

Managing resilience to reverse phase shifts in coral reefs

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Both coral-dominated and degraded reef ecosystems can be resistant to change. Typically, research and management have focused on maintaining coral dominance and avoiding phase shifts to other species compositions, rather than on weakening the resilience of already degraded reefs to re-establish coral dominance. Reversing degraded coral-reef states will involve reducing local chronic drivers like fishing pressure and poor water quality. Reversals will also require management of key ecological processes – such as those performed by different functional groups of marine herbivores – that both weaken the resilience of the degraded state and strengthen the coral-dominated state. If detrimental human impacts are reduced and key ecological processes are enhanced, pulse disturbances, such as extreme weather events, and ecological variability may provide opportunities for a return to a coral-dominated state. Critically, achieving these outcomes will necessitate a diverse range of integrated approaches to alter human interactions with reef ecosystems.

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Ecological resilience is the capacity of ecosystems to absorb disturbances and respond to change while retaining essentially the same function, structure, and feedbacks (Holling 1973; Scheffer *et al.* 2001). If resilience is undermined sufficiently, a phase shift – to an alternate state dominated by a different suite of organisms – can occur (Scheffer *et al.* 2001). These alternate states are generally considered undesirable if they provide fewer or less valuable ecosystem goods and services (Panel 1). Furthermore, degraded states can also be resilient to change, complicating their reversal (Suding *et al.* 2004; Lebel *et al.* 2006). Some disciplines routinely conceptualize the resilience of unwanted states; for example, there is a large amount of literature in the social sciences on social traps, whereby potentially beneficial short-term behavior can lead to detrimental long-term outcomes

that are very difficult to withdraw from or avoid (Platt 1973). This interest has led to burgeoning research on mechanisms for escaping from social traps, with application to issues ranging from poverty to natural resource management (Barrett and Carter 2001; Steneck *et al.* 2011). Importantly, this literature emphasizes how shocks may be used as opportunities to escape traps (McSweeney and Coomes 2011). Ecologists working on coral reefs, on the other hand, more commonly focus on how to avoid phase shifts from coral-dominated to degraded states (Nyström *et al.* 2008). However, phase shifts away from a coral-dominated state to an alternate composition of species, such as macroalgae or soft corals, have been well documented on coral reefs, particularly in the Caribbean Sea (Roff and Mumby 2012) but also in the Indo-Pacific (Ledlie *et al.* 2007). Whether these degraded conditions represent stable states on coral reefs is a topic of some controversy, with indications that these alternate compositions are likely stable in the Caribbean, but evidence for stability is less conclusive for the Indo-Pacific (eg Hughes *et al.* 2010; Mumby *et al.* 2013). Clearly, widespread degradation indicates a pressing need to think and act innovatively about reversing phase shifts. Reversibility of coral-reef phase shifts has proved to be possible, but typically only in relatively small-scale localized instances (eg Bellwood *et al.* 2006; Carpenter and Edmunds 2006; Stockwell *et al.* 2009).

Feedbacks play a critical role in stabilizing or destabilizing both coral-dominated and degraded states (Scheffer *et al.* 2001; Mumby and Steneck 2008; Hughes *et al.* 2010; Nyström *et al.* 2012). For example, after a phase shift from a coral-dominated reef state to one dominated by macroalgae, stabilizing feedbacks can strengthen the macroalgae state if macroalgae prevent successful coral recruitment (Kuffner *et al.* 2006) or outcompete corals

In a nutshell:

- Many coral-reef ecosystems have been degraded to resilient assemblages no longer dominated by live coral
- Reversing this degradation will require a reduction in human pressures on reefs and improved management of ecosystem processes that weaken the degraded condition and promote corals
- If reefs are managed in this way, disturbances such as storms or seasonal variability of seaweeds may be harnessed as opportunities to help reefs recover
- Innovative changes in human interactions with reef ecosystems may be necessary to achieve more sustainable reef futures

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(Rasher and Hay 2010). Conversely, destabilizing feedbacks can weaken the macroalgae state. For instance, rabbitfishes (*Siganus* spp), one of the main herbivorous fish groups that feed directly on mature macroalgae (Hoey and Bellwood 2011), preferentially settle from the plankton into macroalgae and use this habitat as juveniles (Soliman *et al.* 2008). Thus, increases in macroalgae may lead to large cohorts of rabbitfishes reaching maturity and ultimately reducing macroalgal cover. The interplay between the strength of stabilizing and destabilizing feedbacks affects how easily phase shifts may be reversed. Reducing chronic drivers of change – such as fishing or sedimentation – beyond the threshold at which the original phase shift occurred may sometimes be necessary (known as a “hysteresis effect”). However, if feedbacks are weak, then phase-shift reversals are likely to be much easier (Nyström *et al.* 2012). An understanding of both stabilizing and destabilizing feedbacks is therefore important for identifying the processes that weaken the resilience of degraded states and bolster the resilience of coral-dominated states.

In many cases, reversing a phase shift back to coral dominance will fail to fully reinstate the original assemblage structure (Panel 2). Indeed, coral-dominated reefs

have changed through time as a result of escalating human use and climate change, with few contemporary reefs existing in a “pristine” state (eg Pandolfi *et al.* 2003; McClanahan *et al.* 2007). Returning reefs to a pristine condition is therefore not a realistic goal. Future coral reefs are not, however, necessarily doomed to exist only within a range of degraded alternate states (Bellwood *et al.* 2004; Hughes *et al.* 2010). A different path may be possible, whereby phase shifts could be reversed and a greater number of coral reefs could be maintained in coral-dominated (albeit not pristine) states. Here we explore the theory and practice of how phase shifts may be reversed and provide broad guidelines applicable to all marine ecosystems, using coral reefs as a focal example.

■ Drivers of change in coral reefs

Climate change is a major threat to coral reefs. Rising sea-surface temperatures and increasing ocean acidification are chronic global drivers operating over long timescales that can influence processes (such as calcification) in complex ways (Cooper *et al.* 2012). Yet climate change is also resulting in more frequent pulse disturbances such as coral bleaching events, which can cause substantial

Panel 1. Societal beneficiaries of different reef states

Although phase shifts in reef ecosystems are likely to affect the generation of ecosystem services, few studies have explicitly investigated how the provision of ecosystem services changes after a shift in community composition. While reefs with high coral cover and associated diversity will likely provide the highest tourism-related services, other alternate states, such as soft-coral-dominated reefs, can still attract tourists. Although macroalgal states may support a less commercially valuable fish catch than that of coral-dominated reefs, some macroalgae-dominated reefs can support a relatively high biomass of fish important for local consumption (McClanahan *et al.* 2008). How phase shifts to soft coral, sponge, and other benthic assemblages will influence reef fish communities and fisheries yields represents an important knowledge gap.

Ultimately, appreciating how phase shifts affect people's well-being will require a better understanding of not only the ecosystem services provided by alternate states but also how these services are valued by different segments of society. The concept of resilient coral-dominated systems being desirable is normative, value-laden, and generally constructed by outsiders rather than local resource users. Different groups of people have differing, and sometimes polar, views about what is and what is not desirable, often based on the benefits they can capture from a specific ecosystem condition (Lebel *et al.* 2006). For example, although biodiverse, coral-dominated reefs contribute to a multi-billion-dollar tourism industry, profits from tourism, which are generally higher than those from fisheries, often do not benefit poor fishing communities (Hicks *et al.* 2009). In contrast, heavily fished, degraded reefs may support fewer recreational services but provide important food security for low-income households (Figure 1). Therefore, phase shifts that diminish ecosystem services to one sector of society are likely to lead to inequitable outcomes.

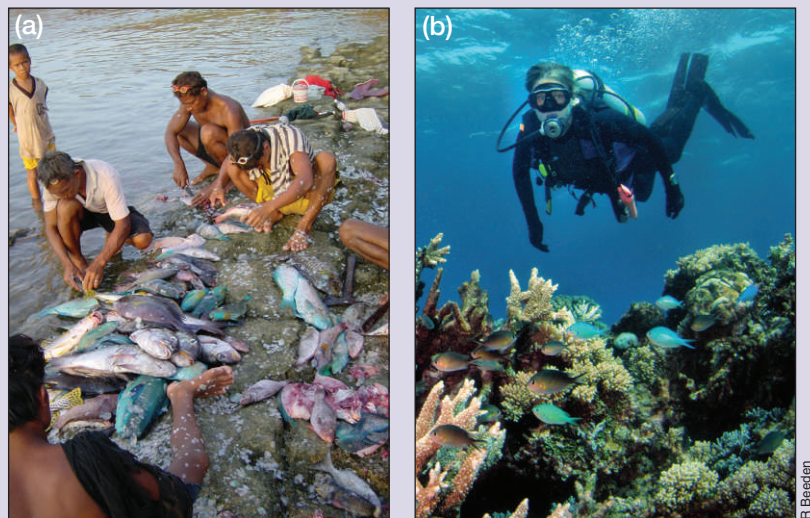


Figure 1. Examples of ecosystem services provided by coral reefs of differing condition and to different segments of society. (a) Fishing provides important food security to many low-income people in coral-reef nations, whose catch can often be dominated by herbivores, particularly if the reefs are heavily degraded. (b) Dive tourism is a popular recreational activity, particularly among wealthier people, who often want to visit coral reefs in good condition.

mortality of live coral. At a local scale, little can be done to mitigate climate-change impacts, which would require global reductions in carbon emissions. However, the interplay between climate change and local drivers of change suggests that managing local drivers may maintain reef resilience, bolstering their ability to cope with climate change in the medium-term future (Bellwood *et al.* 2004; Hughes *et al.* 2010). For example, climate-related disturbances like coral bleaching events affect a different portion of the fish community than fishing (Graham *et al.* 2011). Critically, fishing, a local to regional driver, mediates the abundance of functionally important reef fish species that can control algal growth and promote coral recovery after a major bleaching event (Graham *et al.* 2011). In addition, much of the ongoing deterioration of coral reefs is attributable to centuries of local human impacts, including overfishing and declining water quality (Pandolfi *et al.* 2003), further highlighting the need to address local chronic drivers of change in order to reverse phase shifts and maintain coral-dominated reefs.

Overfishing and water quality are the two dominant local drivers of change on most reef systems. Importantly, these drivers affect key ecosystem processes and feedback mechanisms in both coral-dominated and degraded reef states. Depletion of herbivorous fishes, for instance, can

reduce grazing of seaweed and contribute to a phase shift away from a coral-dominated state (Hughes 1994; McClanahan *et al.* 2011). Conversely, restricting fishing through well-enforced no-take reserves can lead to a recovery of herbivorous fish stocks, reductions of fleshy macroalgal cover, and enhanced rates of coral recruitment (Mumby *et al.* 2007; Stockwell *et al.* 2009). Declining water quality can also promote growth of seaweed (De'ath and Fabricius 2010). On Australia's Great Barrier Reef, where marine herbivores are generally unexploited, inshore reefs in close proximity to river outlets – with greater sediment, pesticide, and nutrient loads – are associated with high macroalgal cover, whereas reefs farther offshore are characterized by greater cover of corals (De'ath and Fabricius 2010; Hughes *et al.* 2010).

Even so, there are some important differences in how fishing influences processes key to different ecosystem states. For example, on Indo-Pacific coral reefs, the herbivorous reef fish species that maintain cropped turf algae (multi-species algal assemblages typically <10 mm in height), preventing a phase shift away from the coral-dominated state, are different from those that feed on macroalgae (mature, often anatomically complex algae >10 mm in height), potentially contributing to the reversal of degraded states. Specifically, various species of parrotfish and surgeonfish of the genera *Acanthurus* and

Panel 2. Realistic goals for the future of coral-dominated reefs

Coral reefs can exist in coral-dominated states or alternate states dominated by other organisms, such as macroalgae (Hughes 1994; Bellwood *et al.* 2004; Mumby *et al.* 2013). Relatively pristine coral-dominated reef states are characterized by high fish biomass (including apex predators), copious coral recruitment, and high grazing rates, resulting in structurally complex habitats with rich taxonomic diversity. However, the condition and composition of coral-dominated reef states has changed through time on most reefs, and it is unlikely that reefs will return to these historical conditions. Many contemporary reef systems have experienced a reduction in fish biomass, reduced diversity, and loss of structural relief as a result of overfishing, reduced water quality, and anthropogenic climate change (eg Pandolfi *et al.* 2003; McClanahan *et al.* 2011). Yet, while many of the species and their abundances have changed, this state is still coral-dominated, net carbonate accretion rates are positive, and critical ecosystem services are provided to humans.

The resilience of reef states can be heuristically expressed as deep or shallow valleys in a stability landscape (Figure 2). Deeper valleys indicate higher levels of resilience, whereas shallow valleys are indicative of low resilience. As natural and anthropogenic drivers have changed reef systems, the coral-dominated state has become less resilient, while the algal-dominated state has become more resilient. In the future, it is unlikely that any reefs worldwide will be in a fully pristine state (Figure 2, vertical dashed line in coral-dominated valley), and it is unrealistic to try to return reefs to this historical condition. Continuing the “business as usual” trajectory – typified by accelerating carbon emissions, overexploitation, high land-derived nutrient loads, and weak governance of tropical coastlines – will result in very few reefs maintained in a coral-dominated state. Nevertheless, if appropriate policies are implemented, more reefs can be sustained or returned to a coral-dominated (but non-pristine) state, providing society with critical goods and services.

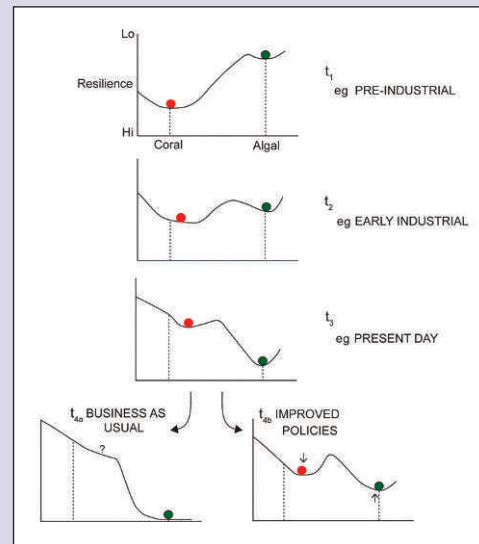


Figure 2. A chronology of alternate states in coral reefs. The condition and composition of the coral-dominated state has changed through time, away from a pristine state (dashed vertical line above “coral”). Furthermore, the coral-dominated reef state has become less common through time (t_1 – t_3), and could become uncommon in the future (t_{4a}) under a “business as usual” scenario. However, if appropriate policies are implemented, more reefs may be maintained in or shifted back to coral-dominated states, with a reduction of the resilience of the algal-dominated state and increased resilience of the coral-dominated state (t_{4b}).

Ctenochaetus provide the detritivorous, grazing, scraping, and excavating roles that maintain sediment fluxes, control turf algae, and promote coral recruitment and recovery dynamics (Bellwood *et al.* 2006; Ledlie *et al.* 2007). Conversely, a separate suite of herbivores – including species of rabbitfish, drummers (Kyphosids), surgeonfish of the genus *Naso*, and the batfish *Platax pinnatus* – is responsible for removing mature macroalgae (Bellwood *et al.* 2006; Hoey and Bellwood 2011).

Differences in the feeding preferences of herbivorous fish functional groups are important, because in some locations herbivorous fishes are vulnerable to fishing (Graham *et al.* 2007), and the suite of species targeted varies depending on the type of fishing gear being used (Cinner *et al.* 2009). Simplistically this may indicate that when trying to reverse macroalgae phase shifts, fisheries policy could focus on increasing the abundance of the species that control macroalgae, while exploitation of scarids (parrotfish) and many acanthurids (surgeonfish) can continue. Yet even if stocks of macroalgal browsers were rebuilt sufficiently to return to a coral-dominated state, the system would still be precariously vulnerable to perturbations leading to a shift back to the degraded state, especially if grazing species were overharvested. Under these conditions, turf algae – if persistent and undergrazed – can also be detrimental to coral recruitment (Arnold *et al.* 2010). It is therefore important to bolster both the resilience of the coral-dominated state (ie increase the abundance of species that maintain cropped turf algae) at the same time as weakening the resilience of the degraded state (ie increase the abundance of macroalgae browsers). In this way, feedbacks that stabilize a coral-dominated state – such as parrotfishes cropping turf algae and promoting successful coral recruitment (Mumby *et al.* 2007) – will already be in place after a phase-shift reversal.

■ Rebuilding coral-dominated systems

Acting early

Once a system has crossed a threshold, transition to a new stable state may take many years. Several agents of mass coral mortality (eg coral bleaching, coral disease, crown-of-thorns starfish [*Acanthaster planci*] outbreaks) result initially in dead coral structures that may remain intact for several years before they break down, initiating a long chain of events (Pratchett *et al.* 2008). In such cases, the initial impacts of coral loss on the rest of the ecosystem can be relatively small, with only specialist coral-feeding and coral-dwelling adult fish decreasing in abundance (Wilson *et al.* 2006). The loss of live coral does, however, affect successful recruitment of larval fish, given that many fish species require live coral at settlement (Pratchett *et al.* 2008). Further changes can occur later, when the physical structure of the dead corals erodes, causing marked declines in abundance of smaller size classes of large fish species (Graham *et al.* 2007).

Subsequently, it can take many years for reduced recruitment success and declines in small size classes to result in a reduction in abundance of large size classes of many ecologically important groups of fish (such as parrotfishes; Graham *et al.* 2007).

The probability of reversing a given phase shift is much greater in the initial phase of this sequence of events, rather than after the system has stabilized in a new state. Before the dead corals erode, timely fisheries management practices aimed at reducing mortality and enhancing the abundance of fish reaching large size classes, and thus bolstering key ecosystem processes such as herbivory, are likely to be more successful than delayed action. If management efforts are delayed and small size classes of fish decline through failed settlement and reduced survivorship after erosion of the reef structure, enhancing the abundance and ensuring the longevity of fish populations is less certain. Therefore, during a phase shift to a degraded state, the earlier that managers act to protect fish groups, the more successful they are likely to be at reinforcing key processes (such as algal control and successful coral recruitment) that encourage coral re-establishment.

Taking advantage of shocks

If feedback mechanisms are weak, reversing macroalgal phase shifts may simply require a long-term commitment to rebuilding herbivore stocks and improving water quality, which will lead to a steady decline of algal abundance and eventual coral recovery (assuming that coral recruitment continues; Figure 3a). Conversely, if feedbacks are strong, phase-shift reversals may be more difficult, necessitating a reduction in chronic drivers beyond the point at which the original phase shift occurred. For instance, established macroalgae can be resistant to grazing because fish tend to avoid dense algal stands (Hoey and Bellwood 2011) and because mature macroalgae are unpalatable to many herbivorous fish (Ledlie *et al.* 2007). Reversals, however, could possibly be aided by natural episodic disturbances or shocks (Holmgren and Scheffer 2001; Suding *et al.* 2004). Indeed, such events play a key role in phase shifts away from coral-dominated assemblages (Hughes 1994), but are rarely considered for their potential role in reversing phase shifts on coral reefs. Pulse events have reversed phase shifts in arid ecosystems that had previously shifted from a vegetated state to a degraded desert state. In combination with controls on grazing pressure, episodic El Niño events that deliver 4–10 times as much rainfall as in “normal” years can enhance vegetation productivity sufficiently for the system to shift back from desert to permanent woodland (Holmgren and Scheffer 2001).

Exceptional weather events may also create windows of opportunity for phase-shift reversals on coral reefs. After dominating reef slopes in Kaneohe Bay (Hawaii) for decades, cover of the green macroalgae *Dictyosphaeria cavernosa* decreased dramatically following an unusually long period (42 days) of rain and overcast skies. These

conditions of low irradiance caused algae to lose mass, which ultimately led to a reduction in percent cover from ~40–70% to 0%, which persisted for the 2 years of the study (Stimson and Conklin 2008). Events like tropical storms, hurricanes, and cyclones, although often destructive for corals (Woodley *et al.* 1981), can be more disruptive to macroalgae (Lapointe *et al.* 2006), again creating a potential opportunity for a phase-shift reversal. However, reversals will occur only if key ecosystem processes, such as herbivory, are bolstered in advance of an anticipated event, to maintain algae in a cropped state and promote successful coral recruitment.

Aside from shocks, inherent variability may also provide opportunities for novel management. The brown algae *Lobophora variegata* became extremely abundant (up to 70% cover) on an inshore group of reefs of the southern Great Barrier Reef after a coral bleaching event in 2006. Nevertheless, corals recovered on some reefs within months. This rapid recovery was due to the macroalgal cover being naturally arrested by an inherent seasonal dieback, and corals re-growing from surviving fragments (Diaz-Pulido *et al.* 2009). Such seasonal diebacks of macroalgae are common on coral reefs and can occur for extended periods of the year. On reefs of the southern Red Sea, the dominant macroalgae die off from June to December (Ateweberhan *et al.* 2006). Importantly, this event aligns with the peak coral-spawning period in the Red Sea, which occurs from May to August (Shlesinger and Loya 1985), suggesting that the open space created by seasonal dieback of algae may be utilized by newly recruited corals if algae cover can be kept low (eg by augmenting herbivore abundance). Hence, in some locations where phase shifts have occurred, seasonality in environmental conditions and/or episodic population dynamics (eg die-offs of reef-associated organisms due to disease and pulses of reproduction, dispersal, and settlement) could offer natural opportunities for innovative management aimed at phase-shift reversals.

Harnessing the potential benefits from shocks or seasonal variability is dependent on reefs being managed to respond positively to such events, otherwise the system will likely return to a degraded state once the initial effect of the shock or variability has faded, because algal growth rates are considerably faster than coral growth rates (Figure 3b; Roff and Mumby 2012). Exploiting natural variability will also require long-term commitments to reducing chronic drivers, such as improving water quality or reducing fishing, and bolstering key processes important to reinforcing the coral-dominated state, in tandem with those important for weakening the degraded reef state. If management can successfully strengthen important processes (eg by maintaining or increasing the abundance of key groups of herbivores), then a pulse event, such as a hurricane, or extreme seasonal variability may facilitate a phase shift back to a coral-dominated state if the whole reef or patches thereof can be maintained in a cropped algae

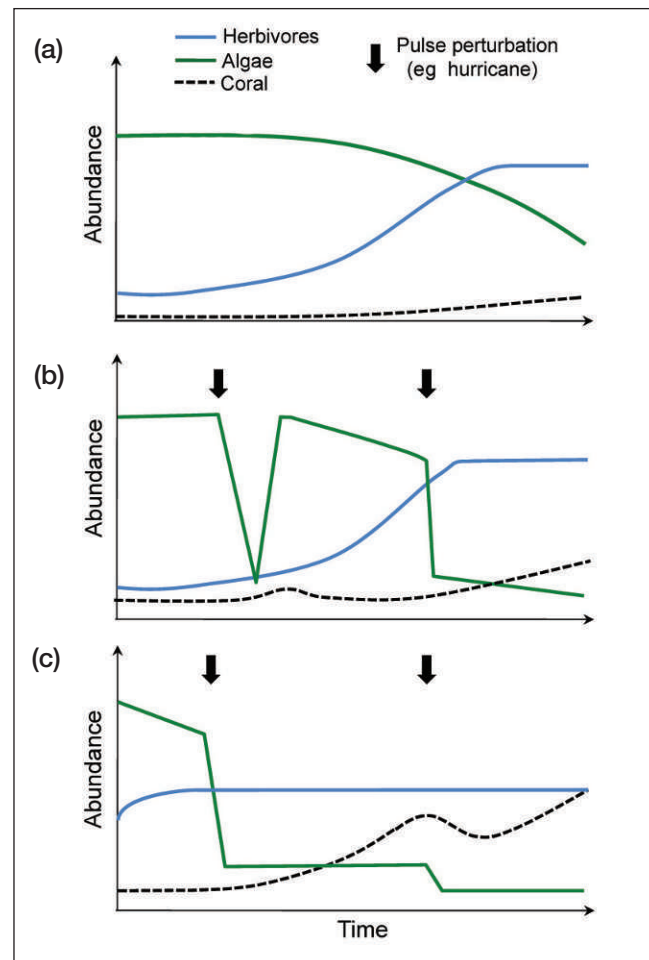


Figure 3. Heuristic model of phase-shift reversals, indicating the potential role of pulse disturbances. (a) Reduction of fishing for marine herbivores creates a slow increase in their abundance with concomitant reductions in algae and eventual recovery of coral. (b) Although too scarce to promote a phase-shift reversal after an initial pulse disturbance, herbivores have built up sufficient numbers to create a shift after a second disturbance. (c) Management has proactively enhanced herbivore abundance; in this case, the system recovers after the first pulse disturbance.

state (Figure 3c). However, the ability to reverse phase shifts and harness the effects of shocks may not always be possible if feedbacks remain sufficiently strong.

Managing reef futures

Reinstating functional redundancy

Managing reef systems to take advantage of shocks or extreme variability and to reverse unwanted phase shifts will require enhancement of key ecosystem processes. Reinstating functional redundancy (ie more than one species performing an ecosystem function) could help sustain reef ecosystem processes, particularly in low diversity systems. Sea urchin (*Diadema*) densities in some parts of the Caribbean prior to the disease-mediated die-off in the early 1980s exceeded 20 individuals

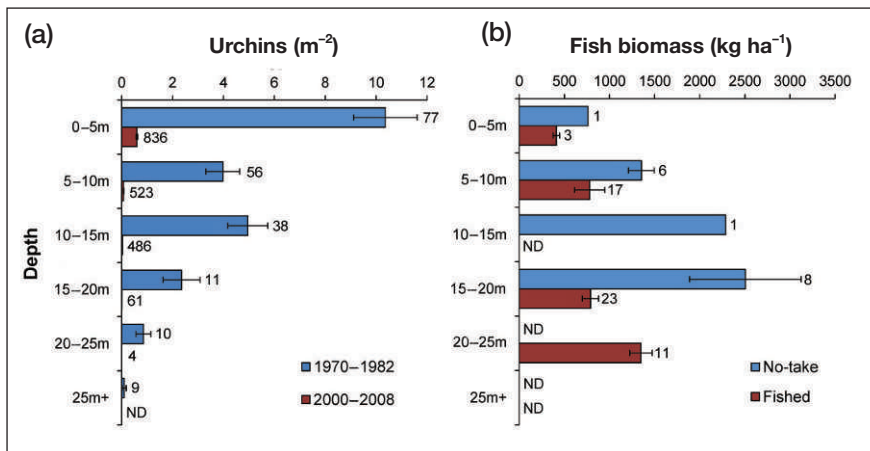


Figure 4. Densities of sea urchins and reef fishes across depth zones in the Caribbean Sea. (a) Mean *Diadema antillarum* densities by depth between 1970–1982, before a die-off from disease in 1983, and between 2000–2008. (b) Mean reef fish biomass (all diurnally active, non-cryptic species) by depth across 70 reef sites in both no-take marine reserves and open-access fished areas. Number of sites sampled per depth–time combination given adjacent to bars. ND = no data. Error bars indicate standard error. Data sources for *Diadema* densities given in Hughes *et al.* (2010). Data sources for fish biomass provided in WebTable 1.

per m^2 , with a mean density in shallow water of ~ 10 individuals per m^2 (Figure 4a), and urchins had replaced fish as the dominant grazer (Hay 1984; Hughes 1994). Subsequent mass mortality of sea urchins led to unprecedented macroalgae blooms that persist today throughout much of the Caribbean (Hughes *et al.* 2010). The limited recovery of *Diadema* in recent years is restricted to shallow water (Figure 4a), where macroalgae have declined and coral recruitment rates have increased (Carpenter and Edmunds 2006). However, the current densities of *Diadema* at 0–5 m are still only one-fifth of their former magnitude, and there has been little or no recovery at many locations or in deeper water (Figure 4a). Although the long-term recovery of *Diadema* populations is uncertain, including extending to greater depths, population recovery to pre-1980s densities would likely be unsustainable given the risk of a new disease epidemic or increased bioerosion caused by dense echinoid aggregations. Enhancing reef fish biomass and diversity across depth zones may contribute toward a more stable future for Caribbean coral reefs. Specifically, enhancing fish biomass and diversity will rebuild functional redundancy in herbivory and enable predatory control of sea urchin densities. Higher total fish biomass (including herbivore and predator groups) is evident in some small Caribbean no-take marine reserves (Figure 4b). Increases in fish biomass and diversity are also necessary across the much larger areas open to fishing, a goal that will require a range of approaches that alter human behavior (WebPanel 1).

Reducing drivers of change to reverse phase shifts

Conventional approaches to reduce chronic drivers of change on coral reefs have generally focused on a limited

set of actions, principally involving marine reserves. Although offering substantial ecological benefits locally (Stockwell *et al.* 2009), marine reserves typically protect only small areal extents of coral reefs, and weak compliance and enforcement often limit reserve effectiveness (Pollnac *et al.* 2010). Novel management approaches that reduce drivers of change across wider seascapes – by altering the way that people interact with reefs – are clearly necessary (WebPanel 1; WebFigure 1). Here, we expand on three approaches that can reduce chronic drivers and enhance ecosystem processes across seascapes.

First, improved understanding of the functional role of reef fish species (Bellwood *et al.* 2006; Ledlie *et al.* 2007; Hoey and Bellwood 2011) has enabled fishing gear use to be restricted or modified (eg escape gaps

in fish traps), thereby limiting mortality of functionally important fish species while maintaining profitability for fishers (Cinner *et al.* 2009; Johnson 2010). Specifically, the gear used by artisanal reef fishers selectively targets species with different body sizes/shapes and feeding characteristics. This selectivity could be used to minimize the capture of key functional groups where an outright ban on fishing is not socially acceptable. Up to 50% of the catch targeted by some artisanal fishing gear, such as spearguns, includes species important for preventing or reversing phase shifts (Figure 5). Nevertheless, the proportion of these key species in catches can vary as a result of local factors such as fishing pressure, suggesting gear management could be tailored to local contexts. As an example, to reduce the catch of macroalgal feeding fishes (and some turf feeding fishes), net fishing could be restricted in the Philippines, whereas reducing speargun use or encouraging selective harvesting would be more effective in Papua New Guinea (Figure 5).

Second, changes to governance systems can improve ecosystem conditions at large scales. Collaborative management (often called co-management) provides resource users with greater ownership and decision-making power over natural resources. Changes to national legislation in Chile, for instance, provided fishing cooperatives with exclusive access to fishery resources in delineated areas. This exclusive access created incentives for fishers to manage and patrol the areas, and resulted in increased harvests and less conflict (Gelcich *et al.* 2010). Co-management arrangements are increasingly common in many coral-reef nations and have resulted in both livelihood and ecological benefits (Cinner *et al.* 2012). Indeed, co-management in the Solomon Islands has formed the basis for systems of protected areas, resulting in a doubling of parrotfish biomass (Aswani and Sabetian 2010).

Third, improved water-quality management could also help to reverse phase shifts on degraded coastal reefs. Elevated nutrients and particulates favor phytoplankton, macroalgae, and suspension feeders such as oysters and sponges, whereas high sediment loads in runoff are detrimental to many corals, particularly juveniles, through smothering. The experience of Kaneohe Bay, Hawaii, in the 1970s demonstrated that improving water quality – in this case by diverting a sewage outfall – can reverse an unwanted phase shift by reducing the abundance of algae and suspension feeders and increasing coral cover (Smith *et al.* 1981). The ongoing decline of coastal reefs along the Great Barrier Reef (Sweatman *et al.* 2011) highlights the need for improving water quality, even where herbivorous fish stocks are lightly exploited. Managing water quality, especially at a catchment scale, is expensive and is often challenging from a governance perspective, because it invariably involves multiple agencies and stakeholders that operate on land as well as the sea. In Australia, efforts to manage coastal pollution and sedimentation are contingent on a strengthening of cooperation between local, state, and federal governments. If ambitious water-quality targets are achieved, a decline in macroalgae cover and an increase in hard coral species richness should occur on inshore reefs (De'ath and Fabricius 2010).

Conclusion

Although the community composition of coral reefs will likely continue to vary over time, it may be possible to maintain coral-dominated reefs and their associated ecosystem goods and services. Doing so will require scientists, policy makers, managers, and resource users to act collectively to develop long-term commitments to improve reef management. Better outcomes for reefs and the people who depend on them also warrant further research to understand how ecosystem trajectories can be influenced and managed. With such knowledge, linked social and ecological thinking can be used to develop novel integrated approaches that reduce chronic drivers of change and bolster key processes across seascapes, to enable phase-shift reversals and strengthen the resilience of coral-dominated states. Finally, scientists and managers could take advantage of opportunities for change by harnessing shocks and natural variability as potential stimuli for beneficial shifts in ecosystem states.

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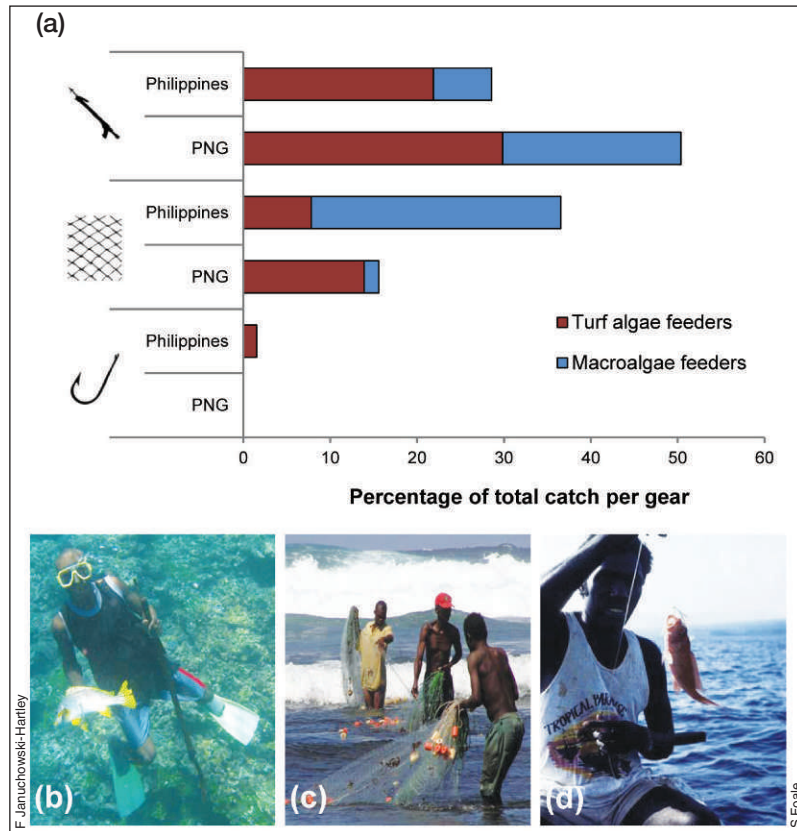


Figure 5. Gear-based fisheries management can potentially help to prevent or reverse phase shifts to degraded reef states. (a) Percentage of total catch (abundance) comprising species that feed on turf algae (ie maintain coral-dominated state) and species that feed on mature macroalgae (ie weaken macroalgae state). Catch is separated by three different types of fishing gear – (b) speargun, (c) net, and (d) hook and line – in two countries (Philippines and Papua New Guinea [PNG]), to illustrate differences in selectivity. Data from PNG adapted from Cinner *et al.* (2009); data from Philippines from DRB.

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