chapter 15

The Ecology of Coral Reefs

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*I*n the simplest sense, coral reefs are wave-resistant piles of limestone and calcareous sediments built by a thin veneer of living organisms (Hubbard 1997). But these piles are of great ecological and resource significance for their massiveness, extremely high biodiversity, and distinct trophic structure and primary production. Reefs grow most prolifically in clear, warm, shallow, and nutrient-poor waters of the western tropical Atlantic and Indo-West Pacific, and more poorly in the eastern Pacific and eastern Atlantic where upwelling and high planktonic productivity inhibit reef development (Achituv and Dubinsky 1990). Scleractinian corals, hydrocorals, and coralline red algae are the primary framework constructors of coral reefs, although a host of other algae and invertebrate phyla also contribute to reef mass.

The scale of reefs is enormous, and they are the largest durable bioconstruction projects on earth. The Panama Canal is still one of the most significant human construction projects, but it is paltry by comparison with the unexceptional coral reefs along the Caribbean coast of Panama. Moreover, modern reefs are only youngsters—less than 10,000 years old—because older reefs were drowned by the rapid Holocene rise in sea level (Hubbard 1997). Over the longer term of millions of years, even small atolls like Enewetak have accumulated 2- to 3-km-thick piles of limestone, just as Darwin (1842) predicted.

There are two aspects of the scale of reef bioconstruction that define the ecological setting for everything else in this chapter. First, reefs determine the physical structure of the coastline and that of adjacent environments and ecosystems (Ogden 1997). Wherever they co-occur, reefs are the protective barrier against the sea for seagrass beds (see Williams and Heck, Chapter 12, this volume) and mangroves (see Ellison and Farnsworth, Chapter 16, this volume), just as man-

groves and seagrasses trap and stabilize runoff from the land and thereby prevent reefs from being drowned in sediments. These linkages can also have negative effects; for example, contaminated sediments continued to kill offshore reef corals for years after a large oil spill killed the mangroves along the central Caribbean shoreline of Panama (Jackson et al. 1989; Guzmán et al. 1994). Thus, in a very real sense the actual habitats as well as all their inhabitants are alive.

The second major point about bioconstruction is that the apparent physical stability of reefs belies an underlying natural turmoil of growth, death, and destruction of calcareous organisms (Glynn 1997; Hallock 1997; Hubbard 1997). Much like a modern city, reefs are constantly being rebuilt and torn down at the same time. Corals are the bricks, broken pieces of plant and animal skeletons the sand, and algal crusts and chemical cements the mortar. The production, accumulation, and cementation of all this calcareous material into solid limestone determine reef growth. Destruction is due to storm damage and even more to pervasive grazing and excavation by organisms. The key point is that even small changes in rates of construction or destruction may cause big increases or decreases in reef mass. For example, eastern Pacific reefs virtually disappeared after the strong El Niño of 1983 due to coral death and intense bioerosion (Glynn and Colgan 1992). This fragility also scales up in geological time; the history of reefs over the past half billion years is punctuated by long episodes of little or very different kinds of reef development that were modulated by shifts in oceanographic regimes (Hallock 1997; Wood 1999).

Coral reefs are the most taxonomically diverse of all marine ecosystems, but the nature and extent of this diversity is known only in the broadest outlines for most groups (Paulay 1997). Coral reefs probably contain at least a million species,

but fewer than 100,000 of these have been described (Reaka-Kudla 1997). Our ignorance of the extent of biodiversity on coral reefs is not limited to obscure, poorly studied phyla; taxonomic uncertainty hinders ecological understanding in many corals, sponges, mollusks, and crustaceans (Knowlton and Jackson 1994). The widespread occurrence of sibling species in groups that have been genetically analyzed (Knowlton 1993, 2000) suggests that much diversity remains to be documented.

One can in many cases ignore this cryptic biodiversity by concentrating on "guilds" or functional groups (Jackson 1977, 1979; Steneck and Watling 1982; Steneck and Dethier 1994; Mumby and Harborne 1999). For example, studies of the replacement of corals by macroalgae capture the essence of this ecological phenomenon even if the species compositions of these two groups are ignored. Studies of the reproductive ecology of reef organisms, on the other hand, are seriously compromised by ignoring species boundaries, because individual organisms recognize such distinctions even if scientists currently do not. The importance of subtle ecological differences between morphologically similar forms is largely unknown in most specific cases, although we favor the view that overly conservative taxonomy has obscured the extent to which species are ecologically specialized and biogeographically limited (Knowlton and Jackson 1994).

With that caveat in mind, we organize this chapter from the bottom up, moving from the individual organisms themselves, to the interactions involving competition, consumption, disease, and to the physical disturbances affecting reef organisms. We then consider coral reefs as communities and ecosystems, and the Phanerozoic history of coral reef development. We conclude with a discussion of the future of reefs in the face of massive anthropogenic impacts. We draw most of our examples from the Caribbean and the Great Barrier Reef because of our greater familiarity with these systems.

THE MAJOR PLAYERS ON CORAL REEFS

Coral Animals

Two groups of anthozoans are important reef builders: the true stony corals (Anthozoa, Scleractinia) and stony hydrozoans (especially the Milleporina). Like other cnidarians, members of these groups contain nematocysts, which may be used in the capture of prey (zooplankton), as well as in defense. Many, however, rely nutritionally to varying degrees on their symbiotic dinoflagellates.

Most reef-building corals are clonal, and many form substantial colonies consisting of numerous interconnected polyps. Clonal organisms are defined by their ability to engage in asexual as well as sexual reproduction; growth and asexual reproduction are often equivalent in these groups (Jackson 1977; Jackson and Coates 1985). Asexual reproduction can also result in the establishment of genetically identical individuals at new locations on a reef. Corals have several different modes of asexual propagation (Kramarsky-Winter

and Loya 1996; Kramarsky-Winter et al. 1997; Richmond 1997), but the most common form in corals is fragmentation, particularly in species with branching growth forms (Highsmith 1982; Richmond 1997). Fragments may be produced by predation, bioerosion or waves, and subsequently dispersed by currents or wave action. Many fragments fail to successfully reattach to the bottom, but the probability of survival for asexual fragments is much greater than that of sexual propagules because the former are so much larger (Hughes 1985). Physiologically isolated colonies can also be produced by partial mortality and lost by fusion. Together with the more conventional processes of sexual recruitment and whole-colony death, these various mechanisms of colony creation and disappearance lead to complex life history matrices in which size and age are decoupled (Figure 15.1) (Hughes and Connell 1987).

Most corals also reproduce sexually (Figure 15.2) and, like many other groups of marine invertebrates, have an enormous array of reproductive alternatives (Harrison and Wallace 1990). These include selfing versus outcrossing, hermaphroditism versus separate sexes (gonochorism), brooding versus broadcasting of eggs, short versus long reproductive

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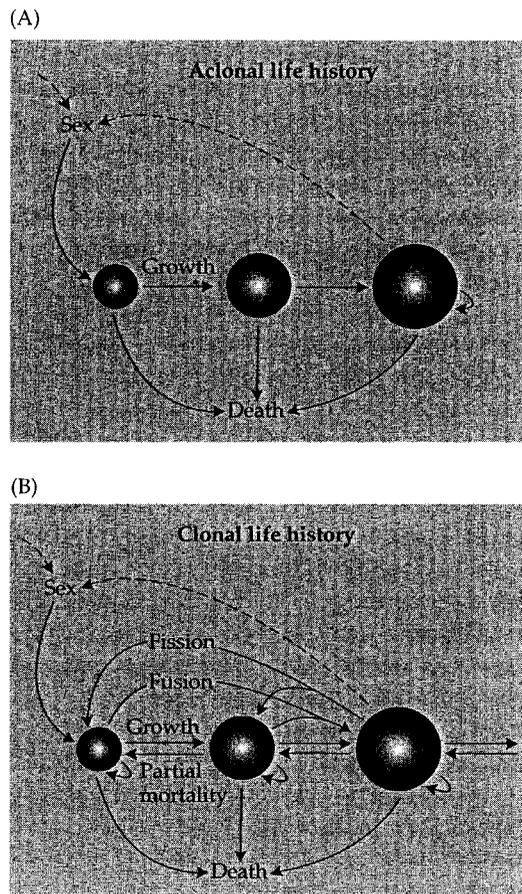
Figure 15.1 (A) Aclonal and (B) clonal life histories represented schematically in terms of individual size, with the arrows indicating all possible transitions among size classes and mortality. (Diagrams courtesy of T. Hughes.)
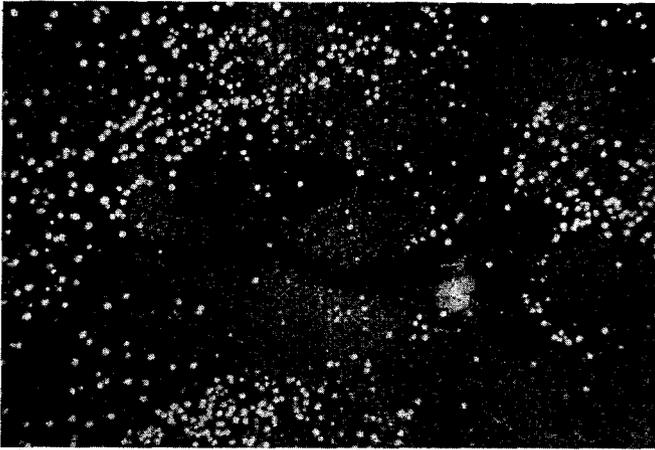
Figure 15.2 Release of egg–sperm bundles by the coral *Montastraea faveolata*. (Photo courtesy G. J. Gast.)

seasons, and limited versus wide dispersal of young. These different options, together with asexual reproduction, have important ecological as well as genetic consequences (Knowlton and Jackson 1993).

Sexual reproduction involves the union of egg and sperm to produce a zygote. Corals release sperm into the water. Eggs may also be released, or they may be retained in the mother until after fertilization. In either case, success in fertilization is strongly influenced by the distance between mates. For example, percentages of fertilization can be close to zero for corals greater than 2 m apart (Morse et al. 1996). These data suggest that coral species may be subject to strong Allee effects and experience nearly complete reproductive failure when they become rare (Levitan 1998).

Sessile forms rely on close synchronization in their reproductive output in order to maximize the probability of fertilization (Oliver and Babcock 1992). However, coral reproduction is often synchronized not only within species but also between them (Harrison et al. 1984; Richmond 1997). On the Great Barrier Reef, where mass spawning was first discovered, over one hundred species reproduce during a single one-week period each year, and slicks of gametes and larvae that extend for hundreds of meters can be seen from the air after spawning occurs (Oliver and Willis 1987). One of the consequences of community-wide mass spawning may be the swamping of potential predators on eggs and larvae, although the phenomenon may simply reflect multispecific use of common cues (Levitan 1998).

Although many coral species release unfertilized eggs or zygotes and engage in mass spawning, others brood fertilized eggs and release them as planula larvae. Most brooders do not participate in annual mass spawning events, but release their larvae on a lunar cycle. Their reproductive season varies in length from a few months to year round. All brooded larvae contain symbiotic algae from their mother, while most eggs and zygotes released in mass spawning species do not (Richmond 1997). Brooding is proportionately much more common in the Caribbean than in the Indo-Pacific and Red

Sea, and seems to be associated with a somewhat weedy lifestyle, small colony size, or specialized environmental conditions (Knowlton and Jackson 1993; Shlesinger et al. 1998). These are also the only corals that appear to self-fertilize at high rates (Carlon 1999).

The potential for dispersal of asexual, brooded, and broadcast propagules varies widely (Jackson 1986). Typically, fragments have the most limited dispersal and small larvae produced by broadcast spawners the greatest. It has been argued that the zooxanthellae of brooded coral larvae allow them to travel long distances. However, brooded offspring of most marine invertebrates typically settle very close to their parents (e.g., Olson 1985), and this is likely for corals as well. Nevertheless, rare long-distance dispersal events could be important in range expansions and recolonization following local extinction. Rafting of recruits attached to floating debris also may lead to very long distance movements (Jokiel 1984). Unfortunately, as with most marine organisms, we know almost nothing about the actual distribution of dispersal distances for coral reef animals and plants. Such information is crucial for determining the extent to which populations on different reefs are interconnected ecologically and genetically by dispersal (Benzie 1999), and their potential, for example, to behave according to the dynamics of metapopulations (Stone et al. 1996; Mumby 1999).

Factors that influence settlement behavior of coral larvae on reefs are poorly understood. However, Morse and colleagues (1996) have shown that distantly related corals, including both broadcast spawners and brooders, all require crustose coralline red algae for successful metamorphosis and settlement. These algae require moderately intense grazing by herbivorous fishes or limpets to clean their surfaces of rapidly growing fleshy algae. Thus coral recruitment must also depend on grazing. Within the coral genus *Agaricia*, different species exhibit different degrees of stringency and specificity in their settlement cues, which could promote niche diversification (Morse et al. 1988).

Algal Symbionts of Corals

All multicellular organisms host communities of microbial symbionts, but these communities are often ignored when discussing the ecology of their hosts. However, one cannot understand the ecology of reef-building corals without understanding the biology of the mutualistic dinoflagellate algae (often referred to as zooxanthellae) that live within them (Trench 1987; Muscatine 1990; Falkowski et al. 1993; Rowan 1998). Zooxanthellae fix inorganic carbon photosynthetically and pass some of this fixed carbon to their hosts (Muscatine 1990). The nutritional benefits received by the corals from their symbiotic algae are responsible for the high rates of calcification that underlie the creation of reefs (Muller-Parker and D'Elia 1997).

For many years, the zooxanthellae in corals and other marine invertebrates were all thought to represent a single species, *Symbiodinium microadriaticum*. Perhaps for this reason, the study of coral–algal symbiosis was typically the

province of physiologists and was ignored by ecologists. This perspective has changed with the realization that symbiotic zooxanthellae exhibit substantial genetic and ecological diversity, not only with respect to the hosts with which they associate (Trench 1987; Rowan 1998), but also with respect to other ecological factors such as ambient light levels (Rowan 1998). The discovery that even single coral colonies may host multiple types of symbionts has led to the recognition that the coral host represents a landscape of differing environmental conditions over which members of the symbiotic community interact (Rowan et al. 1997).

The landscape ecology of coral–algal symbiosis has been studied in greatest detail for the Caribbean species complex *Montastraea annularis*. Each generation, these corals acquire their symbionts anew from the environment (eggs and sperm lack zooxanthellae), and they can host all of the known major groups of zooxanthellae (Rowan et al. 1997; Toller et al., in press b). In the shallowest water on offshore reefs, the symbiotic community is dominated by genotypes that are tolerant of high light (types A and B), while in deeper water, shade-loving symbionts (type C) prevail. At intermediate depths, one typically finds light-tolerant symbionts on the tops of colonies and shade-loving symbionts on the sides or in other low-light microenvironments (Rowan et al. 1997). Nearshore reefs also show complex patterns, with a fourth type of zoo-xanthella (E) that is rare on offshore reefs being relatively abundant (Toller et al., in press b). Several lines of evidence indicate that these zonation patterns are maintained dynamically. For example, although the daily and seasonal pattern of incident illumination that a coral receives is generally fairly stable (barring natural toppling or overgrowth by a neighbor), experiments altering the orientation of colonies result in a shift in the communities of symbionts (Rowan et al. 1997). Extreme disruption of these symbioses can lead to dramatic changes in types of zooxanthellae present; the uncharacteristic dominance by type A zooxanthellae in corals recovering from the effects of prolonged experimental darkness suggests that type A is an ecological weed (Toller et al., in press a).

Temperature can have profound effects on coral–algal symbioses, most vividly seen in the phenomenon known as coral bleaching. High water temperature, often in synergy with high light, damages the photosynthetic capabilities of the algae (Warner et al. 1999) and results in their expulsion or death. In a study of bleaching of *Montastraea* in Panama, it was found that only certain genotypes in certain locations (Figure 15.3) were severely affected, in particular, the shade-loving symbionts at the high-light end of their distributions (Rowan et al. 1997). Moreover, another genotype appeared to increase in response to the temperature stress, perhaps as a consequence of the reduction in numbers of one of its competitors. Similar associations of the type of zooxanthellae with vulnerability to bleaching have also been reported across reef corals generally in Belize (McField 1999). Bleaching can occur in response to a variety of other stresses (Brown 1997a). This breakdown in the coral–algal symbiosis reflects the in-

Figure 15.3 The coral *Montastraea faveolata* exhibiting characteristic blotch bleaching due to the presence of more than one type of zooxanthella in the colony. (Photo courtesy of A. Baker.)

trinsic instability of many mutualisms (Herre et al. 1999); such associations have both costs and benefits, so that when one partner is unable to provide the normal level of benefits due to stress, the other partner may be better off in the short-term by terminating the relationship.

We have only begun to explore the ecological complexity of these symbiotic associations. Some patterns seem to be general; for example, in other species of corals capable of hosting multiple types of symbionts, types A or B are typically shallower than type C, although the actual depth at which symbiont type changes varies widely across coral taxa (Rowan 1998). However, not all coral species host multiple symbionts (Rowan 1998), and some corals acquire their symbionts directly from the mother rather than environmentally (Trench 1987; Muller-Parker and D'Elia 1997). There are also important biogeographic differences in the distributions of the major types of symbionts (Baker and Rowan 1997). Thus the ecology of coral–algal symbiosis will continue to be a fruitful topic of experimental research in the future, and also has considerable applied importance in the context of global climate change.

Sessile Organisms

MARINE INVERTEBRATES. Other sessile marine invertebrates that occupy substantial space on reefs include other cnidarians [horny corals (Gorgonacea), soft corals (Alcyonacea), zoanthids

(Zoanthidea), thorny (e.g., "black") corals (Antipatharia), sea anemones (Actinaria) and corallimorphs (Corallimorpharia)], as well as sponges, bryozoans, and ascidians. All of these are filter feeders, suspension feeders or carnivores, but may also host photosynthetic symbionts (Rowan 1998).

Many of these groups, like corals, have a clonal life history and are capable of extensive asexual reproduction, typically by fragmentation (Karlson 1986; Wulff 1991). Their patterns of sexual reproduction are diverse. Large organisms often produce widely dispersing propagules, but most small, encrusting reef animals produce large, nonswimming or weakly swimming larvae that commonly disperse only a few centimeters to meters before settlement (Jackson 1986). All sessile organisms are potentially vulnerable to Allee effects. For example, fertilization success is very low for female gorgonians 4 m from the nearest spawning male (Coma and Lasker 1997). Mass spawning events often involve other taxa besides corals (reviewed in Levitan 1998).

MACROALGAE. Algae on coral reefs fall into several functional groups (Littler and Littler 1984; Steneck and Watling 1982; Steneck and Dethier 1994). Coral reef algae have been comparatively little studied reproductively, although by extrapolation from other algae it seems likely that all but the weedy, ephemeral taxa have fairly limited powers of dispersal (Santelices 1990). Mass spawning in green algae has recently been documented (Clifton and Clifton 1999), but in contrast to mass spawning corals, gametes are negatively buoyant, reproductive thalli die following gamete release, and reproduction occurs over a several month period. Thus despite superficial similarities, these two groups are quite distinct in their reproductive ecologies.

Mobile Organisms

INVERTEBRATES. The most important mobile marine invertebrates on reefs are polychaete worms, gastropods, crustaceans, and echinoderms (including sea urchins, starfish, brittlestars, crinoids, and holothurians). Several species have been well studied because of their critical roles as grazers (e.g., the sea urchin *Diadema*) and as coral predators (e.g., the polychaete *Hermodice*, the snails *Drupella* and *Coralliophila*, and the crown-of-thorns starfish *Acanthaster*), as discussed below. Other groups clearly play important roles as micrograzers, predators, and deposit feeders, but very little is known ecologically about most mobile marine invertebrates on reefs.

The great majority of mobile marine invertebrates on reefs are aclonal, although there are exceptions (e.g., in echinoderms, Mladenov 1996). Direct transfer of sperm into the reproductive tract of females has evolved in some groups, but others spawn eggs and sperm into the water column. Aggregation is important for high success in fertilization in these groups. For example, fertilization of the gregarious urchin *Diadema antillarum* dropped to 7% with only one male per square meter (Levitan 1991). On the other hand, more than 20% of *Acanthaster planci* eggs were fertilized by a single male

60 m upstream (Babcock et al. 1994), although the high fertilization potential of *Acanthaster* appears to be exceptional.

FISHES. Coral reef fish occupy a diverse array of trophic niches on reefs, including herbivores, planktivores, and small and large carnivores (Sale 1991a). Like vertebrates generally, coral reef fish exhibit much less diversity in ecologically important aspects of reproduction than do marine invertebrates. All are outcrossing and most have separate sexes. Reproduction typically occurs daily to monthly, and offspring are usually capable of considerable dispersal, either as the egg and larva, or as a larva following the hatching of benthic eggs (Victor 1991; Warner 1997). Despite this great potential for dispersal, many reef fishes may recruit back to or near their natal reefs (Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000). Moreover, the behavioral biology of reef fish reproduction differs widely within and among groups. Analysis of this diversity has played a critical role in furthering our understanding of, for example, the evolution of hermaphroditism and the operation of sexual selection (e.g., Warner 1984).

INTERACTIONS AND DISTURBANCE

Competition

Competitive interactions occur frequently on coral reefs. They are especially conspicuous among sessile organisms, because scleractinian corals, other coelenterates, sponges, ascidians, or algae cover much of the available hard substratum. As in other habitats, consumers of these different groups may modulate the outcome of competitive interactions.

COMPETITION AMONG SESSILE ORGANISMS. Competition among sessile reef invertebrates and algae may be for space, light, or food (Jackson 1977; Buss 1979, 1986; Stimson 1985). Modes of competition are often categorized as being either direct (involving physical contact) or indirect (occurring at a distance) (Connell 1973). Because of the enormous diversity of reefs, competition is typically more frequent between members of different species (interspecific) than between members of the same species (intraspecific), and indeed often occurs between members of different phyla or kingdoms (Woodin and Jackson 1979). Studies of reef organisms prompted considerable interest in the extent to which interactions are transitive (hierarchical) or intransitive (nonhierarchical), and the possible implications of such patterns of interaction for maintenance of species diversity (Jackson and Buss 1975, Buss and Jackson 1979, Connell 1978).

Competition among scleractinian corals may involve numerous mechanisms (Lang and Chornesky 1990). Direct competition (Figure 15.4) occurs by digestion of tissues, damage of tissues from contact with tentacles, and even smothering by mucus. Indirect interactions most often involve shading of neighbors, although competition via the release of toxic chemicals has also been documented. The latter may be of particular importance for the inhibition of settlement near
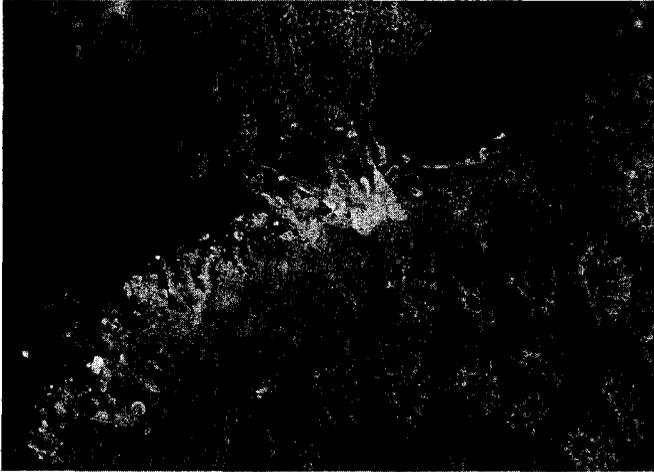
Figure 15.4 Direct competition between two corals. (Photo courtesy of H. Moody.)

adult colonies (Fearon and Cameron 1997). Slowly growing colonies often excel at direct competition, but ultimately, in the absence of other factors, rapidly growing corals that can overtop and shade their neighbors are often competitively dominant (Stimson 1985). These corals also inhibit recruitment by other corals below them, by mechanisms that are probably not limited to reduction of light alone (Fisk and Harriott 1993). Although competitive interactions are typically assumed to have costs in addition to those associated with mortality per se, comprehensive studies of the broader fitness consequences (e.g., reduction in growth and reproduction) for corals engaged in competition are surprisingly limited (Rinkevich and Loya 1985; Tanner 1997).

Other sessile organisms, such as soft corals, sponges, ascidians, bryozoans, and algae, are also abundant on reefs and are often competitively dominant over corals (Rützler and Muzik 1993; Bak et al. 1996; Aerts and van Soest 1997; Griffith 1997; Hill 1998). Many have rich biochemical defense mechanisms and complex allelochemical interactions (Jackson and Buss 1975), although simple overgrowth without chemical mediation may also result in competitive success (Griffith 1997). Competitive dominance between neighbors in cryptic communities depends on sensitivity to allelochemicals, relative rates of growth, interference competition for food, the ability to produce specialized overgrowth and defensive structures, as well as idiosyncratic aspects of the particular interaction, such as angle of attack and colony surface condition (Jackson and Buss 1975; Buss 1979, 1986; Jackson 1979; Palumbi and Jackson 1982; Lidgard and Jackson 1989; McKinney and Jackson 1988). Because species differ in these features and conditions vary, no one species is clearly dominant over all others and patterns of overgrowth are typically intransitive (Jackson and Buss 1975; Buss 1986).

COMPETITION AMONG MOBILE ORGANISMS. Studies of the sea urchin *Diadema antillarum* provide some of the best data for intra- and interspecific competition in mobile coral reef organisms (Levitan 1989; Robertson 1991; Lessios 1995). Prior to catastrophic mortality in the 1980s, population density and body size tended to be inversely correlated. This relationship suggests substantial intraspecfic competition for food, which has been confirmed experimentally (Levitan 1989). Body size and gonad volume (but not mortality rates) were highly sensitive to crowding in the field and the amount of food provided in the laboratory. Individual urchins achieved this through size regulation – large urchins shrank but small urchins grew until all achieved the size appropriate for the amount of food available. The regional demise of *Diadema* provided further opportunities to explore the roles of intra- and interspecific competition, but the results of this natural experiment have been somewhat contradictory. Not all sites show the expected increase in body size following enormous decreases in density (Lessios 1995). Moreover, although herbivorous surgeonfish increased in abundance (Robertson 1991), the herbivorous sea urchin *Echinometra viridis* did not (Lessios 1995), despite the fact that earlier, small-scale experiments suggested competition between it and *Diadema* (Williams 1981). Furthermore, Lessios (1995) found that recruitment or juvenile survivorship of *Diadema* appeared to be aided by the presence of *E. viridis*, suggesting that the effect of *E. viridis* on *Diadema* is not negative across all life stages of the latter.

Studies of interspecific competition among co-occurring territorial damselfish (*Stegastes planifrons*, *S. partitus*, and *S. variabilis*) also reveal complex competitive interactions (Robertson 1996). Removal of the larger and more aggressive *S. planifrons* resulted in a doubling of the population sizes of the other two species, although these increases did not result in as high a level of total biomass as *S. planifrons* had before its removal. Removal of *S. partitus*, on the other hand, had no effect on the abundance of the other two species. Competition in these damselfishes is thus highly asymmetric in its effects.

Mutualism

Positive interactions among sessile reef taxa are probably widespread but have received surprisingly little attention by ecologists. Positive interactions help to maintain the physical integrity of salt marshes (Bertness and Hacker 1994) and coral reefs (Wulff and Buss 1979). Positive interactions are especially common among reef sponges, perhaps because of their extreme homogeneity and flexibility of design (Wulff 1997a). Sponges protect corals from competitors and excavating organisms (Goreau and Hartman 1966), reduce harmful effects of predators and physical disturbances (Wulff 1997a), and hold together the physical structure of reef rubble until it becomes cemented by slower-growing calcareous algal cements (Wulff and Buss 1979).

Positive interactions involving mobile reef invertebrates and fishes have received greater attention, but the behaviors associated with these interactions are typically far better known than the ecological consequences. For example, experiments designed to assess the benefits associated with "cleaning" symbioses between fish and other fish or shrimp

are surprisingly equivocal (Grutter 1997; Spotte 1998). Similarly, many mobile organisms receive clear protection from predators by sheltering near corals or sea anemones, but the benefit to the latter has only occasionally been documented (Meyer et al. 1983; Liberman et al. 1995).

Predation and Herbivory

Sessile organisms on coral reefs commonly defend themselves against predators or herbivores by a great variety of chemical or physical means (Jackson and Buss 1975; Steneck 1983). Associates of these defended organisms, such as small crustaceans living in distasteful algae or sponges, are often protected from predation as well (Hay 1997; Sotka et al. 1999). As in other ecosystems, however, predators have evolved that can overcome these defenses.

Many reef animals and plants are grazed rather than eaten in their entirety, a phenomenon termed partial predation (Bak et al. 1977; Palumbi and Jackson 1982; Steneck 1983; Jackson and Hughes 1985). Partial predation generally is accompanied by the potential to regenerate. Regeneration varies among species, and also as a function of the size, depth, and location of the injury. Larger wounds generally require longer to repair, and successful establishment of a superior competitor in the area of predation is consequently more likely. Partial predation may occur along the edges of an organism, or it may divide clonal organisms into physiologically separate entities that may remain separate or subsequently be rejoined through fusion.

Figure 15.5 The crown-of-thorns starfish, *Acanthaster planci*, with nearby recently consumed coral (white skeleton). (Photo courtesy of T. Hughes.)

PREDATION. Numerous studies and reviews (Glynn 1990; Carpenter 1997; Hixon 1997) have focused on predators on corals. Starfish (*Acanthaster, Culcita*), sea urchins (*Eucidaris*), snails (*Coralliophila, Drupella, Jenneria*), polychaetes (*Hermodice*), many butterflyfish (Chaetondontidae), some pufferfishes (Tetraodontidae), and some triggerfishes (Balistidae) are the predators that have the greatest impact on corals. Most of these predators prefer rapidly growing species of corals, so they probably contribute in important ways to maintaining diversity on reefs. Predators on other sessile invertebrates are comparatively less studied.

The crown-of–thorns starfish, *Acanthaster planci*, is the most conspicuous and extensively studied predator on coral reefs (Moran 1986; Bradbury 1990; Johnson 1992; Carpenter 1997)(Figure 15.5). The starfish digests away the living tissues of corals by everting its stomach over their surfaces. The large size of the starfish, coupled with a propensity for spectacular population explosions, can result in massive coral mortality. To give but one example, on Green Island in the Great Barrier Reef, nearly 90% of the corals were killed over a several month period in 1979–1980 by aggregations of starfish whose numbers were estimated at between 350,000 and 2,000,000 (Moran 1986). Modeling suggests that the population structure of corals before the outbreak is not consistent with levels of predation to which reefs are currently subject, implying that outbreaks were either less frequent or less intense in the past (Done 1988).
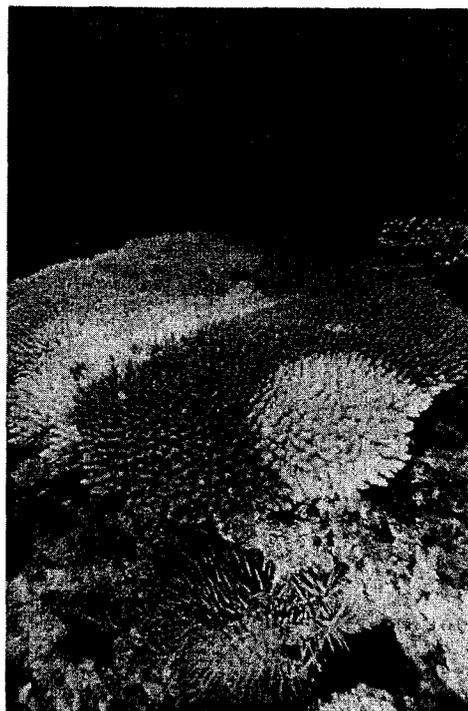
Other invertebrate predators on corals are smaller and often less conspicuous in their effects (Carpenter 1997), and some are functionally parasites rather than conventional predators (Oren et al. 1998). However, outbreaks of snails in the genus *Drupella* can result in substantial coral mortality (Cumming 1999). Predation by fishes on corals may be locally intense, but is generally of minor importance on reefs today, perhaps because of overfishing.

For sponges, in contrast, fishes are now the most important predators on reefs (Wulff 1997b; Pawlik 1998; Hill 1998), although hawksbill turtles, which are obligate sponge feeders, were probably more important in the past (Meylan 1988). Sponges are more conspicuous on Caribbean reefs than in the Indo-West Pacific, and the limited number of fishes that feed on sponges in the Caribbean led to the suggestion that predation was less intense there than in the Pacific (Wulff 1997b). However, several studies suggest that many Caribbean sponges are restricted to mangrove, grass bed, or cryptic reef habitats due to predation by angelfishes, filefishes, boxfishes, and parrotfishes (Wulff 1997b; Pawlik 1998). Moreover, experimental exclusion of fishes can result in increased overgrowth of corals by sponges (Hill 1998).

HERBIVORY. The most important ecological interactions on reefs commonly involve indirect effects of herbivores as mediators of competition between algae and corals (Pennings 1997). Macroalgae grow much more rapidly than corals un-
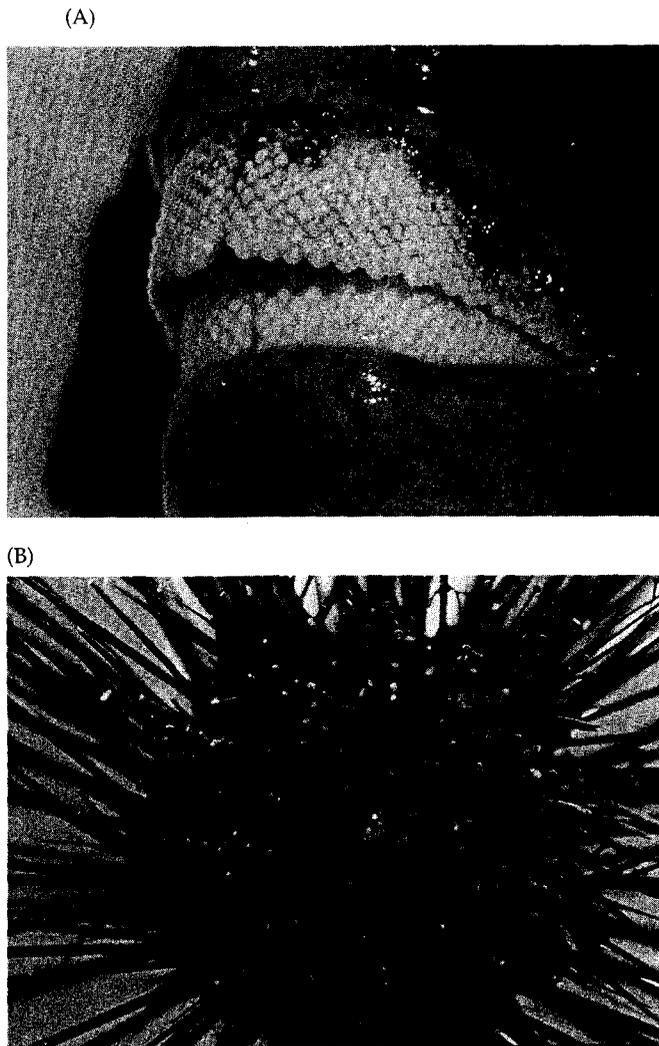
(A)

(B)

Figure 15.6 Herbivores on reefs. (A) The massive teeth of a parrot fish. (Photo courtesy of D. Bellwood.) (B) Sea urchin showing teeth of Aristotle's lantern. (Photo courtesy of R. Steneck.)

ga 1998) that were avoided by herbivorous fishes in Morrison's (1988) study. The recent proliferation of these distasteful algae is presumably due to the demise of the less selective *Diadema*. A variety of typically smaller polychaetes, molluscs, and crustaceans also graze on algae, but their ecological effects are not so well known (Carpenter 1997).

"Herbivores" do not eat only plants (Figure 15.7). When urchins become very abundant, their indiscriminant grazing also results in consumption of coral (McClanahan and Shafir 1990). Large "herbivorous" fish, such as the stoplight parrotfish *Sparisoma viride*, may graze heavily on some corals and limit their distributions to primarily non-reef habitats (Miller and Hay 1998). Territorial damselfish also kill coral to provide surfaces on which to grow their algal gardens (Kaufman 1977; Hixon 1997). Many herbivores contribute substantially to bioersion in the course of their feeding (Bellwood 1995).

Disease

Diseases have been documented in a number of tropical marine plants, invertebrates and vertebrates, and their effects can be severe (Peters 1997; Richardson 1998). Reports of diseases on reefs, particularly of corals, seagrasses, sponges, and sea urchins, have increased dramatically since the early 1970s (Richardson 1998; Harvell et al. 1999). Most of these diseases are poorly understood, and in many cases even the causative agent is unknown. The apparent increase in the incidence of diseases over the last 25 years may be a symptom of the general stress on reef ecosystems associated with multiple anthropogenic effects (e.g., global warming, introduction of novel pathogens from terrestrial run-off and ballast water, eutrophication, pollution). However, hard evidence to support this claim is largely lacking.

The ecological importance of disease has been particularly striking in the Caribbean, where major changes in reef community structure have occurred following the drastic declines of elkhorn and staghorn acroporid corals and the sea urchin

der most conditions, so that the existence of reefs as coral-dominated assemblages often depends on the removal of algae by grazers (Hay 1997). Hence, understanding herbivory is critical to understanding the ecology of reefs.

The two most important groups of herbivores on reefs are sea urchins and fish (Figure 15.6). Herbivorous fishes may bite coral reefs at rates of over 150,000 bites/m²/day, and either fishes or urchins alone may remove nearly 100% of algal production (Hay 1997). Members of these groups are not all equivalent in their effects, however. For example, parrotfish can be classified as either excavators or scrapers; their distinct feeding modes result in very different patterns of algal mortality and rates of bioerosion (Bellwood and Choat 1990). Urchins are generally less selective feeders than fishes, so that these two groups of herbivores are also not ecologically equivalent (Morrison 1988). Caribbean reefs are now often dominated by precisely those groups of algae (*Lobophora*, *Dictyota*, and *Halimeda*) (Hughes 1994; McClanahan and Muthi-

Figure 15.7 Damselfish garden in colony of staghorn coral (*Acropora cervicornis*). The coral is killed by the fish to provide a substrate for algal growth. (Photo courtesy of L. Kaufman.)

Diadema antillarum. Acropora palmata and *A. cervicornis* were dominant corals at shallow to moderate depths throughout the Caribbean in the mid 1970s, but they are now rare throughout much of their former range, primarily due to mortality from "white band" disease (Gladfelter 1982; Aronson et al. 1998). Even more strikingly, an unknown pathogen reduced the formerly abundant *D. antillarum* to less than 2% of its former numbers over a one-year period in 1983–1984 (Figure 15.8a) (Lessios 1988), and populations have largely failed to recover (Lessios 1995, but see Aronson and Precht 2000). Changes in reef community structure associated with these two diseases have been profound. Moreover, Caribbean reefs in the 1990s appear to be confronting a new suite of emerging

(A)

(B)

Figure 15.8 Effects of disease on reef organisms. (A) Dying *Diadema antillarum*. (Photo courtesy of T. Hughes.) (B) *Montastraea faveolata* coral showing extensive mortality from disease. (Photo courtesy of W. Toller.) In both cases the pathogens are unknown.
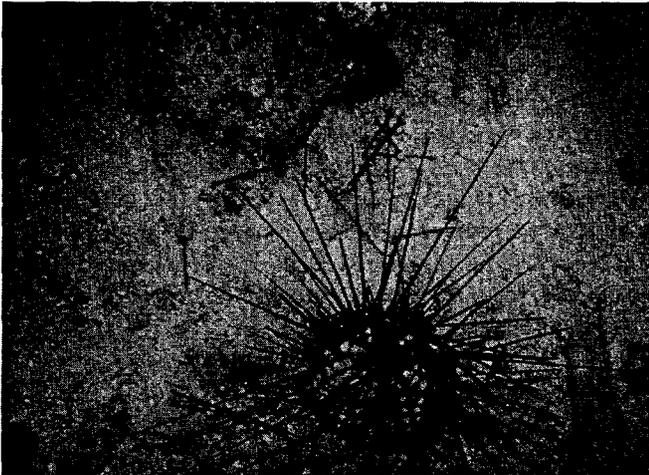
diseases (Richardson 1998; Harvell et al. 1999), and prominent among the victims are species of the abundant *Montastraea annularis* complex (e.g., Santavy et al. 1999) (Figure 15.8B). It is thus conceivable that disease will ultimately play a major role in the decline of all the formerly dominant corals of the region.

Physical Disturbance

Wave energy (Rogers 1993; Connell et al. 1997), lowered salinity (Jokiel et al. 1993), extreme temperatures (Porter et al. 1982; Glynn 1993; Fadlallah et al. 1995), excessive sedimentation (Rogers 1990; Riegl 1995), extremely low tides (Fadlallah et al. 1995), uplift or destruction by earthquakes, and changes in flow patterns (Connell et al. 1997) are among the most common natural sources of physical disturbance on reefs. Some of these disturbances have increased or may increase in the future due to human activities. Extreme disturbances, as measured by either their maximum strength or duration, happen rarely, by definition. However, events that are rare during a human lifetime may be routine for many corals and other reef taxa that may live for centuries (Jackson 1991, 1992; Woodley 1992). Although more extreme events typically produce more disturbance, the past history of disturbance can influence the relationship between the intensity of an event and the amount and kind of destruction that results (Paine et al. 1998; Hughes and Connell 1999).

Hurricanes and typhoons are the strongest physical disturbances to which most reefs are subjected (Figure 15.9). Nevertheless, regions with the greatest number of typhoons and hurricanes overlap to a substantial extent with areas of greatest reef development (Scoffin 1993). Damage caused by major storms has been quantified in both the Pacific and the Atlantic (Woodley et al. 1981; Harmelin-Vivien and Laboute 1986; Rogers 1993; Connell et al. 1997). Mortality is typically greatest in shallow water, but "avalanches" on steep deeper slopes can sometimes result in nearly 100% destruction. In
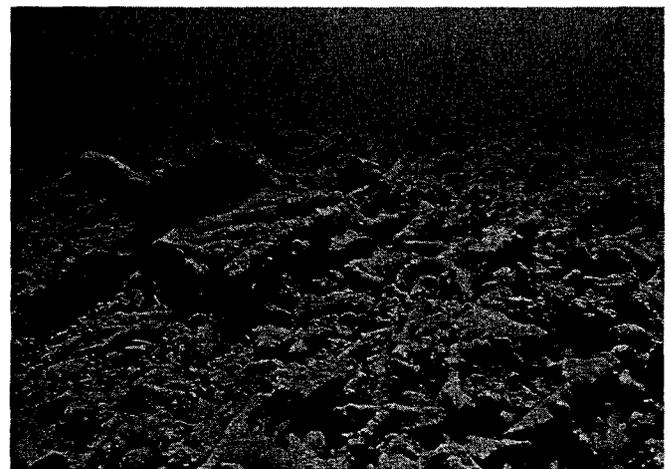
Figure 15.9 Field of coral rubble in the *Acropora palmata* zone of Discovery Bay, Jamaica, caused by waves from Hurricane Allen. (Photo courtesy of L. S. Land.)

general, more rapidly growing branching corals are most vulnerable to storm damage, and more slowly growing massive corals are least vulnerable. For this reason, sporadic major storms often favor species that are competitively subordinate during routine conditions, thus promoting the coexistence of both types (Rogers 1993).

THE STRUCTURE AND ASSEMBLY OF CORAL REEF COMMUNITIES

Community structure is determined by processes that bring species to the community and the population dynamics and species interactions of its members (Roughgarden 1989). Marine species with a planktonic larval phase commonly fluctuate in adult abundance more than species without planktonic larvae, suggesting that processes affecting larval survival, transport, and settlement are important determinants of pattern (Thorson 1950; Roughgarden et al. 1988; Grosberg and Levitan 1992). Renewed attention to this "supply side" of marine ecology is commonly associated with a Gleasonian view of density-independent community structure (Connell 1978; Doherty 1991; Sale 1991b; Williams 1991; Hubbell 1997). On a suitably large scale, however, larval recruitment depends on the abundance, fecundity, and proximity for fertilization or mutual defense of reproductive adults (positive feedback), and the availability of suitable habitat free of competitors or predators (negative feedback). This density dependence brings the biology of species and their niches back into the equation (Chesson 1997). Indeed, as we have seen, corals and other reef organisms may be injured or die from a great variety of causes, and their vulnerability to these processes varies greatly among species (Jackson and Hughes 1985, Knowlton and Jackson 1994).

Many kinds of biological interactions, physical disturbances, and processes affecting dispersal and recruitment have been shown to affect small-scale patterns of community structure and assembly on coral reefs (Doherty 1991; Karlson and Hurd 1993; Carpenter 1997; Connell et al. 1997; Hay 1997; Hixon 1997; Peters 1997). However, we do not know the relative magnitude of the direct and indirect effects of all these different processes, and their synergisms, in more than a handful of cases. Two general problems have impeded progress. First, basic patterns of distribution and abundance, community structure and zonation on coral reefs are poorly documented on all but a few reefs (e.g., Goreau 1959; Loya 1972; Glynn 1976; Done 1982; Liddell and Ohlhurst 1992), so that it is difficult to generalize beyond the simplest patterns (Done 1983, 1992; Jackson 1991; Wilkinson and Cheshire 1988). Thus, in the most basic sense, we often do not know what we are trying to explain.

Second, landscape patterns of interactions, disturbance, and succession on coral reefs comparable to those documented for rocky intertidal communities (Paine and Levin 1981; Roughgarden et al. 1988) and kelp forests (Dayton et al. 1992, 1999) can rarely be observed over appropriate spatial and temporal scales that characteristically extend beyond the re-

sources and lifetimes of ecologists. Extreme hurricanes occur on decadal to century scales, generation times of dominant coral species are commonly measured in decades to centuries, and pivotal successional events are set and reset by fluctuations in sea level measured in tens of thousands of years (Jackson 1991, 1992). Differences among species in competitive abilities, resistance to predation, life histories, and the resulting patterns of community succession on reefs, can be viewed as evolutionary adaptations to characteristic patterns of interaction and disturbance (Jackson and Hughes 1985). But these hypotheses are not directly testable because the longest running study of reef community structure involving observations of individual organisms is only 30 years (Connell et al. 1997). In spite of all these problems, real progress has been made in a few reef systems that have been studied using numerous complementary approaches across a range of spatial and temporal scales.

Recruitment

Local populations of species with weakly dispersing larvae and sessile or sedentary adults are demographically closed; they exhibit potentially high levels of inbreeding (Knowlton and Jackson 1993) and stability in abundance (Jackson and Hughes 1985; Jackson and Kaufmann 1987) compared to species with planktonic larvae or highly vagile adults. Many small incrusting marine invertebrates and macroalgae have larvae that disperse very little. In contrast, virtually all reef fishes and about 85 percent of reef coral species have a planktonic larval stage (Leis 1991; Richmond 1997), so that larval recruits in these groups may be almost entirely or exclusively derived from elsewhere. This implies that their local populations are demographically open and that their populations cannot be regulated by local fecundity (Roughgarden et al. 1988; Caley et al. 1996). However, new evidence suggests that potentially widely dispersed larvae of reef fishes may return to their natal population (Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000). It is thus especially unfortunate that almost all ecological studies of reef fishes and corals have been made on the small spatial scale of local populations for logistical reasons.

At a larger scale, however, groups of local populations (metapopulations) are effectively closed, with boundaries set by limitations to larval dispersal (Caley et al. 1996). It is only on this larger scale that relations among adult abundance, fecundity, and recruitment of species with planktonic larvae can be examined (Hughes et al. 2000). Moreover, the evolution of life history traits and larval behaviors, such as the selection of specific habitats for recruitment, can only be understood at these larger scales (Paine and Levin 1981; Jackson 1991; Warner 1997).

CRYPTIC REEF COMMUNITIES. Undersurfaces of plating corals and coral rubble, crevices in reef framework, and the walls and roofs of caves are dominated by hundreds of species of small encrusting bryozoans, colonial ascidians, sponges, and calcareous algae (Vasseur 1974; Jackson 1977, 1983; Jackson and Hughes 1985; Kobluk et al. 1988; Hughes and Jackson

1992; Harmelin 2000). Recruitment limitation at early stages of community development is evident in extremely low rates of larval settlement on panels suspended from racks situated more than a few meters from a reef (Jackson 1977; Buss and Jackson 1981; Winston and Jackson 1984). Recruitment also drops off to nearly zero after substrates are entirely encrusted, except when substrate is bared by injury to established colonies (Palumbi and Jackson 1983; Winston and Jackson 1984; Jackson and Kaufmann 1987).

REEF CORALS. Connell et al. (1997) observed changes in coral populations in fourteen 1-m^2 quadrats at four low intertidal reef sites at Heron Island over 30 years (Figure 15.10). The sites include exposed pools, exposed reef crest, protected reef crest, and inner reef flat environments situated from 300 to 2000 meters apart. Recruitment of corals was measured by the first appearance of juveniles observed in photographs taken 1 to 4 years apart, thereby comprising some unknown but small fraction of the original larval recruits. Recruitment was highly concordant among the 2–5 replicate quadrats at a site but not among sites. Recruitment varied independently from year to year with no obvious temporal pattern over 30 years. However, recruitment was positively correlated with amount of free space for settlement at three of the four sites; the only exception was the protected crest, where free space never fell below 25%. Thus, recruitment of juvenile corals into the sessile population was strongly density dependent.

A similar 16-year photographic study of coral populations in replicate 1-m^2 quadrats in deeper water in Jamaica (Hughes and Jackson 1985; Hughes 1985, 1990; Hughes and Tanner, 2000) provides a basis for comparison between the Caribbean and Indo-West Pacific. Rates of recruitment of juvenile corals visible in photographs (aged 7–12 months) were similar to those at Heron Island (Connell et al. 1997), even though recruitment rates of very young corals (< 3 months) in the Caribbean are typically about 1% of those on the Great Barrier Reef. Thus survival of juveniles must be much higher in the Caribbean than Australia, a relationship that is in keeping with the higher proportion of brooding coral species in the Caribbean (Richmond 1997). Coral recruitment in Jamaica was also strongly density dependent, as demonstrated by the significant positive correlation of recruitment rate with percent free space. This result was confirmed experimentally by removal of all corals from 6 quadrats and measuring the subsequent severalfold increase in recruitment (Hughes 1985).
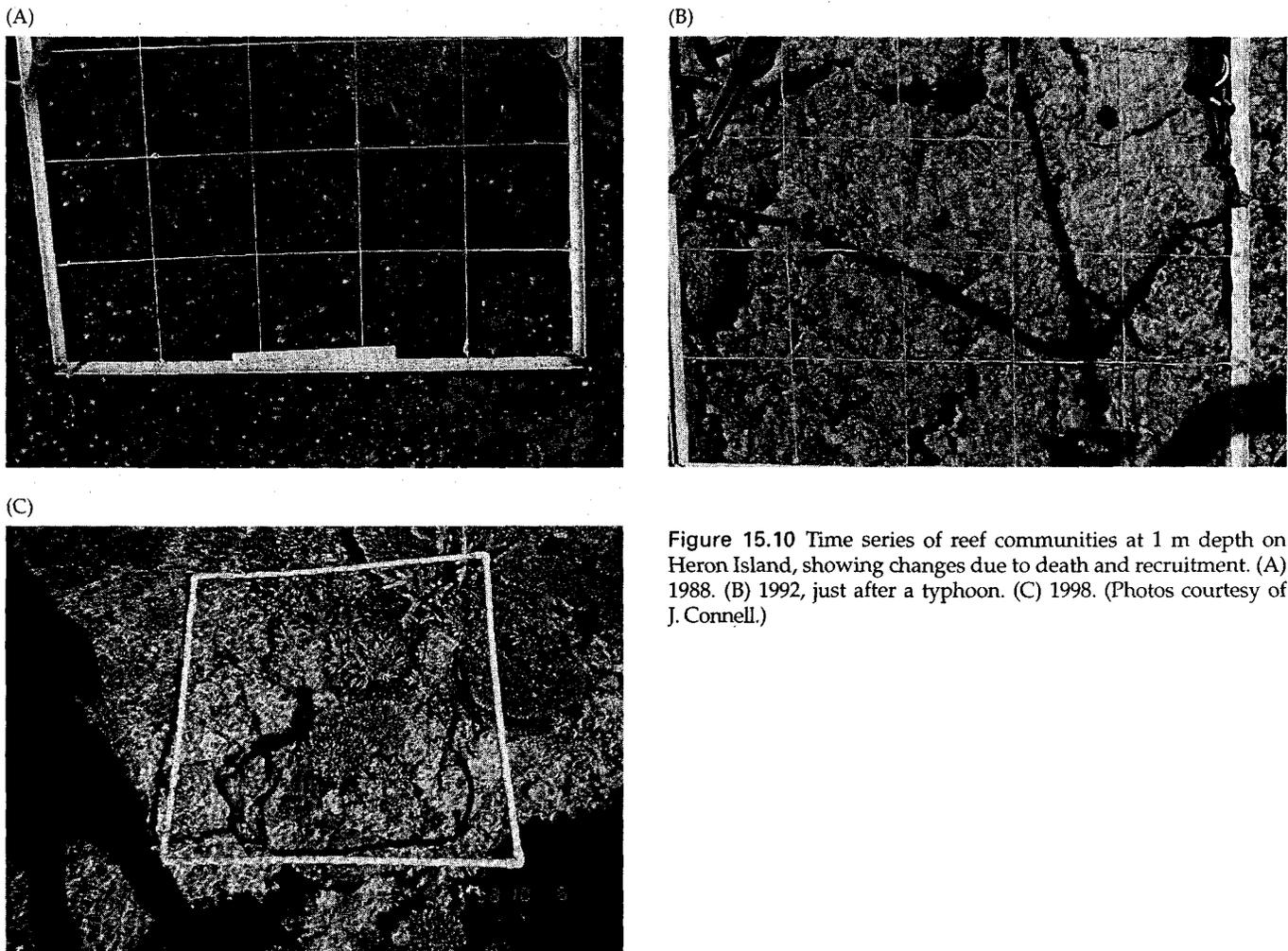
(A)

(B)

(C)

Figure 15.10 Time series of reef communities at 1 m depth on Heron Island, showing changes due to death and recruitment. (A) 1988. (B) 1992, just after a typhoon. (C) 1998. (Photos courtesy of J. Connell.)

The most comprehensive analysis of stock-recruitment relations, involving a variety of spatial scales, is the product of a two-year study of coral abundance, fecundity, and larval recruitment along the entire Great Barrier Reef (Hughes et al. 1999, 2000). Rates of recruitment and total coral abundance and cover were measured on the crests of 33 reefs. Sites were chosen in a hierarchical sampling design consisting of sectors (250–500 km), reefs (10–15 km), sites (0.5–3 km), and replicates (1–5 m). Recruitment rates for spawning species varied more than 25-fold among sectors and more than 200-fold among sites and replicates, versus 5–8-fold for brooders among sectors and 100-fold among sites and replicates. In contrast, adult abundance in transects at the same sites did not vary significantly among sectors, so that there was no relationship between adult abundance and recruitment. However, proportions of gravid colonies of common species of *Acropora* varied from 15 to 100% among the same sites 10 days before the predicted mass spawning. When applied to the entire *Acropora* population, coral abundance weighted by these variations in fecundity explains 72% of the variation in recruitment on the sector scale and no other factors were significant (Figure 15.11). This strong stock-recruitment effect was nonlinear, with numbers of recruits increasing exponentially towards higher values of fecundity. This suggests a threshold density for increases in fertilization success or satiation of predators, and thus strong positive feedback in the stock-recruitment relationship.

REEF FISHES. Local populations of coral reef fishes may be open in the extreme because of the very long planktonic phase of larval development that typically lasts from 10 to more than 100 days (Leis 1991). Indeed, many species are panmictic on the scale of the entire Caribbean or Great Barrier Reef (Doherty et al. 1995; Shulman and Bermingham 1995). Most work on fish recruitment has been done on artificial or natural patch reefs 1 m² or smaller (Doherty 1991). Large and apparently stochastic variations in recruitment into these miniature habitats comprise the primary basis for the hypothesis that population sizes and assembly of communities of reef fishes are mainly determined by insufficient and unpredictable larval recruitment (Sale 1977, 1991b; Doherty 1991). If recruitment is indeed limiting, then patterns of adult abundance in similar environments should be predictable on the basis of recruitment statistics alone (Doherty and Fowler 1994; Caley et al. 1996). However, if numbers of adults are independent of recruitment then recruitment alone cannot be limiting.

The small, common damselfish *Pomacentrus moluccensis* exhibits highly variable recruitment on the southern Great Barrier Reef (Doherty and Fowler 1994). Rates of recruitment measured over 9 years varied consistently by more than an order of magnitude among patch reefs in seven lagoons across 70 km. The historical average of recruitment explained 84% of the variance in adult abundance in the different lagoons. Moreover, the abundance of fishes in different age classes (determined from numbers of rings in their ear bones) at the end of the experiment clearly reflected the magnitude of recruitment of their year class. Thus the abundance and population structure of this species can be explained almost entirely by its magnitude of recruitment. In contrast, Robertson (1988a,b,c) showed that densities of adults were not correlated with settlement patterns over 6 years in three species of surgeonfishes, a triggerfish and a damselfish in Panama. In addition, many studies have demonstrated positive and negative density-dependent effects (as well as no effects) of the presence of resident adult fishes on the rate of larval recruitment (Sweatman 1983, 1985; Jones 1991); some density-dependent effects on recruitment are expressed primarily at the earliest stages immediately after settlement (Caselle 1999; Schmitt and Holbrook 1999). Remarkably, given the level of controversy, large-scale stock-recruitment relations have not been studied for any coral reef fish species.

Post-Recruitment Processes

CRYPTIC REEF COMMUNITIES. Undersurfaces of platy corals support a highly diverse encrusting community of mostly sponges, bryozoans, colonial ascidians, and coralline algae (Jackson and Buss 1975; Jackson and Winston 1982). Most of the undersurface is occupied, so that growth of one organism almost inevitably involves partial or complete mortality of a neighbor. Grazing by sea urchins and other predators is also common in shallow environments but decreases with depth. Analyses of weekly photographs under corals in Jamaica (Figure 15.12) demonstrate that community composition at any fixed point changes rapidly due to grazing and overgrowth, but other processes appeared unimportant (Jackson and Kaufmann 1987). Grazing killed organisms occupying one-third of the surface per year prior to the demise of *Dia-*
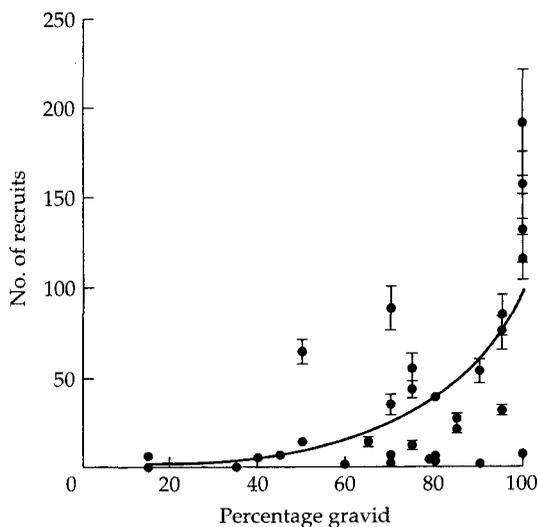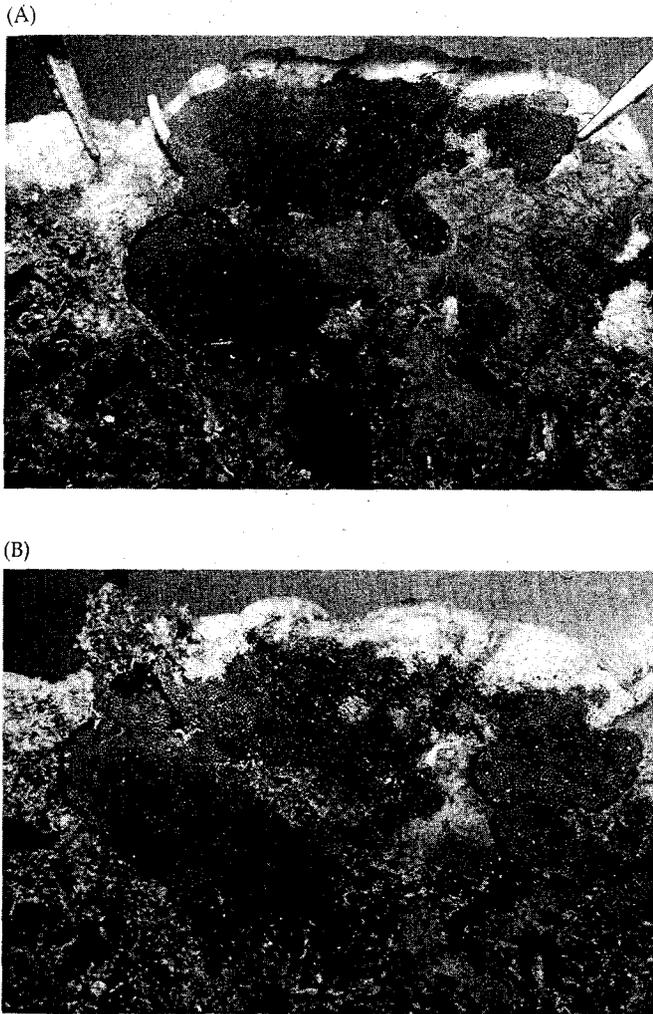

Figure 15.11 Relationship between abundance weighted by fecundity and recruitment for *Acropora* corals on the Great Barrier Reef. (From Hughes et al. 2000.)

(A)

(B)

Figure 15.12 Time series of changes for cryptic community under coral in Jamaica. (A) June 1983. (B) September 1983. (Photos by J. B. C. Jackson.)

dema, and overgrowth killed another third. Nevertheless, community composition was stable across the reef because growth and regeneration by dominant species approximately equaled their losses. Rates of predation decreased greatly after the *Diadema* died, but community composition changed little over two years because *Diadema* had grazed mostly upon competitively inferior organisms. Slow increases in abundance of erect animals previously eaten by *Diadema* suggest that they could eventually grow to dominate the community the way seaweeds overgrew corals (Hughes 1994), but there are no data.

REEF CORALS. Most mortality of reef corals measured in long-term studies in Australia and before the demise of *Diadema* in Jamaica was due to routine processes of competition, predation, and sedimentation rather than catastrophic storms or outbreaks of predators or disease (Hughes and Jackson 1985; Bythell et al. 1993; Connell et al. 1997; Hughes and Connell

1999). However, we have little idea of the relative importance of different routine causes of mortality, nor their magnitude compared with recent outbreaks of disease, crown-of-thorns starfish, coral bleaching, and overgrowth of corals by seaweeds in the Caribbean in the 1980s (Hughes 1994; Connell et al. 1997; Done 1997, 1999; Richardson 1998). For example, various species of *Acropora* form dense, nearly monospecific stands at the expense of other species. Rapid growth, clonal propagation, resistance to breakage by all but the most severe storms, and tall, arborescent colony form allow *Acropora* to overtop and shade out slow growing corals (Kaufman 1977; Porter et al. 1981; Stimson 1985; Jackson 1991; Fisk and Harriott 1993). However, we cannot scale these competitive effects relative to those of predators, disease, or routine physical disturbances. The same problem affects all other forms of competition involving corals, such as digestive dominance, although the strong inverse correlation between aggressive rank and growth rates suggest that these factors were once highly important (Lang 1973; Lang and Chornesky 1990).

Many studies of effects of predation on corals concern small invertebrates and fishes (Kaufman 1977; Knowlton et al. 1990). Rates of partial predation may be as high as in cryptic reef communities, but have not been followed closely. Effects of predators may change radically with prey density, as in the case of the continued decline of staghorn coral *Acropora cervicornis* due to predation after the coral's mass mortality following a severe hurricane (Knowlton et al. 1981, 1990). Concentrations of predators on survivors of a strong El Niño event in the eastern Pacific similarly contributed to the continued decline of corals after normal temperatures returned (Glynn and Colgan 1992). In contrast, recruitment of benthic macroalgae after the mass mortality of *Diadema* exceeded the abilities of other resident herbivores to consume them, resulting in the massive buildup of seaweed populations that have overgrown corals throughout the Caribbean (Lessios 1988; Hughes 1994). These threshold effects of relative predator and prey densities, and other nonlinear interactive effects of competition and predation, modulate variations in community structure and may lead to the existence of alternate stable or quasi-stable states (Knowlton 1992; Done 1992, 1997).

There has been a major effort in Australia to model the dynamics of outbreaks and dispersal of the crown-of-thorns starfish *Acanthaster planci* along the Great Barrier Reef using a variety of approaches (Bradbury 1990; Johnson 1992; Bradbury and Seymour 1997). The frequency and movement of starfish outbreaks, and the patterns of outbreaks relative to prevailing hydrodynamic conditions are reasonably well understood; less clear are the key issues of shifts between low- and high-density populations and stock-recruitment relationships (McCallum 1992). The dynamics of outbreaks are also changing because the proportion of reefs available to host major outbreaks is declining (Figure 15.13) (Bradbury and Seymour 1997).

There has also been considerable progress in modeling responses to devastation by *Acanthaster* and subsequent successional dynamics of the sessile reef community, compara-
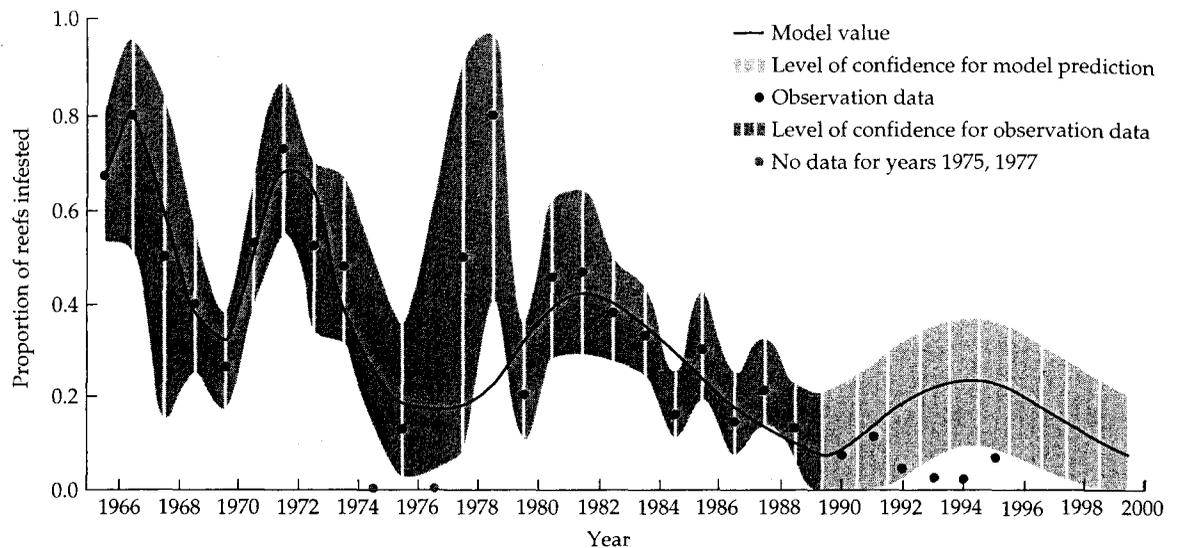
Figure 15.13 Changes in the frequency of outbreaks in crown-of-thorns starfish over the last two decades. (After Bradbury and Seymour 1997.)

ble to Paine and Levin's (1981) analyses of the landscape dynamics of temperate rocky intertidal mussel beds. The main difficulty is to obtain data on changes in benthic community composition on appropriately large spatial and temporal scales. Transition-matrix models have been used to project periods of recovery of coral populations (Done 1992, 1997, 1999). Recognition of deliberately simplified alternative sessile communities (algal, colonizing coral, recovering coral, old coral, and other) permits observations of the persistence of different states and rates of shifts between them. However, a century or more of data may be required to test alternative predictions because the relevant time scales are so long (Jackson 1991).

REEF FISHES. The importance of post-settlement processes in the assembly and structure of reef fish communities has been obscured by the rhetoric of recruitment limitation (Jones 1991; Williams 1991). Larval habitat selection has also been treated as an evolutionary black box (Doherty 1991; Doherty and Fowler 1994) without consideration of the natural selection (i.e., ecology) necessary to maintain such otherwise costly behavior (e.g., Morse and Morse 1996 for corals). However, recent work is reviving interest in post-recruitment processes. Detailed surveys of 75 reefs around two adjacent islands on the southern Great Barrier Reef demonstrate much greater predictability in fish distributions among habitats on large, contiguous reefs than among small, isolated patch reefs (Ault and Johnson 1998). This is important because, as we have seen, most of the support for recruitment limitation comes from studies of very small patches. In addition, Robertson (1996) has demonstrated intense, asymmetric interspecific competition among adult damselfish based on removals of two common species over many years. The experiments are highly unusual in their duration, which exceeds the average generation times of the species involved, and in the consider-

able number of years required to begin to see persistent effects (Yodzis 1988).

ECOSYSTEM STRUCTURE AND FUNCTION

Reef Ecosystems Today

Ecosystem ecology concerns the processes that link the physical and chemical environment to the resident, interacting assemblage of organisms, and the boundary conditions, physical scales, and rate constants that affect the action of these processes (Hatcher 1997). The most important ecosystem processes on coral reefs are trophic and bioconstructional (Done et al. 1997). The outstanding trophic characteristics are the (1) overwhelming contribution of endosymbiotic zooxanthellae and benthic algae to primary production, and the correspondingly minor role of phytoplankton (Hatcher 1988, 1990; Kinsey 1991); (2) sensitivity of benthic production to nutrient inputs and sedimentation (Hallock and Schlager 1986; Birkeland 1987); and (3) large number and high diversity of trophic levels in food webs (Figure 15.14, Grigg et al. 1984). The outstanding bioconstructional features are the enormous biogenic production of limestone and calcareous sediment, and the conflicting balance of processes that bind these materials together into reef framework versus processes of physical and biological destruction and erosion that break down framework into sediment (Figure 15.15) (Buddemeier and Hopley 1988; Hubbard 1988, 1997; Glynn and Colgan 1992).

In essence, what makes a reef a reef is determined by the relative amounts of carbon invested in trophic pathways versus bioconstruction, and this in turn depends upon the relative abundance and production of calcifying versus noncalcifying primary producers. There is an enormous literature on the mechanisms and controlling factors of the productive and calcifying pathways on coral reefs (Hatcher 1988, 1990, 1997;
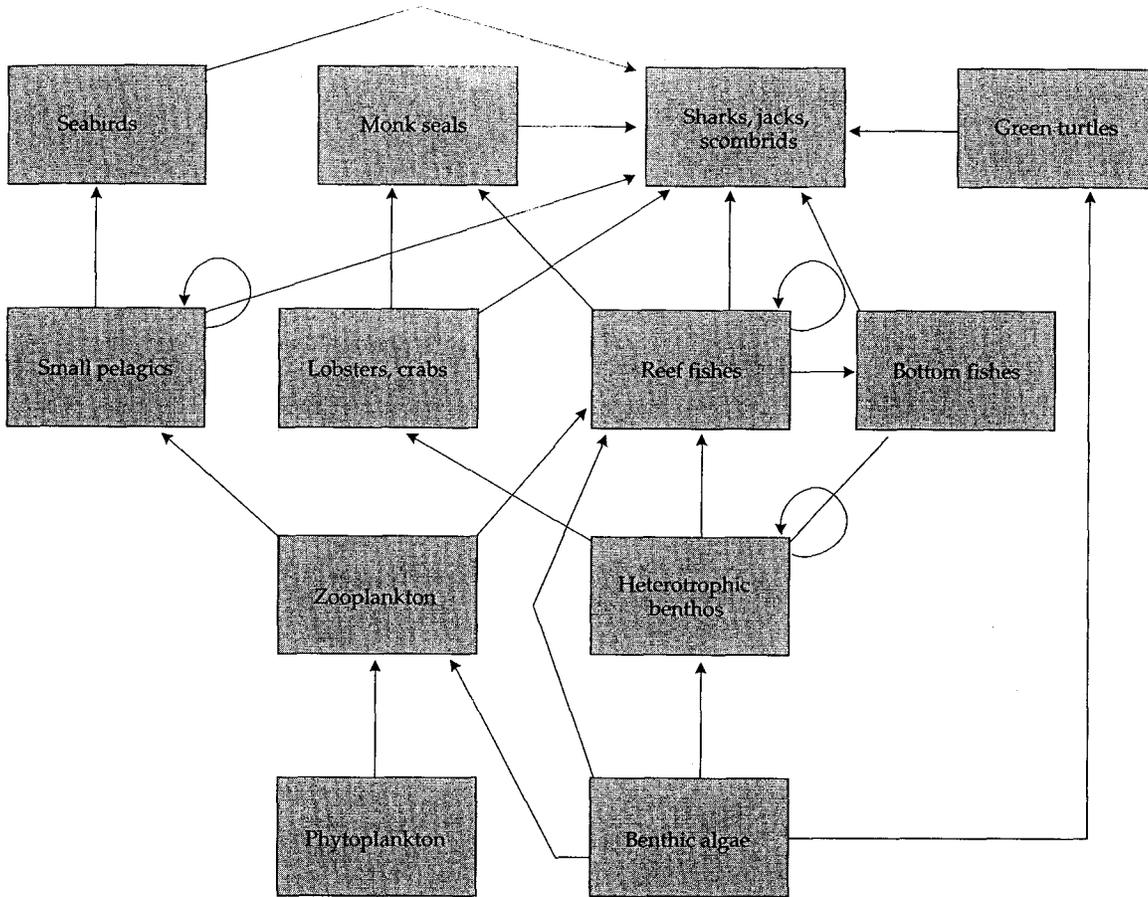
Figure 15.14 Food web for French Frigate Shoals. (After Grigg et al. 1984.)

Kinsey 1991; Done et al. 1997; Muller-Parker and D'Elia 1997), the details of which are beyond the scope of this review. Here we concentrate on two basic kinds of interactions among population and ecosystem processes that are of particular relevance to the recent degradation of coral reef communities.

The first concerns the balance between calcifying organisms, noncalcifying organisms, and bioeroders that deter-

Figure 15.15 Massive bioerosion caused by sea urchins on Caribbean reefs. (Photo from Jackson 1983.)

mines whether or not reef mass increases or decreases. This balance can be shifted by catastrophic mortality of the first group, particularly corals, due to hurricanes (Knowlton et al. 1981, 1990; Woodley et al. 1981), coral bleaching (Glynn and Colgan 1992), and outbreaks of predators (Done 1992, 1997) or disease (Richardson 1998). In all these cases, continued predation on surviving corals further tips the balance in favor of uncalcified benthic animals and fleshy algae that cover the substratum and inhibit coral and coralline algal settlement and recovery (Knowlton 1992; Done 1992, 1999). Patterns of carbon flux and structure of food webs change dramatically (Kinsey 1988; Johnson et al. 1995). The mass mortality of the sea urchin *Diadema antillarum* also permitted an explosion in growth of fleshy algae that overgrew and killed their coral and coralline algal neighbors (Figure 15.16) (Lessios 1988; Hughes 1994). This shift from dominance by corals to fleshy algae also greatly reduces rates of calcification and increases rates of erosion by grazing animals (Glynn 1997). Reef accretion stops and reef mass decreases in size, further decreasing chances of the reestablishment of corals (Buddemeier and Hopley 1988; Hubbard 1997).

Increased nutrient inputs also have deleterious effects on coral abundance and reef growth for many reasons (Hallock and Schlager 1986; Done et al. 1997). Increased nutrients fertilize phytoplankton whose increased growth reduces water transparency and thus the light available to zooxanthellae at
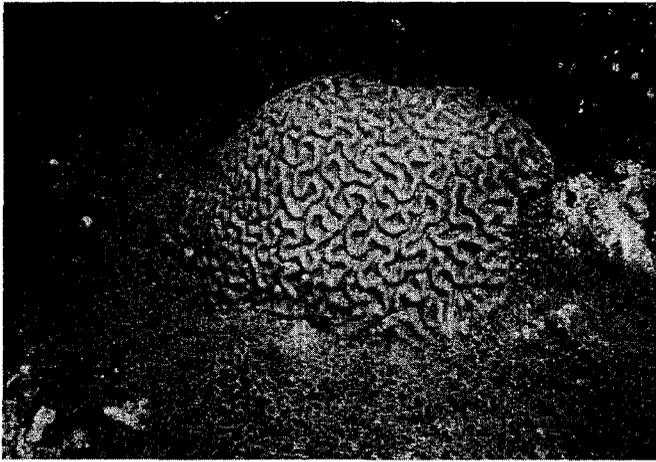
Figure 15.16 Effects of mortality of *Diadema antillarum*; note the lush growth of algae on the bottom. (Photo courtesy of T. Hughes.)

the bottom. Increased phytoplankton also favors recruitment and growth of benthic suspension-feeding animals that overgrow or bioerode coral skeletons (Highsmith 1980; Hallock and Schlager 1986; Birkeland 1987; Hallock 1988). Finally, increased nutrients favor growth of benthic fleshy algae that overgrow corals. All of these different effects of increased nutrients and the catastrophic disturbances discussed above act synergistically to suppress the growth of Caribbean corals and coral reefs (although the loss of herbivores appears to have had a greater effect than increases in nutrients; Hughes et al. 1999; Miller et al. 1999).

Half a Billion Years of Reef Ecosystems

Geologists agonize about what and what not to call a reef (James 1984; Fagerstrom 1987; Hallock 1997). Their most important criteria for "true" coral reef development include (1) presence of framework built by colonial metazoans containing endosymbionts or by crustose coralline algae, (2) topographical relief of the living reef surface above the surrounding sea floor, and (3) resistance of the framework to wave action and storms. By this definition, large-scale development of true reefs occurred during just three episodes of geologic time that altogether lasted about one-quarter of the Phanerozoic or roughly 125 million years (Wood 1999). Principally tabulate corals and stromatoporoid sponges constructed extensive Silurian and Devonian reef tracts as large as the Great Barrier Reef. Highly integrated growth across the colony surface over which small polyps were arrayed strongly suggests that tabulates possessed endosymbionts that contributed to their extensive calcification (Coates and Jackson 1987), but there is no definitive evidence that stromatoporoids contained endosymbionts. The second and third major phases of extensive and geographically widespread framework development occurred in the Jurassic and in the mid to late Cenozoic to recent. These reefs were built largely by colonial scleractinian corals with varying contributions by larger foraminifera, and calcareous

or coralline algae. Both stable isotopic and morphological analyses indicate that scleractinians possessed endosymbionts in the Late Triassic or Early Jurassic (Coates and Jackson 1987; Swart and Stanley 1989). In all three episodes, the surface area of cryptic reef environments within the reef framework greatly exceeded that of open reef surface, and was inhabited by a highly characteristic assemblage of calcareous sponges and other encrusting animals.

Regional changes in nutrient levels also have been implicated as the controlling factor for turning on or off major episodes of reef development over geological time (Hallock and Schlager 1986; Edinger and Risk 1994). Patterns of extinction selectivity and distribution of endolithic organisms in coral skeletons across the Oligocene-Miocene boundary 25 million years ago suggest that collapse of extensive Oligocene reef tracts and coral diversity in the Caribbean was associated with eutrophication. Species diversity of reef corals slowly recovered until the end of the Pliocene about 2 million years ago, when there was another mass extinction of reef corals (Budd and Johnson 1997) associated with oceanographic changes and intensifying sea level fluctuations (Jackson 1994b). Throughout this period of increasing diversity, large-scale reef buildups were absent, and sedimentological evidence suggests that water-column productivity remained high. Then, after the second mass extinction, reef development increased dramatically with declining productivity (Collins et al. 1996), even though coral diversity never recovered.

In contrast, "reef" development during the remaining three-quarters of the Phanerozoic was limited to low-lying buildups, or bioherms, of carbonate skeletal debris in a mud matrix without any obvious structural framework (Wood 1999). However, uncalcified sponges may have helped hold such structures together just as they hold corals together today (Wulff and Buss 1979). The two major groups responsible for such buildups were (1) cyanobacteria, calcareous algae, and weakly calcified or hexactinellid sponges and (2) heterotrophic, mostly solitary animals including corals, bivalve mollusks, brachiopods, bryozoans, and archeocyathids. Only one or the other of the two groups was generally abundant at any time. The most abundant and geologically spectacular heterotrophs are early Cambrian archeocyath sponges (Wood et al. 1993), middle Paleozoic solitary and simple colonial rugose corals (Fagerstrom 1987), Permian calcified sponges, bryozoans and brachiopods (Wood et al. 1995), and Cretaceous rudist bivalves (Ross and Skelton 1993). Animals with endosymbionts were apparently rare or absent, and cryptic environments were much less developed than in reefs with true framework.

Much of this variation in mode and extent of Phanerozoic reef development and taxonomic composition can be explained by (1) relations between variations in nutrient availability and modes of growth and life histories of dominant reef builders, as well as (2) types and abundance of predators (Figure 15.17) (Wood 1999). However, the record of nutrient levels and productivity in Phanerozoic seas is still preliminary, and their role in reef development is largely inferred
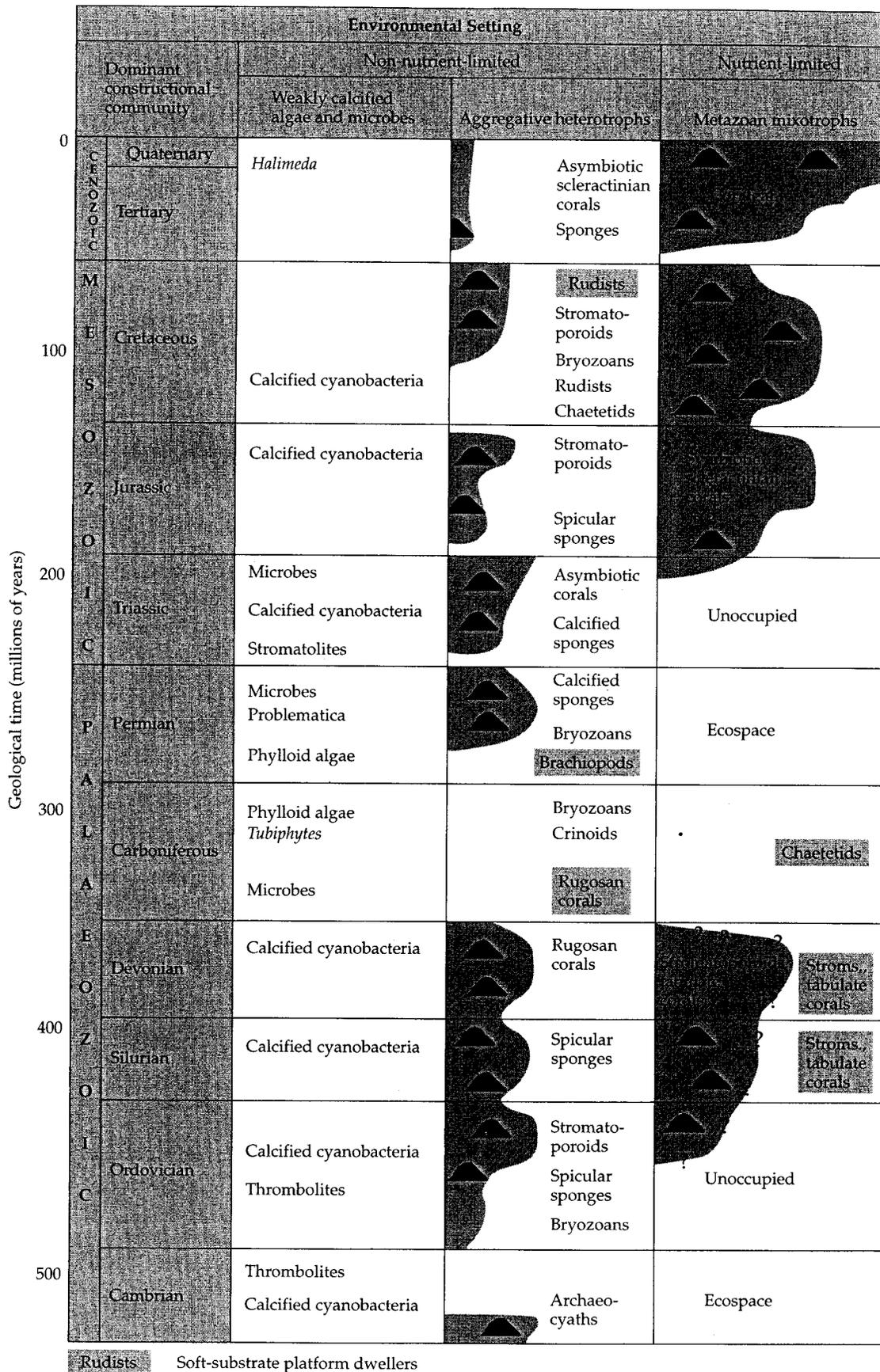
| | Environmental Setting | | |
| Dominant constructional community | Non-nutrient-limited | | Nutrient-limited |
	Weakly calcified algae and microbes	Aggregative heterotrophs	Metazoan mixotrophs
CENOZOIC — Quaternary / Tertiary	*Halimeda*	Asymbiotic scleractinian corals Sponges	
MESOZOIC — Cretaceous	Calcified cyanobacteria	Rudists Stromato-poroids Bryozoans Rudists Chaetetids	
MESOZOIC — Jurassic	Calcified cyanobacteria	Stromato-poroids Spicular sponges	
MESOZOIC — Triassic	Microbes Calcified cyanobacteria Stromatolites	Asymbiotic corals Calcified sponges	Unoccupied
PALAEOZOIC — Permian	Microbes Problematica Phylloid algae	Calcified sponges Bryozoans Brachiopods	Ecospace
PALAEOZOIC — Carboniferous	Phylloid algae *Tubiphytes* Microbes	Bryozoans Crinoids Rugosan corals	Chaetetids
PALAEOZOIC — Devonian	Calcified cyanobacteria	Rugosan corals	Stroms., tabulate corals
PALAEOZOIC — Silurian	Calcified cyanobacteria	Spicular sponges	Stroms., tabulate corals
PALAEOZOIC — Ordovician	Calcified cyanobacteria Thrombolites	Stromato-poroids Spicular sponges Bryozoans	Unoccupied
PALAEOZOIC — Cambrian	Thrombolites Calcified cyanobacteria	Archaeo-cyaths	Ecospace

Geological time (millions of years): 0, 100, 200, 300, 400, 500

Rudists | Soft-substrate platform dwellers

Figure 15.17 Geological record of reef development, showing relationships between abundance of major reef builders and physical conditions. (From Wood 1995.)

from what is known about variations in growth and life histories of reef dwellers in relation to nutrients in recent seas.

Factors leading to episodes of reef building by solitary heterotrophs can be understood in terms of factors that regulate the relative abundance of solitary and colonial animals today (Jackson 1977, 1983; Jackson and Coates 1985). Dense aggregations of benthic organisms can form by aggregative larval recruitment or by indeterminate growth and clonal propagation across the substrate. Larval aggregation is most common among aclonal, solitary animals like oysters, mussels, and tube worms that are poor overgrowth competitors for space except in very high densities, when they may dominate the entire community. Clonal propagation is characteristic of many algae, sponges, and colonial animals like corals that are excellent overgrowth competitors.

Levels of nutrients and primary production in the plankton modulate the balance of power between aclonal and clonal groups (Littler and Littler 1984; Birkeland 1988; Hallock 1988). Eutrophic conditions with very high levels of nutrients and planktonic productivity favor solitary animals. This is because increased food supplies allow enormous production of larvae and suppress growth of photoautotrophs and mixotrophs like algae and corals. Low productivity favors clonal organisms that do not require constantly high recruitment to maintain high population densities. Significantly, fossil reefs built by heterotrophs predominate in mudstones that almost certainly reflect high turbidity, nutrients, and planktonic productivity (Wood 1999; Ross and Skelton 1993), the same conditions that favor aggregations of solitary animals like oysters today.

In contrast, dominance by fleshy algae over corals and coralline algae in recent seas is favored by (1) moderate levels of nutrients that promote algal growth and (2) low abundance of grazers that otherwise maintain hard substrates clean of fleshy algae (Littler and Littler 1984; Birkeland 1988; Hallock 1988). Significantly, the geological first appearance of many of the most important grazers immediately precedes or follows closely upon the beginning of each of the three major episodes of framework reef building (Steneck 1983; Signor and Brett 1984; Vermeij 1987). The relative importance of reef building by algae in the absence of heterotrophs also falls off throughout the Phanerozoic as grazers with more and more effective dentition evolved.

The Last Two Million Years, the Last Five Hundred Years, and the Foreseeable Future

Pleistocene Perspectives on the Structure and Assembly of Reef Communities

The fossil record is the only source of long-term ecological data on time scales that encompass the natural variability of coral reef ecosystems (Hubbard 1988; Jackson 1991, 1992; Pandolfi 1999). Individual coral skeletons provide a wealth of paleoenvironmental data (Dodge and Vaisnys 1977; Fair-

banks et al. 1997) that can be used to determine time series of major climatic perturbations and their ecological consequences (Glynn and Colgan 1992), as well as recording past biological interactions and physical disturbance (Jackson 1983). Corals are commonly preserved in life position or with minimal transport. Thus, line transects or quadrats laid across outcrops of uplifted reefs can be used to record paleocommunity composition and diversity just as on a living reef (Figure 15.18A) (Stemann and Johnson 1992; Pandolfi 1996; Pandolfi and Jackson, in press). This method is commonly used on Late Pleistocene or Holocene reefs that have been uplifted above sea level. Alternatively, cores can be obtained or trenches dug into subtidal reef framework to obtain a record of more recent events leading up to present-day communities (Macintyre and Glynn 1976; Fairbanks 1989; Aronson and Precht 1997; Aronson et al. 1998). This approach is most useful for the Holocene record of sea level rise over the past 10,000–15,000 years. Environments of deposition and

(A)

(B)

Figure 15.18 Fossil reefs of New Guinea. (A) Corals in growth position. (B) Reef terraces created by uplift and sea level changes. (Photos courtesy of J. Pandolfi.)

water depths can be determined independently of the corals themselves to avoid circularity in interpretation (Pandolfi et al., in press). Moreover, comparisons of distributions and abundance of live coral and dead coral on recent reefs with similar fossil data demonstrate that fossil coral communities faithfully record the original living coral community (Greenstein et al. 1998a).

Pandolfi (1996, 1999) examined coral community composition on nine Late Pleistocene reef terraces on the Huon Peninsula of Papua New Guinea that were formed by the interaction of local tectonic uplift and glacial sea level fluctuations over 95,000 years (Figure 15.18B). Each uplift event comprised a separate ecological experiment in coral community assembly following a major disturbance. Reef crest and reef slope assemblages were recognized and sampled separately at three sites along 35 km of coast. There were no significant differences in community composition or species richness in each environment over time (among the nine terraces) but there were consistent differences among sites along the shore.

Community membership over 95,000 years was much more stable than expected from a random sample of the habitat-specific species pools (i.e., only those species known to occur in each specific environment rather than all species known from the geographic region). Restriction of the analysis to the habitat-specific species pool is essential because far fewer species occur in any local habitat than occur in the regional species pool. Indeed, this is a basic problem (Westoby 1998) with the analysis of so-called local versus regional effects on coral community structure and diversity (Karlson and Cornell 1998). For example, only 18 species of *Acropora* occur along the coast of the Huon Peninsula today, out of the roughly 125 species of *Acropora* from the broader West Pacific region, and only four of these 18 species are common. These same four *Acropora* species dominate Pandolfi's Pleistocene communities and, in general, both the reef crest and reef slope communities were dominated consistently by fewer than 25% of the 66–92 species encountered in each environment in the Pleistocene and the recent. Moreover, dominant species are no more widely distributed than rarer species in the same environments. Thus, consistent dominance does not appear to result only from superior dispersal ability as predicted by Hubbell (1997).

The New Guinea study was criticized (Aronson and Precht 1997) for using only presence or absence of corals. However, similar community stability was observed using the same methods of analysis with relative abundance data from three different reef environments on the 125,000-year-old terrace in Curaçao (Pandolfi and Jackson 1997, in press). Community composition was different among environments but not over distances of as much as 40 km within the same environments. As in New Guinea, coral communities were dominated by only a small percentage of the roughly 30 species recorded from each paleocommunity, which is similar to recent species richness along the same coasts. Dominant species were no more widely distributed than rarer species in the same habitats.

Curaçao is rarely subjected to hurricanes (Pandolfi and Jackson, in press). Woodley (1992) suggested that the extreme dominance of shallow water Jamaican reefs by *Acropora palmata* and *Acropora cervicornis* was an artifact of infrequent damage by hurricanes during the early studies of reef zonation in Jamaica (Goreau 1959; Kinzie 1973). However, paleoecological studies in areas strongly affected by hurricanes demonstrate apparently uninterrupted dominance by one or the other of these *Acropora* species for thousands of years during individual high stands of sea level (Jackson 1992; Aronson and Precht 1997; Aronson et al. 1998; Greenstein et al. 1998b). In general, growth rates of acroporid corals are so high that competitive dominance occurs over intervals shorter than the average period between major hurricanes at any particular site.

The paleontological data provide an ecological baseline of predictable patterns of coral community assembly and membership over large spatial and temporal scales before intense modern human disturbance (Jackson 1992; Pandolfi and Jackson 1997, in press; Pandolfi 1999). The probability approaches certainty that the community at any particular reef site will be devastated by some form of disturbance over decades to millennia (Connell 1978; Jackson 1991; Woodley 1992; Connell et al. 1997; Hughes and Connell 1999). Recovery will be varyingly affected by recruitment limitation, interactions among established organisms and further disturbance (Done 1992, 1997, 1999; Connell et al. 1997; Hughes and Tanner 2000); and diversity commonly, although not always, peaks at intermediate levels of disturbance (Tanner et al. 1994) as hypothesized by Connell (1978). Nevertheless, the fossil data require that these disturbances are (or were) sufficiently predictable over large scales of the reefscape for the development of predictable coral community composition, just as on rocky intertidal shores (Paine and Levin 1981).

With this perspective, distinctions break down between equilibrium and nonequilibrium communities, open versus closed populations, and Gleasonian versus Eltonian community assembly (Chesson 1997). On the scale of the regional landscape, interspecific differences in life histories and niches produce predictable patterns of community development (Jackson and Hughes 1985; Jackson 1991; Knowlton and Jackson 1994; Tanner et al. 1994; Hughes 1996; Hughes et al. 2000). However, none of these conclusions require or imply tightly integrated mechanisms of community structure (Jackson 1994a) as has sometimes been assumed by paleoecologists (Aronson and Precht 1995; Jablonski and Sepkoski 1996).

What Was Natural on Coral Reefs?

Until the 1980s, most coral reef ecologists assumed that reefs they were studying were "natural" (Sheppard 1995), despite evidence to the contrary from fisheries (Munro 1983; Hatcher et al. 1989) and absence of baseline data before industrialization and the modern, exponential rise in human populations (Jackson 1995, 1997). Opinions changed, however, with increasing reports of catastrophic mortality of corals due to out-

breaks of disease, predators, bleaching, overgrowth by fleshy algae, over-fishing, eutrophication, oil spills, and a host of other factors (Hay 1984; Tomascik and Sander 1987; Jackson et al. 1989; Ginsburg 1993; Hughes 1994; Brown 1997a, b; Done 1997, 1999; Peters 1997; Richardson 1998; but see Grigg 1992). Coral cover declined precipitously and relative abundance of surviving species changed at sites around the world over the last two decades (Wilkinson 1992; Hughes 1994). Effects of repeated disturbances appear increasingly severe, suggesting that reefs do not entirely recover before new perturbations (Done 1988; Paine et al. 1998; Hughes and Connell 1999). This negative synergism is equally apparent for natural disturbances such as hurricanes and anthropogenic impacts such as oil spills.

In spite of widespread basis for concern, we cannot quantify using standard ecological methods how much of this decline is within the range of natural variability of coral reef ecosystems, and how much is due to anthropogenic change (Jackson 1992; Sapp 1999). This is not a trivial problem. Well-documented, natural variations in other marine ecosystems may be extremely large. For example, the order of magnitude, boom–bust cycles in abundance of anchovies and sardines in the eastern Pacific are driven by climatic fluctuations with a periodicity longer than the longest environmental time series from the region (Baumgartner et al. 1992; MacCall 1996; McGowan et al. 1998). There are no comparable observational records from any coral reef environment.

Paleoecological, archeological, and historical data (hereafter collectively referred to as paleo data) are therefore the only means for obtaining the necessary long-term perspective (Jackson 1992, in press). Paleo data are necessarily descriptive rather than experimental, but they uniquely encompass the time scales necessary to distinguish natural from anthropogenic variation. Moreover, most long-term ecological studies of living reefs are also entirely descriptive (Connell et al. 1997; Hughes and Tanner 2000), and that fact has not hindered their application to similar ecological problems (Hughes 1994; Connell et al. 1997). The application of paleo data to coral reef ecology is still in its infancy, but there are already clear examples of the power of the approach for both corals and mobile consumers such as sea urchins, fish, and turtles.

We have seen how detailed surveys of Pleistocene and Holocene reef corals can provide an ecological baseline for the apparently low natural variability in coral community composition (Pandolfi 1996, 1999; Aronson and Precht 1997; Aronson et al. 1998; Greenstein et al. 1998a; Pandolfi and Jackson, in press). The same studies demonstrate that recent dominance of Caribbean shallow-water reefs on exposed coasts by comparatively opportunistic, brooding species of *Agaricia* and *Porites* instead of *Acropora* are unprecedented on fossil reefs so far examined extending back for 125,000 years. Prehistoric shifts to dominance of reefs by soft-bodied organisms like fleshy algae (Lessios 1988; Hughes 1994) should be detectable by detailed analyses of horizons of extensive bioerosion on fossil reefs, but this has not been attempted. Nevertheless, there is clearly no paleontological evidence for anything like the modern situation on Caribbean reefs.

There also are good historical data showing that the decline of shallow-water *Acropora* in the Caribbean began in Barbados as early as the nineteenth century (Lewis 1984). Extensive tracts of *Acropora palmata* persisted around much of the island until the 1920s but had disappeared before the first modern ecological surveys in the 1950s (Lewis 1960), apparently due to increased eutrophication and runoff that began with the deforestation of the island for sugarcane in the seventeenth century. This historical discovery helps to explain the apparently anomalous difference between the persistence of dense stands of *Acropora* spp. throughout the past half-million years on Barbados and its earlier reported absence in the recent in Barbados (Jackson 1992).

Paleontological data for mobile reef animals have produced less consistent results because of greater problems of sampling and reworking of sediments that mix skeletal remains. For example, the vast amounts of skeletal debris formed by the mass mortality of *Diadema antillarum* in the Caribbean were soon mixed unrecognizably into older sediments (Greenstein 1989). On the other hand, preservation of fossil *Diadema* is sufficient to determine that it was the most abundant sea urchin on Caribbean reefs 125,000 years ago (Gordon and Donovan 1992), long before overfishing began. Likewise, we still do not know if outbreaks of crown-of-thorns starfish happened in the past, because abundant skeletal remains of the starfish sampled at depth in cores of reef sediments may have been reworked (Keesing et al. 1992; Pandolfi 1992). However, this problem could be easily resolved by analysis of Holocene reefs in New Guinea or elsewhere that were uplifted before observed outbreaks of starfish began. Similar constraints and possibilities apply to fossil otoliths of reef fishes that could be used to determine the taxonomic composition and body size of reef fish populations and communities before intensive human exploitation.

Historical data clearly demonstrate the great magnitude of ecological effects of human exploitation on reefs. Large predatory fishes and sharks were extremely abundant in the Caribbean in the sixteenth and seventeenth centuries (Oviedo 1526; Dampier 1729). These were fished down to levels so low that inhabitants shifted their efforts to smaller and smaller carnivores and herbivorous fishes (Munro 1983; Jackson 1997). The net effect on reef environments was to fish down the trophic level of reef fish communities, just as has been documented for larger commercial fisheries worldwide (Pauly et al. 1998).

The best historical data are for green turtles in the Caribbean because of the enormous importance of these animals in the colonial economy of the Caribbean, where populations of human slaves were fed on turtles for more than a century (Jackson 1997). Historical reports of voyagers describe populations so huge that ships could navigate in the fog by the noises of migrating animals, that could also impede the progress of ships that sailed directly into the vast aggregations! Green turtles used to crop "turtlegrass" (*Thalassia testudinum*) at hundreds of sites around the Caribbean whose names (e.g., Dry Tortugas) refer to the once abundant turtles that are now very rarely, if ever, seen. Estimates of adult abundances based on

hunting data produce astonishing numbers ranging from approximately 16- to 35-million 100-kg adult turtles for the entire tropical western Atlantic (Jackson 1997; Bjorndal et al. 2000). Estimates based on experimental data for the carrying capacity of turtle grass beds yield numbers up to 10–20 times higher. Even the smallest, conservative estimates exceed the biomass of large vertebrates in east Africa today; and there is every reason to believe that abundances of other large vertebrates including other sea turtles, manatees, and sharks were of comparable size.

Clearly, studying grazing and predation on reefs today is like trying to understand the ecology of the Serengeti by studying the termites and the locusts while ignoring the wildebeest and the elephants. The remaining small fishes and invertebrate predators and grazers feed very differently from their larger precursors (Figure 15.19) because they nibble at rather than break apart their prey and (unlike turtles and manatees) cannot digest cellulose. Loss of megavertebrates drastically reduced and qualitatively changed grazing and excavation of seagrasses, predation on sponges, export of pro-
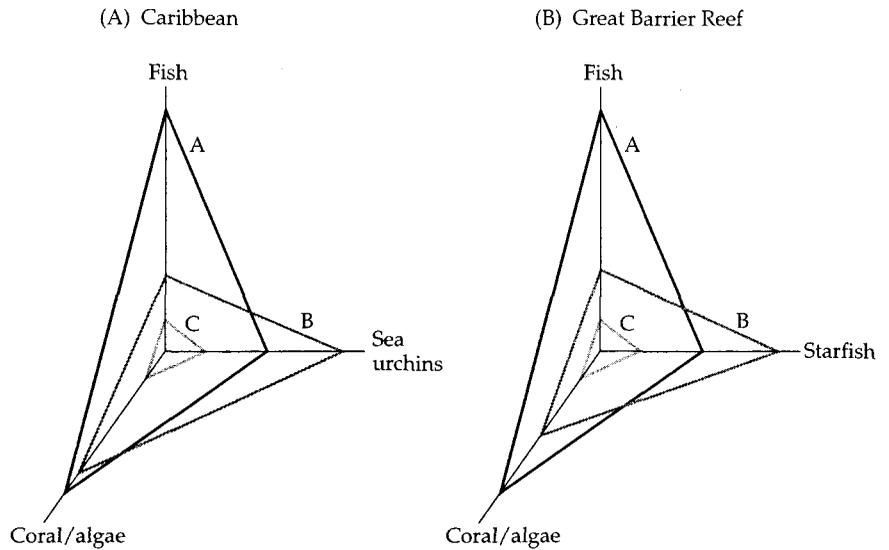
(A)

(B)

Figure 15.19 (A) A dugong feeding. (B) Aerial photo illustrating massive disturbance to seagrass beds associated with grazing by these large vertebrates. (Photos courtesy of H. Marsh.)

duction to adjacent ecosystems, and the structure of food chains. Likewise, patterns of carbon flux were changed on the Great Barrier Reef after devastation by crown-of-thorns starfish (Johnson et al. 1995). It is no accident that the only published food web for coral reef environments that includes large vertebrates is for the French Frigate Shoals (Figure 15.14) (Grigg et al. 1984), thousands of kilometers from any human populations. No large vertebrates are even mentioned in Sale's (1991a) compendium on the ecology of coral reef fishes.

Whither Coral Reefs?

Coral reefs were already greatly altered by human activities long before the first coral reef ecologists began to study them. Nevertheless, we are beginning to understand the magnitude of these changes and their consequences (Done 1992, 1997, 1999; Bradbury 1990; Hughes 1994; Bradbury and Seymour 1997; Jackson 1997, in press). These insights can be summarized in two elementary models of the causes and consequences of outbreaks of crown-of-thorns starfish *Acanthaster planci* on the Great Barrier Reef and the demise of the sea urchin *Diadema antillarum* in the Caribbean (Figure 15.20). Both models ignore for simplicity important spatial questions of hydrodynamics and larval dispersal that are essential to the metapopulation dynamics of these systems.

On Caribbean and East African reefs, abundant predatory and herbivorous fish once suppressed sea urchin and macroalgal abundance, and coral cover was high (Figure 15.20A, plane A) (Hughes 1994; McClanahan et al. 1996). Fishing initially decreased predatory fish populations, resulting in increases in sea urchins and small herbivorous fishes that grazed on algae, and coral abundance remained high (plane B). Eventually, intense subsistence over-fishing also greatly reduced herbivorous fish abundance which, after the mass mortality of *Diadema antillarum* in the Caribbean, permitted enormous increases in unpalatable macroalgae that are progressively overgrowing corals throughout the region (plane C). Increased nutrient levels due to agriculture and human waste, decreased coral abundance due to hurricanes, increased sedimentation due to deforestation, and outbreaks of disease or coral bleaching have further lowered thresholds for macroalgal dominance over corals in all cases (Harvell et al. 1999; Jackson, in press).

More hypothetically on the Great Barrier Reef, high densities of fish (and other predators) probably suppressed *Acanthaster* population growth, so that outbreaks did not occur or were very rare (Bradbury and Seymour 1997). Coral cover greatly exceeded that of macroalgae, soft corals, or other potentially dominant sessile taxa (Figure 15.20B, plane A). Reduction of predatory fish populations below some unknown threshold density due to moderate fishing contributed to the increased frequency of starfish outbreaks, that decimated coral cover (plane B) and resulted in presumably unstable limit cycles of starfish-coral-macroalgal abundance. Finally, we can speculate that increased fishing will further reduce abundance of less preferred herbivorous species. Then, the sudden growth of macroalgae following coral mortality due to starfish outbreaks would greatly exceed consumption by

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