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Resilience of Coral Reefs

Tim R. McClanahan, Nicholas V. C. Polunin,
and Terry J. Done

Coral reef ecosystems are restricted to tropical latitudes (within 30° of the equator) and therefore experience relatively constant environmental conditions on the basis of the seasonal cycles. This relative stability may produce organisms and ecosystems that are poorly adapted to environmental fluctuations. It is, therefore, arguable that coral reefs may be among the least resilient ecosystems on the planet and may be good indicators of environmental changes such as global warming (Glynn 1993; Brown 1997). There is good evidence, however, that tropical environments and coral reefs experience significant intra- and inter-annual variation in environmental conditions, such as temperature and light (McClanahan 1988; Sheppard 2000), albeit less than temperate latitudes. Reefs are also one of the most persistent ecosystems over the Earth's geological history (Veron 1995). The species that have created reefs have, however, waxed and waned over time and the species and even taxonomic orders dominant in the present Cenozoic era are significantly different from those of the Mesozoic and Paleozoic eras (Veron 1995). Consequently, there has been considerable debate among reef ecologists and geologists over the issue of reef resilience and stability and whether the geologic past is relevant to the scale and types of contemporary disturbances (Brown 1997).

Coral are exposed to a large number of natural and human-influenced disturbances that affect their species and ecological adaptations and organization (Connell 1978; Rogers 1993; Hughes 1993; Brown 1997). Many of these ecological disturbances may, however, be averaged out, and reefs may appear to be more stable over geologic (Pandolfi 1996) than ecological time (Connell et al. 1997). Over geologic time (more than hundreds of years) the species composi-

tion of geologic deposits may remain fairly stable even in the presence of disturbances over ecological time (days to tens of years). In some cases species composition may change while total species richness remains similar, because newly evolved species can compensate for species extinctions (Jackson et al. 1993; Budd et al. 1996), but this may vary between ocean basins (Jablonski 1998). Gains and losses of species appear to occur on the scale of millions rather than of hundreds of thousands of years, and most extant reef species have been present over the past few million years or a number of glacial cycles (Veron 1995; Jackson et al. 1996).

Despite the potential long-term stability of reefs in the face of many disturbances, there is concern that recent human-induced environmental changes may be exceeding the limits of tolerance of reef organisms to factors such as water temperature, ultraviolet radiation, and predation by humans (Glynn 1993). For example, the warmest temperatures of the last 100,000 years were only about 1°C above today's. To find temperatures 3°C warmer, as predicted by global climate change models, one must look back several million years to the Pliocene, when the Earth's and coral reef biota were different from today's (Veron 1995; Livingstone 1996). These changes in background environmental factors will be associated with the rapidly rising use of reefs for fisheries and other types of resource extraction (coral building blocks, medicine, and so forth). Dual stresses could have variable consequences, with some counteracting each other and others being synergistic. Some synergistic relationships may lead to species losses and novel ecosystems with lost ecological services in cases where single stresses might have been tolerable.

Below we will introduce some of the basic aspects of reef ecology and discuss the conditions that appear to lead to characteristics of both resilience and non-resilience of ecological structures, functions, and their management at different spatial scales. Our analysis relies heavily on a number of recent case studies where reefs have or have not been resilient to environmental and human disturbances.

Reef Functions

One of the simplest ways to view the ecological function of coral reefs is through two of the main outputs of reefs—organic and inorganic (calcium carbonate) carbon production (figure 5.1). Carbon, largely available as bicarbonate ions dissolved in seawater, is fixed by reef organisms for the production, maintenance, and reproduction of the organisms themselves as well as their skeletal structures. The production of skeletal structure or the calcium carbonate production ranges from 1 to 10 kilograms per square meter per year (Kinsey 1985,

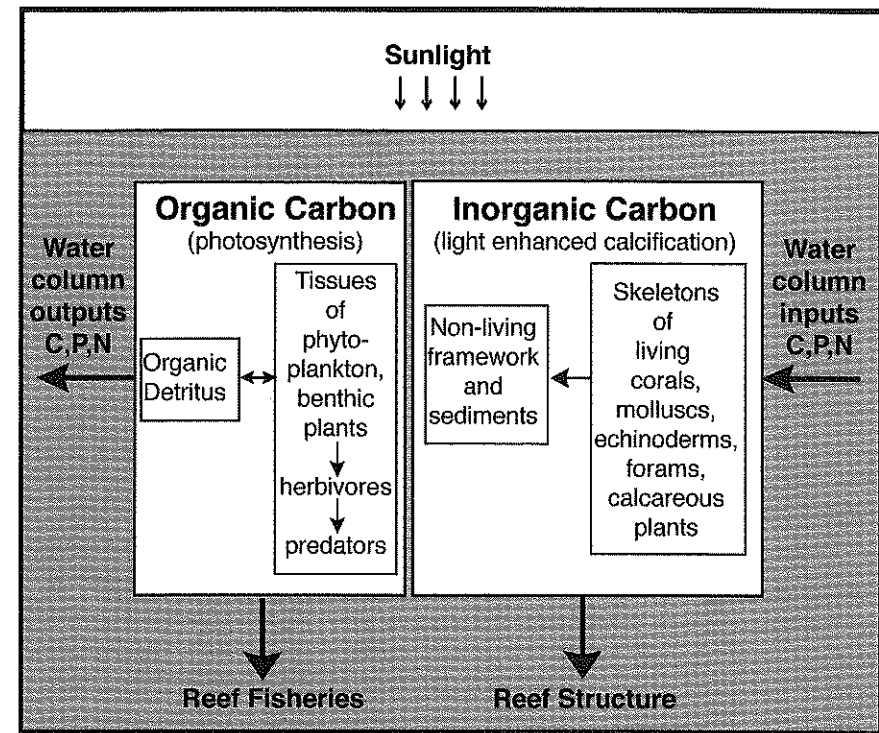


Figure 5.1. Diagrammatic representation of the pathways of carbon fixed in coral reef ecosystems. Diagram aggregates carbon accumulation by organic and inorganic (calcium carbonate) pathways.

1991). Skeletal structure is also broken down into sediments that form sandy bottoms and beaches and are an important fraction of the inorganic carbon pathway (figure 5.1). Gross organic production, as well, is also high at 1 to 9 grams of carbon per square meter per day, which is equivalent to 3.5 to 32.2 kilograms wet per square meter per year. Such production supports the complex and diverse organisms and food webs found on most coral reefs.

Primary production is largely dependent on a variety of algae that principally include four main functional groups. These are symbiotic algae living in hard corals (zooxanthellae), fast-growing filamentous turf-forming algae (turfs), larger fleshy red, brown, and green algae (fleshy algae), and algae that deposit calcium carbonate skeletons (red coralline and green calcareous algae) (Steneck and Dethier 1994). Each of these groups exhibits a slightly different balance between organic and inorganic production, or tissue growth versus skeletal or defensive structures. Corals and their zooxanthellae and coralline algae generally

Table 5.1. (a) Energy inputs into a typical coral reef system, and (b) standards of metabolic performance for three main types of benthic substratum

(a)

<i>Energy Input</i>	<i>Actual Energy, joules/m²/y</i>
Solar energy	7.1E+9
Waves, absorbed	9.9E+8
Currents, kinetic	6.6E+8
Tides	1.1E+8
Rain, physical	3.1E+4

Source: Data from McClanahan 1990 based on East African data.

(b)

<i>Substratum*</i>	<i>Photosynthesis gC/m²/day</i>	<i>Production/Respiration</i>	<i>Calcification kg CaCO₃/m²/y</i>
Continuous coral	20	1	10
Algal pavement	5	> 1	4
Sand and rubble	1	< 1	0.5

Source: Data from Kinsey 1991.

* These three categories are the dominant substrata in the "framework," "pavement," and "sand" zones, respectively, of coral reefs. Varying proportions of one or both of the other two categories may be present.

have relatively low organic production but higher inorganic carbon production, while turfs and fleshy algae have the opposite pattern (table 5.1). As we will show later, reefs can be dominated by different functional groups that can greatly affect the ratios of organic to inorganic production.

Undisturbed coral reefs seldom seem severely nutrient limited. Field studies indicate that, as water passes over coral reefs, there is no net uptake of phosphorus and an export of nitrogen (Pilson and Betzer 1973; Wilkinson et al. 1984). This indicates that the physicochemical factors that influence production of both organic and inorganic carbon are primarily dependent on sunlight and water motion from waves, tides, and currents (table 5.1). Sunlight is the largest single energy input, but the total energy in water motion, of tides, currents, and waves combined is also large and is important in transporting resources and waste products of the reef. Perhaps equally important for maintaining high production are disturbances to the primary producers, which maintain an early

stage of ecological succession and, therefore, high photosynthesis and growth rates of turf-forming and fleshy algae (Carpenter 1988; Choat 1991). Consequently, some investigators have argued that the abundance of grazers is the main limitation to primary production on coral reefs (Larkum 1983). Consumers, in general, frequently disturb their prey and they, therefore, may often be responsible for the high production of reefs by maintaining their prey in high-growth phases and by supplying concentrated nutrients to their prey (Polunin 1988; Meyer and Schultz 1985).

Ecological Services

Disturbances are important in maintaining high biological production and shaping general reef ecology. It should be recognized, however, that many ecological processes have a unimodal (hump-shaped) response to disturbance or production factors, and either too little or too much of the factor can reduce production or structure from a maximum level. It is the net production of resources that is available for humans, not the gross. Net productivity of both organic and inorganic carbon are considerably lower than gross measures because a significant portion of the production is lost from the reefs or, more importantly, consumed by the coral-reef organisms themselves, largely in respiration, self-maintenance, or reproduction (Polovina 1984; Birkeland 1997). In the case of inorganic calcium carbonate production, there are whole suites of organisms that erode these skeletal structures into sand (Glynn 1997). Sand can be exported from the reef to form sand-based ecosystems such as seagrass meadows and beaches. Consequently, as little as 1 percent of the gross organic production of reefs is available for humans, largely in the form of various seafood (Birkeland 1997). Few estimates of the amount of inorganic carbon available for human resources have been made, as humans do not directly use most inorganic carbon. Instead, inorganic carbon constitutes an indirect ecological service such as shoreline protection and the formation of beaches. Coral blocks from dead or living corals are important for building in many tropical coastal settlements, but little effort has been made to determine the sustainable level of extraction of calcium carbonate (Risk and Sluka 2000).

Alternate Structures and Interacting Processes

Coral reef ecologists have reported a variety of community or ecosystem states that are often described by the dominant organisms or functional groups (figure 5.2). These states are often attributed to human influences, where the two most common environmental concerns of reef ecologists have been the influences of

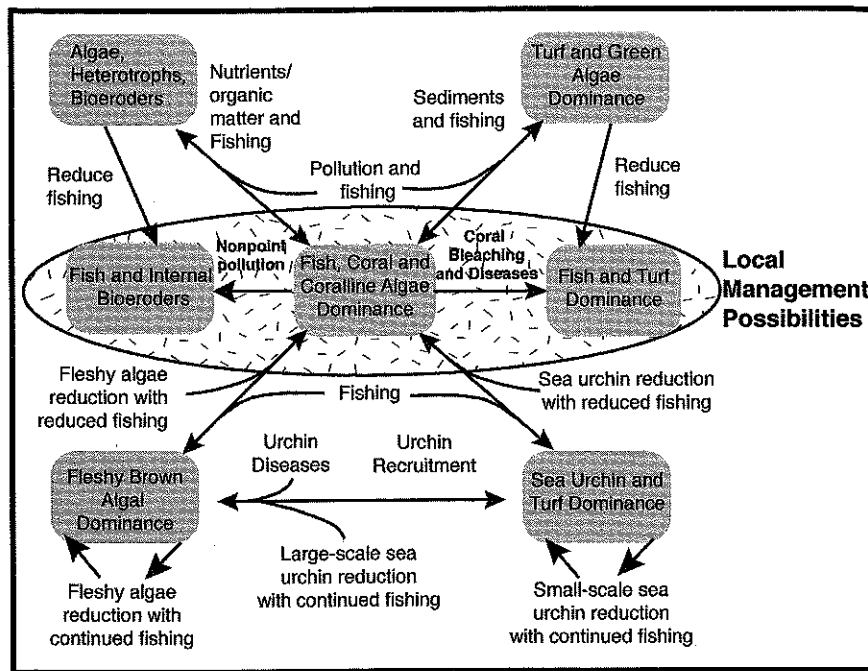


Figure 5.2. A simple conceptual model (meta-model), depicting the different ecological states (gray polygons) of coral reefs and the factors that may cause or maintain these states.

harvesting and pollution. A conceptual model based on major functional groups (figure 5.2) predicts a variety of ecological states, depending on combinations of pollution, fishing, sediments, diseases, and other natural disturbances such as cyclones and human management. Because reefs are often exposed to a combination of human and natural influences, individual reefs may be an amalgamation of many of these states.

Many reef ecologists believe that increases in nutrient concentrations in waters will switch dominance from corals to various forms of fleshy and filamentous algae and bioeroding sponges (Smith et al. 1981; Cuet et al. 1988; Bell 1992; Lapointe et al. 1997; Rose and Risk 1985; Risk et al. 1995). Nutrification, or the addition of growth-promoting nutrients such as nitrogen and phosphorus, has the potential to increase the growth rates of some fast-growing algae and heterotrophic invertebrates relative to corals (Littler et al. 1991; Lapointe et al. 1997). Many studies have shown, however, either only small or no responses to nutrient additions (Kinsey and Domm 1974; Kinsey and Davies 1979;

Hatcher and Larkum 1983; Larkum and Steven 1994; McClanahan et al. 2002). Some algae, such as browns, actually decrease in the presence of nutrification while others, such as greens and blue-greens, increase (Borowitzka 1972; McClanahan et al. 2002). In the Caribbean, some sites considered to be oligotrophic have high cover of macroalgae (e.g., Williams and Polunin 2001). All other variables being equal, an increase in nutrients and algal growth might be expected to cause a reef dominated by late-successional fleshy algae, sponges, and soft corals. In practice, however, there are a number of disturbances, particularly to algae, which prevent this from occurring. Most important, herbivory (Hatcher and Larkum 1983; McCook 1999), but also physical disturbances like water movement and the saltation of sediments along the seafloor, can frequently reduce algae and compensate for increased algal growth (McClanahan 1997a). Fishing, sometimes associated with a reduction in herbivory, and nutrification may interact to produce algal growth responses (figure 5.2).

The combination of fishing and pollution does not always shift reefs from dominance by corals and early successional algae to late-successional algae. For example, fishing can promote the abundance of herbivorous sea urchins (Hay 1984; McClanahan and Shafir 1990) that graze intensely and reduce the abundance of algae to levels even lower than when fish dominate grazing (McClanahan 1995a, 1997a). In a second example, when nutrient additions are associated with sediments from a river or a dredging operation, the physical disturbance per se can retard the successional development of algae (McClanahan and Obura 1997; McClanahan 1997a). Additionally, in areas or seasons with high wave or current energy, algae may be constantly disturbed and unable to maintain high levels of abundance (McClanahan et al. 1996). The abundance of macroalgal may also be increased by spatial escapes from grazing with the loss of coral cover through disease and other disturbances (Williams et al. 2001). Food webs are one way in which the functional linkages among ecosystem components are perceived, but because predation is only one process affecting abundance of organisms, their ability to predict indirect effects in ecosystems is very limited (Polunin and Pinnegar 2002). Consequently, there are a number of contingent outcomes to pollution and fishing disturbances depending on how these factors interact among themselves (McCook 1999) and with diseases and other physicochemical conditions.

In order to achieve the conservation objective of increasing the abundance and diversity of corals and fishes, managers have the option of trying to reduce fishing and pollution as well as reducing pest species or groups such as sea urchins and unpalatable fleshy algae. In many cases, it is important to attempt a combination of these management options as the outcome will often depend on an interaction of two or more factors (McClanahan et al. 1996, 2001).

Disturbances, Time Scales, and Reef Ecology

The kinds, scales, and intensities of disturbance vary both regionally and locally (Scoffin 1993), and may be modified by human population growth, resource exploitation, and industrialization. Episodic events (those lasting a few hours to months) that can injure, kill, and collapse most corals over scales of hectares include hurricanes (Woodley et al. 1981; Scoffin 1993; Rogers 1993; Massel and Done 1993), freshwater (Hedley 1925), predators (Endean 1976; Moran 1986), stress-related bleaching (Glynn 1993; Brown 1997), and sedimentation (Cortes and Risk 1985). Other disturbances, such as the many diseases reported in Caribbean corals in recent years, may take years to decades to decimate local population of corals (Antonius 1985; Aronson and Precht 1997). While we suggest elsewhere in this chapter that the quantity (frequency, intensity, and distribution) of each of these types of episodic and long-term disturbances has been modified greatly by humans, most disturbances, we believe, are qualitatively similar to disturbances reefs have experienced since their origin.

Natural Disturbances: Cyclones

The statistical likelihood of a particular coral reef being exposed to strong wave forces varies greatly. It is negligible in the doldrums, which extend to 10° north and south of the equator. Reefs between these latitudes are subject, instead, to weaker monsoonal storms. When and where extreme events do occur, the reefs involved are, at the very least, substantially set back to an earlier successional stage dominated by coral rubble and algal turf. At most, cyclones destroy the entire coral architecture and redistribute rubble and biogenic sediments (Woodley et al. 1981; Scoffin 1993; Dollar and Tribble 1993). Within cyclone latitudes, the expected "cyclone-free" longevity of a massive coral (Massel and Done 1993), which may also be thought of as a surrogate for the longevity of uninterrupted succession, first increases, then decreases with increasing distance from the equator. In some reef areas, the length of "cyclone-free" successional runs are predicted to shorten as cyclone frequencies increase under current global climate change scenarios (Pittock 1999; Done 1999).

Crown-of-Thorns Starfish

Populations of coral-eating crown-of-thorns starfish *Acanthaster planci* are a normal part of Indo-Pacific coral reefs. They are the cause of the largest known pest-related disturbances on Indo-Pacific reef systems and are regarded as a major management problem (see Moran 1986 and Birkeland and Lucas 1990 for reviews). The starfish eats coral tissue, favoring abundant fast-growing plate and

branching corals but also consuming the tissues of rarer, slow-growing massive types that take much longer to replace themselves (Done 1987, 1988). The starfish have periodically killed more than 90 percent of the corals on many reefs throughout the region since the 1960s, returning to individual reefs after about fifteen years. In the first few years following such outbreaks, algal-covered reef-scapes are drab compared to their coral-dominated predecessors and successors.

Human-Induced Disturbances

Humanity may be affecting the frequency, intensity, and distribution of many types of disturbance. For any given reef in the Great Barrier Reef, for example, the average interval between cyclone impact and inundation by a flood plume is likely to decrease under all global climate change scenarios (Pittock 1999). The amount of terrestrial sediments re-suspended by those storms and delivered by those floods will likely increase as a result of elevated soil erosion from land used for many decades to centuries for various urban, industrial, water conservation, and rural activities. Humans, through fishing down of keystone predators (Ormond et al. 1988; McClanahan 1995c) or elevating nutrients (Birkeland 1982), may increase the frequency and intensity, and increase the geographic extent of, coral predators such as crown-of-thorns starfish (*Acanthaster planci*) and gastropods (*Drupella* spp.).

Nutrients and Sediments

On the Great Barrier Reef, small-scale experiments have in the past indicated negative effects of inorganic nutrient additions on two major ecological functions of reefs (figure 5.1), namely total primary productivity (Kinsey and Domm 1974) and coral calcification (Kinsey and Davies 1979). More recent controlled exposures to ammonium and phosphate, either individually or together, indicated that the most important primary producers, the epilithic algae, may be nutrient sufficient (Larkum and Koop 1997). In fact, in some areas, factors other than nutrients may be limiting to algal production, such as light (Adey and Goertemiller 1987), inorganic carbon supply, space availability (Williams et al. 2001), or, indirectly, water movement (Larkum and Koop 1997). Nutrients may stimulate the production of algae that could potentially overgrow and kill corals (Tanner 1995; Lapointe et al. 1997). Nonetheless, other disturbances such as grazing and saltation of sediments often compensate for this increased growth (Hatcher and Larkum 1983; McClanahan 1997a; McCook 1999) such that the predicted competitive exclusion does not occur. It appears that many reefs are, therefore, resilient to inorganic-nutrient additions, and this may be

governed by a number of circumstances. Thus, reefs generally have substantial nutrient stores in sediments and biota, and external supply may be substantial (Tribble et al. 1994; Polunin 1996). There is better evidence, however, that erosion of reef structure increases with increased nutrients (Risk et al. 1995).

Large-scale nutrient additions to reefs from human activities will generally come from the land, but these additions are often accompanied by other changes in water quality, such as increased concentrations of suspended particulate matter and reduced salinity. Thus, where large-scale degradation has occurred in inshore reef communities, attribution of this degradation to specific factors such as nutrients is uncertain (Kinsey and Davies 1979; Tomascik and Sanders 1987; Tomascik et al. 1997).

Corals are generally considered to be sensitive to sedimentation effects, but primary framework-building corals vary in their ability to withstand sediment deposition on them and some may thus be considered resilient (Rogers 1993). Sediments may change the generic composition of corals but not the total coral cover (McClanahan and Obura 1997) or may arrest the successional development of algae at the turf stage rather than accelerating it toward erect fleshy algae (McClanahan 1997a). Because these studies were undertaken in marine protected areas, where fishing was excluded, it was easier to distinguish river sediment effects from other likely human influences. Whatever the specific mechanism, coral reefs in areas with human development can be expected to display ecological changes. These include the maximum depth of water to which corals grow (Tomascik et al. 1997), coral community composition (Randall and Birkeland 1978; van Katwijk et al. 1993), fish abundance and species composition (Amesbury 1981; Green et al. 1997), and processes such as grazing and sediment turnover (McCook 1996; Green et al. 1997).

Resource Extraction

Fisheries are the most extensive extractive use of living reefs. Fishing reduces the abundance and mean size of target species such as snappers (Lutjanidae), groupers (Serranidae), grunts (Haemulidae), and emperors (Lethrinidae), and it is evident, even on lightly fished reefs, that the decline in biomass may be rapid (Jennings and Polunin 1996a). Since many such fishery-target species are carnivorous, the abundance of whole trophic groups of fishes, such as invertebrate-feeders, is thought to be sensitive to exploitation (figure 5.3a). This swift depletion of target species is the basis for contention that reefs are sensitive to fishing, and indeed the catch per unit effort does decline in a similar fashion (figure 5.3b). However, as in other fishery stocks, decline in biomass is evidently accompanied by increased productivity (Jennings and Lock 1996). The stocks

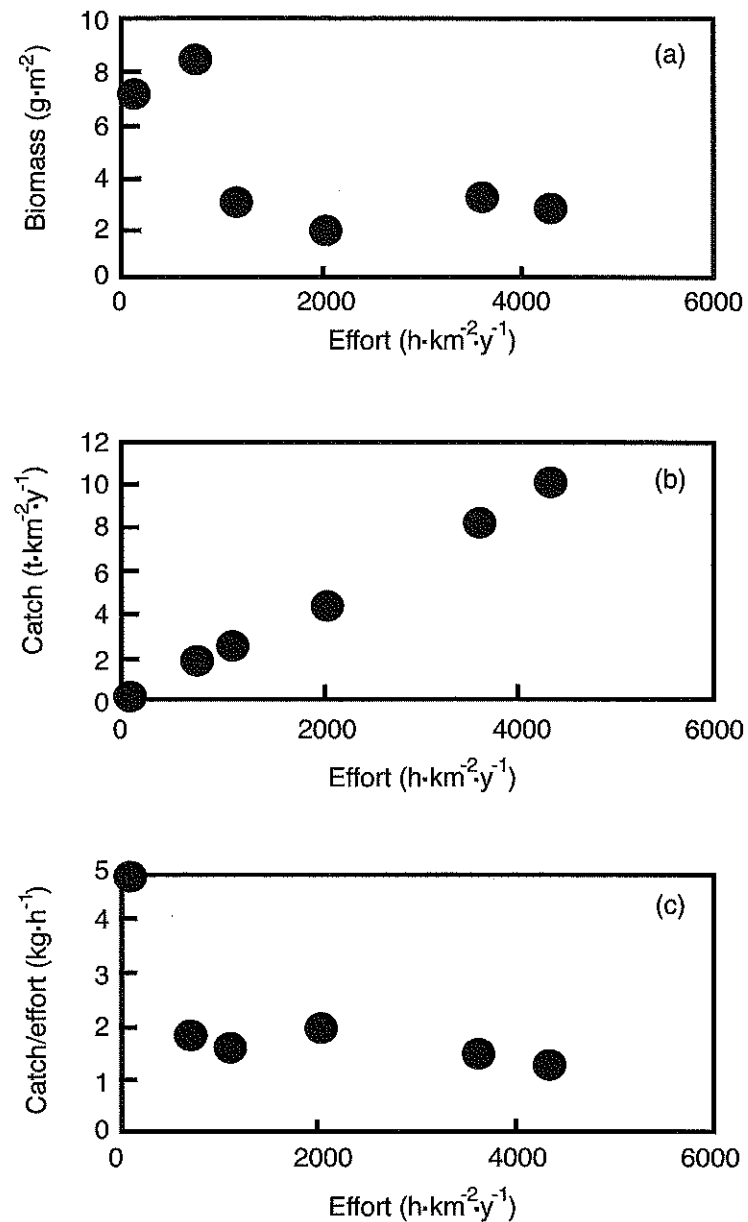


Figure 5.3. Depletion and sustainability of small-scale reef fisheries in Fijian traditional fishing grounds (*goliqoli*) subject to different levels of fishing pressure: (a) decline in biomass of invertebrate-feeding fishes estimated by underwater visual census (UVC) at low levels of fishing effort (Jennings and Polunin 1996a), (b) evidence that the catch rate per unit of reef area increases linearly as fishing effort increases (after Jennings and Polunin 1995a), and (c) catch and effort data corroborate those from the UVC analysis (after Jennings and Polunin 1995a).

involved, therefore, may be quite resilient to exploitation in productivity terms (figure 5.3c). In spite of earlier impressions to the contrary, reef fishery stocks in the South Pacific are able to support yields that are high on a per unit reef area basis (fresh weights of 10 to 30 tons per square kilometer per year). The sustainability of these high levels of productivity is corroborated by modeling studies (Polunin et al. 1996) and by their own persistence in time (more than ten years), although in interpreting existing fisheries yield data, care should be taken with the units of comparison (Munro 1996). Field studies on Kenyan coral reefs suggest that fish catch, through the use of seine nets that catch small fish, is reduced on a per-area and per-effort basis compared to sites without this gear (McClanahan et al. 1997; McClanahan and Mangi 2001). Modeling studies suggest that catch rates and selection can affect fisheries yields (McClanahan 1995b).

Substantial contributions to reef fisheries yields may, however, be made from adjacent unexploited coral reefs or from other ecosystems such as seagrass, plankton, and sandy-bottom ecosystems (Polunin 1996). Consequently, high fishing pressure may in many such cases be substantially supported by recruitment from distant reefs that are lightly exploited, as may be the case in archipelagoes such as Fiji (Jennings and Polunin 1996a). On many Kenyan fringing reefs, fisher folk fishing within protected lagoons often catch fish that have migrated in from deeper and less-fished reefs. Additionally, many of the coral-associated species are not an important part of the fisheries at high levels of fishing effort. The catch from coral reefs is frequently composed of species of generalists that are only weakly associated with coral reefs, or of species more frequently associated with other ecosystems or food sources, such as plankton, sandy bottom, or seagrass meadows.

Fishing has had profound and often indirect influences on reefs in areas such as the Caribbean and Kenya (figures 5.2 and 5.3, and see below). A number of studies have shown increased abundance and diversity of small-bodied damselfish, parrotfish, and wrasses on heavily fished reefs (Russ and Alcalá 1989; McClanahan 1994, 1997c) and losses of species at the highest levels of fishing (McClanahan 1994, 1997c; Ohman et al. 1997). A comparative study of Kenya's fringing with patch reefs of Tanzania found a 50 percent loss of species diversity on the fringing reefs but not the patch reefs (McClanahan 1997c). This may be due to habitat differences. It is more likely, however, that the fringing reef environment has the effect of compressing fisher folk behind the reef, resulting in high population densities (7–14 per square kilometer) in shallow (less than 5 meters deep) reef and seagrass habitats (McClanahan and Kaunda-Arara 1996; McClanahan et al. 1997). The densities of Tanzanian fisher folk are less (2–4 per square kilometer) and reefs are typically separated by deeper water

(McClanahan et al. 1999). Consequently, many of the indirect changes associated with fishing may be dependent on the density of fisher folk and their catch selection, as also suggested by model simulations (McClanahan 1995b), and the densities on Fijian reefs are typically low.

Unsustainable exploitation may occur where fishing is extensive and recruitment overfishing occurs. In the central Pacific, there is as yet little evidence that these high levels of human disturbance have detrimental side effects on the wider ecosystem. Koslow et al. (1988) presented evidence for changes occurring in the fish community of Jamaican reefs as a result of exploitation, but these may be best explained by selectivity of the fishing process, and ecosystem or indirect effects of fishing are not necessarily involved. The expectation that prey fishes, such as those of small size, or those of many nontarget groups, should increase in abundance when piscivorous fishes are removed by fishing has not been corroborated by work focused on some of the larger target species (Jennings and Lock 1996; Jennings and Polunin 1996a).

Interactions between Disturbances

In many cases, disturbances interact to cause ecological change on coral reefs. For example, one prediction of the effect of sedimentation on coral reefs is that soft corals should increase in abundance (De'ath and Fabricius 2000), but in Kenya, this appeared to be the case only in areas with high water movement (McClanahan and Obura 1997). Coral bleaching may also result from a combination of elevated water temperatures, low water movement, and light or ultraviolet radiation (Gleason and Wellington 1993; Brown et al. 1994; Dunne 1994), and each of these factors may modify the level at which bleaching occurs. There are probably cases where more than two disturbance factors interact, and future investigations will need to consider this possibility.

Recovery Rates of Reefs

In coral reefs, recovery following catastrophic disturbance may or may not result in a return to the predisturbance community structure (Hatcher 1984; Done 1992; Knowlton 1992; Hughes 1994; McClanahan and Obura 1995). Whatever the specific details, the rate of recolonization and growth is as much a function of the location of the coral reef as a property of the recolonizing populations (Done et al. 1996). Within large and dense archipelagos arranged along major current systems (such as the Great Barrier Reef) most reefs regularly receive dense aggregations of the larvae released from upstream reefs (Doherty and Williams 1988; Oliver and Willis 1987). In this setting, high degrees of

gene flow have been demonstrated in a number of invertebrate taxa (Benzie 1994). There is, nonetheless, enormous interannual variation in larvae supply and recruitment success among patch reefs and across whole regions (Doherty and Williams 1988).

At reefs separated from their neighbors by great distances, unfavorable currents, or both (as in French Polynesia), it seems likely that larvae from other reefs would arrive less reliably. There may be intervals of many years, decades, or even longer, between "good years" for exogenous larval inputs, and they would depend much less on them than on retention of their own reproductive output (Planes et al. 1993).

Corals

The Great Barrier Reef, which is a dense archipelago of individual reefs, would appear to provide optimal conditions for coral settlement, recruitment, and growth following natural disturbance and return to normal conditions (Done 1992). The recovery rate of corals on slopes severely damaged by crown-of-thorns starfish decreased with increasing water depth with rates (expressed as percentage of total substratum) of around about 7 percent, 5 percent, and 2 percent annually at 1 meter, 3 meters, and 6 meters in depth respectively (Done et al. unpublished). After fifteen years, some denuded shallow sites had attained near 100 percent coral cover, while deeper sites were mostly 30 percent or less. By far the greatest contribution at all depths was made by the same fast-growing branching and plating corals that were dominant before the predation event. In Indonesia, the same suite of corals colonized a denuded area at a rate exceeding 12 percent per year (Tomascik et al. 1996). The rapid linear extension rate of individual corals came, however, at the expense of a marked reduction in skeletal density.

The Great Barrier Reef and Indonesian examples contrast markedly with examples from the Caribbean (Connell 1997). For example, in the Dry Tortugas, coral settlement densities were only a fraction of those observed on the Great Barrier Reef (Kojis and Quinn 1994). Combined with a tiny post-settlement survival rate and poor supply and survival rates of coral fragments, negligible recovery was observed. Studies on Florida coral reefs (Patterson et al. 1997) indicate a continued and widespread negative impact on coral cover by a variety of diseases.

Recovery in massive corals on the Great Barrier Reef has been assessed using simulation models (Done 1987, 1988b). These suggest that the currently observed fifteen-year recovery interval may be sustainable only on some reefs. The criterion for a "sustainable disturbance interval" was the time necessary,

under conditions of simulated recurrent disturbance, for the coral population to consistently maintain a balanced size-class distribution, including the oldest class. Differences among the reefs were a function of the preexisting structure of the target coral population, the size-specific damage regime, and inter-episode rates of coral recruitment, survivorship, growth, and repair. All of these parameters, as well as outbreak intervals of the starfish, may change under global climate change scenarios.

Fishes

The common larger reef fishes, including coral trout (Ferreira and Russ 1992), parrotfishes (Choat et al. 1996), and snappers, may only rarely exceed twenty-five years of age. Consequently, if recruitment is sufficient, the time it will take for a depleted stock to approach its unexploited biomass should usually be twelve to twenty years. In cases where depletion is less severe, substantial effects of protection from fishing can be expected in shorter periods of time, and have in fact been indicated by work on marine reserves in the Caribbean (Polunin and Roberts 1993), small-scale fishing in the South Pacific (Smith and Dalzell 1993), and a newly created marine park in Kenya (McClanahan and Kaunda-Arara 1996). Exceptions to such recovery rates can be expected where recruitment is limited, as may be the case at remote sites in the Pacific and certain areas in the Caribbean (Roberts 1995). McClanahan (2000) found that the triggerfish, *Balistapus undulatus*, a keystone predator, was still recovering in marine protected areas after twenty years of protection from fishing. Additionally, there may be differences in the recovery rates of different fish families or species (McClanahan and Kaunda-Arara 1996), and recovery may also be dependent on the ecological or structural state of the reef. For instance, the recovery rate of reef sites in a newly created marine park appeared to depend on the abundance of sea urchins (McClanahan 1997b). Sites that had been protected from fishing for over three years showed only minimal recovery over this time, but an experimental sea urchin reduction led to a recovery of corals and fishes (McClanahan 1997b).

Other Organisms and Reef Structure

Most reef ecologists have focused on the recovery of corals and fishes, and so less is known about other groups and their recovery times from disturbances. Recovery is, however, often closely related to the territory or size of the individual organisms or the structure of the reef (figure 5.4). Most of the primary production is achieved by reef algae and the recovery rate of these algae is usually less

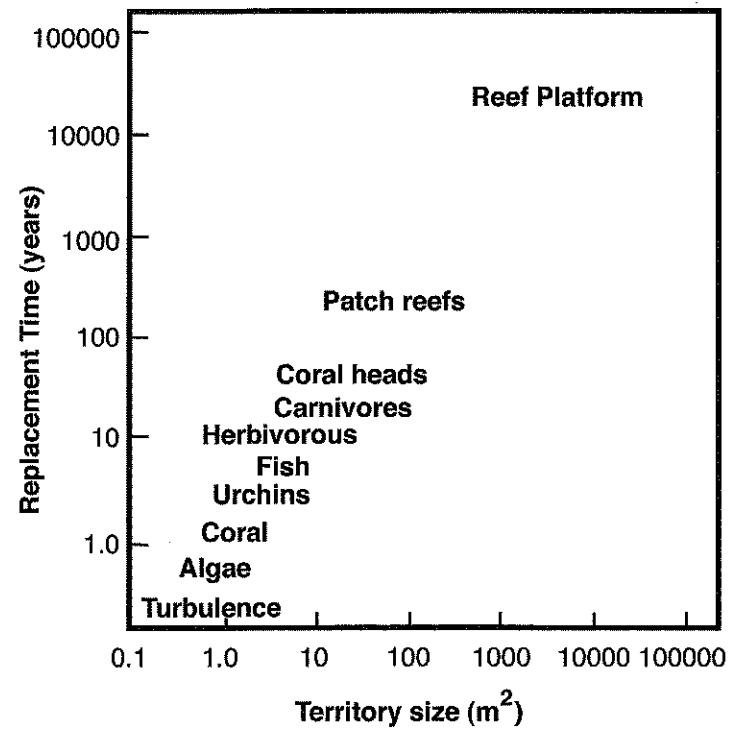


Figure 5.4. Graph showing the replacement time and territory of the major reef components.

than a month for the microscopic filamentous turfs and a few months for the larger erect fleshy and calcareous algae (McClanahan 1997a). The recovery of heterotrophic organisms is usually slower, ranging from years to decades, and the recovery of the reef structures themselves, which include everything from massive coral heads to platform reefs, ranges from decades to millennia. Many of the reef structures we see today have been formed since the last sea-level rise during the past ten thousand years but, in many cases, they were built on reef structures of older origin. Reefs deposit calcium carbonate at a rate of about 1 kilogram per square meter per year, which corresponds to a vertical accretion rate of 0.8 millimeter per year, which is near the global sea level rise of 1.3 millimeters per year over the past one hundred years (Smith 1983). Consequently, reef growth usually keeps pace with the glacially induced sea-level change, but there are some cases, particularly at high latitudes, where reefs can “drown” because they grow too slowly to keep pace with sea-level rise (Grigg 1997). Predictions for the rise in sea level due to global warming are as high as 15 millimeters per year, in

which case many reefs could potentially drown if this rate persists over a few centuries (Buddemeier and Smith 1988).

Factors That Contribute to Resilience

Below we describe factors that appear to increase the resilience of coral reefs, as shown by a number of case studies. Resilience is defined here, as in the rest of the book, as the ability of ecosystems to resist lasting change from disturbances (Gunderson et al. 1997) and not the return time of an ecosystem after disturbance (Haydon 1994). In many cases, the quality of science is not sufficient to distinguish between alternative explanations and in other cases it is frequently a number of factors that have either reduced or increased resilience. Consequently, some of the following case studies and explanations should be considered speculative until further studies test the validity of the proposed explanations. The factors proposed to influence resilience should, therefore, be seen as working hypotheses until better tested.

Species Diversity

Evidence is accumulating, particularly from terrestrial plant studies (Naeem et al. 1994; Tilman and Downing 1994; Tilman et al. 1996; Chapin et al. 1998), that “functional diversity” is able to stabilize or buffer ecosystem processes such as resource uptake and productivity. Consequently, species diversity may have the capacity to increase ecosystem resilience by ensuring that there is sufficient informational redundancy to protect against risks associated with environmental disturbances (Naeem 1998). Evidence to support this hypothesis from coral reefs is at present ambiguous. For example, there is little evidence that regions with lower diversity of corals have lower or more variable rates of calcium carbonate deposition, or that areas with lower diversity of algae have lower rates of productivity (Kinsey 1983; Smith 1983). Even though some regions have lower species diversity than others, all maintain similar functional diversity. Functional diversity appears to be maintained within ecosystems even when species diversity is low. The low number of studies and the limited accuracy of measurements of productivity and net calcium carbonate deposition make any conclusions at this point highly speculative, and future work will need to distinguish between functional and species diversity.

Areas with low species diversity, namely the eastern Pacific and the Caribbean, have experienced dramatic changes in their ecology during the past few decades. In the eastern Pacific, the El Niño warming of 1983 led to a series of ecological changes that devastated many reefs in the region. High water

temperature caused bleaching and mortality of 70 to 95 percent of corals in Costa Rica, Panama, Columbia, and Ecuador (Glynn et al. 1988; Glynn and Colgan 1992). High temperatures also extirpated populations of a crustacean guard of the dominant coral *Pocillopora* that left the coral vulnerable to the starfish predator, *Acanthaster planci* (Glynn 1987). The final insult to these reefs was a largely unexplained increase in the populations of a sea urchin, *Diadema mexicanum*, which, through its feeding activities, began to erode the reef framework to such an extent that many of the reefs are disappearing (Reaka-Kudla et al. 1996). The 1983 El Niño had a one-in-one-hundred-year return frequency, so perhaps reefs are able to form and recover on this time scale. However, most eastern Pacific reefs are low diversity, seldom form extensive reef flats, and are sparsely distributed.

In the Caribbean, a series of diseases has resulted in a basin-wide reduction in the primary reef-building coral, *Acropora palmata* (Antonius 1981; Gladfelter 1982; Aronson and Precht 1997), and in an important grazer, *Diadema antillarum* (Lessios et al. 1984). Many of the reefs in this region are now dominated by erect algae (Carpenter 1990a; Hughes 1994; Shulman and Robertson 1997; McClanahan and Muthiga 1998), and this, in turn, is suppressing a number of fish species and their grazing rates (McClanahan et al. 2000a, 2001). Although there are few reported studies, it is fair to assume that these reefs have changed not only in species composition (McClanahan et al. 2001) but also in terms of the important ecological processes such as organic (Carpenter 1988) and inorganic production (Sammarco 1980, 1982). In addition, the recovery rate of corals after disturbances in the low-diversity Caribbean has been slower than recovery in the high-diversity Indo-Pacific (Connell 1997). Consequently, there is some cause to believe that species diversity increases the capacity of reefs to tolerate and recover from disturbance, but more research into the mechanisms is required.

Keystone Species and Redundancy

Conventional ideas linking diversity and resilience may or may not be useful in understanding coral reefs. High species diversity may confer a measure of redundancy that maintains ecological processes when individual species decline (McNaughton 1977; King and Pimm 1983; Tilman et al. 1996; Naeem 1998), even though stability of species can be reduced in high diversity systems (May 1977; Haydon 1994). In practice, there may be sufficient biological differences among species such that species are not always fully redundant, interchangeable, or replaceable (Rowan et al. 1997). Disturbances may, over the long term, detrimentally affect specialists more than generalists because specialists are

often slow growing, site attached, territorial, and competitive dominants (*K*-selected), while generalists will frequently exhibit the opposite traits (*r*-selected). Disturbances to specialists may result in their replacement by fast-growing and vagile generalists until specialists recover and reoccupy their niche. Differences in species' use of resources may result in only partial filling of the specialist's niche. In other words, it cannot always be assumed that generalists will always replace the role of specialists, nor that one specialist replace the role of another, even if they appear to be fairly similar to each other ecologically. Consequently, the loss of key species, even in high-diversity systems like coral reefs, can result in changes in reef ecology that alter resource use, productivity, or accretion.

Loss and Replacement of Keystone Species

Two cases illustrate the effect of either the loss or replacement of keystone species on the structure and function of reef systems.

SEA URCHIN PREDATOR CASE STUDY

Relationships between sea urchins and their fish predators can greatly affect reef ecology. Sea urchins have been reported in the stomachs of a large number of fish species (Randall 1967), and it might, therefore, be inferred that one sea urchin predator could easily be replaced by another predator. However more careful analyses of sea urchin predators suggest that complete replacement of one predator by another is, in fact, unlikely.

First, many of the species having sea urchin contents in their guts are not actually predators of sea urchins but, rather, scavengers of dead sea urchins (McClanahan 1995c, 1999) (figure 5.5). There are fewer true predators than scavengers, and in many cases one or a few species are doing most of the predation (McClanahan 1995c, 1999, 2000). Of the eight species of predators of the sea urchin *Echinometra mathaei* in Kenya, one species, the red-lined triggerfish (*Balistapus undulatus*), preyed on over 80 percent of experimental urchins. This fish exhibited sophisticated eating and foraging habits compared to wrasse and scavenger predators (McClanahan 1995c). The other predators were a variety of large, often-terminal male wrasses, and a few other invertebrate-feeding fishes (Lethrinidae) that were also common scavengers of sea urchin carcasses. At Mombasa Marine National Park, there was a change in the dominant predator shortly after the cessation of fishing, as the triple-lobed wrasse (*Cheilinus trilobatus*) was replaced by the red-lined triggerfish during the first few years after the park's creation (McClanahan 2000). Observations indicate that the red-lined triggerfish is aggressive toward other predators like the triple-lobed wrasse, and

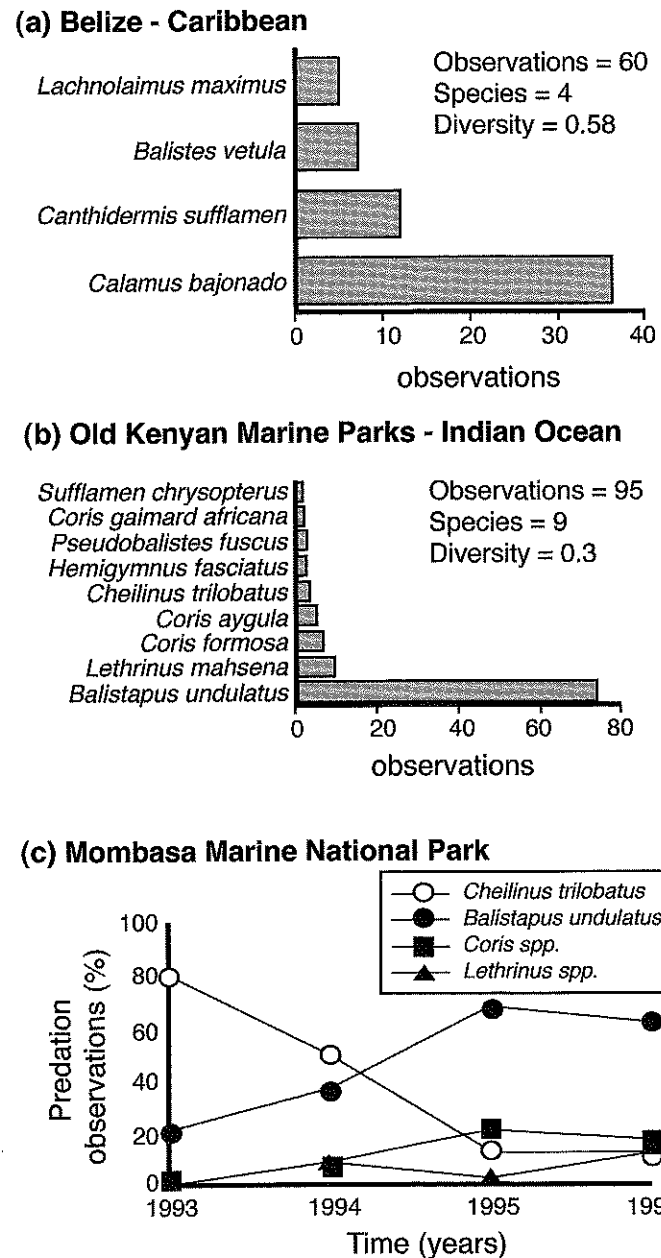


Figure 5.5. Predators of (a) the sea urchin *Echinometra viridis* in Glovers Reef Atoll (Belize), (b) *Echinometra mathaei* in Kenyan marine parks (western Indian Ocean), and (c) the change in predators in the Mombasa Marine National Park over its early stages of protection from fishing.

as its populations recovered it was able to reduce the frequency of predation of its competitors (figure 5.5c).

The red-lined triggerfish is very uncommon in shallow water outside of East Africa's marine protected areas while the wrasses and scavenger species are relatively common (McClanahan 1994, 1997c, 2000). The aggressive behavior of the triggerfish, which may make it the competitive dominant in the sea urchin predator guild, is a disadvantage in heavily fished reefs because it is often among the first species to take bait in traps or on lines. It may also recover slowly after being eliminated by fishing (McClanahan 2000). The red-lined triggerfish is, therefore, uncommon in a well-developed fishery, while the other predators such as some of the wrasses and scavengers are able to tolerate fishing disturbances and continue to be common in the catch of mature fisheries (McClanahan personal observation). Consequently, many of the fished reefs in East Africa have lost the dominant sea-urchin predator through fishing, and the predator role is largely being assumed by other species of wrasse and scavengers.

Sea urchin densities are typically far greater on fished reefs than in older and fully protected marine parks (McClanahan and Shafir 1990; McClanahan 1998). It appears that the subdominant and more naive predators are unable to maintain sea urchin populations at the low levels found in reefs undisturbed by fishing. An increase in sea urchin populations has a series of ecological effects on the reef. A beneficial effect of the sea urchin increase is a reduced biomass of fleshy algae and possibly increased net production and nitrogen fixation (Carpenter 1988; Williams and Carpenter 1988; McClanahan 1997a). Detrimental effects are increased erosion of the reef substratum (Birkeland 1988; McClanahan 1995b) competition with, and a reduction of, herbivorous and other invertebrate-feeding fishes (Carpenter 1990b; Robertson 1991; McClanahan et al. 1994, 1996), and, at the highest levels of sea urchin abundance, a loss of coral cover (Sammarco 1980; McClanahan and Mutere 1994). Consequently, the accumulation of sea urchins is probably associated with an increase in net organic production but a decrease in inorganic carbon production. Much of this net organic production is not transferred beyond the sea urchin grazer guild, so it does not benefit fisheries (McClanahan 1995b). In fact, there is accumulating experimental and theoretical evidence that sea urchin dominance reduces fisheries production (McClanahan 1995b, 1997b; McClanahan et al. 1994, 1996).

In the Caribbean, the queen triggerfish (*Balistes vetula*) may be an ecological equivalent to the red-lined triggerfish in the western Indian Ocean (although experimental evidence is sparse). At remote, but fished, Glovers Reef Atoll, Belize, this species was the third most common predator of *Echinometra viridis*. The more generalized jolt head porgy (*Calamus bajonado*—Sparidae, figure 5.5) was the dominant predator (McClanahan 1999). This may reflect a similar sit-

uation to that found during the early stages of the Mombasa Marine National Park, where a subdominant is the main predator because the dominant has not recovered from the effects of fishing. Further research will be needed to test this hypothesis. Queen triggerfish populations have been reduced to such an extent in the Caribbean that it is being listed as one of the regions threatened species (Hudson and Mace 1996).

LOSS OF A SEA URCHIN

On relatively undisturbed Caribbean reefs, major groups of grazers, particularly sea urchins and herbivorous fishes, contribute substantially to the maintenance of hard-coral cover and recruitment by suppressing algal biomass (Sammarco 1980, 1982; Lewis 1986; Hughes 1994). A certain balance is maintained between the grazer groups by predation and competitive interactions (figure 5.6a). It is likely that the black-spined sea urchin (*Diadema antillarum*) became an important grazer in the Caribbean because both its main fish competitors (including parrotfishes and surgeonfishes) and its predators (including wrasses, triggerfishes, and porgies) were susceptible to fishing pressure. Grazing by an increased abundance of the sea urchin was able to compensate for the loss of fish grazing pressure caused by fishing (figure 5.6b). *D. antillarum* thus came to play a pivotal grazing role in the ecosystem (figure 5.6c).

In 1983–1984, *D. antillarum* declined by about 98 percent across the region, as the result of a pathogen (Lessios 1988a). Experimental removal of *D. antillarum* had earlier shown its role in controlling algal abundance in shallow reef sites (Sammarco 1982). Although there was scope for other herbivores to compensate in grazing (Carpenter 1990b; Robertson 1991; McClanahan et al. 1994, 1996), remaining herbivorous fishes and other species of sea urchin were not able to achieve the grazing levels maintained by *D. antillarum* (Hughes et al. 1987; Lessios 1988b). This is probably because of continuing fishing pressure (Hughes 1994) and perhaps because there was insufficient ecological redundancy between *D. antillarum* and other unfished species (McClanahan 1999). As a result, fleshy frondose algae quickly became dominant (figure 5.6d). Fleshy frondose algae were also promoted by coral mortality as a result of cyclones, coral bleaching (e.g., Williams et al. 2001), and perhaps elevated nutrients (Shulman and Robertson 1997; Lapointe et al. 1997). In this case, therefore, the system was initially resilient to a fundamental shift in structure because macroalgal suppression was maintained by more than one group of grazers. As far as it is possible to tell, resilience was lost when the grazing function became largely reliant on one grazer, which was susceptible to a pathogen. On deeper Caribbean reef areas (e.g., 12–15 meters), the role of urchins in reducing macroalgal overgrowth was small even before the mass mortality. A negative

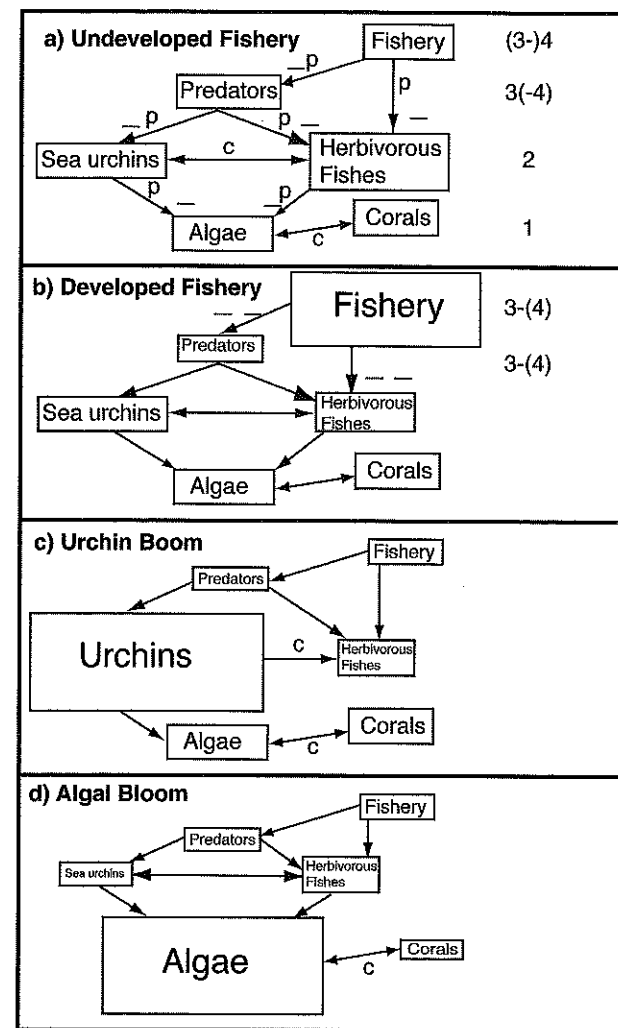


Figure 5.6. Schematization of changes that are thought to have occurred in shallow-water coral reefs of the north coast of Jamaica. Changes in the size of compartments between diagrams suggest changes in the importance of the group or activity (fishery) at each stage, but relative sizes of compartments within diagrams are arbitrary. (a) With light fishing, it is postulated that the biomass of predatory and grazing fishes would have been comparatively great, the abundance of sea urchins would have been relatively low and a certain balance would have been maintained between corals and macroalgae; it is possible that this ceased to be the case many decades ago (Jackson 1997). (b) The fishery depleted predatory and herbivorous fishes, so reducing predation and competitor pressure, respectively on sea urchins. It is supposed that macroalgae did not increase because sea-urchin grazing was substituted for fish herbivory to some extent. Corals remained abundant. (c) Substantial depletion of predators and herbivorous fishes is thought to have led to a sea-urchin boom, which in the early 1980s at least was curtailed by the impact of a microbial pathogen. (d) The reduction in total grazing then led to a bloom of macroalgae, which outcompeted the hard corals. The latter were also reduced by hurricanes. The numbers on the right-hand side of (a) and (b) indicate the trophic levels principally involved. The letters *p* (in [a]) and *c* (in [a], [c], and [d]) indicate predatory interactions and competition, respectively. The minus signs indicate negative effects of interactions (– = significant, – – = substantial)

correlation between abundance of parrotfishes and surgeonfishes and macroalgal cover (Williams and Polunin 2001) is indicative of these grazers controlling that cover today. In shallow reef areas, it is not clear how a return to a balanced grazing by both urchins and grazing fishes might be accomplished.

Spatial Heterogeneity and Refugia

Coral reefs can be resilient to multiple scales of disturbances (Pandolfi 1996; Connell 1997). One important factor that maintains this resilience is the scattered patchy distribution of reefs throughout tropical ocean basins (UNEP/IUCN 1988). The reefs are thus open to recruitment from other reef sources outside of the disturbed areas. Ocean-wide currents can potentially deliver larvae across hundreds to thousands of kilometers (Roberts 1997), although actual dispersal may be more limited (Cowen et al. 2000). Consequently, the combination of spatial heterogeneity and refugia of reef systems, the temporal heterogeneity of dispersal, and a physically stable but moving transport system of currents ensures the connectivity among reefs that are required for recovery. This is an important aspect of ecological resilience.

MARINE PARKS AS REFUGIA

Heavy fishing is now pervasive throughout the tropics and undoubtedly extends farther offshore than in the past (see chapters in McClanahan et al. 2000b). Pollution is often diffuse and many tropical watersheds are heavily influenced by human activities (Lapointe et al. 1997; Hodgson 1997). Consequently, spatial refuge for many reef organisms and ecosystems is often limited to marine protected areas or deep and remote reefs (McClanahan and Obura 1995). The absence of any systematic differences between effectively protected and unprotected areas in the Caribbean indicates, however, that linkages between fishing and benthic structure are weak in these reefs (Williams and Polunin 2000). However, some theoretical (Bohnsack 1993; Roberts and Polunin 1991, 1993) and mathematical modeling (DeMartini 1993; Man et al. 1995; Holland and Brazee 1996; Sladek Nowlis and Roberts 1997), and field studies (Alcala and Russ 1990; McClanahan and Kaunda-Arara 1996; McClanahan and Mangi 2000) of marine protected areas support the possibility that refuge from human disturbances could increase the total resilience of coral reef fisheries by offering refuge to the larger and reproductively mature individuals and to their required habitat.

Two field investigations of the fisheries adjacent to marine protected areas in the Sumilon Island Park in the Philippines and the Mombasa Marine National Park suggest that parks can improve fisheries yields such that they may partially

compensate for the lost fishing area. A seven-year study of the fish catches adjacent to the Mombasa Marine National Park found that, although 65 percent of the fishing area was taken up by the park's establishment in 1991, the total catch decreased only by 35 percent, due to a 110 percent increase in the catch per person of those fishers that remained (figure 5.7). Once the park was reduced from 10 to 6 square kilometers in October 1995, the catch quickly increased and then declined to a level just short of the total catch of the area without protection. The coincidence between beach seine exclusion and the reduction in the refuge make it difficult to distinguish the effect of the park's size and the fisheries management adjacent the park's border. There was, however, evidence that the degree of spillover depends on the adjacent management (McClanahan and Mangi 2000) and the time since the creation of the protected area (Russ and Alcala 1996; Sladek Nowlis and Roberts 1997). In Sumilon Island, however, a similar pattern in fish catch was observed when a small park covering 25 percent of the reefs of the island stopped functioning and fishing began inside the park. The loss of the park resulted in a 54 percent loss in the total yield of fish from the island (Alcala and Russ 1990). These experimental management and modeling studies combined suggest that spillover from refuge such as marine protected areas have a partial ability to compensate for lost fishing grounds and decrease variability in fish catches.

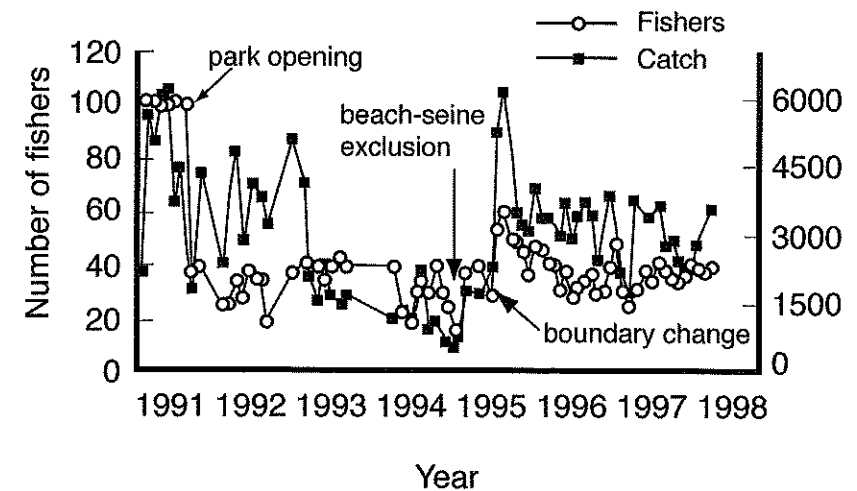


Figure 5.7. Time-series data of the number of fishers and their individual and total catch for a period in which a marine park was created, the size of the park was reduced, and beach-seine fishing was excluded.

CONNECTIVITY

In the long run, isolation can have devastating consequences to ecosystems. Connectivity can aid maintenance of ecological resilience, it can also expose the ecosystem to invasive species and thereby reduce, or at least challenge, the ecosystem's resilience (Simberloff 1991). This is true when the species assemblage is exposed to novel disturbances such as a new pathogen or predator or a keystone species as described above for *Diadema antillarum*. Novelty can challenge ecosystems' resilience, but it is also arguable that over the long-term, disturbance is self-organization around novel events or organisms that incorporates novelty into the total biological diversity. This new diversity, in turn, becomes a part of the ecosystem's resilience. Consequently, the temporal scale of disturbance can result in different conclusions concerning connectivity and resilience.

A complementary alternative to the above novelty-resilience hypothesis, still relevant to connectivity, is the *stress model*. This model makes a series of predictions about the structure of species assemblages based on the idea that smaller and more isolated water basins experience more physicochemical environmental variability than do larger and open environments (Odum 1985; Bertness and Hacker 1994; Kareiva and Bertness 1997). The stress model predicts that small and isolated ocean basins will have (1) fewer, (2) smaller-bodied, and (3) less-ornate species that largely feed low in the trophic web and which are mostly detritivores and herbivores (Vermeij 1978; Bertness 1981; Odum 1985; McClanahan 1992; Rapport and Whitford 1999). These predictions are, however, based more on population dynamic considerations (Pimm 1982) and less on an adaptive system or species accumulation model (Odum 1983; Kauffman 1995). Fluctuating environments will largely and by chance have fewer species that can tolerate the environment, and those that can tolerate it are likely to feed on the most abundant food and have fugitive strategies. Consequently, large, shallow, and oxygen-demanding bodies are likely to do poorly in stressed environments.

An example in support of this stress theory is the assemblage structure of gastropods in shallow waters of different ocean basins (Vermeij 1978; Stanley 1986; McClanahan 1992). Gastropods are a good assemblage with which to test some of these hypotheses because they are largely adapted to hard bottom aquatic environments, they are relatively easy to see and identify, are noncolonial, eat a variety of foods, and leave a fossil record. Based on searches of shallow-water environments in the Caribbean (Belize and the Florida Keys) and the Indian Ocean (Madagascar and Kenya), there is good support for these hypotheses (figure 5.8). In addition, a similar pattern was seen when comparing a bay (Florida Bay) in the Caribbean with a more open environment (Hawk Channel, figure 5.9, McClanahan

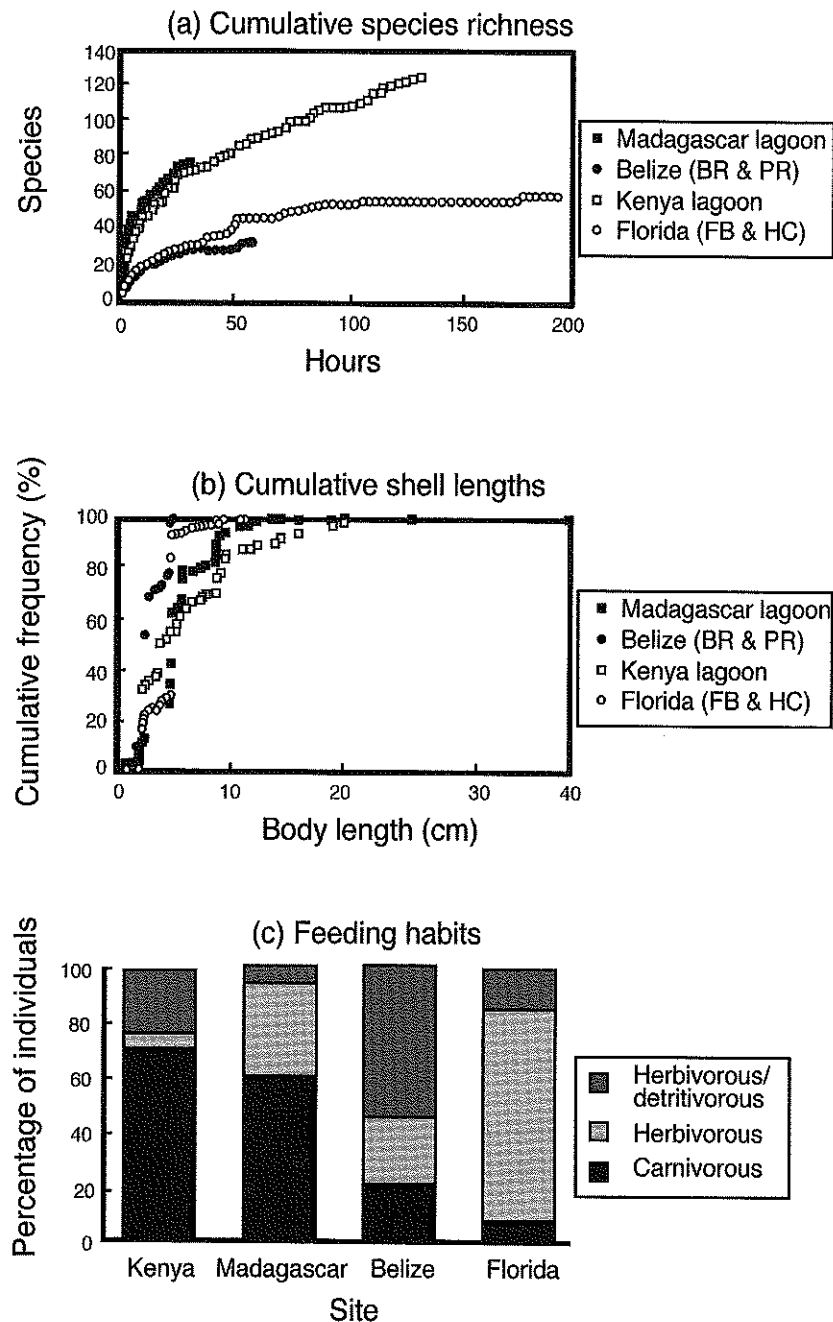


Figure 5.8. Comparison of the prosobranch snail populations in two regions of the western Indian Ocean and Caribbean (McClanahan unpublished data): (a) cumulative species observed as a function of cumulative search time, (b) cumulative frequency of shell lengths, and (c) feeding habits.

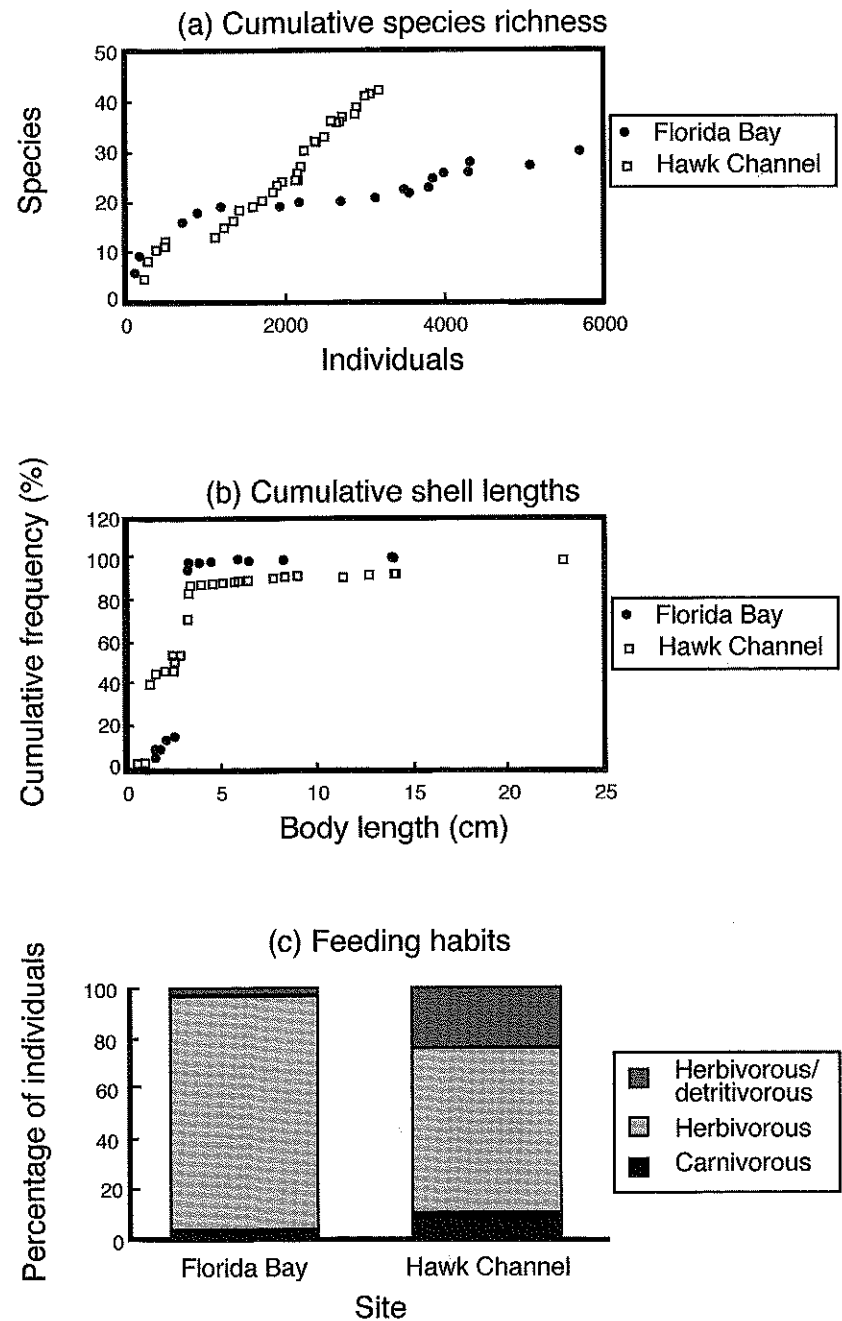


Figure 5.9. Comparison of the prosobranch snail assemblages on the oceanic (Hawk Channel) and bay sides of the Florida Keys (data from McClanahan 1992): (a) cumulative species observed as a function of cumulative search time, (b) cumulative frequency of shell lengths, and (c) feeding habits.

han 1992). Consequently, isolation should have the effect of increasing the variation in the physical environment that, in turn, should affect ecological and evolutionary organization of the species assemblages. This ecological organization can be independent of the level of connectivity but more a measure of species' tolerance to environmental fluctuations. This model predicts the opposite of an ecosystem adaptive-learning model. It predicts that smaller and more fluctuating environments will be more resilient to disturbances because the species that persist in these environments are already adapted to fluctuations and are less likely to be perturbed by new or additional fluctuations.

The alternative hypotheses are more compatible when one considers that the organization of species assemblages under different levels of environmental stress is often a process that works more on ecological than on evolutionary time. In fact, many of the species in stressed environments are ancestral species or species that were formed prior to the formation of the organisms that now inhabit less environmentally stressed surroundings (Vermeij 1978). For instance, the evolutionary origin of most of the marine snail species found in the Florida Bay is on the order of many millions of years, while the bay itself was formed by the recent sea level rise and is, therefore, less than ten thousand years old. These ancestral species have not persisted in much of their original range because, in theory, they have been replaced by more recent evolutionary forms and presumably find refuge from detrimental species interactions in stressed or low-productivity environments that are uninhabitable by their potential competitors. In essence, these ancestral species find refuge from biological forces like predation that are more intense in the less environmentally stressed surroundings (Vermeij 1978; McClanahan 1992). Consequently, species assemblages in stressed environments have not been an active part of the main evolutionary process but are relicts of and peripheral to it.

Ecological stress and information accumulation, or evolutionary and ecological organization, are counteracting forces. Environmental stress works to reduce species diversity and redundancy to those species most able to tolerate large environmental fluctuations but not additional species of potential competitors and predators. Ecological and evolutionary organization often work to increase species diversity and redundancy as species divide up resources more finely over evolutionary and ecological time. Despite the long-held view that closely related species cannot coexist, more recent models suggest there is more tolerance of species overlap than previously recognized (Abrams 1996).

Synergistic Stressors

The number and extent of environmental stresses can influence resilience of coral reefs. This occurs because stresses can act in multiplicative rather than

additive ways, or because the sum of two stresses can exceed a threshold where a single stress would not. Consequently, two or more stresses or disturbances working independently may have a much smaller effect than the two factors working together. The opposite or inhibitory interactions or synergies can also occur when one factor would have an effect except that a second factor is nullifying this influence. There are numerous examples of these types of interactions, and we will briefly describe some examples relevant to coral reef conservation and management.

Reef ecologists believe that the largest human influences on coral reefs, manageable on a local scale, are fishing, pollution, and sedimentation (Ginsburg 1994). Because these influences are common throughout the tropics, it has been difficult to distinguish their independent influences. In order to study the effects of nutrification alone, it may be necessary to study its effects in marine protected areas that exclude fishing or in areas without human influences. These factors are frequently associated with human population densities, and few governments will establish marine protected areas in polluted waters or allow marine scientists to artificially pollute protected areas. However, there are studies that suggest that the response of coral reefs to these factors combined may be different from them in isolation (e.g., Umar et al. 1998; McCook 1996, 1999; Miller and Hay 1996).

The Malindi-Watamu Marine National Park in Malindi, Kenya, is an example of a protected area that has been nutrified over the last two decades. The park has been receiving increasing sediment and nutrients from the Sabaki River over the last fifty years associated with an increase in land uses that promote soil loss (Dunne 1979; Finn 1983). However, this river influence appears to have only minor influence on the corals (McClanahan and Obura 1997). The total cover of hard coral and algae benthic cover remained nearly the same over a seven-year period despite periods of three months or more per year when waters were brown and turbid. The largest change over the study period was a shift in the species composition of the corals such that those species more tolerant of the increased nutrient and sediment conditions increased while less-tolerant species decreased. This minor shift in species composition was unexpected. Many reef ecologists believe that, depending on levels of herbivory and other disturbances to algae, nutrified reefs will be dominated by fast-growing reef algae that will eventually overgrow and kill corals (Littler et al. 1991; Bell 1992; Delgado and Lapointe 1994; Lapointe et al. 1997).

The unexpected response was probably attributable to two factors: sediments from the river discharge, and a lack of fishing. The sediments acted as a physical disturbance that retarded ecological succession to an early-successional turf algae stage rather than a carrier of nutrients that accelerated it toward fleshy

algae dominance (McClanahan 1997a). Lack of fishing meant that herbivorous fishes were abundant in this reef, and the persistence of these consumers may have kept fleshy algal abundance in spite of any stimulation of growth by nutrients. This interpretation is consistent with the views of Szmant (1997) and McCook (1999), which suggest that the maintenance of fishes and their feeding responses as well as the physical structure of the reef may be important factors that can inhibit algal overgrowth of coral reefs. These studies suggest that it is often the combined effect of the loss of reef consumers, the reef structure, and nutrification that cause drastic changes in reef ecology. Consequently, if reefs are being nutrified, it may prove useful to restrict or eliminate fishing to improve the chances of maintaining coral phase ecology.

A second example of increased resilience was shown during a sea urchin reduction experiment in the Mombasa Marine National Park, which was created in 1991 (McClanahan et al. 1994, 1996). Sea urchins are so abundant in many Kenyan reefs that they can be considered pests that require active management. Consequently, this study reduced the abundance of sea urchins by about 85 percent in the park, as well as at two fished reefs. In the fished reefs (low fish herbivory) where sea urchins were reduced, fleshy algae and seagrasses colonized and reduced living coral by about 35 percent over the one-year study. In contrast, the increase in fleshy algae in the Mombasa Park (high fish herbivory) was smaller and resulted in little change in the coral cover. The reason for these differences is, again, attributable to the greater abundance of surgeonfish and parrotfish in the park, which increased after the sea urchin reduction and kept fleshy algae from increasing and smothering coral. In unprotected reefs, there was a moderate increase in small-bodied damselfish and juvenile parrotfish, but this increase appeared insufficient to keep fleshy algae from dominating the site. Consequently, the greater functional diversity of herbivores in the protected areas acted to inhibit algal overgrowth of the reef and maintain its ecological stability. In general, unfished reefs have greater diversity on the small scale, more ecological redundancy, and, therefore, are more likely to buffer the effects of species deletions or reductions. Consequently, in order to maintain resilience, it behooves managers of coral reefs to maintain species of functional diversity and reduce the number of simultaneous disturbances or stresses.

Human Institutions and Coral Reef Resilience

Humans, through their cultural institutions, have the ability to reduce or increase the resilience of ecosystems depending on various cultural and environmental conditions and interactions. With the exception of the recent rise of tourism and marine protected areas, the human relationship with coral reefs has

been that of hunter-gatherer, even when exploited by otherwise agrarian or industrialized humans. Below we will describe, from an historical perspective, some case studies of the development and decay of human cultural institutions associated with coral reef fisheries and discuss their relevance to ecological resilience.

The Economic Evolution of Watersheds

The history of coral reefs adjacent to high islands and continents is often closely associated with the economic development of watersheds. On high islands and continents, coral reefs and their fisheries are often just one of a number of domestic and wild ecosystems that humans will utilize. In the absence of strong cultural taboos, human populations that have a high reliance on agriculture will partition their effort among ecosystems in such a way that their labor is best rewarded with resources in the short term. In many tropical areas, rainfall or other environmental factors required by crops are seasonal, with either one or two planting, weeding, and harvesting cycles per year. When human population densities are low and human labor limits the production of crops, it is common to have people of many ages and both sexes attending to crops during these critical periods. Consequently, at low levels of domestication of the watershed, fishing is often a seasonal activity largely undertaken by men, when their labor is not required for crop production or hunting on land.

As human population densities increase, agricultural labor becomes less limiting, greater partitioning of labor occurs among the various production systems, and a guild of full-time fishers develops. Fishing becomes less a subsistence activity and more a commercial activity where fishers will attempt to catch far beyond their household requirements. As human populations increase, fishing can become one of the few ways to meet deficits and earn extra money to support impoverished people. In such cases, fishes in nearshore waters may be quickly depleted, and fishers adopt boats, technologies, and patterns of movement that will allow them to exploit fisheries farther offshore. Many fishing communities now occupy and exploit land and sea areas with insufficient productivity to fully support them. They, therefore, often emigrate to expand their access to resources.

The development and cultural adoption of fossil fuels and associated technologies greatly increased production and reduced the human labor requirement. It led to further specialization and accelerated aggregation of people into towns and cities. Fishing grounds and technologies expanded, but in probably the majority of cases nearshore fisheries were already fully exploited, and the high capital and costly technologies caused many fisheries to collapse or to

expand to offshore waters (Berkes 1987). The pressures on fished populations became governed more by the complex interplay of market demands, supply, subsidies, and the cost of fishing, and less by the direct interactions between local needs, skill, and effort (Thomson 1980). Costly and high-technology fisheries were not necessarily the most beneficial for local communities (Kamukuru 1992).

Associated with the development and expansion of resource use were common patterns of waste production. Sediments and nutrient run-off increased along a gradient from indigenous forest to plantation forest to shifting agriculture to permanent agriculture to pasture (Dunne 1979; Young 1996). Run-off from large tropical cities and towns was seldom treated and further added to the eutrophication of the nearshore and coral-reef environments. This run-off in combination with fishing added to the deterioration of the oligotrophic coral-reef environment.

Low-Lying Atolls and Islands

Low-lying islands and atolls can differ from high islands and continents because the lower capacity for agriculture on these islands makes dependence on seafood and trade more important. Consequently, the capacity to maintain human populations on these islands is more limited, and the maintenance of humans may require that they (1) develop trading partners or tourism, (2) rely on offshore fisheries, or (3) develop a fugitive strategy of exploiting resources and moving on. In fact, these three economic strategies and their various combinations are common to many of the low-lying islands of the tropics. For example, inhabitants of the low-lying Maldivian Islands off of southern India have historically relied almost entirely on the catch of pelagic tuna and until recently did not fish on their reefs. Recently, outsiders interested in exporting live fish to other Asian countries have developed reef-based fisheries there.

Fisheries Management and Its Contribution to Ecological Resilience

In order to adapt to the changing conditions of the human needs/resource abundance ratio, a variety of fisheries management policies and actions have developed (Berkes 1985; Smith 1988; McGoodwin 1990; Smith and Berkes 1991; Berkes et al. 1995). In the early stages of the economic evolution, this largely included ways to more fully exploit resources, with little efforts toward conservation (Smith 1988). Nonetheless, there is evidence for conservation of resources among small-scale fishers and hunter-gatherer, agrarian, and industrialized cultures that could potentially result in conservation and increased

resilience of the human fisheries resource (Johannes 1981; McGoodwin 1990; Smith and Berkes 1991; Zerner 1994; Ruddle 1996; McClanahan et al. 1997). Regardless of the state of the culture, conservation of resources is largely achieved through restrictions on (1) gear, (2) access to the resource or the limitation of effort, and through use of (3) time limits, (4) size restrictions, and (5) spatial restrictions such as sacred, dangerous, or marine protected areas. Below, we will discuss how each of these restrictions has developed in different cultural conditions and their effect on conservation and ecological resilience of coral reefs.

SMALL-SCALE FISHING SOCIETIES: MIJIKENDA OF EAST AFRICA

The Mijikenda are an association of largely agrarian Bantu people that have lived as a distinct ethnic group along the East African coast for approximately four hundred years (Spear 1978). Their oldest settlement is located in the forest watershed of the East African coastal mountain range, but their second oldest known settlement is situated just behind a coral-sand beach adjacent the East African fringing reef (Spear 1978). These people have developed a number of cultural institutions that have parallels with modern fisheries and resource management. These institutions are, however, closely linked to the spiritual view of these people and not explicitly or, perhaps, consciously developed in order to manage fisheries or natural resources (McClanahan et al. 1997; Glaesel 1997).

Fish landing sites in this area are now largely managed by a group of elders, who include two *kaya* elders and two fisheries cooperative leaders. *Kaya* elders are traditional leaders who inherit their positions from their fathers and take this leadership role after the death of their father. Fisheries cooperative leaders are a more modern institution, and these leaders are voted into their positions by the fishers that utilize the landing site. *Kaya* elders teach, oversee, and perform traditional cultural institutions. Interviews with the *kaya* elders indicate that a number of them believe that their ancestors placed restrictions on the gear used to catch fish, the size of fish caught, access to resources by fishers, and times as well as the places when fishing is allowed (McClanahan et al. 1997). For example, if fishers from outside the community would like to fish in the waters adjacent the landing site, they are expected to pay a fee, called *ubani*, to the elder and this is seen as a communal gift to the fishing community. If the fishers are not wanted for reasons of their gear use or other matters, then the elders can refuse to accept *ubani* and the foreign fishers are expected to leave and not fish in "their waters." This institution suggests a degree of territorial control of fishing grounds.

Ubani is traditionally used for communal activities such as purchasing goods—a goat or chicken, rice, and sweets—or for the annual sacrifices that

these communities perform. During sacrificial times no one is allowed to fish. Additionally, most of these landing sites have a series of areas where these sacrifices are performed, called *kaya* or *mzimu*. *Mzimu* are unusual features such as large coral heads, springs, and caves on the beach or at sea that are believed to be inhabited by spirits that can influence fish catches, births, marriages, and other important events in these peoples' lives. *Mzimu* were identified by ancestors during their dreams, and their locations were passed down through the generations. Traditionally, *mzimu* were considered dangerous locations, because of the spirits, and sites should be visited only when making sacrifices. Consequently, many of these areas were unfished until recently and might be viewed as traditional marine protected areas despite the fact that this was never their stated purpose.

A recent study examined the utility of these institutional practices in sustaining resources by comparing the traditional knowledge, fish catches, and coral reef ecology adjacent to landing sites maintaining different levels of adherence to these traditions (McClanahan et al. 1997). It was discovered that fish catches adjacent to two landing sites with the most-strict adherence to traditional practices had 40 percent higher catches per person than those that did not, but the ecological condition of the reefs was similar and indicated a high level of ecological degradation. One reason for this is that the more tradition-adhering communities did not adhere to all traditions (for example they fished in *mzimu* and young fishers used spear guns, which are not condoned by some *kaya* elders) and they were unable to exclude foreign fishers or those from adjacent landing sites. This was largely because the national government institutions, including police and government fisheries officers, did not allow them to use physical force as part of their enforcement program. These communities were, therefore, limited to passive means of enforcement that included discussions with foreign fishers, not buying or allowing foreign fishers to sell their fish at the landing site, and also pushing their boats onto dry land. Consequently, it was common for foreign fishers to use nontraditional gear such as pull-seine nets in the waters of the tradition-adhering communities. This created a great deal of animosity between the tradition-adhering communities with foreign fishers and their national governments, and may be one of the reasons for the poor ecological state of their reefs.

SMALL-SCALE FISHING SOCIETIES: FIJI AND THE PACIFIC

In the Pacific and Southeast Asia, reef and lagoon resources and areas were widely subject to traditional use rights, and many of these controls persist to this day (Ruddle et al. 1992). In many parts of Indonesia, natural resource use may generally be subject to traditional laws (called *adat*), and management systems

such as those in parts of the Moluccas (*sasz*) help to constitute a form of coastal territoriality. In Fiji, traditional fishing grounds are known as *qoliqoli*. Restraint of the level of exploitation by such practices, which are essentially a form of ownership, is nevertheless strongly contested for many areas in Southeast Asia and Melanesia (Polunin 1984). Carrier (1996) specifically argued, for a site in northern Papua New Guinea with a sophisticated pattern of marine tenure, that resource depletion was unlikely to be recognized. Whatever the origins, there is overwhelming evidence that this customary tenure tended and tends to be opportunistic (Polunin 1984); it can scarcely alone restrain current resource use, where a resource suddenly gains in value, or exploitation steadily increases through human population growth (Tomascik et al. 1997).

A forceful case for the development of customary reef tenure having been accompanied by conservation awareness has been made for small islands in the South Pacific, where marine resources have traditionally been an essential source of human sustenance (Johannes 1978). Ruddle et al. (1992) argued that in the South Pacific, where customary marine tenure exists, there are plentiful examples of their resilience to outside pressures. But, for Southeast Asia, there is a lack of critical analysis and where semi-quantitative analysis has been made the conclusion has been that the tenure systems lacked resilience (Jennings and Polunin 1996b).

The Fijian *qoliqoli* appear to vary substantially in their management aptitude; specific regulations are only variably enforced such that their performance in the face of growing resource pressure is unpredictable (Cooke et al. 2000). Smaller Pacific islands are currently the focus for developing sustainable resource use (Dalzell et al. 1996), and, despite the variable performance of existing tenure systems, many will persist and may even be further strengthened by national government constitutions. Consequently, any future management regime will have to cooperate with indigenous tenure even if the evidence for its management resilience, and in particular management aptitude, to internal or external pressures remains weak. If such resilience and aptitude could be demonstrated or strengthened, it could be employed, in partnership with central-government authorities, to maintain resource persistence, or indicate where it is most likely to be achieved through co-management projects.

National Governments

In the global context, national governments are middle-level institutions with both upward and downward responsibilities and opportunities for husbanding coral reefs. Upward, national governments often enter into regional and global agreements, each designed to improve overall human welfare; these include

agreements on trade, the environment, climate change, sustainable development, and biodiversity. Downward, their most pressing domestic demands will be to meet the demands and aspirations of a population, most of which will care very little for international agreements. For example, the East African and Fijian examples above have shown that sustainable use of coral reefs is often rooted in tradition, but traditions can be weakened by diminishing resource/people ratios combined with conflicting policies of national governments. Thus it is important that detailed specific description and analysis of the cultural and socioeconomic dimensions of resource use and coral reef ecology is suitably communicated to politicians, policy makers, and resource managers. Works of this type (Birkeland 1997; Hodgson 1997; McClanahan et al. 1997, 2000) may only have an influence when the executive summaries of key findings are made easily accessible to the aides of the responsible government ministers, or to the ministers themselves. If government will exists, such information transfer from credible scientists should be critical for seeking sound decisions and the management needed to produce ecologically and socially beneficial outcomes.

Commitment by national governments to international agreements can influence the national debate over the best ways to implement or develop domestic economic and environmental policies. Different sectors of society have different perspectives on the freeing up of world trade: "The key challenge is to limit the current tendency toward greater use of trade measures for environmental purposes in order to avoid undue erosion of the global trading system" (Drake-Brockman and Anderson 1994). In other words, they are suggesting that bringing environmental criteria to bear on international trade agreements tends to erode the global trading system and hence its capacity to pay for environmental protection. Opponents of current arrangements for world trade, on the other hand, suggest that it is the burgeoning global trading system itself that is ultimately the greatest driver of environmental degradation.

Zarsky and Hunter (1998) suggest that national governments can catalyze good environmental outcomes through use of policy and incentive schemes. They note that the national government usually has the role of regulator and enforcer as well as that of financier of public goods and operator of public utilities. For East Asia, Afseh et al. (1996) suggest that the model of environmental management should be based on the concept of multiple agents and multiple incentives. The three key agents that should interact in setting social norms for environmental management are government, markets, and communities. Government can act directly to influence the other sectors, or it can achieve social goals by indirect action; for example, it can design policies and build capacities that enable communities to play a role in regulating industry and markets (and communities) to play a role in the provision of public goods. In this "triangular

model," governments can influence the other two sectors in raising environmental performance, thereby overcoming the three universal obstacles of fiscal constraint, lack of regulatory capacity, and political will.

Depending on whether resources are being under or overused relative to sustainable levels, governments can create incentives or disincentives for markets and communities to regulate resource use around sustainable levels. This is a commonly stated goal of national government practice in fisheries and park management in developed countries. However, its implementation depends on having good information and models on the status and trends of fisheries and having the appropriate citizenry and political will in the face of uncertainty and—often—communities with more pressing short-term personal economic goals.

When communities come to accept the need to implement other ecological measures, such as conservation of biodiversity and protection of indirect ecological functions and services, the need for monitoring and ecological understanding becomes even larger. Consequently, the lack of reliable information for managers and users, their lack of confidence in the information, or the inability of communities to change in the face of this information are all obstacles that can cause sustainable resource management to fail. Management can become passive and rely on environmental and economic disasters as the key form of negative feedback unless there is a knowledgeable and adaptable citizenry (Rose-nau 1997; Thompson and Trisoglio 1997). The role of scientists to share their unique knowledge to influence public policy to be guided by knowledge and principles of precaution can not be underestimated (Haas 1997).

National governments are in a position to create international and nationwide systems of marine protected areas with potential to be effective contributors to biodiversity conservation and fisheries support. For example, the United States has its National Marine Sanctuary Program and Australia its National System of Marine Protected Areas. In both countries, the protected areas are "multiple use protected areas" with or without strictly protected exclusion zones, a decision that exposes the viability of the areas somewhat to the uncertainties and risks of fisheries management. Included within these multiple-use protected areas are the Florida Keys Marine Sanctuary (United States) and the Great Barrier Reef World Heritage Area and Marine Park (Australia).

Australian governments from both sides of politics have provided strong institutional support for the management of the 380,000-square-kilometer Great Barrier Reef World Heritage Area as a multiple-use marine protected area. Until 1998, the management of the Marine Park and World Heritage Area was funded by a government appropriation. Now, funds for the management of the area, and for research and monitoring underpinning management, are generated

by economic activity in the area—specifically, a few dollars per person per day "environmental management charge" on tourists using a commercial carrier to visit the Area. A 1975 Act of the federal parliament created the Great Barrier Reef Marine Park and the Great Barrier Reef Marine Park Authority, excluded mining and mineral exploration from the park, and prescribed areas ("zones") in which different types and levels of activity are permitted and excluded.

There are many opportunities for community input into zoning and management of the area both through regional management advisory committees and through public review of any proposed changes in regulations. The Authority, an arm of the Australian government, has legally binding agreements with the state of Queensland to jointly develop and implement policies and regulations in relation to people's use of the park and the conduct of fisheries. The fisheries regulations abide by principles of ecologically sustainable development, which it defines as "development (1) carried out in a way that maintains biodiversity and the ecological processes on which fisheries resources depend, and (2) that maintains and improves the total quality of present and future life" (Anonymous 1994).

There are major difficulties in transforming these fine sentiments into effective action. Clearly, for the individual fisher, sustaining poorly comprehended ecosystem processes and biodiversity does not carry the same weight as feeding their family or sustaining their fishing boat or next year's mortgage payments. For peak representative groups of commercial fishers, the issues are how many licenses and how much total catch should be allowed in the different types of fisheries (e.g., line and trawl) to maintain the quality of life and income of the fishers, as well as how to develop more environmentally friendly technologies and determine sustainable catch rates for target and by-catch species. These groups collect substantial levies from their members that are matched by government and used for wide-ranging research. For example, there are major ongoing research and monitoring efforts into coral reef fish and sustainable fisheries (Mapstone et al. 1996), monitoring and ecological studies of water quality (Furnas et al. 1997), reef health (Sweetman 1997), ecological values (Done 1995; Done and Reichelt 1998), and connectivity of representative protected areas (Done et al. 1996). Done and Reichelt (1998) have advocated the use of biodiversity, life history information, and oceanographic and risk analysis in the selection and management marine protected areas (Done et al. 1996).

Concluding Remarks

Most coral reef resources have a number of organizations interested in the welfare of this ecosystem. Each level in this potential management hierarchy may

have slightly different desires, local communities being most interested in food resources, national governments in tourism and shoreline protection, and international governments in biodiversity or global element cycles. Consequently, there is a potential for conflict in the types of management that each organization will want as well as the information that they will need for determining the status of their desired objectives. One of the greatest challenges to management, therefore, is to achieve greater synergy among the human organizations in this hierarchy. This has remained difficult because of the diverse cultures of the different organizations involved and the conflict arising from the desire to maintain decision power and resource control by different sectors in society.

Conflicting desires are not easily overcome unless a constructive dialogue is created among the organizations, each organization stating their desires in order that areas of overlap and conflict are identified and mutually acceptable solutions derived from these discussions. Trust is also an additional element critical to negotiations and the political process. All of these suggestions suggest that trustworthy information is important in determining the status of the resources and the views and desires of the human organizations. Consequently, it is important that the organizations trust the quality of the information. This can be achieved if representative members of each level of the human hierarchy are involved in either the collection or confirmation of this information or that all human organizations approve of the group mandated to collect information. Scientists, therefore, have the potential to play a key role in this process because of their shared and, hopefully, objective methodology. Co-management is difficult to achieve because of conflicting desires and because only rarely does any one level in the hierarchy have sufficient resources to research, monitor, and protect the resources unless there are some strong economic incentives to cooperate. Thus, information, key players, connectivity, and cooperative synergy are likely to be important elements, not only in the resilience of natural ecosystems, but also within human organizations.

Literature Cited

- Abrams, P. A. 1996. Limits to the similarity of competitors under hierarchical lottery competition. *American Naturalist* 148:211–219.
- Adey, W., and T. Goertemiller. 1987. Coral reef algal turfs: Master producers in nutrient poor seas. *Phycologia* 26:374–386.
- Afshar, S., B. Laplante, and D. Wheeler. 1996. Controlling industrial pollution: A new paradigm. Policy research working paper no. 1672, World Bank. Available online at http://www.worldbank.org/nipr/work_paper/1672/index.htm.
- Alcala, A. C., and G. R. Russ. 1990. A direct test of the effects of protective manage-

- ment on abundance and yield of tropical marine resources. *Journal Consueil Internationale du la Exploration de Mer* 46:40–47.
- Amesbury, S. 1981. Effects of turbidity on shallow water reef fish assemblages in Truk, Eastern Caroline Islands. *Proceedings of the 4th International Coral Reef Congress* 6:491–496.
- Anonymous. 1994. *Queensland fisheries*. Queensland, Aus.: Queensland Government Printing Office.
- Antonius, A. 1981. The “band” diseases in coral reefs. *Proceedings of the 4th Coral Reef Symposium* 2:6–14.
- . 1985. Coral diseases in the Indo-Pacific: A first record. *PSZNI: Marine Ecology* 6:197–218.
- Aronson, R. B., and W. F. Precht. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23:336–346.
- Bell, P. R. F. 1992. Eutrophication and coral reefs—Some examples in the Great Barrier Reef Lagoon. *Water Research* 26:553–568.
- Benzie, J. A. H. 1994. Patterns of genetic variation in the Great Barrier Reef. Pp. 67–79 in *Genetics and evolution of aquatic organisms*, edited by A. S. Beaumont. London: Chapman and Hall.
- Berkes, F. 1985. Fishermen and the “Tragedy of the Commons.” *Environmental Conservation* 12:199–206.
- . 1987. The common property resource problem and the fisheries of Barbados and Jamaica. *Environmental Management* 11:225–235.
- Berkes, F., C. Folke, and M. Gadgil. 1995. Traditional ecological knowledge, biodiversity, resilience and sustainability. Pp. 281–299 in *Biodiversity conservation: Problems and policies*, edited by C. A. Perrings, K.-G. Mäler, C. Folke, C. S. Holling, and B.-O. Jansson. Dordrecht, Netherlands: Kluwer Academic Publishers.
- Bertness, M. D. 1981. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. *Ecology* 62:411–425.
- Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363–372.
- Birkeland, C. 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology* 69:175–185.
- . 1988. The influence of echinoderms on coral-reef communities. *Echinoderm Studies* 3:1–79.
- . 1997. Symbiosis, fisheries and economics development on coral reefs. *Trends in Ecology and Evolution* 12:364.
- Birkeland, C. E., and J. S. Lucas. 1990. *Acanthaster planci*: Major management problem of coral reefs. Boca Raton, Fla.: CRC Press.
- Bohnsack, J. A. 1993. Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36:63–71.
- Borowitzka, M. A. 1972. Intertidal algal species diversity and the effect of pollution. *Australian Journal of Marine and Freshwater Research* 23:73–84.
- Brown, B. E. 1997. Coral bleaching: Causes and consequences. *Coral Reefs* 16:S129–S138.
- Brown, B. E., R. P. Dunne, T. P. Scoffin, and M. D. A. Le Tissier. 1994. Solar damage in intertidal corals. *Marine Ecology Progress Series* 105:219–230.
- Budd, A. F., K. G. Johnson, and T. A. Stemmann. 1996. Plio-Pleistocene turnover and