



Coral–algal phase shifts on coral reefs: ecological and environmental aspects

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Abstract

This paper briefly reviews coral–algal phase shifts on coral reefs, with particular regard to summarizing the exogenous and endogenous factors in support of a proposed conceptual model, and to identifying critical information gaps. A phase shift occurs on a coral reef when the cover of a substrate by scleractinian corals is reduced in favor of macroalgal dominance, and resilience of the former condition is retarded because of ecological processes and/or environmental conditions. The change is often, but not always, associated with a perturbation such as coral bleaching, outbreaks of a coral-eating species, or storm damage. The new state is generally associated with some combination of reduced herbivory (from disease and/or fishing) and nutrient enrichment, although the relative importance of these factors is under debate and may vary among locations and even across single reefs. Disturbances that result in a state of generally low biotic three-dimensional structural complexity often precede a phase shift. Following such a disturbance, the system will pass to a state of higher biotic structural complexity, with either macroalgae or coral dominating. As the community progresses towards larger and more three-dimensionally complex corals or macroalgae, it exhibits greater resistance to shifting dominance from one state to the other. Studies of the phase-shift phenomena have been generally conducted at scales that are small relative to the sizes and inherent variability of whole coral reefs and systems of reefs. There is an urgent need for studies aimed at quantifying and simulating cause and effect aspects of the phase shift, including human–environment coupling, particularly in support of coral reef decision-making.

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1. Introduction

The term “coral–algal phase shift” refers to the phenomenon of coral reefs shifting to unusually low levels of coral cover, associated with persistent states of high cover of fleshy macroalgae (seaweed). It is widely recognized that persistence times of these shifts have increased in the past few decades. This has led to concern over declining coral reef ecosystem health and integrity, losses of biodiversity, and decreases in social, cultural and economic values (Hughes et al., 2003; McManus, Meñez, Reyes, Vergara, & Ablan, 2000). There have been a number of reviews on various aspects of the subject (e.g. Done, 1992; Hughes et al., 1999a,2003; Hughes, Szmant, Steneck, Carpenter, & Miller, 1999b; Knowlton, 1992; McClanahan, Polunin, & Done, 2002b; McManus et al., 2000; Szmant, 2002). In this paper, we will focus on characteristics of the phenomenon relevant to comparisons with regime shifts in other ecosystems. In particular, we will discuss evidence concerning three issues raised by Steele (2004) in the introduction to this volume:

1. The general dynamic nature of the shifts, including potential hysteresis associated with alternate successional processes, as well as the nature of exogenous forcing (combinations of stress and perturbation) involved in the shifts.
2. The relative importance of endogenous factors, including bottom-up (benthic) vs. top-down (herbivory) aspects.
3. The relevance of these to management issues, including the identification of critical knowledge gaps.

For the purposes of this paper, we shall use the term “resilience” to refer to the rate of return to coral dominance. This is in keeping with the use of the term by Pimm (1991), accepting, however, that dominant here does not necessarily imply “more than 50% bottom cover”. It has been shown that near-pristine reef slopes often have less cover by living coral than by other benthic elements (McManus, Vallejo, Meñez, & Coronado, 1995). Thus, coral dominance of a reef community is that in which living scleractinian corals play a major role in structuring other elements of the ecological community at local scales of a few tens of meters in diameter.

We begin with a general description of the relationships between disturbance and resilience on coral reefs, and briefly discuss the loss of resilience. Next, we propose a conceptual model to summarize the broad range of factors potentially involved in the coral–algal phase shift and discuss evidence for causative

explanations, including nutrient loading, loss of herbivory, the combination of these, and other potential exogenous and endogenous factors. We then describe the dynamic nature of the shift, and expand upon earlier suggestions that three-dimensional (3D) heterogeneity plays a role in terms of hysteresis. Finally, we discuss the gap in scale between existing investigatory approaches and the needs of management decision-making, emphasizing recent efforts to refocus research appropriately.

2. Coral reef disturbance and resilience

Early studies on coral reefs often emphasized their constancy over decades to centuries (e.g., Gladfelter & Gladfelter, 1978; Odum & Odum, 1955; Smith & Tyler, 1972). Gradually, coral reefs came to be seen as a temporal mosaic of communities in various stages of recovery from various disturbances (Brown, 1997). It is now widely accepted that the benthic communities of coral reefs can change radically, such as over periods of a few years and sometimes over only a few hours during a disturbance such as a hurricane. Typically, the change is from areas that were formerly dominated ecologically by scleractinian corals toward dominance by some form of algae, either calcareous encrusting algae (CEA), turf algae (mixed species, low stature, filamentous algae), calcareous frondose macroalgae (CFM – usually *Halimeda* spp.), and/or fleshy frondose macroalgae (FFM) which occurs in creeping and upright growth forms. All of these forms of algae are normally present on a coral reef in low densities, although FFM can be very rare on outer reef slopes in pristine areas. Initially following a disturbance, the algae typically cover dead coral pieces and patches of exposed hard calcareous substrate. In some circumstances, turf, CFM or FFM will then spread rapidly beyond these footholds to cover large areas of reef slope or other former coralline zones.

Many coral reefs undergo such changes several times in a decade. In response to physical damage, some corals, especially large coral heads, recover by “resheeting” with live tissue (e.g., *Porites lobata*) (Hillis & Bythell, 1998). Elsewhere, corals are replaced by newly settled coral recruits. Some forms of CEA facilitate this resettlement (Heyward & Negri, 1999; Morse, Hooker, Morse, & Jensen, 1988), perhaps through chemical inducers. Additionally, other components of the reef are known to induce settlement, including exposure to the skeleton of the massive coral *Goniastrea retiformis* and to coral rubble (Heyward & Negri, 1999). Although corals grow in the range of approximately 2–185 mm/year (Harriott & Banks, 2002), the collective growth of many colonies across a large area can return the area to coral dominance within a few years (McManus, Nañola, & Reyes, 1997).

The process of disruption and resilience has been well-documented along the individual reefs of the Great Barrier Reef System of Australia, where resilience from episodes of coral bleaching, attacks of coral-eating *Acanthaster planci* starfish, major storms, or other disturbances is often on the order of 2–7 years, although cases from 1 to 14 years have been recorded (Connell, 1997). Other recovery periods recorded from Indonesia, Thailand and the Red Sea ranged from 1 to 11 years (Connell, 1997). Indeed, the commonness of natural disturbances and the long-term survival of coral reefs around the world indicate that coral reef resilience has, at least until recently, been the norm rather than the exception.

Within the last two decades, increasing reports have been made of coral communities, whether parts of structural limestone reefs or associated with other substrates, showing a shift to dominance by macroalgae (usually FFM) that persists for a decade or more (Connell, 1997; Done, 1992; Knowlton, 1992). The most well-known case occurred along the north coast of Jamaica, where dominance by macroalgae has persisted since severe coral damage associated with Hurricane Allen in 1980 (Hughes, 1994). Major factors identified by Hughes (1994) and thought to contribute to the long-term persistence of algal dominance are a reduction in herbivory by fish (due to overfishing) and a reduction in the sea urchin *Diadema antillarum* (due to disease).

Gardner, Côté, Gill, Grant, and Watkinson (2003) used monitoring data from 1977 to 2003 to show that coral cover declined across the Caribbean from an initial average of 50% to a current average of 10%. Although, the choice of monitoring sites near areas of high disturbance, high interest, accessibility, etc. may have biased the estimate (Buddemeier & Ware, 2003), it is widely agreed that a dramatic drop in coral cover has occurred across the region. The Global Reefs at Risk analysis (Bryant, Burke, McManus, & Spalding, 1998) used a quantitative Geographic Information System (GIS) model calibrated with reports from ReefBase, the Global Coral Reef Database (McManus et al., 1995), to estimate that 60% of the world's reefs were at risk from cumulative stresses and perturbations. A more intensive Reefs at Risk analysis of Southeast Asia (Burke, Selig, & Spalding, 2002) estimated that 88% of that region's reefs were at risk. The higher values in that region were attributed to factors including rampant deforestation (leading to increased terrestrial runoff) and the high densities of impoverished coastal populations who concurrently overfish, destructively fish, and pollute nearby fringing reefs, the latter due largely to direct sewage inputs (McManus, 1996; McManus et al., 1997).

Although much of this decline has been associated with subsequent persistent increases in macroalgal cover, it is generally difficult to separate the process of fleshy algae retarding coral settlement and recovery from the effects of repetitious and diverse perturbations. In the Caribbean, coral disease is a growing problem, responsible for waves of coral losses region-wide (Aronson & Precht, 2001; Bruckner & Bruckner, 1997; Harvell et al., 1999; Patterson et al., 2002). In the Florida Keys Reef Tract, the combinations of disease outbreaks, boat groundings, storm damage, coral bleaching and other perturbations make it difficult to determine what has led to any particular decline, and how important might be the exclusion of coral larvae from settlement areas by macroalgae (Miller, Swanson, & Chiappone, 2000; Porter, 2003).

Resilience to sudden disturbances does not always appear to be the issue. In some cases, it appears that constant stresses may push a reef beyond a resistance threshold. For example, in Kaneohe Bay, Hawaii, a sewage outfall into the bay seems to have caused a gradual increase from the late 1960s and 1970s in the creeping macroalga *Dichtyosphaeria cavernosa*, until it dominated the substrate of the reefs, without the incidence of a major perturbation (Laws, 1992; Szmant, 2002). Once the source of sewage was removed, the reefs returned gradually to coral dominance (Connell, 1997; Szmant, 2002).

Coral reef degradation is not a recent phenomenon. Pandolfi et al. (2003) gathered a variety of evidence to infer the historical states of 14 reef systems around the world. They show that most of these were seriously degraded before 1900, primarily because of overfishing (though they suggest that land-based pollution may have acted synergistically with overfishing in some areas). They express concern that recent attention paid to global phenomena such as bleaching and coral disease may be distracting attention from these long-term trends of reef degradation. However, it is generally accepted that the coral–algal phase shift has been rapidly accelerating in recent decades, and this problem serves as an appropriate target for corrective coral reef management.

In this paper, we review some of the most recent studies, both observational and experimental, that are helping determine the relative roles of each factor and the interaction of contributing factors in the coral–algal phase shift phenomenon.

3. A conceptual model for the coral–algal phase shift

It is important to understand the broader range of factors involved in determining the abundances of major benthic components on a reef. Major factors involved in the coral–algal phase shift are illustrated in Fig. 1. The ratio of coral to algae is the focus. However, it is recognized that merely a reduction in coral does not constitute a coral–algal shift. This new synthesis is based largely on linkages that have been described in McManus et al. (2000) and McClanahan et al. (2002b). The linkages are briefly described here, and supportive material and references can be found in sections below.

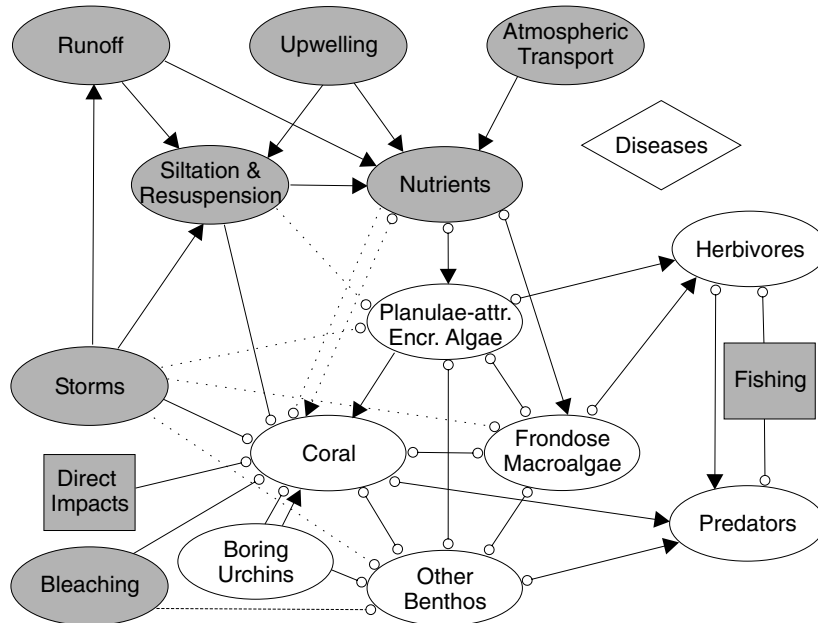


Fig. 1. Conceptual model of major factors involved in the coral–algal phase shift. Exogenous factors are in shaded enclosures. Specifically anthropogenic effects are in rectangles. Diseases (diamond) affect all living components, and the links have been omitted for simplicity. Arrows represent a gain to the component they touch, circles represent a loss. Dashed lines represent weak links or those with impacts under extreme conditions.

Normally, when coral is dead, the resulting space (substrate after the removal of the colony and/or the surface of the dead coral) is filled within weeks by algae or other benthos (anthozoans, gorgonians, sponges, benthic foraminifera, etc.). Within months, a resilient community will exhibit settled coral planulae or asexual propagules. This settlement can be enhanced by “planulae-assisting” encrusting CEA as discussed previously. If the settlement or survival of these planulae is substantially inhibited because of FFM, then a phase shift is the likely result. However, the reduction of reproductively active corals can be a contributory cause, particularly given that most coral planulae spend times in planktonic stages from a few hours to a few days (McManus & Meñez, 1997). Asexual propagation by medusa-like behavior in coral polyps (Sammarco, 1982) or by broken portions of colonies (Highsmith, 1982) generally involves minimal dispersion and is successful under limited circumstances, and so cannot offset losses due to reductions in the success of sexual reproduction. Thus, a reduction in coral, a reduction in the success of the production or settling of coral planulae, or an enhancement of FFM can potentially facilitate or prolong a phase-shift.

Corals can be reduced by the boring away of substrate by sea urchins, and by breakage due to diver actions, boat groundings, dredging, use of fishing gear and other direct impacts. Bleaching and siltation are well-known causes of coral reduction. Although nutrients are necessary for coral growth, excessive levels can inhibit the success of coral settlement (Tomascik, 1991). Storms often break or damage corals, and very large storm waves can substantially reduce other components, including FFM, CEA, other benthos, and even herbivores and predators (not shown). However, the primary impact for the first months to years afterwards is normally a reduction in scleractinian coral. Runoff, upwelling and atmospheric deposition can all at least potentially increase nutrient levels. Nutrients enhance algal growth. Herbivores reduce algal standing stock. Predators reduce herbivory, but some predators (certain parrotfish, crown-of-thorns

starfish, coralivorous snails, etc.) negatively impact corals. Fishing reduces many predators and herbivores, but may alleviate predation on some of each, such as the harvesting of piscivorous fish potentially permitting herbivores to proliferate.

4. Increased nutrients as a causative factor

Conceptual models have proposed that nutrients play a leading role in determining coral reef community structure (Birkeland, 1987; Littler & Littler, 1984; Steneck & Dethier, 1994). In general, these studies suggest that corals will dominate over fleshy macroalgae under low nutrient conditions, with the competitive advantage shifting toward macroalgae as nutrient levels increase (Szmant, 2002), leading to the assumption that nutrients are the, or at least the primary, cause of the coral–algal phase shift.

In regard to the predictions founded on community structure models, the predominant models are based on the common assumption that reef algae are nutrient-limited. Szmant (2002) argues that this assumption is, so far, poorly supported. Firstly, many coral reefs around the world are subject to frequent, constant and/or high levels of nutrient enrichment under natural conditions. Secondly, macroalgae, on the whole, have not been shown to be nutrient limited. In fact, the entire range of responses, from none to luxuriant responses, has been seen in various nutrient addition studies (Szmant, 2002). Finally, McCook (2001) challenged the assumption that algae are normally competitively dominant over corals by showing experimentally that corals out-competed turf algae on a reef in close proximity to terrestrial nutrient sources. McCook, Jompa, and Diaz-Pullido (2001) asserted that while there clearly is direct competition between corals and algae, the competitive hierarchy is determined by many more factors than simply nutrient availability.

In the ENCORE nutrient enrichment experiment on the Great Barrier Reef, Australia, epilithic algal community growth was not enhanced by long-term increases in nutrients in the water column, reportedly because the dense patches of algae were nutrient rich already or diffusion was limited across the water strata immediately above the algae (Larkum & Koop, 1997; McCook, 1999). In Cocos Lagoon, Guam, (Thacker, Ginsburg, & Paul, 2001) and Glovers Reef, Belize, (McClanahan, Cokos, & Sala, 2002a) nutrient addition alone did not significantly increase cyanobacterial or macroalgal biomass. However, studies by Abram, Gagan, McCulloch, Chappell, and Hantoro (2003) indicate that iron from atmospheric deposition during the 1997 Indonesian wildfires could have caused unusually intense red tides that led to coral deaths by asphyxiation in the Mentawai Islands reef ecosystem, located off-shore of southwest Sumatra, Indonesia.

The bulk of studies conducted to address how much of the global decline in coral reefs is being caused by nutrient over-enrichment as opposed to other known factors seem to demonstrate that the levels of nutrient enrichment found as a result of anthropogenic-enrichment are not likely to be the sole or major cause of shifts in coral–algal abundances (Szmant, 2002), except in extreme cases.

5. Loss of herbivory as a causative factor

All over the world, in practically every marine habitat, fishing activities have severely reduced the population sizes as well as the average size of individual fish within a species for almost every commercially sought-after species for which data are available (Jackson et al., 2001; Meyers & Worm, 2003; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Pauly et al., 2002). Coral reef ecosystems have not been exempt. The removal, by fishing, of the major herbivores in tropical and subtropical food webs has resulted in decreased grazing, and hence increased proliferation of algae on many coral reefs (McManus et al., 2000).

This effect is generally expressed following a major disturbance, such as a storm. In most cases, algae will flourish immediately following a disturbance event in which large areas of reef substrate were cleared. Normally, excess algal growth is then quickly limited and/or controlled by herbivore grazing (Lewis, 1986),

allowing corals to reestablish successfully (Hughes, Ayre, & Connell, 1992). However, if grazers are not present in sufficient numbers, algal communities will succeed toward more permanent forms and species, preventing the recovery of the reef to its previous coral-dominated state (Szmant, 2002).

Fish are not the only major herbivores on reefs. In many areas, echinoderms, especially sea urchins, exert the primary control over algal populations. When these ecologically important organisms are removed in great numbers, as was the case with the outbreak of the Caribbean-wide *Diadema antillarum* epidemic in the 1980s, increased algal growth (principally FFM) can lead to severe inhibition of coral settlement and thus reduce community resilience.

In 1983–1984, *D. antillarum* populations were reduced across the Caribbean by approximately 93%, because of what was apparently a Caribbean-wide epidemic of an unidentified disease (Carpenter, 1997; Lessios, Robertson, & Cubit, 1984). This sea urchin was a major herbivore on Caribbean reefs, and its severe population reductions may have lowered coral reef resilience across the region. Others have suggested that gradual increases in nutrients in Jamaican waters, probably due to increases in coastal populations and construction (Lapointe, 1997), may contribute to the changes witnessed on Jamaican reefs. There are recent reports of improvements in coral cover, with the greatest increases occurring at 5 m depth (2.3–17.8%), correlated with increases in *D. antillarum*. This correlation, plus the fact that low nutrient levels alone did not result in recovery, have been interpreted as evidence that *D. antillarum* exerts top-down control on macroalgal abundance (Cho & Woodley, 2002). The fact that increases in macroalgal cover have occurred in reefs in Belize where *D. antillarum* has been reduced but not other herbivores indicates that the sea urchin may have played a unique role in preventing macroalgal dominance in that area (Carpenter, 1997). Despite the strong emphasis on the widespread loss of this sea urchin as a factor in phase-shifts in the Caribbean, it is important to note that this species is primarily abundant only in the upper 10 m of a reef. The fact that shifts to macroalgal dominance have frequently occurred in deeper portions of reefs, including those in Jamaica, indicates that factors other than the loss of *D. antillarum* have been important. Indeed Hughes (1994) emphasized the reduction of herbivorous fish by over-harvesting as a potentially major cause.

In the Indo-West Pacific, there seems to be no single herbivorous species whose loss would severely impact reef resilience. The reef flat of Santiago Island in Bolinao, Philippines, includes herbivorous sea urchins of which two, *Tripneustes gratilla* and *Salmacis sphaeroides* are particularly common. Investigations by Klumpp, Salita-Espinosa, and Fortes (1993) revealed that *T. gratilla* fed primarily on attached seagrass fronds (77–89% of diet), particularly the abundant *Thalassia hemprichii*. *Salmacis sphaeroides* was demonstrated to be a generalist, consuming *T. hemprichii* fronds (13–65%), detached seagrass debris (5–39%), the red alga *Amphiroa fragilissima* (0–30%), and algal-coated sediment and rubble (0–51%) depending on their local availability. This may indicate that in the more speciose Indo-West Pacific, there is a greater chance of one species functionally replacing another, and thus that the reefs are less sensitive to the loss of particular species through epidemics.

Despite the heavy emphasis in the literature on the role of herbivorous sea urchins as a factor in the phase shift, this can only explain limited aspects of the phase-shift problem. Outside of the Wider Caribbean, herbivory is associated with complexes of multiple species across phylogenetic boundaries (McClanahan et al., 2002b). Williams, Polunin, and Hendrick (2001) interpreted experimental results in Belize as implying that a gradual reduction of coral cover and increases in macroalgae have crossed a threshold, beyond which herbivorous fish were unable to limit macroalgal proliferation. This suggests that the fish populations were limited by factors other than the availability of their food, such as the protection from predation afforded by coral cover. These results indicate that there may be circumstances in the Caribbean where neither reductions in *D. antillarum*, nor increases in fishing pressure are sufficient to explain the coral–algal phase shift, and suggests that coral reduction itself may be critical in an unexpected way. Gardner et al. (2003) were able to explain some coral declines in the Caribbean as associated with the loss of *D. antillarum*, but had to invoke a wide range of explanations to account for the

overall picture of regional decline, including coral disease, bleaching, storms, predation, and various human impacts.

To determine the effects of herbivory and competition on interactions between a hard coral and a brown alga on the Great Barrier Reef, Jompa and McCook (2002) manipulated both coral and algal densities and used cages to exclude grazers. They showed that reduced herbivory resulted in the overgrowth of brown algae that then smothered and killed coral, whereas coral viability and expansion were demonstrated in the absence of brown algae. Competitive inhibition of the two organisms was mutual when the coral and algae were in direct contact, indicating that, in this case, coral was able to limit the overgrowth of the brown algae and vice versa. On Glovers Reef, Belize (McClanahan et al., 2002a), and the Mariana Islands, Guam (Belliveau & Paul, 2002), caging experiments to exclude herbivores resulted in higher total algal cover.

6. Combined effects of herbivory and nutrients

It is likely that the ability of a coral reef to withstand increases in nutrients is related to the integrity of the food chain. In a healthy reef, additional nutrients may be passed up the food chain, distributing biomass effects across all levels. In a reef in which natural herbivory has been reduced, the effect on the reef of increased nutrient levels may be to accumulate biomass at the primary production level – hence resulting in the dominance of macroalgae (Littler & Littler, 1984). The nature of this loss in nutrient absorptive capability is not known, and could result in a linear relationship between absorptive capacity and herbivory, or nonlinear immediate or direct effects (Fig. 2). This relationship would be crucial to quantitative analyses in support of management decision-making, and warrants specific analyses.

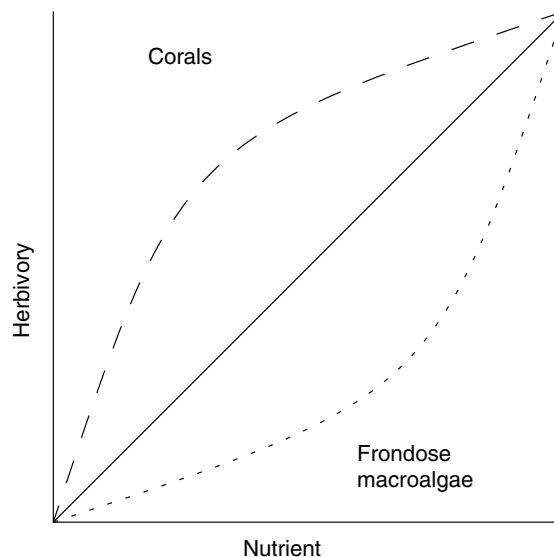


Fig. 2. Three potential relationships in synergy of herbivory and nutrient levels in influencing the tendency toward coral or macroalgal dominance. At any point in the graph, representing a combination of herbivory and nutrients, one would expect either more coral or more macroalgae. The lines represent potential combinations resulting in generally equal coral and macroalgae. If the middle line is the true case, then the synergy would be a constant, near-linear relationship, in which more nutrients must be accommodated by more herbivory in order for corals to be dominant. If the upper line is the true case, then very high levels of herbivory would be required to accommodate small increases in nutrients for corals to dominate. However, beyond some point, adding more nutrients would have little additional effect. In the case of the lower line, even low levels of herbivory can accommodate all but very high levels of nutrient additions for corals to dominate.

Jompa and McCook (2002) studied how herbivory, nutrients and competition between a hard coral and a brown alga interact to control benthic algal abundance. They found that nutrients had a small effect on algal abundance and consequent coral death but that this effect was only present when herbivores were excluded and the competing algae were already present in the caged sites. They conclude that nutrient enrichment will impact the competitive balance between corals and algae only when herbivore pressure is significantly reduced. A similar caging and nutrient enrichment study on outer slope reefs also demonstrated that nutrients had an effect on algal turf biomass and productivity only when herbivores were excluded (Hatcher & Larkum, 1983).

Using a combination of herbivore-excluding cages and nutrient enrichment, Thacker et al. (2001) found that herbivore exclusion shifted the algal community toward more palatable species and, overall, had a much greater effect on cyanobacterial and macroalgal biomass and community structure than nutrient enrichment. They speculate that reduced, but not fully absent, grazing pressure may encourage the dominance of less palatable macroalgal species. In their study, nutrient enrichment did not significantly affect the final biomass of any cyanobacterial or macroalgal species, regardless of the herbivory treatment.

Unfortunately, very few experiments have included simultaneous manipulations of herbivory and nutrient levels. Szmant (2002) argues that such multifactorial studies are essential to understanding the relative impacts of nutrients and herbivory because background levels of grazing on coral reefs will likely swamp any differences in algal growth resulting from nutrient enrichment.

7. Other contributing factors

The competition for space between hermatypic corals and macroalgae is potentially influenced by a broad range of factors (Fig. 1). Here, we briefly describe some other factors involved in determining coral or algal dominance. Expanded discussions of these can be found in McManus et al. (2000) and McClanahan et al. (2002b).

Siltation by silt, sand, mud, and mud-bacterial complexes known as “marine snow” (Wolanski, Richmond, McCook, & Sweatman, 2003) can reduce coral proliferation. In addition to the effects of nutrients discussed above, excess nutrients resulting in plankton blooms can reduce light, thereby inhibiting coral growth. The same process can potentially reduce macroalgal growth.

A variety of fish species graze on corals (Hixon, 1997; Randall, 1974), but this has substantial effects on coral proliferation only in specific instances. For example, the large bumphead parrotfish *Bolbometapon muricatus* eats living coral (Choat, 1991; Randall, 1974). In some cases in the Caribbean, the spotlight parrotfish has been known to proceed beyond the usual coral scraping and to dig deep into corals (Bythell, Gladfelter, & Bythell, 1992; Bruggemann, van Oppen, & Breeman, 1994; Bruckner & Bruckner, 1998). Coral proliferation can be drastically reduced by outbreaks of coral-eating mollusks, *Hermodice* worms, and other invertebrates in all reef areas, and in particular by outbreaks of *Acanthaster planci* starfish in the Indo-Pacific. Thus, there is a category of “Other Benthos” that can substantially limit coral proliferation.

Fishing for herbivores is likely to enhance macroalgal proliferation. Fishing for predators on the herbivores will, conceptually, tend toward reversing this effect. However, the result of fishing for predators has been shown to be unpredictable, particularly given that the level of predation may vary with the life stage of a fish (Morinière et al., 2003). It is believed by some researchers that fishing on the commercially important predatory fish *Lethrinus* spp. along the Great Barrier Reef has contributed to outbreaks of the coral-eating crown-of-thorns starfish *Acanthaster planci*, on which it preys. A study of gut contents of these fish in the vicinity of an *Acanthaster* outbreak failed to verify this, though the small sample size may have been a factor (Sweatman, 1997). If losses of *Lethrinus* spp. have been important in proliferating *Acanthaster* outbreaks, this, then, becomes an example where removing a predator allows for the increase of a coralivore, leading to reduced coral proliferation which potentially favors macroalgal proliferation.

The burrowing sea urchin *Echinometra mathaei* (de Blainville) can enhance coral settlement by providing suitable settling spaces (grooves) on reefs with substantial FFM, as demonstrated by Birkeland and Randall (1981) for Taiwan and Guam. However, in high densities they can cause a reduction in suitable substrate for coral proliferation, as described for Kenya by McClanahan (1995). Thus, fishing away predators on burrowing sea urchins can have unpredictable effects on reef resilience. Many other potential secondary effects of fishing are not well-investigated.

8. Characteristics of the phase shift and possible hysteresis

A conceptual model of the responses of FFM, CEM and coral to a major disturbance is illustrated in Fig. 3. FFM reproduces and grows quickly, followed by the slightly slower proliferation of CEM over dead

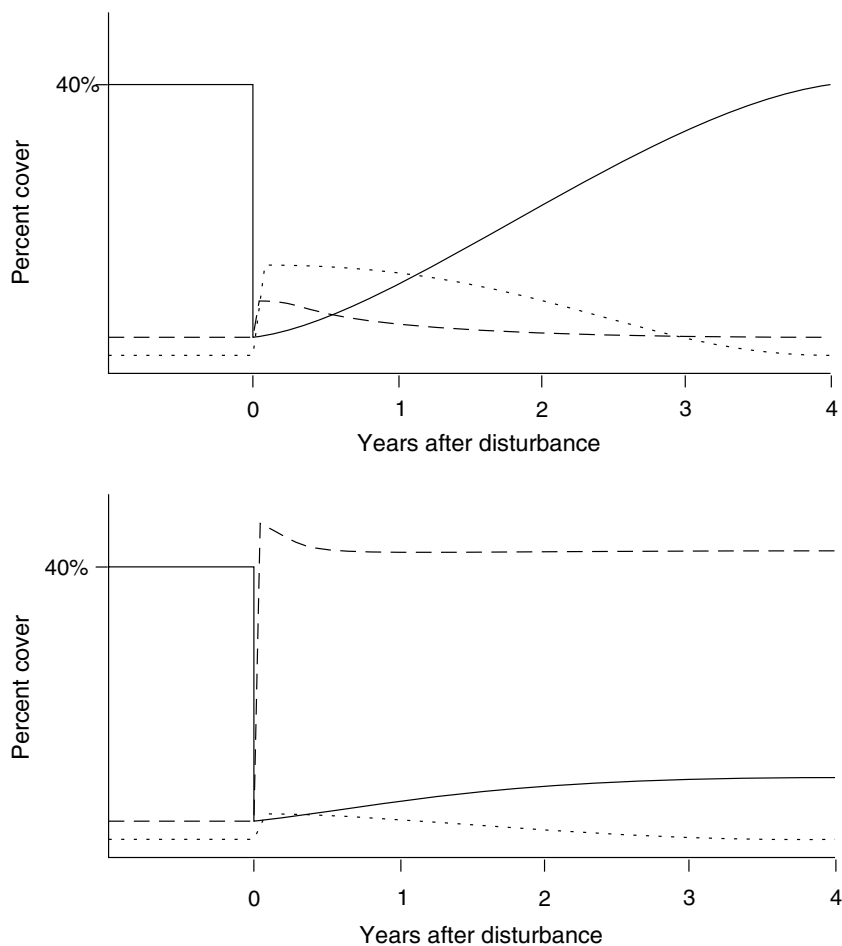


Fig. 3. Responses of coral communities with normal (top) and low (bottom) resilience to a major disturbance. Solid lines are coral, dashed are frondose macroalgae, and dotted are encrusting red algae that facilitate the settlement of coral planulae. It is generally believed that high nutrient loading, low herbivory, or a combination of these, are the primary factors leading to the phase shift to macroalgal dominance. Forty percent is the approximate global average of reef slope coral cover (McManus et al., 1995). However, scales of axes are only illustrative.

corals. However, in a “healthy” reef situation, the coral slowly recovers. Under conditions of reduced herbivory and/or increased nutrients, the macroalgae maintains its dominance.

Steneck and Dethier (1994) demonstrated that macroalgae in both tropical and temperate marine ecosystems tend to pass through successive assemblages that show a gradual increase in 3D complexity and height. Szmant (2002) suggested that this increase in complexity over time occurs within the coral community as well, as corals grow gradually from low to high colonies. We illustrate the two alternate courses of increased complexity following a disturbance in Fig. 4.

The diagram can be compared to that of Scheffer and van Nes (2004, their Fig. 3) for the two trajectories of biota in shallow lakes in the Netherlands, and the “hysteresis” effect wherein a reversal along one trajectory (turbidity) makes possible a switch to the other trajectory (a benthic plant assemblage). In the case of coral reefs, there may be cases wherein (envisioning a “reversal” of the time axis via perturbation) a reduction in the 3D structural complexity of the macroalgal community (e.g., removal of tall *Sargassum* spp. and *Turbinaria* spp.) may enhance resilience by increasing the likelihood of settlement and proliferation of corals. For example, it has been suggested that the tall *Sargassum* in parts of the Jamaican coral reefs may inhibit movement of grazing *Diadema*, thus delaying coral recovery (Jeremy Woodley pers. comm.). It is likely that the circular scrubbing of hard substrate by *Sargassum* plants under wave motion removes a majority of newly settled organisms. Steneck and Dethier (1994) point out that shading by successively larger FFM tends to remove competitive algae, thereby enhancing the stability of increasingly more complex macroalgal communities. McClanahan, Hendrick, Rodrigues, and Polunin (1999) have shown in Belize that the coverage of reef areas by dense FFM tends to decrease the abundance of herbivorous fish. Although invertebrate-feeding fish were also reduced, there was little evidence that this would enhance herbivory by invertebrates. Thus, the net effect was a stabilizing of the macroalgal community.

This tendency to follow a general trajectory, toward increasing macroalgal or coral dominance, is illustrated in Fig. 5. In this conceptual model, the effect of increased nutrients and/or decreased herbivory is

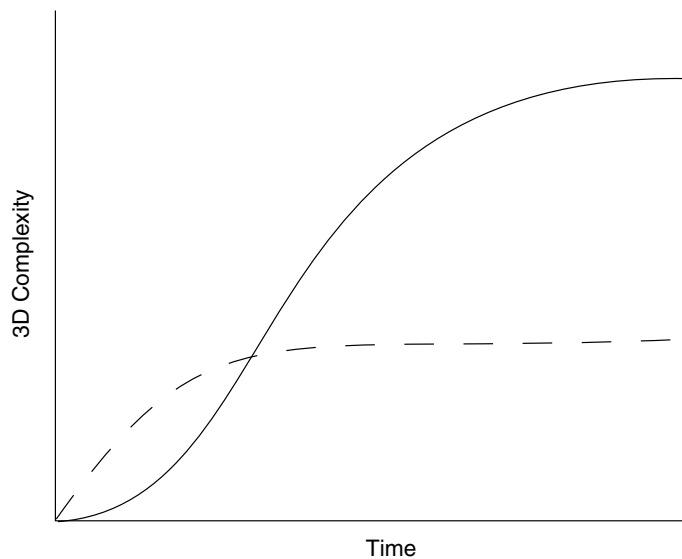


Fig. 4. Two potential trajectories of reef dominance following a major disturbance. The solid line indicates a succession toward high levels of coral complexity. The dashed line represents succession toward complex macroalgae, such as *Sargassum* spp. Shifting trajectories is easiest at low levels of 3D complexity. Note that the lines merely represent generalized trajectories, about which there could be considerable variation.

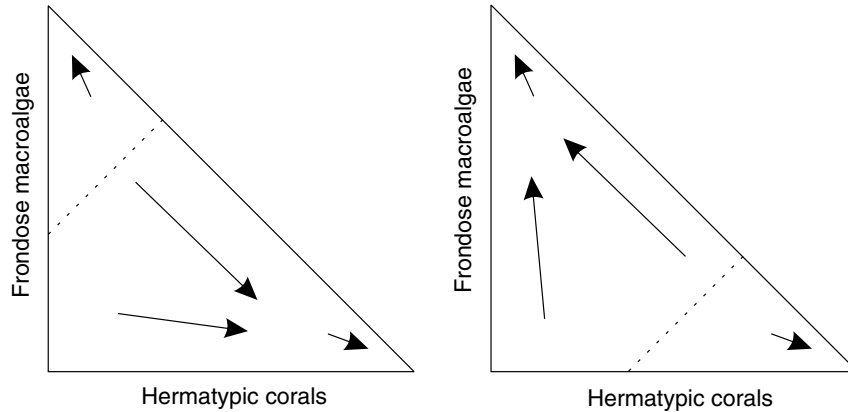


Fig. 5. State space of percent cover showing tendency for increasing coral or macroalgal cover over time, depending on starting ratio. The space is triangular because the two groups cannot total more than 100% cover. Each point within the triangle represents a starting combination of corals and frondose macroalgae. The arrows represent trajectories macroalgae (upper left corner) or coral cover (lower right corner). The dashed line is a threshold in starting combinations of the two components, dividing those that result in trajectories toward either exclusive macroalgae or coral cover. Stressed communities (right triangle) have a greater range of starting combinations that will result in trajectories toward macroalgal dominance. A disturbance (e.g., a storm) tends to reset the starting combination by creating new space for settlement, and the new combination depends on what is available to settle or expand horizontally. Long times between disturbances permit one or the other component to more completely dominate, and to progress to more complex growth forms and species, thus reducing the likelihood that a new disturbance of given impact will result in enough of a change to switch to trajectories leading to the opposite “corner” over a large area of reef (i.e., a hysteresis effect). Stress alters these probabilities in favor of macroalgae.

to shift the “ridge” dividing the starting points that lead to increasing coral complexity and those leading to increasing macroalgal complexity.

9. Studying coral reefs at appropriate scales

The hypothesis that stressors have reduced resilience in favor of macroalgal dominance on a global scale could perhaps be tested by analyzing the results of global-scale perturbations. The 1997–1998 El Niño resulted in patches of unusually warm seawater, especially in the Indian Ocean, wherein an estimated 50–95% of the shallow reef-building corals in surveyed areas were killed due to bleaching (expulsion of symbiotic single-celled zooxanthellae algae from the coral tissue) (Souter, Obura, & Lindén, 2000). It was suggested (McManus et al., 2000) that this perturbation could result in major net losses of coral cover because of decreased resilience. Although post-bleaching studies are underway in parts of the Indian Ocean and elsewhere (Souter et al., 2000), it will be a few more years before a net decline related to the bleaching can be verified with certainty.

Most studies of coral reef resilience, such as nutrient enrichment or herbivore removal experiments, have been conducted at a scale of a few tens of square kilometers, under very specific environmental conditions. However, coral reefs are extremely heterogeneous systems (Fig. 6).

The aspect of a particular part of a reef to storm waves, its proximity to freshwater sources, its depth and slope, and numerous other factors strongly influence the nature and degree of disturbances leading to reductions in coral cover as well as rates of coral growth. Patterns of circulation heavily influence the rates at which exposed areas can be resettled and at which fish and mobile invertebrate populations can be renewed. Basically, reef ecology varies across a reef as well as among reefs and reef systems (Edmunds, 2002;

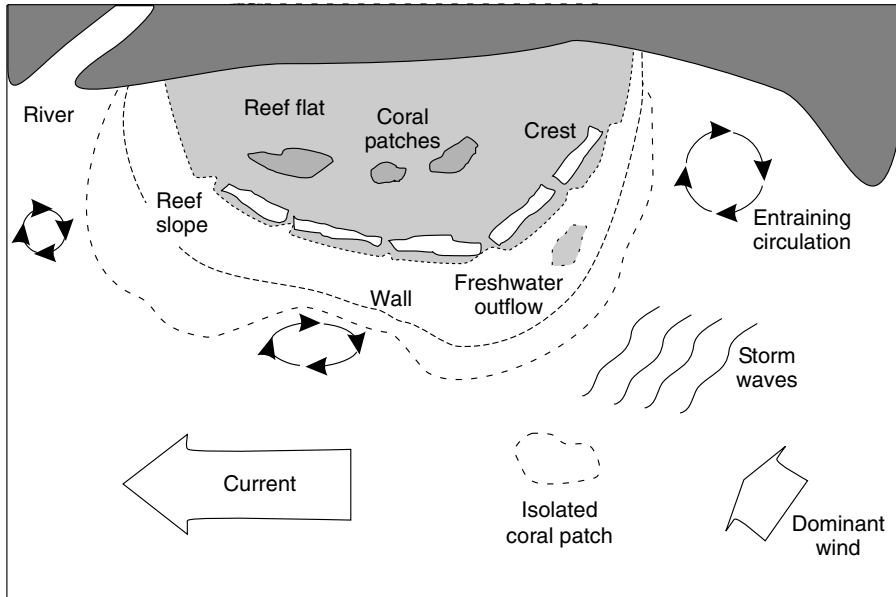


Fig. 6. Schematic of a fringing reef showing factors influencing spatially differential resilience.

Ninio & Meekan, 2002). Social and economic factors vary as well, particularly among reef systems. This spatial variability is best managed and modeled using a spatio-temporal approach.

Seen in this context, there is really very little known quantitatively about any of the processes concerning coral reef resilience at the whole-reef scale. Rates of herbivory in one part of a reef may differ greatly from those at another where environmental conditions, rates of settling of key species, and species composition also may be very different. Studies at the scale of a few quadrats in one area may tell us little about the cause and effect responses at another. This problem has been highlighted recently by Hughes et al. (2003):

Research in support of reef management urgently needs to increase the scale of experiments, sampling and modeling to match the scale of impacts and key biological processes (e.g., dispersal, bleaching, overfishing), and go beyond the current emphasis on routine monitoring and mapping. Indeed, most coral reef research is parochial and short-term, and provides little insight into global or longer-term changes. . . International integration and scaling-up of reef management is an urgent priority.

An example of a study at appropriate scales has been the study by Hughes et al. (1999a, 1999b) of coral recruitment along the length of the Great Barrier Reef which involves more than 40 scientists engaged in coordinated coral settling observations. Even at the scale of a single coral reef, a meaningful study of, for example, rates of herbivory, could be scaled up to the whole reef by stratifying the reef and conducting the study within quadrat areas selected via stratified random sampling (or an approximation thereof). Thus, the sampling is of the cause and effect responses of a reef by observation and/or experimentation so as to answer questions at the scale of the reef.

Providing answers managers can use requires the simultaneous study of many aspects of coral reef resilience along with linkages to the social and economic factors that impact these aspects. For example, various types and levels of fishing are involved in the loss of resilience on many reefs. The decisions as to which types of fishing should be reduced to what levels involve tradeoffs that include not only ecological impacts, but social and economic consequences as well. Thus, the analysis of resilience in support of reef management is best conducted in an interdisciplinary context, including ecological, physical, social and

economic studies aimed at determining ranges of potential interventions and their consequences across the disciplines.

It has been widely recognized for more than 30 years that the best approach to understanding coral reefs as ecological systems would be to conduct long-term, large-scale, model-driven studies comparatively on a variety of reef systems around the world (McManus, 2001; Sachet & Dahl, 1974). The new Comparative Analysis of Reef Resilience Under Stress (CARRUS) Alliance is intended to address this concern (www.ncoremiami.org). It will involve independently-supported, long-term, model-driven studies on major reef systems around the world, conducted in such a way as to facilitate the comparison of cause and effect relationships among reef systems in widely varying environments and with different species compositions.

10. Conclusions

1. The coral–algal phase-shift phenomenon in coral reefs is generally believed to be the result of gradual increases in stress due to loss of herbivory and/or increases in nutrient levels, but is usually triggered by a major perturbation such as a hurricane, crown-of-thorns infestation, outbreak of coral disease, or bleaching event. There is some evidence that the shift may occur in the absence of a single strong perturbation, as with the Kaneohe Bay overgrowth in Hawaii in the 1980s. Thus, susceptibility to a “red noise” cause (Steele, 2004) is not to be ruled out. Hysteresis is highly likely in terms of the increased resistance to perturbations as corals grow large given long times between perturbations. There is some evidence that a similar hysteresis may apply to the succession of macroalgae, once a phase shift has been initiated – the macroalgae becoming larger and increasingly more resistant to perturbations and to infiltration by coral recruits, given a reasonable chance to proliferate.
2. A widely accepted hypothesis that susceptibility to nutrient loading is greatly enhanced by a loss of herbivory would, if better reinforced by field studies, indicate that a strong top-down factor is important in the phase shift. The herbivory includes that by mobile invertebrates and fish (endogenous factors), and the decline in herbivory has been enhanced by fishing (anthropogenic exogenous forcing). The phase-shift itself can be maintained for decades by endogenous benthic processes (bottom-up forcing), but there is little evidence that this occurs without concurrent stresses such as overfishing and nutrient loading.
3. Small-scale experiments have been helpful in determining the mechanisms involved in the phase shifts. As suggested by Szmant (2002), additional multifactorial experiments focused on the combination of herbivory and nutrient loading would add greatly to this understanding. However, ecological processes vary widely across a given reef system, such that it is unlikely that a quantification of causes in one area, determined at a scale of tens of meters, would be a valid basis for management decisions and intervention at whole-reef levels. Recent efforts to promote large-scale, long-term, whole reef studies and to organize comparative analyses among reef systems are intended to fill this critical gap between scientific inquiry and management needs.

Acknowledgements

We thank our colleagues at the National Center for Caribbean Coral Reef Research and the Rosenstiel School of Marine and Atmospheric Science for superb discussions regarding this manuscript. The manuscript has benefited from critical comments from three anonymous reviewers. Funding in support of this effort was provided by the National Centers for Environmental Research of the United States Environmental Protection Agency (Grant EPA-R-82802001) and by NSF (Grant OCE 0119976).

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