

Sale, P.F., and M.A. Hixon. 2015. Addressing the global decline in coral reefs and forthcoming impacts on fishery yields. Pages 7-18 in S.A. Bortone (ed.) *Interrelationships Between Corals and Fisheries*. CRC Press; Boca Raton, Florida.

chapter two

Addressing the global decline in coral reefs and forthcoming impacts on fishery yields

Peter F. Sale and Mark A. Hixon

Contents

| | |
|---|----|
| An immediate problem for one fifth of humanity..... | 7 |
| Decline of coral reefs..... | 8 |
| Effects of coral declines on reef fishes..... | 10 |
| Delaying coral reef decline..... | 11 |
| Adaptation to coral reef loss..... | 13 |
| References..... | 14 |

An immediate problem for one fifth of humanity

LandScan data (Bright et al. 2012) reveal that, worldwide, 1.36 billion people now live within 100 km of a tropical coastline—that is, almost one fifth of the global population live on a narrow strip that is just 7% of the available land. These people occupy 9 megacities (10 million inhabitants or larger), but also live in numerous much smaller settlements. The average population density (145 people/km²) of this strip is twice that of inland populations, with coastal populations growing more rapidly (Sale et al. in press). Most of these people live in developing countries and many depend on their immediate coastal waters for much of their animal protein food, other resources, and their livelihoods. Only the wealthy are sufficiently well connected to global markets that they do not depend directly on their local coastal waters. Coastal fisheries provide both food and livelihoods for millions of poor people along these tropical coasts (Donner and Potere 2007).

Coral reefs are one of the principal habitats of these coastal waters, and while there are many coastal fisheries over nearby seagrass beds, sand flats, and rocky hardbottom habitats, the fish taken are mostly ecologically associated closely with coral reefs (Ogden and Gladfelter 1983). Whether this close ecological connection means that fishery production is heavily dependent on the status of nearby coral reef habitat is not yet clear.

In developing countries, coastal fisheries are principally artisanal and small scale (Newton et al. 2007, Cochrane et al. 2011). Fish are caught from shore and from small boats using nets, traps, and spears, as well as by hand (some of these “fish” are shallow-water invertebrates taken from reef flats at low tide). Use of chemicals or dynamite to catch fish is generally illegal, but still widespread and chronically damaging (Fox and Caldwell 2006). Numerous families depend on these fisheries for the majority of the protein in their diets and major portions of the catch never enter a commercial market. Coastal fisheries are

generally open and only weakly regulated, and evidence of overfishing is widespread (Friedlander and DeMartini 2002, Robbins et al. 2006, DeMartini et al. 2008, Sandin et al. 2008, Stallings 2009).

Coral reefs are currently experiencing severe anthropogenic impacts of several types, and worldwide, coral reef habitat is becoming seriously degraded (Pandolfi et al. 2003, 2005, Bellwood et al. 2004, Birkeland 2004, Wilson et al. 2006). Recent data from Australia (De'ath et al. 2012), the Caribbean (Perry et al. 2013), and elsewhere (Carpenter et al. 2008, Wilkinson 2008) show substantial reductions in coral cover and in coral growth rates, and increases in the rate of reef erosion over the last couple of decades. Over the last 27 years, 50% of cover on the Great Barrier Reef has been lost (De'ath et al. 2012); loss of cover across the Caribbean is even more severe (Jackson et al. 2013). The impacts responsible include overfishing, inappropriate coastal development, pollution with nutrients, heavy metals, and other chemicals, siltation, and coral mining, all of which are essentially local in their effects. Causes also include ocean warming, sea-level rise, increased intensity of storms, and more variable precipitation leading to more extreme flooding and siltation, all of which are due to anthropogenic climate change and cannot be mitigated by local effort (Maina et al. 2011). Finally, the release of CO₂ into the atmosphere, in addition to causing climate change, is resulting in increased rates of transfer of CO₂ to ocean waters, which in turn leads to the reduction in pH termed ocean acidification (Feely et al. 2004, Sabine et al. 2004, Doney et al. 2009). Each of these impacts has effects on corals and on coral reefs that lead to reef decline (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011, Meissner et al. 2012), with likely deleterious effects on artisanal reef fisheries and the social systems they support (Munday et al. 2008, Cinner et al. 2012, 2013, Sale et al. in press).

Decline of coral reefs

Coral reefs are now declining at such a rate, and on such a geographical scale, that it is no longer possible to dismiss claims the loss will be total by 2050 (Hoegh-Guldberg et al. 2007, Sale 2008, 2011). Coral reefs, as we knew them during the 1960s, will no longer exist in 2050 unless we institute far more effective management of locally acting threats. Simultaneously, we should take real steps to reduce the global emissions of CO₂ and other greenhouse gases, because if we do not, even the best-managed coral reefs (with respect to local threats) may very well fail to survive the warming and acidification. Given that it has now been 16 years since the global epidemic of mass coral bleaching in 1997–1998, and our emissions of CO₂ continue to rise steeply while local management of coral reefs remains largely ineffective, optimism about our ability to stem the decline of coral reefs is very difficult to muster.

There are several reasons for the decline of coral reefs (Sale 2008, 2011), all related to the dependence of reef ecosystems on the survival and health of a group of ecologically delicate species, the corals themselves. The rocky structure of coral reefs with its complex topography is the result of calcification by a broad range of organisms, especially the corals (Kinsey and Davies 1979, Barnes and Chalker 1990). Erosional forces, some also biogenic, modify the accreted structure, and prevailing patterns of water flow further shape the resulting reef, so that a stable coral reef is a dynamic equilibrium between processes of growth in which new rock is created as calcified skeletons, and processes of erosion in which the rocky structure is broken down by a variety of bioeroders, by storms, by changes in sea level, and by the routine effects of wave action and currents.

Bioeroders range from minute sponges and worms to 1 m long parrotfishes, and their rasping, burrowing, and dissolving activities gradually reduce consolidated limestone

rock into sand (Glynn 1997). A single, 1 m long, green humphead parrotfish (*Bolbometopon muricatum*) can remove 5 tons of structural reef carbonates per year, almost half of it living coral (Bellwood et al. 2003). Cyclonic storms break up living coral, shift rubble and sediments, scour and abrade corals and other sessile species, and generally wear down coral reefs, while also throwing rock and sediment up onto reef flats to add to or form new islands of up to 3–4 m elevation above high tide levels. Changes in sea level, whether due to global shifts, subsidence, or elevation of underlying rock, can lift a reef above sea level resulting in rapid death, lower it modestly allowing it to flourish, or take it deeper at rates too quick for compensation by reef-building processes, causing it to be drowned. Normal wave action and currents have continual low-level erosional impacts on a reef (Glynn 1997).

The modern corals (order Scleractinia) have been present since the early Mesozoic period and are likely derived from earlier rugose corals dominant in the Paleozoic era (Veron et al. 1996). Most Scleractinia contain symbiotic single-celled dinoflagellates (zooxanthellae) within their tissues that greatly increase the capacity of the coral to calcify. Zooxanthellate Scleractinia necessarily are restricted to shallow water by the photosynthetic requirements of the algae, but some azooxanthellate forms occur in deep water where they build slow-growing reefs. We know a lot less about the ecology of deepwater reefs; this chapter deals with the shallow-water reefs built by tropical zooxanthellate corals, while recognizing that fishery species may also depend on deepwater reefs.

Zooxanthellate corals are limited to the tropics by temperature, and to clear, oceanic, low-nutrient waters. Further, because they are restricted to shallow waters, they typically occur relatively close to coastlines—coastlines that are increasingly occupied by human settlements. The present-day global decline in coral reefs began at different times in different locations as humans interacted with reefs (Bell et al. 2006). Inappropriate coastal development has caused increased siltation and pollution, changes to patterns of water flow, and physical destruction of inshore reefs. Agricultural and industrial activities well inland have contributed to coastal pollution and nutrient enrichment of coastal waters. In some places, corals are mined for building materials, lime, and the curio trade. Overfishing, or fishing using inappropriate methods, has led to some direct loss of corals and substantial trophic shifts in reef ecosystems (Hughes et al. 2007). The latter are most damaging when important grazers and bioeroders such as the larger parrotfishes (Scaridae) are harvested. Paradoxically, bioerosion by parrotfishes, which directly destroys reef structure, also creates bare rocky surfaces that favor coral settlement and growth (Bellwood et al. 2003). Removal of herbivores more generally reduces controls on algal growth and can result in a phase shift from a coral-dominated to an algae-dominated system (Hughes 1994, Mumby 2006, 2009, Hughes et al. 2007, Ledlie et al. 2007). The latter tend to be less diverse, and less productive of fishery species, although primary production may be as high as, or higher than, that of a coral-dominated system.

Given the generally weak legal structures governing activities in most coastal waters, this suite of human impacts is present to varying degrees along most tropical coasts. As human populations have grown, these impacts have intensified, contributing to a general downward spiral in reef condition. Technical solutions are available to remedy all of these local impacts on coral reefs, but, as is often the case, societal, cultural, and political factors impede their application (Bell et al. 2006, Lotze et al. 2006). How does a fishery manager reduce fishing effort, or prohibit taking of certain species, in an artisanal fishery in which a major portion of the catch never enters an open market and in a community where there are few other sources of employment? How does a government control coastal development and the release of nutrients from upstream agricultural districts, when the human

population is growing, poverty is rife, and efforts to feed and house people deplete all available resources?

In recent decades, the global effects of greenhouse gases have added to the burden on coral reefs. Rising sea surface temperatures have meant that periods of unusually warm water have become more prevalent, and since corals live close to their thermal maxima, these warm episodes have led to mass bleaching (Baker et al. 2008). When conditions causing the bleaching last for three or more weeks, extensive coral mortality can result. Ocean acidification appears to have already progressed far enough that it is measurably slowing the rates of growth of at least some coral species, thereby slowing the regenerative capacity of reefs (Pandolfi et al. 2011, Meissner et al. 2012). With increased coral mortality and slowed regeneration, any past equilibrium has shifted toward reef decline (Hoegh-Guldberg et al. 2007).

De'ath et al. (2009) recently reported the results of analysis of 328 cores from colonies of *Porites* spp. collected from 69 sites across the Great Barrier Reef. These cores showed a 14.2% decrease in rate of calcification and a 13.3% slowdown in growth (extension) rate since 1990. Both the extent and the abruptness of the changes are greater than any over the past 400 years. The authors attributed this regionwide decline to a combination of growing thermal stress and decreasing ocean pH—the capacity of corals of this genus to calcify was being measurably reduced. Tanzil et al. (2009) showed very similar results in a smaller study for corals at Phuket, Thailand. Subsequent work elsewhere has confirmed these trends while revealing important interspecific variation (Manzello 2010, Friedrich et al. 2012), and it remains unclear whether the data for individual genera of coral scale-up to a measurable decline in rate of reef accretion. In any case, the percentage cover of live coral is declining rapidly in many regions (Carpenter et al. 2008, Wilkinson 2008, De'ath et al. 2012, Jackson et al. 2013, Perry et al. 2013).

Effects of coral declines on reef fishes

Fishes are a highly diverse and vital component of the coral reef ecosystem. Some 8000 species of fish are associated with coral reefs (Bellwood et al. 2012), and reef fishes have a broad range of life histories, body sizes, and trophic roles, ranging from tiny prey to large apex predators. Energy flow upward through trophic levels including fishes ultimately supports reef fisheries that provide a major source of protein for associated human communities (Polunin and Roberts 1996). Consequently, it is highly likely that the decline of coral reefs will lead to loss of fishery productivity in tropical coastal waters (Bellwood et al. 2004, Cinner et al. 2012).

Living corals provide both food and living space for fishes, as well as settlement cues for incoming larvae (Kingsford et al. 2002, Gerlach et al. 2007, Munday et al. 2010). The food provided by corals includes not only the coral polyps themselves (supplying food for corallivores), but also a broad variety of prey that inhabit corals (supplying food for herbivores, invertivores, piscivores, and omnivores). The living space provided by the coral structure includes actual home sites (settlement, nursery, or permanent) as well as spawning/nesting sites, cleaning stations, refuges from strong currents, and especially, spatial refuges from predation (Graham and Nash 2013, Hixon 2014).

Recent major empirical reviews have demonstrated that reef fishes are closely associated with living corals. Coker et al. (2014) reported 93 species of coral inhabited by fishes, mainly branching species in the genera *Acropora* and *Porites*. They listed 39 fish families that inhabit live coral habitats, the species richness of which is dominated by smaller forms, including damselfishes (Pomacentridae), gobies (Gobiidae), wrasses (Labridae),

cardinalfishes (Apogonidae), and butterflyfishes (Chaetodontidae). Many species inhabit corals only as juveniles (Coker et al. 2014), with a trend for larger fish to be less associated with coral, likely as individuals shift from spatial prey refuges to size refuges from predation (Alvarez-Filip et al. 2011). Consequently, there is often a strong positive relationship between reef structural complexity and fish density, biomass, and species richness (Gratwicke and Speight 2005, Graham and Nash 2013), as well as between coral species richness and fish species richness (Belmaker et al. 2008, Belmaker 2009, Messmer et al. 2011), and more complex reefs support more trophic levels (Alvarez-Filip et al. 2011). A recent modeling study using an Ecopath with Ecosim model parameterized for a rich coral reef system in Indonesia predicts a direct link between loss of coral biomass and loss of the capacity to produce fishery species, such that a loss of 50% of coral would reduce fishery production capacity by 30% (Sale et al. in press).

It is not surprising, therefore, that fish abundance and perhaps species richness decline substantially as coral reefs degrade, a pattern increasingly well documented in a variety of regions, including the Pacific (Sano 2000, Booth and Beretta 2002, Jones et al. 2004, Feary et al. 2007, Holbrook et al. 2008, Wilson et al. 2010a,b), the Atlantic/Caribbean (Acosta-Gonzalez et al. 2013), the Indian Ocean (Garpe et al. 2006, Graham et al. 2006), and globally (Wilson et al. 2006, Pratchett et al. 2008, 2011). These losses may undergo time lags: dead yet structurally intact corals may initially support most fishes except live-coral specialists, but then gradually erode into rubble inhabited by relatively few species (Garpe et al. 2006, Pratchett et al. 2008). Time lags may also occur as recruitment fails, reducing replenishment of local populations (Graham et al. 2007, McCormick et al. 2010). In some cases, there may be substantial shifts in species composition and/or evenness of reef fishes despite few changes in overall fish abundance and species richness (Lindahl et al. 2001, Bellwood et al. 2006, Cheal et al. 2008). In any case, the threat of extirpation and even extinction now looms large for coral reef fishes, especially obligate corallivores (Graham et al. 2011). This threat will accelerate through a variety of mechanisms as the oceans continue to warm and acidify (Munday et al. 2008).

Delaying coral reef decline

As noted earlier, the locally acting stressors that help degrade coral reefs are all amenable to local intervention, and the technologies for intervening successfully are largely well understood (Bell et al. 2006, Lotze et al. 2006). In most cases, the primary need is simply enhanced awareness of potential problems before they arise. For example, it is relatively easy to plan coastal improvements with due recognition of existing patterns of freshwater runoff and awareness that disrupting these patterns can kill nearby reefs. Similarly, if patterns of water flow are known, it can be obvious that sediment or pollutants released into the water at particular locations will be deposited on downstream reefs, smothering or poisoning them. While straightforward conceptually, the successful application of environmental insights during major coastal development projects depends on a rigorous environmental impact assessment (EIA) process backed up by regulatory structures that are strong enough to encourage compliance instead of violation followed by the willing payment of assessed penalties. Rigorous EIA procedures and a culture of compliance with environmental regulations are not hallmarks of developing countries, and are often bypassed in the more advanced countries when political will is weak, profit margins consequent on development are high, or the value of coastal marine ecosystems is poorly appreciated by stakeholders (Wanless and Maier 2007, Lindeman et al. 2010).

Addressing chronic, and growing, coastal pollution due to agricultural and industrial activities far inland can be more difficult. The jurisdiction of agencies responsible for

the management of coastal areas seldom extends inland, and the economic value of the upland activities may be such that a collaborative approach to encourage agriculture and industry to act in the interests of a distant coastal ocean will achieve very little change in behavior. Stable political systems, and an electorate well informed on the economic value of sustainably managed coastal ecosystems, are essential if any remission of pollution is to be gained. Our difficulty in the developed world in restoring coastal dead zones, such as those at the mouth of the Mississippi River or in Chesapeake Bay, shows how difficult it is to apply common sense to the management of nutrients and pollutants on a watershed-wide scale (Diaz and Rosenberg 2008, Doney 2010).

In developing countries, the chronic overfishing of reefs, including frequent use of inappropriate methods, is a particularly vexing stressor on coral reefs (Cinner et al. 2009). These problems are due to the fact that large populations of poorly educated people adopt fishing as the employment of last resort, and because coastal fisheries, to the extent they are managed at all, are managed as open-access fisheries. The obvious solution would be a reduction in fishing effort. However, sustained social, economic, and political effort over many years would first be needed to create other employment opportunities, to encourage fishers to stop fishing, and to enforce a no-take status in networks of marine protected areas. Such sustained effort is difficult to achieve when most fishery management agencies are poorly resourced by governments that have often given up on the idea that creation of alternative employment is even possible (Bell et al. 2006, Sale et al. in press).

The development of open aquaculture in pens and on subtidal leases could generate alternative employment while subsidizing food production from traditional capture fisheries (Naylor and Burke 2005). However, too often, inadequately managed aquaculture development leads directly to new coastal pollution, degradation of coastal ecosystems such as mangroves, which are important as nursery habitat for capture fishery species, and acrimonious conflict among stakeholder groups—not a way of solving stresses due to overfishing (Goldburg and Naylor 2005).

Overriding all such efforts to mitigate local stressors is the near universal tendency for environmental (including fishery) management to be fragmented among agencies and between tiers of government, with few agencies able to build a cadre of technically well-informed staff, or a holistic view of the problems and solutions. While simple technical fixes are available for most locally acting stressors, culture, tradition, politics, and failure of leadership ensure that the solutions are seldom implemented or sustained (Bell et al. 2011, Sale et al. in press).

Globally acting stressors are becoming progressively more intense. This is due both to the environmental consequences of greenhouse gas emissions, and to the increasing pressure on coastal fisheries caused by growing worldwide demand for fishery products as communities grow and become more affluent (Halpern et al. 2008, Mora et al. 2013). These stressors cannot be addressed by local interventions alone. It might be possible to reduce demand and thereby reduce fishing effort in a community by closing opportunities for export trade, but such barriers are usually pierced by enterprising individuals willing to violate the law. However, the effects of globally acting stressors can be reduced in some cases by addressing local impacts effectively. For example, it has been shown both on the Great Barrier Reef (Wooldridge 2009) and in the Florida Keys (Wagner et al. 2010) that the extent of coral bleaching during major warming events was less severe where waters contained lower nutrient levels. By reducing the strength of locally acting stressors, it should thus become possible to “buy time” for coral reefs, enabling them to better withstand stresses such as warming. Ultimately, however, unless we act globally to reduce greenhouse gas emissions, coral reefs as we know them are going to largely disappear (Pandolfi et al. 2003, Carpenter et al. 2008).

Adaptation to coral reef loss

The decline and ultimate loss of coral reefs will not bring an end to coastal fisheries, but catches are likely to change in composition, and the capacity of reefs to produce fishery species also seems likely to fall. Indeed, the abundance of reef fish is already clearly declining, severely in some cases (Jones et al. 2004, Paddock et al. 2009, Stallings 2009). While humans will probably find ways to adapt as the situation changes, just as we have been adapting to changing yields as coral reefs are degraded, the substantial decline of fishery production capacity on a global scale will become a serious issue for food security in future decades (Garcia and Rosenberg 2010). Food insecurity, driven by growing human populations, expanding affluence, and worsening impacts of climate change on food production, is already increasing and will continue to do so. Experts differ in the degree of optimism they display. In a recent review, Wheeler and von Braun (2013) report that the positive effects on plant growth due to increased CO₂ in the atmosphere are now known to be less than had been anticipated, and that food production is going to fall most severely across the tropics as climate change advances. They quote Knox et al. (2012), who stated that yields across Africa are predicted by 2050 to change by -17% (wheat), -5% (maize), -15% (sorghum), and -10% (millet), and across South Asia by -16% (maize) and -11% (sorghum). While their emphasis is on agricultural crops, Wheeler and von Braun conclude that committed climate change requires that we begin to adapt to global food insecurity in the next 20–30 years.

Under these circumstances, any actions that can improve the likelihood of tropical coastal fisheries remaining productive should be pursued aggressively. Obviously, a far higher priority should be being given to maintaining the sustainability of present-day coastal fisheries, using recognized technical solutions: strong prohibitions on the use of inappropriate fishing methods such as dynamite and chemicals, provision of alternative livelihoods and reduction of fishing effort, strengthening and effective enforcement of regulations governing coastal pollution and habitat destruction, and the creation of networks of marine protected areas to reduce fishing effort while enhancing fishery and reef conservation. Beyond these actions, there should be continued research on the cues used by reef fishes to return to reef habitat at the end of larval life, and consideration of methods for enhancing the availability of such cues, or of preserving those cues as reefs degrade. With the right cues in place, it may become possible to enhance settlement of fishes to a site where they can be protected during the first critical weeks or months (see Almany and Webster 2006), thereby enhancing ultimate yields.

With further reef decline, the loss of living reefs could be mitigated by providing artificial reefs, built specifically to provide the habitat attributes needed by fish. How best to do this is not yet clear, but reefs should be carefully designed not simply thrown together using whatever surplus materials or vehicles happen to be at hand (Bohnsack and Sutherland 1985). It is sometimes asserted that reef fishes are drawn only to the three-dimensional physical structure of reefs, so that only physical structure is important in artificial reef design. In reality, as shown in the section on Effects of coral declines on reef fishes, the fishes that inhabit coral reefs are dependent on far more than structural shelter; the high productivities of coral reef ecosystems provide the food source for reef fishes, as well as the remainder of the entire reef food web of which fishes are one part. While relatively few fishes directly consume corals, the living reef provides the broad variety of algal and invertebrate prey that supports the productivity and diversity of reef fishes. Therefore, artificial reefs intended to mitigate coral reef loss must be designed with the benefit of detailed comparisons with living reefs (Carr and Hixon 1997), and especially with the goal of increasing local production rather than merely aggregating fish from surrounding habitats (Grossman et al. 1997).

What is called for, in fact, is the kind of ecosystem-based management of fisheries that has long been promoted, but taken to a new level where those facilities or services that degraded coral reefs can no longer deliver are provided in order to facilitate the continued production of fishery species (McClanahan et al. 2011, Aswani et al. 2012, Sale et al. in press). The good news in an otherwise bleak future is that these possible steps, available if we decide not to just “muddle through,” do not require global agreement: a local community can unilaterally decide to improve its fisheries, to sustain its reefs, or to replace lost reefs with artificial structures. The possibility of effective local action needs to be promulgated widely, in the hope that some local communities will show the wisdom that most of us, at least to now, appear to have lacked (McClanahan et al. 2008). To put this last point more bluntly, what is needed is a dramatic improvement in management performance, addressed to all locally acting stressors with the aim of sustaining or improving fishery yield; at present, most nations show little inclination to embark on this journey.

An immediate effort to improve all aspects of the management of tropical coastal waters, including management of fisheries, could be a major boost to tropical coastal ecosystems. This approach would best equip us to cope with reef degradation due to greenhouse gas emissions while we make a major global effort to reduce those emissions. Billions of people depending on tropical coastal seas will be severely affected if the largely piecemeal, unsustainable, and otherwise ineffective management of coastal waters is allowed to continue.

References

- Acosta-Gonzales G, Rodriguez-Zaragoza FA, Hernandez-Landa RC, Arias-Gonzalez JE. 2013. Additive diversity partitioning of fish in a Caribbean coral reef undergoing shift transition. *PLoS ONE*. 8(6):e65665.
- Almany GR, Webster MS. 2006. The predation gauntlet: Early post-settlement mortality in coral reef fishes. *Coral Reefs*. 25:19–22.
- Alvarez-Filip L, Gill JA, Dulvy NK. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere*. 2(10):118. Available from: <http://dx.doi.org/10.1890/ES11-00185.1> via the Internet. Accessed 1 February, 2014.
- Aswani S, Christie P, Muthiga NA, Mahon R, Primavera JH, Cramer LA, Barbier EB, Granek EF, Kennedy CJ, Wolanski E, et al. 2012. The way forward with ecosystem-based management in tropical contexts: Reconciling with existing management systems. *Mar Policy*. 36:1–10.
- Baker AC, Glynn PW, Riegl B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Shelf Sci*. 80:435–471.
- Barnes DJ, Chalker BE. 1990. Calcification and photosynthesis in reef-building corals and algae. *In*: Dubinsky Z, editor. *Coral reefs. Ecosystems of the world*. Volume 25. Amsterdam: Elsevier. p. 109–131.
- Bell JD, Johnson JE, Hobday AJ. 2011. Vulnerability of tropical Pacific fisheries and aquaculture to climate change. Noumea: Secretariat of the Pacific Community.
- Bell JD, Ratner BD, Stobutzki I, Oliver J. 2006. Addressing the coral reef crisis in developing countries. *Ocean Coast Manage*. 49:976–985.
- 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, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature*. 429:827–833.
- Bellwood DR, Hughes TP, Hoey AS. 2006. Sleeping functional group drives coral-reef recovery. *Curr Biol*. 16:2434–2439.
- Bellwood DR, Renema W, Rosen BR. 2012. Biodiversity hotspots, evolution and coral reef biogeography: A review. *In*: Gower D, Johnson KG, Richardson J, Rosen BR, Williams ST, Rüber L, editors. *Biotic evolution and environmental change in southeast Asia*. London: Cambridge University Press. p. 216–245.

- Belmaker J. 2009. Species richness of resident and transient coral-dwelling fish responds differentially to regional diversity. *Glob Ecol Biogeogr.* 18:426–436.
- Belmaker J, Ziv Y, Shashar N, Connolly SR. 2008. Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. *Ecology.* 89:2829–2840.
- Birkeland C. 2004. Ratcheting down the coral reefs. *BioScience.* 54:1021–1027.
- Bohnsack JA, Sutherland DL. 1985. Artificial reef research: A review with recommendations for future priorities. *Bull Mar Sci.* 37:11–39.
- Booth DJ, Beretta GA. 2002. Changes in a fish assemblage after a coral bleaching event. *Mar Ecol Prog Ser.* 245:205–212.
- Bright EA, Coleman PR, Rose AN, Urban ML; LandScan 2011 [Internet]. Oak Ridge, TN: Oak Ridge National Laboratory; 2012. Available from: <http://www.ornl.gov/landscan/> via the Internet. Accessed 1 February, 2014.
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science.* 321:560–563.
- Carr MH, Hixon MA. 1997. Artificial reefs: The importance of comparisons with natural reefs. *Fisheries.* 22(4):28–33.
- Cheal AJ, Wilson SK, Emslie MJ, Dolman AM, Sweatman H. 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. *Mar Ecol Prog Ser.* 372:211–223.
- Cinner JE, Huchery C, Darling ES, Humphries AT, Graham NAJ, Hicks CC, Marshall N, McClanahan TR. 2013. Evaluating social and ecological vulnerability of coral reef fisheries to climate change. *PLoS ONE.* 8(9):e74321. Available from: <http://dx.doi.org/10.1371/journal.pone.0074321> via the Internet. Accessed 1 February, 2014.
- Cinner JE, McClanahan TR, Daw TM, Graham NAJ, Maina J, Wilson SK, Hughes TP. 2009. Linking social and ecological systems to sustain coral reef fisheries. *Curr Biol.* 19:206–212.
- Cinner JE, McClanahan TR, Graham NAJ, Daw TM, Maina J, Stead SM, Wamukota A, Brown K, Bodin O. 2012. Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Glob Environ Chang.* 22:12–20.
- Cochrane KL, Andrew NL, Parma AM. 2011. Primary fisheries management: A minimum requirement for provision of sustainable human benefits in small-scale fisheries. *Fish Fish.* 12:275–288.
- Coker DJ, Wilson SK, Pratchett MS. 2014. Importance of live coral habitat for reef fishes. *Rev Fish Biol Fisher.* 24:89–126.
- 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.
- De'ath G, Lough JM, Fabricius KE. 2009. Declining coral calcification on the Great Barrier Reef. *Science.* 323:116–119.
- DeMartini EE, Friedlander AM, Sandin SA, Sala E. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Mar Ecol Prog Ser.* 365:199–215.
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science.* 321:926–929.
- Doney SC. 2010. The growing human footprint on coastal and open-ocean biogeochemistry. *Science.* 328:1512–1516.
- Doney SC, Fabry VJ, Feely RA, Kleypas KA. 2009. Ocean acidification: The other CO₂ problem. *Ann Rev Mar Sci.* 1:169–192.
- Donner SD, Potere D. 2007. The inequity of the global threat to coral reefs. *BioScience.* 57:214–215.
- Feary DA, Almany GR, Jones GP, McCormick MI. 2007. Coral degradation and the structure of tropical reef fish communities. *Mar Ecol Prog Ser.* 333:243–248.
- Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science.* 305:362–366.
- Fox HE, Caldwell RL. 2006. Recovery from blast fishing on coral reefs: A tale of two scales. *Ecol Appl.* 16:1631–1635.
- Friedlander AM, DeMartini EE. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: The effects of fishing down apex predators. *Mar Ecol Prog Ser.* 230:253–264.

- Friedrich T, Timmerman A, Abe-Ouchi A, Bates NR, Chikamoto MO, Church MJ, Dore JE, Gledhill DK, González-Dávila M, Heinemann M, et al. 2012. Detecting regional anthropogenic trends in ocean acidification against natural variability. *Nat Clim Chang.* 2:167–171.
- García SM, Rosenberg AA. 2010. Food security and marine capture fisheries: Characteristics, trends, drivers and future perspectives. *Philos Trans Roy Soc B Biol Sci.* 365:2869–2880.
- Garpe KC, Yahya SAS, Lindahl U, Öhman MC. 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar Ecol Prog Ser.* 315:237–247.
- Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V. 2007. Smelling home can prevent dispersal of reef fish larvae. *Proc Natl Acad Sci U S A.* 104:858–863.
- Glynn PW. 1997. Bioerosion and coral reef growth: A dynamic balance. *In:* Birkeland C, editor. *Life and death of coral reefs.* New York: Chapman and Hall. p. 69–98.
- Goldburg R, Naylor R. 2005. Future seascapes, fishing, and fish farming. *Front Ecol Environ.* 3:21–28.
- Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, MacNeil MA, McClanahan TR, Öhman MC, Polunin NVC, Wilson SK, et al. 2011. Extinction vulnerability of coral reef fishes. *Ecol Lett.* 14:341–348.
- Graham NAJ, Nash KL. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs.* 32:315–326.
- 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, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv Biol.* 21:1291–1300.
- Gratwicke B, Speight MR. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol.* 66:650–667.
- Grossman GD, Jones GP, Seaman WJ. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries.* 22(4):17–23.
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, et al. 2008. A global map of human impact on marine ecosystems. *Science.* 319:948–952.
- Hixon MA. 2014. Predation: Piscivory and the ecology of coral-reef fishes. *In:* Mora C, editor. *Ecology and conservation of fishes on coral reefs: The functioning of an ecosystem in a changing world.* Cambridge, UK: Cambridge University Press.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science.* 318:1737–1742.
- Holbrook SJ, Schmitt RJ, Brooks AJ. 2008. Resistance and resilience of a coral reef fish community to changes in coral cover. *Mar Ecol Prog Ser.* 371:263–271.
- Hughes TP. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science.* 265:1547–1551.
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschanivskyj N, Pratchett MS, Steneck RS, Willis B, et al. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol.* 17:360–365.
- Jackson J, Donovan M, Cramer K, Lam V, editors. 2013. *Status and trends of Caribbean coral reefs: 1970–2012.* Washington, DC: Global Coral Reef Monitoring Network, c/o International Union for the Conservation of Nature, Global Marine and Polar Program.
- Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci U S A.* 101:8251–8253.
- Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J. 2002. Sensory environments, larval abilities and local self-recruitment. *Bull Mar Sci.* 70(1):309–340.
- Kinsey DW, Davies PJ. 1979. Carbon turnover, calcification and growth in coral reefs. *In:* Trudinger PA, Swaine DJ, editors. *Biogeochemical cycling of mineral-forming elements.* Studies in Environmental Science 3. Amsterdam: Elsevier. p. 131–162.
- Knox J, Hess T, Daccache A, Wheeler T. 2012. Climate change impacts on crop productivity in Africa and South Asia. *Environ Res Lett.* 7(3):034032. Available from: <http://dx.doi.org/10.1088/1748-9326/7/3/034032> via the Internet. Accessed 1 February, 2014.

- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs*. 26:641–653.
- Lindahl U, Ohman MC, Schelten CK. 2001. The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Mar Pollut Bull*. 42:127–131.
- Lindeman KC, Gibson HT, Yu H. 2010. Participatory climate adaptation in coastal Florida: Increasing roles for water-users and independent science. *Proc Gulf Caribb Fish Inst*. 62:7–11.
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*. 312:1806–1809.
- Maina J, McClanahan TR, Venus V, Ateweberhan M, Madin J. 2011. Global gradients of coral exposure to environmental stresses and implications for local management. *PLoS ONE*. 6(8):e23064. Available from: <http://dx.doi.org/10.1371/journal.pone.0023064> via the Internet. Accessed 1 February, 2014.
- Manzello DP. 2010. Coral growth with thermal stress and ocean acidification: Lessons from the eastern tropical Pacific. *Coral Reefs*. 29:749–758.
- McClanahan TR, Graham NAJ, MacNeil MA, Muthiga NA, Cinner JE, Bruggemann JH, Wilson SK. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc Natl Acad Sci U S A*. 108:17230–17233.
- McClanahan TR, Hicks CC, Darling ES. 2008. Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. *Ecol Appl*. 18:1516–1529.
- McCormick MI, Moore JAY, Munday PL. 2010. Influence of habitat degradation on fish replenishment. *Coral Reefs*. 29:537–546.
- Meissner KJ, Lippmann T, Gupta AS. 2012. Large-scale stress factors affecting coral reefs: Open ocean sea surface temperature and surface seawater aragonite saturation over the next 400 years. *Coral Reefs*. 31:309–319.
- Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ. 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*. 92:2285–2298.
- Mora C, Frazier AG, Longman RJ, Dacks RS, Walton MM, Tong EJ, Sanchez JJ, Kaiser LR, Stender YO, Anderson JM, et al. 2013. The projected timing of climate departure from recent variability. *Nature*. 502:183–187.
- Mumby PJ. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl*. 16:747–769.
- Mumby PJ. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*. 28:761–773.
- Munday PL, Dixon DL, McCormick MI, Meekan MG, Ferrari MCO, Chivers DP. 2010. Ocean acidification alters larval behaviour and impairs recruitment to reef fish populations. *Proc Natl Acad Sci U S A*. 107:12930–12934.
- Munday PL, Jones GP, Pratchett MS, Williams AJ. 2008. Climate change and the future for coral reef fishes. *Fish Fish*. 9:261–285.
- Naylor R, Burke M. 2005. Aquaculture and ocean resources: Raising tigers of the sea. *Ann Rev Environ Res*. 30:185–218.
- Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK. 2007. Current and future sustainability of island coral reef fisheries. *Curr Biol*. 17:655–658.
- Ogden JC, Gladfelter EH. 1983. Coral reefs, seagrass beds and mangroves: Their interaction in the coastal zones of the Caribbean. *UNESCO Rep Mar Sci*. 23:133.
- Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, et al. 2009. Recent region-wide declines in Caribbean reef fish abundance. *Curr Biol*. 19:590–595.
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science*. 301:955–958.
- 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, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, et al. 2005. Are U.S. coral reefs on the slippery slope to slime? *Science*. 307:1725–1726.

- Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat Commun.* 4:1402. Available from: <http://dx.doi.org/10.1038/ncomms2409> via the Internet. Accessed 1 February, 2014.
- Polunin NVC, Roberts CM. 1996. Reef fisheries. London: Chapman and Hall.
- Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ. 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity.* 3:424–452.
- Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR. 2008. Effects of climate-induced coral bleaching on coral-reef fishes: Ecological and economic consequences. *Oceanogr Mar Biol Ann Rev.* 46:251–296.
- Robbins WD, Hisano M, Connolly SR, Choat JH. 2006. Ongoing collapse of coral-reef shark populations. *Curr Biol.* 16:2314–2319.
- Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, et al. 2004. The oceanic sink for anthropogenic CO₂. *Science.* 305:367–371.
- Sale PF. 2008. Management of coral reefs: Where we have gone wrong and what we can do about it. *Mar Pollut Bull.* 56:805–809.
- Sale PF. 2011. Our dying planet: An ecologist's view of the crisis we face. Berkeley, CA: University of California Press.
- Sale PF, Agardy T, Ainsworth CH, Feist BE, Bell JD, Christie P, Hoegh-Guldberg O, Mumby PJ, Feary DA, Saunders MI, et al. In press. Transforming management of tropical coastal seas to cope with challenges of the 21st century. *Glob Environ Chang.*
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, et al. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE.* 3(2):e1548. Available from: <http://dx.doi.org/10.1371/journal.pone.0001548> via the Internet. Accessed 1 February, 2014.
- Sano M. 2000. Stability of reef fish assemblages: Responses to coral recovery after catastrophic predation by *Acanthaster planci*. *Mar Ecol Prog Ser.* 198:121–130.
- Stallings CD. 2009. Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. *PLoS ONE.* 4(5):e5333. Available from: <http://dx.doi.org/10.1371/journal.pone.0005333> via the Internet. Accessed 1 February, 2014.
- Tanzil JTI, Brown BE, Tudhope AW, Dunne RP. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand, between 1984 and 2005. *Coral Reefs.* 28:519–528.
- Veron JEN, Odorico DM, Chen CA, Miller DJ. 1996. Reassessing evolutionary relationships of scleractinian corals. *Coral Reefs.* 15:1–9.
- Wagner DE, Kramer P, van Woesik R. 2010. Species composition, habitat, and water quality influence coral bleaching in Southern Florida. *Mar Ecol Prog Ser.* 408:65–78.
- Wanless HR, Maier KL. 2007. An evaluation of beach renourishment sands adjacent to reefal settings, southeast Florida. *Southeast Geol.* 45:25–42.
- Wheeler T, von Braun J. 2013. Climate change impacts on global food security. *Science.* 341:508–513.
- Wilkinson C. 2008. Status of coral reefs of the world: 2008. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre.
- Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA, Tinkler P. 2010a. Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: The importance of coral and algae. *PLoS ONE.* 5(12):e15185. Available from: <http://dx.doi.org/10.1371/journal.pone.0015185> via the Internet. Accessed 1 February, 2014.
- Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC. 2010b. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol Appl.* 20:442–451.
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Glob Chang Biol.* 12:2220–2234.
- Wooldridge SA. 2009. Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar Pollut Bull.* 58:745–751.