosystem structure of coral reefs. *Conserv Biol* 9:988–995
- Robertson DR, Gaines SD (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67:1372–1383
- Robertson DR, Polunin NV, Leighton K (1979) The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebbrasoma scopas*): their feeding strategies, and social and mating systems. *Environ Biol Fish* 4:125–170
- Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. *Trends Ecol Evol* 27:404–413

- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr Biol* 24:1000–1005
- Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *Am Nat* 111:337–359
- Sale PF (1980) The ecology of fishes on coral reefs. *Oceanogr Mar Biol Annu Rev* 18:367–421
- Shephard S, Fung T, Houle JE, Farnsworth KD, Reid DG, Rossberg AG (2012) Size-selective fishing drives species composition in the Celtic Sea. *ICES J Mar Sci* 69:223–234
- Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol Lett* 9:835–845
- Soulé ME, Mills LS (1998) No need to isolate genetics. *Science* 282:1658–1659
- Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA, Kininmonth SJ, Airoidi L (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501:539–542
- Swain DP, Sinclair AF, Hanson JM (2007) Evolutionary response to size-selective mortality in an exploited fish population. *Proc R Soc Lond B Biol Sci* 274:1015–1022
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799–802
- Tanaka Y (1998) Theoretical aspects of extinction by inbreeding depression. *Res Popul Ecol (Kyoto)* 40:279–286
- Vinebrooke RD, Cottingham KL, Norberg J, Scheffer M, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos* 104:451–457
- Wainwright PC, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, pp 33–55
- Walsh MR, Munch SB, Chiba S, Conover DO (2006) Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol Lett* 9:142–148
- Ward-Paige CA, Mora C, Lotze HK, Pattengill-Semmens C, McClean L, Arias-Castro E, Myers RA (2010) Large-scale absence of sharks on reefs in the Greater Caribbean: a footprint of human pressures. *PLoS One* 5:e0011968
- Wells S (1997) Giant clams: status, trade and mariculture, and the role of CITES in management. IUCN—the World Conservation Union, Gland, Switzerland
- Wenger AS, Fabricius KE, Jones GP, Brodie JE (2015) Effects of sedimentation, eutrophication and chemical pollution on coral reef fishes. In: Mora C (ed) *Ecology of fishes on coral reefs*. Cambridge University Press, Cambridge, pp 145–153
- Wilkinson C (2002) Status of coral reefs of the world. Australian Institute of Marine Science, Townsville, Australia
- Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Mar Ecol Prog Ser* 222:187–196