Invertebrate Predators and Grazers

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Coral reefs are among the most productive and diverse biological communities on earth. Some of the diversity of coral reefs is associated with the invertebrate organisms that are the primary builders of reefs, the scleractinian corals. While sessile invertebrates, such as stony corals, soft corals, gorgonians, anemones, and sponges, and algae are the dominant occupiers of primary space in coral reef communities, their relative abundances are often determined by the activities of mobile, invertebrate and vertebrate predators and grazers. Hixon (Chapter X) has reviewed the direct effects of fishes on coral reef community structure and function and Glynn (1990) has provided an excellent review of the feeding ecology of many coral reef consumers. My intent here is to review the different types of mobile invertebrate predators and grazers on coral reefs, concentrating on those that have disproportionate effects on coral reef communities and are intimately involved with the life and death of coral reefs.

The sheer number and diversity of mobile invertebrates associated with coral reefs is daunting with species from several major phyla including the Annelida, Arthropoda, Mollusca, and Echinodermata. Numerous species of minor phyla are also represented in reef communities, but their abundance and importance have not been well-studied. As a result, our understanding of the effects of predation and grazing by invertebrates in coral reef environments is based on studies of a few representatives from the major groups of mobile invertebrates.

Predators may be generalists or specialists in choosing their prey and this may determine the effects of their feeding on community-level patterns of prey abundance (Paine, 1966). Feeding preferences are determined by a suite of factors that include predator and prey vagility, morphological structures for prey capture and processing, relative availabilities of different prey species, and the relative sizes of predator and prey. Each of these factors is important in both an ecological and evolutionary context. Relative constancy of prey abundance often can lead to specialization by a predator on a single prey type (Emlen, 1973). Some of the more spectacular examples of feeding specialization have been found in coral reef communities. Examples include opisthobranchs feeding on algae (Taylor, 1971), fishes that specialize on cleaning parasites from other fishes (Losey, 1974), and butterflyfishes that specialize on corals
(Reese, 1977). However, some invertebrate predators and grazers are more generalist, and while their prey are restricted to certain groups of organisms (e.g., corals, algae), they exhibit little preference or discrimination between different species within these groups. Many invertebrate predators and grazers appear to exhibit limited preferences within major groups of prey that likely are the result of prey morphology relative to the handling capability, feeding mode, and feeding apparatus of the predator. For example, the crown-of-thorns seastar, *Acanthaster planci*, feeds preferentially on branching and tabulate acroporid corals, leaving poritid, fungiid, and faviid corals behind (Moran, 1986; Birkeland, 1989a; De’ath and Moran, 1998a). However, depending on the relative abundances of coral species, *Acanthaster* may feed on a variety of other prey species (Glynn, 1990). Many herbivorous invertebrates, such as majid crabs and echinoids, feed preferentially on filamentous algal turfs, avoiding macroalgae species, but do not discriminate between species within the algal turf functional group (Steneck, 1988). Again, depending on prey availability, some primarily herbivorous echinoids may feed on live coral (Bak and van Eys, 1975; Carpenter, 1981). It appears that dietary plasticity and the ability to exploit a wide range of prey contributes to the success of several species of invertebrate predators and grazers associated with reefs (Birkeland, 1989a).

In general, the two most common types of benthic prey in many coral reef environments are scleractinian corals and algae. On most shallow reefs (<20 m), these two components cover in excess of 80% of the substratum. Deeper reefs, especially in the Caribbean, may have a significant cover of sponges, and soft corals are common on some Pacific reefs (Wilkinson and Cheshire, 1989). Nevertheless, corals and algae are prey for a large number of invertebrates and it is the relative abundances of these two components, and how this balance is regulated by some species of predators, that underlies the transition between a thriving, growing, coral-dominated reef and an algal-dominated community that ceases to expand laterally and to accrete vertically (Adey, 1978; Hubbard, Chapter II).

The generic, direct effects of invertebrate predators and grazers on their prey is to reduce their abundance. In the simplest terms, the extent to which predators limit their prey depends on predator abundance and efficiency of prey capture and the availability to the prey of spatial and/or temporal refugia from predators. Several combinations of these conditions can lead to stable predator-prey cycles (Pianka, 1988). However, predator-prey relationships in most environments probably are not at equilibrium. Most invertebrate predators and grazers on coral reefs are intermediate-level consumers and are themselves, the prey for higher level predators. Likewise, the abundance of prey species for invertebrate predators and grazers may be controlled in part by nutrient and/or light availability (Hatcher, 1990; Muscatine, 1990). As a result, both top-down and bottom-up processes, together with stochastic processes, such as recruitment and physical disturbance, regulate the relative abundances of invertebrate predators and their prey and set the stage for numerous indirect effects that cascade throughout the coral reef trophic web (Pennings, Chapter XI).

The list of invertebrate predators and grazers on corals and algae given in Table 1, while not exhaustive, includes the majority of organisms known to feed on these prey items on coral reefs. They have been divided into two categories (those with major and minor impacts) based on their typical abundances and their demonstrated effects on
9.1. INVERTEBRATES HAVING MINOR IMPACTS

9.1.1. Corallivores

A variety of invertebrates have been reported to feed on live coral, including polychaetes (Robertson, 1970; Ott and Lewis, 1972; Witman, 1988), gastropods (Robertson, 1970; Moyer et al., 1982; Hayes, 1990a,b; Turner, 1994a), and crabs (Glynn, 1983a; Gilchrist, 1985; Stimson, 1990). Under normal circumstances, species within these groups are not exceedingly abundant and coupled with their small body size and limited mobility, they appear to have only minor and localized effects on coral reef communities. For example, Witman (1988) reported that the polychaete Hermodice carunculata was responsible for removing 0.13% per day of the hydrocoral Millepora spp. on one Caribbean reef and this resulted in a change in the relative abundance of this species and species that colonized the damaged colonies. However, the abundance of H. carunculata on most reefs is low and their impact in changing live coral biomass is minimal (Ott and Lewis, 1972; Knowlton et al., 1990). Likewise, brachyuran crabs and hermit crabs have limited direct impact as coral predators and the association of some crabs, such as Trapezia spp., with corals are much more important due to their deterrence of other coral predators (Glynn 1983a,b; Stimson, 1990).

Some gastropod corallivores can have more significant effects on corals. In the Caribbean, Corallophilia abbreviata was found on up to 64% of the coral colonies examined on a reef in Panama and the gastropods were associated with coral mortality in experiments where corals were stressed (Hayes, 1990). O n reefs in the Florida Keys, Baums et al. (2003) found up 50% of coral colonies infested with C. abbreviata although snail abundance varied among coral species. Similarly, Knowlton et al. (1990) examined the effects of C. abbreviata on the coral Acropora cervicornis in Jamaica where approximately 10% of the coral colonies had snails associated with them. They found that recent coral mortality was related to the presence of C. abbreviata and that coral predation, combined with other stresses had significant effects on coral mortality. Because the changes in the coral reef community at this site were also related to the mass mortality of the echinoid, Diadema antillarum, it was not possible to attribute which of these changes might have been caused directly by C. abbreviata. However, it appears that predation by this species may be important locally where snails are abundant and when other environmental conditions result in additional stresses to corals. This is in contrast to the conclusions reached by Ott and Lewis (1972), who reported that C. abbreviata had minimal effects on corals on the reefs of Barbados.

Other gastropods that have been demonstrated to have significant effects on coral mortality on some Pacific reefs are the ovulid snail Jenneria pustulata (Glynn, 1982) and muricid snails in the genus Drupella (Moyer et al., 1982; Turner, 1994a). Glynn (1982) found that J. pustulata consumed the coral Pocillopora spp. on reefs in Panama. At least four species of Drupella (D. cornus, D. elata, D. fragum, and D. rugosa) have been shown to cause extensive reef damage in areas where their densities have reached outbreak dimensions. Reported densities of Drupella spp. include abundances of <1
Table 1

Taxa of invertebrate corallivores and herbivores that have minor and major effects on coral reefs.

<table>
<thead>
<tr>
<th>CORALLIVORES</th>
<th>HERBIVORES</th>
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<td><strong>Taxa</strong></td>
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<td><strong>Groups Having Minor Impacts</strong></td>
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<tr>
<td><strong>ANNELIDA</strong></td>
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<tr>
<td><em>Hermodice carunulata</em></td>
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<td>Witman, 1988</td>
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<td><strong>MOLLUSCA</strong></td>
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<tr>
<td><em>Corallophilia abbreviata</em></td>
<td>Robertson, 1970</td>
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<td>Hayes, 1990a, b</td>
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<td>Knowlton et al., 1990</td>
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<tr>
<td><em>Drupella cornus</em></td>
<td>Wilson and Stoddart, 1987</td>
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<td></td>
<td>Turner, 1994a</td>
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<tr>
<td><em>D. elata</em></td>
<td>Moyer et al., 1982</td>
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<td><em>D. fragum</em></td>
<td>Moyer et al., 1982</td>
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<tr>
<td><em>D. rugosa</em></td>
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<tr>
<td><em>Jennaria pustulata</em></td>
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<td>other gastropods</td>
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<td><strong>ECHINODERMATA</strong></td>
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<tr>
<td><strong>Asteroidea</strong></td>
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<tr>
<td><em>Culcita novaeguineae</em></td>
<td>Endeán, 1971</td>
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<td>Glynn and Krupp, 1986</td>
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<tr>
<td><em>C. schmideliana</em></td>
<td>Thomassin, 1976</td>
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<tr>
<td><em>Nidorellia armata</em></td>
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<tr>
<td><em>Pharia pyramidalata</em></td>
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</tr>
<tr>
<td><em>Echinaster purpureus</em></td>
<td>Thomassin, 1976</td>
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<tr>
<td>Species</td>
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<tr>
<td>Asterina sp.</td>
<td>Yamaguchi, 1975</td>
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<tr>
<td>Tripneustes spp.</td>
<td>see Birkeland, 1989a for review</td>
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**Echinoidea**

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<tr>
<th>Species</th>
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<tbody>
<tr>
<td>Astropyga radiata</td>
<td>Herring, 1972</td>
</tr>
<tr>
<td>Diadema antillarum</td>
<td>Bak and Van Eys, 1975</td>
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<td></td>
<td>Carpenter, 1981</td>
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<tr>
<td>D. setosum</td>
<td>Herring, 1972</td>
</tr>
<tr>
<td>Echinothrix calamaris</td>
<td>Herring, 1972</td>
</tr>
</tbody>
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**Groups Having Major Impacts**

**ECHINODERMATA**

**Asteroidea**

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<th>Species</th>
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<tbody>
<tr>
<td>Acanthaster planci</td>
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<td></td>
<td>Moran, 1986</td>
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<td></td>
<td>Birkeland and Lucas, 1990</td>
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<td>Diadema antillarum</td>
<td>Randall et al., 1964</td>
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<td>Ogden et al., 1973</td>
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<td>Sammarco, 1982</td>
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<td>Carpenter, 1986, 1990a,b</td>
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<td></td>
<td>Hughes et al., 1987</td>
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<td>Echinoidea</td>
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<tr>
<td>Eucidaris thouarsii</td>
<td>Glynn et al., 1979</td>
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<td></td>
<td>Glynn and Wellington, 1983</td>
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<td>Mathias and Langham, 1978</td>
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<td>Bauer, 1980</td>
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<td>Ormond and Campbell, 1971</td>
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<td>Downing and El-Zahr, 1987</td>
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<td>McClanahan and Muthiga, 1988</td>
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<td></td>
<td>McClanahan and Shafir, 1990</td>
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<tr>
<td>Echinometra mathaei</td>
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<tr>
<td>Echinometra radiata</td>
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ind./m² in the Ryukyu Islands, Japan (Fujoika and Yamazato, 1983), 1-20 ind./m² on the Great Barrier Reef, Australia (Ayling and Ayling, 1992), and 5-19 ind./m² on Ningaloo Reef in Western Australia (Ayling and Ayling, 1987; Turner, 1994b). Outbreak aggregations with densities of 1500 ind./0.5 m² have been reported from some reefs in the Philippines (Moyer et al., 1982). Aggregations tended to be found in areas with high cover of acroporid corals. Drupella spp. appear to be generalist corallivores, although some studies have suggested preferences for acroporid, poritid, and pocilloporid corals (see Turner, 1994a for a review).

The effects of coral predation by Drupella spp. when they reach outbreak densities is to remove up to 95% of live corals in the patchily distributed areas of high snail density and therefore, at this scale, is quantitatively and qualitatively similar to the effects of predation by the seastar Acanthaster planci. In several cases, reefs have been simultaneously infested with high densities of both Acanthaster and Drupella spp., making it difficult to interpret the effects of Drupella spp.. In both cases, dead coral skeletons within the predated patches are quickly colonized by filamentous algae and fouling organisms and as a result, portions of the reef or sometimes the entire reef, is transformed from a coral-dominated system to an algal-dominated one. Increased algal resources can result in higher abundances of grazing fishes and decreased abundances of obligate coral feeders such as chaetodontids (Ayling and Ayling, 1987).

The causes underlying the outbreaks of Drupella spp. on some reefs are not well understood. Whether outbreaks are the result of natural fluctuations in the population sizes of these species due to stochastic processes that determine recruitment success, or to anthropogenic influences that either reduce mortality of Drupella spp. due to overfishing of snail predators, or through modification of the coastal environment as a result of increased run-off and siltation, has not been established (Turner, 1994a). Although the impact of predation by Drupella spp. has been significant on a few reefs, their abundances and impacts on most reefs in the Pacific are minor. However, the capability of forming outbreak populations and subsequently altering the community structure of the reef, should make studies of the causes of population increases in Drupella spp. a priority.

Several species of echinoderms have been shown to feed primarily, or acultivitively on live corals. Birkeland (1989a) lists nine species of asteroids that prey on corals in the Pacific. With one exception (Acanthaster planci), these species are thought to have only minor effects on coral populations. For example, Culepta novaeguineae, due to its smaller size and extruded stomach area (compared to A. planci), prey mainly on smaller, encrusting colonies of acroporid and pocilloporid corals and only have minor effects on reef community structure (Glynn and Krupp, 1986).

Most echinoids associated with coral reefs are herbivorous or omnivorous (Lawrence, 1975). However, several echinoid species have been found to feed, at least occasionally, on live corals. Herring (1972) reported that coral was an important food item for three species of diadematid sea urchins in Zanzibar (Diadema setosum, Echinothrix calamari, and Astropyga radiata). Bak and van Eys (1975) reported that Diadema antillarum fed on live corals in the Netherland Antilles and Carpenter (1981) found that coral predation by D. antillarum varied seasonally on reefs in St. Croix, U.S. Virgin Islands, suggesting that fluctuating algal resources probably influenced the
choice of prey for this echinoid species. The direct effects of coral predation by *D. antillarum* on coral reef community structure were not considered significant in either of these studies.

While the diversity of this minor group of corallivores is high, it appears that given their typical abundances and feeding preferences, predation on live corals by these species does not have a dramatic influence on coral reef community structure. Only for *Drupella* spp., has it been demonstrated that under conditions of high population density, that they have a significant effect on coral abundance and that predation results in a phase shift (sensu Done, 1992) from one community type to another.

9.1.2. Herbivores

The diversity and abundances of herbivorous invertebrates associated with coral reefs are impressive, but studies of the effects of invertebrate herbivores on coral reef algal communities primarily have focused on a few groups. Due to their small size and sometimes cryptic behavior, very little is known about the effects of feeding by species in several groups, including annelids, molluscs, and arthropods.

Polychaetes in the families Eunicidae and Syllidae are the most abundant herbivorous annelids associated with coral reefs (Fauchois and Jumars, 1979). Kohn and White (1977) reported densities of herbivorous polychaetes that exceeded 40,000 ind./m² on algal turf covered substrata in Guam. Carpenter (1986) found densities of syllids associated with algal turfs to be positively related to algal turf biomass and the highest densities (2500 ind./m²) were found in treatments protected from fish predators. Their overall body size and mouthpart size suggest that polychaetes only are capable of ingesting diatoms, cyanobacteria, and the smallest algal filaments, and although numerous, polychaetes do not have a significant effect on reef algal communities (Steneck, 1988). This is supported further by the positive relationship between algal abundance and polychaete density (Carpenter, 1986) and suggests that algal turfs probably are a refuge from fish predators.

Several species of herbivorous molluscs are associated with coral reefs (Steneck and Watling, 1982; Steneck, 1983). Limpets (e.g., *Lottia*, *Fissurella*) are among the most common molluscan herbivores on shallow reefs where they maintain feeding ranges on algal-covered substrata. Depending on the species, limpets feed primarily on small algal filaments and crustose coralline algae within a very limited home range (Steneck and Watling, 1982). Repeated grazing within the feeding range results in the predominance of filamentous turf algae and crustose corallines that are able to persist under the intense grazing regime. Although capable of shifting algal community structure on a very limited spatial scale (centimeters), limpets are never abundant enough on most coral reefs to have a community-wide effect on species composition or affect the balance between the abundance of corals and algae. Similarly, other herbivorous gastropods and chitons (Glynn, 1970), while associated with coral reefs, have not been demonstrated to exert control of coral reef community structure.

Arthropod mesograzers, such as amphipods, isopods, tanaids, and the larger majid crabs commonly are found in coral reef habitats. Amphipods, isopods and majid crabs are herbivorous primarily, while tanaids most often are detritivores. Klumpp et al. (1988) found densities of amphipods associated with algal communities on the Great
Barrier Reef to range from 491 to 22968 ind./m², while isopods in the same areas reached densities of 386 to 3840 ind./m². Carpenter (1986) reported densities of amphipods associated with reef algal turfs up to 1406 ind./m² and densities of tanaids up to 6875 ind./m². In both of these studies, higher abundances of mesograzers were associated with higher biomass (thicker) algal turfs.

As a result of their size and handling capabilities, many amphipods are restricted to feeding on microscopic unicellular and filamentous algae while isopods are capable of feeding on a range of algal types (Brawley, 1992). The effects of grazing by these mesoherbivores suggest that they often can control the abundance of epiphytic algae on larger macroalgae. In a coral reef microcosm, Brawley and Adey (1981) found that grazing by the amphipod, *Ampithoe ramondi*, controlled algal community structure. When amphipods were absent, the algal community was dominated by several species of small filamentous algae. When grazing by amphipods was present, the abundance of filamentous algae declined and a macroalgal species (*Hypnea*) persisted. Similarly, field experiments in Hawaii by Brostoff (1988) demonstrated that amphipod grazing reduced the abundance of filamentous algal epiphytes on two species of macroalgae. Both of these studies were conducted under conditions where mesograzers were not subjected to normal predation. These results suggest that when amphipods are abundant, they may play an important role in reducing epiphytes on macroalgae. It is unclear the degree to which predators control the abundance of these mesograzers on most reefs. Data suggest that algal turfs on open reef surfaces grazed by macroherbivores do not support large populations of mesograzers (Carpenter, 1986), however, adjacent crevices and holes in the reef may provide refugia from predators and the extent of nocturnal grazing by mesoherbivores may be underestimated.

Larger mesoherbivores, such as majid crabs, are capable of feeding on a variety of algal species (Coen, 1988a) and may limit the abundance of algae near their protective crevices. Coen (1988b) found in Carrie Bow Cay, Belize that *Mithrax sculptus* was associated with 28% of the *Porites porites* colonies examined in a shallow reef environment. Experiments where *Mithrax* abundances were manipulated, demonstrated that crabs removed most of the algal epibionts from the coral colonies, perhaps preventing overgrowth of the coral. Their cryptic diurnal behavior suggests that the abundance of majid crabs such as *Mithrax*, is probably controlled by predation. While it is clear that crabs can influence algal community structure over limited spatial scales, their ability to affect algal species composition and/or coral abundance on a community-wide scale has yet to be demonstrated.

Several echinoid species that primarily are herbivorous are associated with some coral reefs. The diadematid, *Astropyga radiata*, is found most often in sandy and seagrass habitats surrounding reefs, where it grazes seagrasses as well as attached algae (personal observations). *Astropyga* is usually rare or absent on most reefs and has not been reported to have significant effects on the coral reef community.

Another diadematid echinoid, *Echinostrephus* spp., often is found inhabiting holes and crevices on Pacific reefs (Birkeland, 1989a). These sea urchins are sedentary, capturing drift algae with their spines and pedicellaria and do not appear to graze the substratum surrounding their protective holes. As a result of this sedentary behavior,
even population densities of several ind./m$^2$ probably have little or no effect on the open reef community (personal observations).

Several sea urchins in the genera Heterocentrotus and Colobocentrotus are found on many Pacific coral reefs (Birkeland, 1989a). While species in both genera are herbivorous, their distributions on the reef generally are restricted to shallow subtidal and intertidal habitats, respectively; both in areas of extreme water motion. Although Ebert (1971) reported an abundance of Heterocentrotus mammillatus from the Kona Coast, Hawaii; these taxa do not appear to maintain high population densities on most Pacific reefs. As a result of their patchy distribution and relatively sedentary nature, these sea urchins have a limited impact in reef environments.

In the Caribbean, Echinometra lucunter and E. viridis occur in varying densities in some coral reef habitats (Lessios, 1995). The rock-boring sea urchin, Echinometra lucunter, is found most commonly in very shallow and intertidal portions of the reef and on algal ridges (Ogden, 1977). In these areas, population densities of 50-100 ind./m$^2$ are common. This species, like Echinostrephus spp., is a sedentary crevice dweller that relies primarily on drift algae for food, although they do graze within their burrows, resulting in bioerosion of the substratum and enlargement of the crevice as the sea urchin grows. The impact of grazing by E. lucunter therefore is very localized, and their impact on the reef community is limited to those areas where they maintain high population densities.

The abundance of Echinometra viridis on reefs varies from site to site. In backreef habitats at Discovery Bay, Jamaica, Williams (1981) reported population densities of 10 to 15 ind./m$^2$. Lessios (1995) has quantified the abundances of E. viridis on reefs in Panama for over ten years and reported population densities of <1 to 4 ind./m$^2$. Population densities of E. viridis in forereef habitats in St. Croix, U.S. Virgin Islands have been <1 ind./m$^2$ (Carpenter, unpublished data). Echinometra viridis, although fairly sedentary, has been reported to compete for algal resources with Diadema antillarum in Jamaica (Williams, 1981). Because it is not abundant at other reef locations, E. viridis does not appear to have a strong impact on reef community structure.

Other echinoids occasionally found on coral reefs include Eucidaris tribuloides, Lytechinus variegata, and L. williamsii in the Caribbean. The former, although occasionally ingesting algae, feeds primarily on encrusting animals (Lawrence, 1975), and L. variegata is found commonly in seagrass beds and is rare on most coral reefs (Ogden and Lobel, 1978). Lytechinus williamsii is rare on most reefs. Tripneustes spp. can be found on both Caribbean and Pacific reefs (Birkeland, 1989a). Although Ogden (1976) reported that T. ventricosus increased in abundance and cropped algae from the reef following the removal of Diadema antillarum from a patch reef, this pattern has not been repeated following the mass mortality of D. antillarum (Hughes et al., 1987; Lessios, 1995). Tripneustes ventricosus is found most commonly in seagrass habitats. Similarly, in the Pacific, the abundance of T. gratilla is patchy and this species does not appear to have any community-level effects on coral reefs.

9.2 INVERTEBRATES HAVING MAJOR IMPACTS
9.2.1. Corallivores

*Eucidaris thouarsii*

In most coral reef environments, cidaroid sea urchins are a minor component of the predator and grazer guild and feed on a variety of encrusting animals and algae (Lawrence, 1975; Birkeland, 1989a). In the Galápagos Islands, the cidaroid, *Eucidaris thouarsii*, has played a much more important role in the coral reef community. On the Eastern Pacific coral reefs of Panama and Ecuador, population densities of adult *E. thouarsii* ranged between 1 and 5 ind./m², although abundances of juveniles occasionally exceeded 50 ind./m². Adult sea urchins in these localities were relatively small with maximum test diameters between 2.7-3.5 cm (Glynn et al., 1979). Similar to cidaroids elsewhere, *E. thouarsii* in these coastal habitats are relatively sedentary, remaining cryptic during the day and foraging nocturnally. Adult populations of *E. thouarsii* in Panama and Ecuador appear to be kept in check by the abundance of echinoid predators, particularly fishes in the families Balistidae, Labridae, and Tetradontidae (Glynn et al., 1979; Glynn and Wellington, 1983).

*Figure 9-1. Eucidaris thouarsii* grazing on *Pocillopora* corals on Isla Onslow, Galápagos.
In contrast, populations of *Eucidaris thouarsii* around several of the Galápagos islands were greater with adult densities between 10 and 50 ind./m² and these populations consisted of much larger individuals with maximum test diameters ranging from 4.3 to 6.2 cm (Glynn et al., 1979). Additionally, *E. thouarsii* in the Galápagos were neither sedentary nor cryptic during the day, but foraged over relatively large distances (1 to 3 m/day) during both day and night. The main prey of *E. thouarsii* on Galápagos reefs also differed from mainland sea urchins. In addition to feeding on crustose coralline algae, a common prey item for mainland populations, sea urchins in the Galápagos preyed heavily on live corals. The primary prey were *Pocillopora damicornis*, *P. capitata*, and *P. elegans*, although sea urchins also were observed to feed on *Pavona clavus* (Glynn et al., 1979). Feeding surveys indicated that on some reefs over 50% of the sea urchins were feeding on live coral with the remainder feeding on crustose coralline algae covering the dead coral skeletons. Most of the coral colonies were fed on from the tips of branches, as sea urchins usually did not have access to the interior portions of the colony.

The effects of predation on live coral by *Eucidaris thouarsii* had significant effects on the community structure and function of the reef (Glynn and Wellington, 1983). As bare space was opened by the removal of coral tissue, other organisms settled on the dead coral branches. The most common organisms to cover the branch tips were crustose coralline algae and barnacles (*Megabalanus galapaganus*). Crustose corallines often are able to persist despite intense repeated grazing by sea urchins because of their crustose morphology and calcification that lessens the amount of biomass removed by grazers (Steneck and Watling, 1982; Steneck, 1988). As a result of sea urchin predation on live corals, the percent cover of live coral was reduced while the abundance of crustose coralline algae and barnacles increased. Glynn et al. (1979) found further, that grazing by *E. thouarsii* resulted in significant bioerosion of the coral framework (see Glynn, *Chapter IV*) and limited both the lateral expansion and vertical accretion of the reef framework.

The predation on live corals in the Galápagos by *Eucidarus thouarsii* was clearly a case of a predator having significant effects on the coral reef community that resulted in a change in the long-term trajectory of the community. Increased abundance and size of *E. thouarsii*, combined with a behavioral shift leading to increased foraging time and a change in diet, led to a change in the community from one dominated by a high cover of live coral that accreted vertically, to a community with reduced coral cover, increased abundances of algae and other organisms, and a reef framework that accreted and expanded more slowly. The central question is, why were sea urchin populations higher in the Galápagos? It appears that high population densities of *E. thouarsii* in the Galápagos were not a recent phenomenon but had persisted for decades. Glynn et al. (1979) indicated that sea urchin predators were more abundant on coral reefs in Panama and Ecuador than in the Galápagos. Although the same species of predators were present in all localities, predation pressure was reduced in the Galápagos due to the lowered abundance of predators. Glynn et al. (1979) speculated that sea urchin predators themselves may be subject to higher predation in the Galápagos from higher level predators (sharks). This suggests the following scenario. Intense predation on sea urchins associated with mainland reefs resulted in not only lower population densities of *E. thouarsii*, but also smaller sized sea urchins, diurnal crypsis, and reduced foraging.
movements. Under these conditions, prey for the sea urchins was abundant and they fed on a variety of encrusting organisms. Under conditions of reduced predation on sea urchins in the Galápagos, sea urchin population sizes increased and selection for diurnal crypsis was reduced, allowing increased time for foraging over larger areas. Due to increased competition for prey as high density populations depleted resources, sea urchins switched to preying on live corals. Sea urchin sizes were greater in these populations because mortality was reduced, or alternatively, sea urchins grew faster when feeding on corals.

However, several questions remain. Why have populations of *Eucidaris thouarsii* exhibited this pattern only on the coral reefs of the Galápagos and not at any other known coral reefs where sea urchin predators are also rare? Was the reduction in predation pressure on sea urchins in the Galápagos a natural phenomenon or human-induced? Or, did the increase in sea urchin populations result, in part, from a stochastic event resulting in high recruitment of juvenile sea urchins that swamped their predators and allowed them to reach a refuge in size? How long had the pattern of high sea urchin densities and high rates of coral predation persisted? Unfortunately, continued study of these questions was prevented by the mass mortality of corals in the Galápagos during the El Niño event in 1982-83.

*Acanthaster planci*

One of the most influential invertebrate predators on Pacific coral reefs is the crown-of-thorns seastar, *Acanthaster planci*. A member of the Acanthasteridae, *A. planci* is distributed from the tropical Indian and western Pacific oceans east to Panama and portions of the Gulf of California (Birkeland, 1989a). Madsen (1955) proposed that *Acanthaster* in the eastern Pacific were a different species (*A. ellisi*), but this has not been accepted generally and Glynn (1976) has regarded *Acanthaster* in the eastern Pacific as *A. planci*. This conclusion has been supported further by genetic evidence (Nishida and Lucas, 1988). The local distribution of *A. planci* is primarily in protected areas of the reef, including lagoons and deeper portions of forereef slopes (Moran, 1986). Shallow, wave-exposed portions of reefs are avoided.

*Acanthaster planci* is a free-spawning, dieocious, sexually reproducing species that is not known to reproduce asexually through arm autonomy (Moran, 1986). Periods and duration of spawning are temperature-dependent and occur primarily during summer. Females have been reported to produce from 12 to as many as 60 million eggs per spawning season. From larval culturing studies, it is estimated that the feeding planktonic larvae spend from 9 to 23 days in the plankton before they settle, although the timing is influenced by environmental conditions of temperature, salinity, and food availability (Lucas, 1982; Olson, 1987). At the end of the planktonic period, larvae become negatively buoyant prior to settlement and this may lead to higher recruitment of juvenile seastars on deeper portions of reefs (Moran, 1986). Recruitment onto reefs in Fiji has been shown to be highly variable both spatially and temporally (Zann et al., 1990).

The juvenile stages of *A. planci* usually are cryptic and feed primarily on crustose coralline algae and grow to a size of approximately 1 cm in total diameter within 4 to 5 months after settlement (Yamaguchi, 1973). The rate of growth is exponential and at an age of approximately 6 months, the diet of the juvenile seastars switches to live coral (Lucas, 1975; Moran, 1986). Birkeland (1989a) and others have pointed out that the
initial rapid growth and dietary plasticity of juvenile *A. planci* may be important characteristics explaining their potential for rapid population increase. Juveniles continue to grow rapidly and attain sexual maturity at an age of approximately 2 years. Adult growth appears to be indeterminate and is influenced by diet and spawning activity (Moran, 1986).

Adult seastars normally range in size from 25 to 35 cm in total diameter and have from 7 to 21 arms that are covered with spines (Moran, 1986). The tissue covering the spines contains one or more compounds that are toxic, and as a result, the spines are thought to function in predator deterrence (Cameron, 1977). The calcareous skeleton in
A. planci is relatively thin and gives the seastar a flattened, elastic, prehensile morphology. This morphology has been proposed as another trait that contributes to the effectiveness of A. planci as a predator on corals, as it allows feeding on branching corals that are unavailable to other asteroid corallivores (Birkeland, 1989a).

Acanthaster planci feeds primarily on corals but will feed on a variety of other benthic organisms, depending on availability (Moran, 1986). A. planci is termed a generalist coral predator by some (Birkeland and Lucas, 1990), while others describe it as a strict coral specialist (Cameron and Endean, 1982). It appears that A. planci is a generalist with distinct preferences for branching corals, especially the acroporids (De’ath and Moran, 1998a). Feeding preferences are determined by a variety of factors, including the relative availability of prey, the nutritional state of the seastar, and the presence and identity of coral crab symbionts (Ormond et al., 1976; Moran, 1986; Pratchett 2001). Although growth is most rapid when A. planci feeds regularly, individuals are able to live without feeding for considerable periods of time.

Acanthaster planci feeds by everting the stomach over the live coral tissue and secreting an enzyme (with protease activity) that breaks down the coral tissue and the products are absorbed; a process that requires 4 to 6 hours. The area of feeding is defined by the size of the stomach and therefore the size of the seastar. Birkeland (1989a) has pointed out that the everted stomach area for A. planci is about 2.5 times that for a same-sized corallivorous seastar, Culcita novaeguiniæ, and suggests that this might contribute to the greater effects of corallivory by A. planci. Once a coral is digested, the seastar moves on to the next branch or colony.

A characteristic of Acanthaster planci that allows it to encounter its prey effectively, is the ability to move relatively rapidly across the reef. The smallest of juveniles have been observed to move one body length per minute (Yamaguchi, 1973), while larger juveniles can move up to 4 m in an hour (for a review see Moran, 1986). Movements of adult seastars of ten meters per day have been measured (Keesing and Lucas, 1992) and there is indirect evidence that A. planci can move large distances between reefs separated by unsuitable habitat (Moran, 1986). Movement and cryptic behavior also have been demonstrated to be related to the nutritional condition of seastars (De’ath and Moran 1998b).

There has been debate about the longevity of Acanthaster planci with some arguing that they have characteristics of a short-lived species (Ebert, 1983), while others have suggested that their longevity is much longer (Cameron and Endean, 1982). The best estimates of longevity, based on laboratory studies, are that seastars live for approximately 8 years (Lucas, 1984), but longevity in the field is not known for most populations. Zann et al. (1990) found that the longevity of different cohorts of A. planci in Fiji varied between 2 and 8 years. Age determination of individuals in the field is hampered by the lack of a reliable method to accurately estimate age (Souter et al., 1997).

The role of predators in controlling populations of Acanthaster planci has been a point of discussion for the past 3 decades. It is known that at least 12 different species can prey on juvenile and/or adult A. planci (Moran, 1986; Endean and Cameron, 1990). These include xanthid crabs, a shrimp, a polychaete, two species of gastropods, and several species fishes. Although some species prey on the egg and larval stages of the seastar, they do not ingest them preferentially and many potential predators actively
avoid them. This led Yamaguchi (1973) to conclude that these stages might contain chemical compounds to deter predators. The gastropod _Charonia tritonis_ was proposed as a major predator on _A. planci_ (Endean, 1977), but the effect of predation by this species on populations of _A. planci_ has been questioned (Moran, 1986). If eggs and larvae are protected somewhat from predation and the heavily-spined adults can resist all but the most effective predators, it may be the juvenile stage of _A. planci_ that is most vulnerable to predation. However, Moran (1986) concluded that there is little evidence that predation controls population sizes of _A. planci_.

Although quantitative data are few, "normal" abundances of _Acanthaster planci_ are considered to be on the order of 1 ind./100m² or <20 ind./km of reef, although as Moran (1986) points out there are no adequate data to define the "normal" density of a population. What has fueled interest in _A. planci_ have been a series of explosions in the population sizes of this seastar since the mid-1950s (Potts, 1981). These outbreaks have occurred fairly synchronously across a large number of localities including reefs in the Ryukyu Islands, Micronesia, Hawaii, Fiji, Tahiti, Panama, and on some reefs of the Great Barrier Reef (GBR) in Australia. The extent of the population increases varied between areas and due to a lack of standardized sampling of the abundance of _A. planci_ and the patchy distribution of seastars, reports of _A. planci_ abundance during outbreaks vary greatly. However, outbreaking populations of _A. planci_ generally have abundances that are 400-600% higher than normal (Birkeland, 1982; Moran, 1986).

Outbreaks of _A. planci_ populations occurred in the Ryukyu Islands beginning in the mid 1950s and spread southward and were reported in Okinawa in 1969. Outbreaks were reported on the reefs near Green Island on the GBR in 1962 and spread southward to the Swain Reefs by 1975. In Micronesia, an outbreak erupted on the reefs in Guam in 1968 and again in the late 1970s. In 1979, a second outbreak occurred at Green Island and again spread southward affecting many of the reefs of the central GBR (Moran, 1986). These outbreaks have been classified as primary or secondary based primarily on their timing and presumed connectance to other outbreaks. The initial outbreaks in the Ryukyu Islands and at Green Island are thought to be primary outbreaks where populations of _A. planci_ increased dramatically. Further outbreaks to the south of these areas were probably secondary outbreaks, resulting from the transport of seastar larvae produced by the outbreaking populations to the north (Moran, 1986; Dight et al., 1990a). For the GBR, this interpretation has been supported by data on the genetics of outbreaking populations (Benzie and Stoddart, 1992). Clearly, some outbreaks are harder to explain (e.g., Hawaii, Panama) and might represent additional primary outbreaks. Other hard to explain patterns include why some reefs within the same region have been susceptible to repeated outbreaks (mid-shelf reefs of the GBR), while outbreaks have never been reported on nearby, outer-shelf reefs (Moran, 1986; but see Dight et al., 1990b).

The impact of the outbreaks of _Acanthaster planci_ have been dramatic in many cases. In Panama, Glynn (1973) reported that _A. planci_ removed only 15% of annual coral growth. In most outbreak areas coral mortality ranged from <50 to nearly 100% (Birkeland, 1989a; Glynn, 1990). Mortality often was patchy spatially because aggregations of seastars disproportionately impacted deeper portions of reefs and reefs protected from wave action (Moran, 1986). Acroporid corals were fed on preferentially at most locations and other coral species often survived, at least as small remnants
This was true particularly for massive species, such as Porites spp.. It was estimated that a single crown-of-thorns seastar could consume 5 to 6 m$^2$ of live coral per year and at outbreak densities, this translated to as much as 6 km$^2$ of reef being consumed per year (Birkeland, 1989a). However, as Moran (1986) emphasizes, outbreaks were variable in their duration and severity such that some reefs were impacted more significantly than others.

The immediate ecological impacts of Acanthaster planci outbreaks on most reefs were that the community structure of reefs was modified because abundances of some coral species were reduced drastically, or they were removed from the reef community entirely, and that significant amounts of substratum were made availability for settlement of other organisms (Moran, 1986; Birkeland, 1989a; Endean and Cameron, 1990; Glynn, 1990). In the short term, algae colonized most of the newly availability space following coral mortality and on some reefs were displaced later by sessile invertebrates such as sponges and soft corals (Birkeland, 1982). If the reef previously was composed largely of coral species that were fed on preferentially by A. planci (i.e., acroporids), mortality was often >80% and the species composition of the community was changed dramatically (second-order effects). Some reefs dominated previously by Acropora spp., were devastated and the framework of the reef collapsed due to increased bioerosion (Moran, 1986; Glynn, Chapter IV), modifying spatial heterogeneity of the reef and further affecting community composition and recovery (Sano et al., 1987). If coral mortality was patchy, due to either the presence previously of mixed coral species stands or to patchy distributions of A. planci, reef communities were modified into mosaics of different successional stages (Figure 1).

Third-order changes in coral reef communities also occurred at some locations (see Pennings, Chapter XI). Increases in algal abundance led to increases in the population sizes of herbivorous fishes at some locations (Wass, 1987; Birkeland and Lucas, 1990; Hart et al., 1996), while the abundances of obligate coral feeding fishes, such as chaetodontids, decreased (Endean and Stablum, 1973; Bouchon-Navaro et al., 1985; Williams, 1986). These examples illustrate how the impact of a single species can have effects that cascade throughout the coral reef community.

Longer-term changes in coral communities subjected to outbreaking populations of Acanthaster planci were related to patterns of coral recruitment and regeneration of coral fragments. Colgan (1987) identified five stages of recovery on corals reefs in Guam: 1) dominance of crustose and filamentous algae, 2) recruitment of coral planulae, 3) differential success of different coral growth forms, 4) coral colony expansion, and 5) competition between corals (Moran, 1986). The reported time frame of recovery of impacted reefs varied between sites and according to the interpretation of the term, "recovery". Relevant components of the coral reef community to consider when evaluating the degree of reef recovery were the percent cover of live coral, coral species composition, and the community structure of the non-coral covered benthos (Done, 1985; 1987; 1988; Done et al., 1991). Several investigators found that impacted reefs
recovered in terms of the percent cover of live coral within a 10 to 15 year period (Pearson, 1981; Colgan, 1982; Done, 1985), although Seymour and Bradley (1999) concluded that recovery times were longer for reefs that had been impacted previously by A. planci.

The time required for coral species diversity to approach previous levels usually was longer and depended in part on previous species diversity of corals, which coral species were killed, and the extent of coral mortality. Cameron et al. (1991) reported long-term changes in the abundance of massive corals on reefs of the GBR, with the massive corals on outbreak reefs dominated by poritids while the massive corals on non-outbreak reefs in the same region were dominated by faviids. Differential mortality of corals due to feeding preferences or distributions of A. planci, together with differential recruitment of corals following the mortalities, gave rise to different trajectories of coral reef community development following outbreaks. Done et al. (1991) compared reef recovery from A. planci predation between and among reefs in French Polynesia and the GBR. They found evidence of significant changes on reefs that had been colonized by macroalgae such as Turbinaria ornata and Sargassum sp., suggesting much slower recovery rates on these reefs or the possibility that these were new alternate community states (Hatcher, 1984; Knowlton, 1992). Done et al. (1991) concluded that recovery of reefs appeared to be governed by local rather than regional processes. This is
supported by studies that have shown substantial variability in rates of recovery of reefs distributed along the GBR (Loury et al. 2000). As Moran (1986) states, the paucity of data available for many sites prior to seastar outbreaks, has made generalizations about reef community recovery difficult.

A key issue underlying the *Acanthaster planci* phenomenon is the cause of the outbreaks. Moran (1986) reviewed six hypotheses that have been proposed to explain outbreaks of *A. planci* (Table 2). The hypotheses can be categorized into two groups; those hypotheses that view outbreaks as natural phenomena that have occurred repeatedly in the past, and hypotheses that are grounded in the premise that outbreaks are recent and novel events. Support for the view that outbreaks of *A. planci* have occurred previous to the 1950s comes from several sources. Birkeland and Randall (1979) and Birkeland (1981) concluded that outbreaks had occurred earlier in this century based on interviews with fisherman in Samoa who remembered extremely high densities of *A. planci* and based on the fact that the seastar is included in several cultures of human populations in Micronesia. Birkeland and Lucas (1990) also reported extensive documentation of outbreaks in Japanese waters by those using *A. planci* commercially as a source of fertilizer.

Table 9-2. Hypotheses Proposed to Explain the Outbreaks of Populations of the Seastar *Acanthaster planci*.

<table>
<thead>
<tr>
<th>Outbreaks as Natural Phenomena</th>
<th>Dana, et al., 1972</th>
<th>Lucas, 1972</th>
<th>Birkeland, 1982</th>
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<tr>
<td>Adult Aggregation Hypothesis</td>
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<td>Larval Recruitment Hypothesis</td>
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<td>Terrestrial Runoff Hypothesis</td>
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<td>Reef Destruction Hypothesis</td>
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<td>Pollution Hypothesis</td>
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<tr>
<td>Predator Removal Hypothesis</td>
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A second line of evidence for outbreaks in the past comes from geological evidence that skeletal elements of *Acanthaster planci* are found in abundance periodically in reef sediments dated over the past 7000 years (Frankel, 1977; 1978; Walbran et al., 1989; Henderson, 1992; Henderson and Walbran, 1992). These authors suggest that predation by *A. planci* has been a recurring influence on the development of reefs on the GBR. Other reef scientists have questioned this stratigraphic evidence due to assumptions about the dispersion of skeletal ossicles and dating methodology (Moran et al., 1986; Fabricius and Fabricius, 1992; Keesing et al., 1992). The issue of whether accumulated skeletal elements represent reliable evidence of past outbreaks of *A. planci* remains unresolved.

On other grounds, Chesher (1969) and Randall (1972) have argued that outbreaks could not have been regular occurrences on reefs in the past or these reefs would be composed entirely of corals that *Acanthaster planci* avoids, such as *Porites* spp.. As
Moran (1986) points out however, recovery of acroporids can occur relatively rapidly (10-15 years) after an outbreak.

The hypotheses proposed under the premise that outbreaks are natural phenomena include the adult aggregation hypothesis forwarded by Dana et al. (1972), which states that *Acanthaster planci* are more common on reefs than once thought, but that the majority of the population lives in deeper portions of the reef where they have escaped previous attention. Following a disturbance such as a storm that causes coral mortality and a disruption in food availability, seastars aggregate in areas with healthy corals and an outbreak ensues. Although this hypothesis explains why all the seastars in an outbreak are of adult size and is consistent with the correlation for some sites between large storms and subsequent outbreaks, it has been suggested that the amount of reef damage required to result in food limitation is much greater than that observed for most storms. Reichelt et al. (1990a, b) and Bradbury (1991) have used data on *Acanthaster planci* outbreaks on the GBR and theoretical models of predator-prey interactions, to conclude that outbreaks are the result of a typical predator-prey cycle that is driven by prey (coral) abundance and recruitment success and survival of the predator (seastar). When corals are reduced in abundance, reefs cannot support large populations of *A. planci* and the outbreak ceases until coral abundance increases again. They have used this reasoning to predict future outbreaks on the GBR.

Lucas (1975) proposed that outbreaks of *A. planci* could occur if environmental conditions were such that larval survival and recruitment were higher than normal, arguing that for such a fecund species, a small percentage increase in survival could lead to massive increases in recruitment. In larval culturing experiments, Lucas (1973) demonstrated that larval survival increased under conditions of low salinity and high temperature and Pearson (1975) suggested that such conditions could occur off the Australian coast, particularly in areas near large rivers. This hypothesis is consistent with the pattern that the majority of outbreaks have occurred on reefs surrounding high islands or near continental land masses where freshwater run-off occurs, at least seasonally.

In a similar vein, Birkeland (1982) proposed the terrestrial run-off hypothesis that stated that nutrients in freshwater run-off, especially from large storms, cause a phytoplankton bloom that increases the food supply for *Acanthaster planci* larvae. Increased survival results in increased recruitment of juveniles and a subsequent outbreak. Like the previous hypothesis, the terrestrial run-off hypothesis explains why outbreaks have been most common near high islands and continents and is consistent with the correlation between large storms and subsequent outbreaks that exists for some sites. This hypothesis assumes that most *A. planci* larvae starve from food limitation under "normal" conditions. Using an *in situ* culturing chamber, Olson (1987) tested this hypothesis and concluded that the development times of larvae raised under conditions simulating a phytoplankton bloom were less than those for larvae in ambient seawater, but that the difference was not great enough to explain the sudden increases in *A. planci* populations. Nevertheless, a combination of temperature, salinity, and food conditions might lead to increased larval survival and recruitment and explain primary outbreaks in some reef locations (Moran, 1986).
Observations that outbreaks of *Acanthaster planci* occurred near centers of human populations led several investigators to hypothesize that outbreaks were not natural events, but instead were human-induced phenomena. Both Fisher (1969) and Randall (1972) proposed that increased pollutant concentrations in nearshore waters resulting from human activities reduced the abundances of predators of *A. planci*, allowing a population explosion. However, no studies in reef environments have shown that pesticides or other pollutants are in significantly higher concentrations in animals near human populations or that predation controls population sizes of *A. planci*. Chesher (1969) proposed that destruction of reefs as a result of human activity, including dredging, blasting, and poor land use practices leading to increased siltation, caused extensive mortality of corals. He presumed that corals were the primary predators of *A. planci* larvae and decreasing coral abundance subsequently led to outbreaks of seastars. Endean (1977) concluded that this did not explain outbreaks in areas not subject to human activities and that in general, this hypothesis was not supported.

Of the hypotheses proposing that outbreaks of *Acanthaster planci* are human-induced events, the predator removal hypothesis of Endean (1969) has received the most attention (although the prior two hypotheses relate to predator removal as well). This hypothesis states that seastar outbreaks are the result of the reduction of predators on juvenile and adult *A. planci* by humans. The initial hypothesis referred to the triton snail, *Charonia tritonis*, which has been collected heavily in many locations. It was known previously that *C. tritonis* was a predator of small adult *A. planci*, but caging experiments to estimate the rate of predation by tritons on *A. planci* suggested tritons did not prefer *A. planci* if there was a choice and only consumed, on average, one seastar per week (Potts, 1981). This suggested that it was unlikely that *C. tritonis* controlled the population sizes of *A. planci*. Endean (1977; 1982) later incorporated other potential predators into the hypothesis, including several species of fishes. This hypothesis, that predators are a major factor controlling the populations of *A. planci* has received limited support from the results of theoretical models that incorporate the role of predation on seastars in the dynamics of seastar-coral interactions (Bradbury, 1991). However, it is unlikely that a reduction in predator abundance could result in sudden increases in the population sizes of *A. planci* in selected years.

The current ideas on the causes of outbreaks of *Acanthaster planci* are that it is unlikely that a single cause underlies the outbreaks at all locations. None of the proposed hypotheses fully explains the variation observed between outbreak locations or in some cases the timing of outbreaks (i.e., why have outbreaks occurred nearly simultaneously in widely separated areas). Given the complexity of the physical and biological interactions between coral reef organisms and their environment, it is more likely that outbreaks of *A. planci* and their spread to other reefs are caused by a complex suite of interacting processes that include some aspects of many of the hypotheses that have been proposed. As Moran (1986) states, "It is worth pondering whether our understanding of the Acanthaster phenomenon is hamstrung because there is a tendency to rely on hypotheses which may provide simplistic answers to what may be a far more complex question? Perhaps the real answer may lie in a collage of the main hypotheses proposed earlier."

From a management perspective, the question of outbreak frequency is acute (Kenchington and Kelleher, 1992). Birkeland (1989b) and others have argued that
outbreaks have become more frequent and *Acanthaster planci* are more chronically abundant in Guam, Fiji, the Ryukyu Islands, and on the GBR (Birkeland, 1982; Yamaguchi, 1986; Reichelt et al., 1990; Zann et al., 1990). For at least some sites, the answer to the question of increasing frequency appears to be a convincing affirmative. It is tempting to correlate the increase in frequency and duration of *A. planci* outbreaks to the continuing (and accelerating) development of coastal zones throughout the Indo-Pacific that lead inevitably to increased erosion, siltation, coastal eutrophication, and increased stress on coral reef communities. Since some of the hypotheses to explain the cause of *A. planci* outbreaks would predict increasing frequency of outbreaks under these conditions, resource managers are left to decide a course of action in the absence of clear-cut recommendations based on expert opinions (Kenchington and Kelleher, 1992). While the economic costs of resource protection through more prudent land use and development and conservative resource management practices would be significant, the potential ecological and long-term economic costs of inaction may be much higher. The *Acanthaster* problem is one that has prompted interdisciplinary scientific approaches and will require further innovative efforts to provide resource managers with the information necessary to make informed decisions about maintaining coral reefs as highly productive and diverse ecosystems with sustainable economic benefits.

9.2.2. Herbivores

*Echinometra mathaei*

Another invertebrate species that has been demonstrated to affect some coral reef communities disproportionately when it is abundant is the echinoid, *Echinometra mathaei* (Dart, 1972; Muthiga and McClanahan, 1987; McClanahan and Muthiga, 1988). *Echinometra mathaei* is a camarodont sea urchin that burrows into rock and coral substrata and is distributed throughout the Indo-Pacific from eastern Africa and the Red Sea to Hawaii (Clark and Rowe, 1971). The habitats in which *E. mathaei* normally are found are shallow reef crests and lagoonal coral heads, and when present in low densities, inhabits holes and crevices in the substratum that are enlarged by erosion of the rock or coral by the spines and grazing activity (Dart, 1972). Sheltering behavior and defense of crevices against conspecifics by *E. mathaei* is thought to be the result of predation pressure from fishes. Under conditions of low population density, *E. mathaei* feed on encrusting and upright algae in and near their protective crevices. When conditions permit high population sizes, *E. mathaei* inhabit open areas of the reef, show less agonistic behavior toward conspecifics and graze attached algae over wide expanses of the reef (McClanahan and Muthiga, 1988; McClanahan and Shafir, 1990).

In several locations on the reefs of Kenya, McClanahan and co-workers have identified a situation where the removal of echinoid predators (primarily balistids and wrasses) has led to increases in the population densities of *Echinometra mathaei* by 2 to 3 orders of magnitude (McClanahan and Shafir, 1990). Reef sites vary in the abundances of echinoid predators by a factor of 5, with high abundances in reef park areas protected from fishing, and lowered abundances on unprotected, fished reefs. As a result of reduced predation, population densities of *E. mathaei* reach 13 ind./m² in some areas, where they outcompete other echinoid species (McClanahan and Kurtis, 1991).

Elevated population sizes of *Echinometra mathaei* have both first and second order effects on the coral reef community. First order effects include lowered algal biomass,
increased cover of algal turfs, lowered cover by live corals, increased bioerosion, and lowered spatial heterogeneity on heavily grazed reefs (McClanahan and Shafir, 1990). The overall species diversity of the benthic community is significantly lower in areas of high E. mathaei abundance. Second order effects are increased cover by sponges on heavily grazed reefs and decreases in the population sizes of herbivorous fishes (McClanahan and Shafir, 1990; McClanahan, 1992).

These results suggest that when released from predation, populations of Echinometra mathaei increase dramatically and that the resulting increase in grazing pressure reduces live coral cover. It is unclear whether the reduction in coral cover is a direct result of predation by E. mathaei or the indirect result of preventing recruitment of corals due to intense, generalized grazing of the reef surface. When population densities are high, E. mathaei apparently is capable of outcompeting other herbivores, including other echinoid species and fishes, through more efficient utilization of algal resources and exploitative competition (McClanahan, 1992). This provides another example of a species that, under conditions of reduced population regulation by predators, can mediate coral reef community structure.

**Diadema antillarum**

The long-spined sea urchin Diadema antillarum is an aulondont echinoid that is distributed from the Gulf of Mexico, throughout the Caribbean to Surinam in South America, northward to Bermuda and eastward to the Azores, Madeira, and Cape Verde

*Figure 9-4 Diadema antillarum* foraging at night at St. John in the U.S. Virgin Islands.
Islands and the Gulf of Guina in west Africa (Ogden and Carpenter, 1987). *D. antillarum* is a free-spawning echinoid with populations having a female-biased sex ratio of 2:1 (Lessios, 1988). Spawning occurs year-round in small aggregations and males and females must be within approximately 20 cm to effect successful fertilization (Levitan, 1991). As a result, successful reproduction is population size dependent. Planktotrophic larvae are produced that are thought to spend at least one month in the plankton and therefore dispersal potential is great. Longevity of larvae is dependent on food quality and abundance and under some conditions, larvae can delay metamorphosis for up to 90 days (Carpenter, unpublished data). Juveniles recruit into small crevices in the reef and recruitment is dependent on algal biomass, which may be a cue for the presence of conspecifics (Bak, 1985). Juveniles grow rapidly (5 mm/month in test diameter) and attain a size of 2.5-3 cm in the first year (Randall et al., 1964; Lewis, 1966). *D. antillarum* exhibit early sexual maturation after approximately one year and continue to grow to a maximum size of >10 cm. Longevity in the field is not known, but 4 years is probably a minimum estimate (Ogden and Carpenter, 1987).

The population densities of *Diadema antillarum* have varied widely between locations throughout the western Atlantic. In some locations, such as Barbados, Curacao, Jamaica, the Virgin Islands, Cozumel, Belize, Puerto Rico, Grand Cayman, and the San Blas Islands in Panama, population densities of 3 to 73 ind./m² have been reported (Bauer, 1980). Population densities at other sites, such as Honduras, Bermuda, and some sites in the Bahamas and in Belize have been much lower (<1 ind./m², Bauer, 1980). Hay (1984) and Levitan (1992) have correlated elevated population densities of *D. antillarum* with the overfishing of sea urchin predators (see below) and competitors (herbivorous fishes) in locations near large human populations. While human activities appear to have influenced population sizes of *D. antillarum* at some locations in the past, other processes such as recruitment limitation may be important in determining population densities on a local scale. Recent evidence based on molecular-based approaches estimating effective population size suggests that populations of *D. antillarum* throughout the Caribbean have been substantial for at least the past 100,000 years (Lessios et al. 2001). This predates any potential effects of anthropogenic origin on the historic abundances of this species. Presently, population densities of *D. antillarum* are reduced drastically throughout the western Atlantic due to the mass mortality event in 1983-84 (see below).

In many reef environments, *Diadema antillarum* inhabits holes and crevices diurnally, emerging at dusk to forage all night and return to their protective crevices in the morning. Individuals have been demonstrated to exhibit crevice fidelity for extended periods of time and crevice fidelity is negatively correlated with sea urchin population densities and positively correlated with predator abundances (Carpenter, 1984). *D. antillarum* is an herbivore primarily, preferring to feed on algal turfs, but will prey on other items such as live coral (Bak and van Eys, 1975; Carpenter, 1981). Under food limiting conditions, *D. antillarum* can increase the size of certain elements of the Aristotle’s lantern, thereby increasing feeding efficiency (Ebert, 1980; Levitan, 1991). This may be one characteristic underlying the success of this species since it can optimally allocate resources to feeding and reproduction and maximize their reproductive output over time. Dietary and morphological plasticity may be important...
characteristics underlying the widespread occurrence and impacts of *D. antillarum* on coral reef communities.

The main predators of *Diadema antillarum* are balistid, sparid, large labrid, and batrachoidid fishes (Ogden and Carpenter, 1987). Based on gut contents, Randall (1967) found that the queen triggerfish, *Balistes vetula* was the main predator on *D. antillarum* in the U.S. Virgin Islands. The king helmet snail, *Cassis tuberosa*, is also known to be a predator (Randall et al., 1964).

Many studies have been conducted to investigate the effects of grazing by *Diadema antillarum* on the coral reef community. The direct effects of grazing by *D. antillarum* are to reduce algal biomass, shift algal community structure and diversity, and increase rates of primary productivity of algal turf communities (Ogden et al., 1973; Sammarco et al., 1974; Carpenter, 1981; 1986; Sammarco, 1982). In a sea urchin removal experiment, Ogden et al. (1973) and Sammarco et al. (1974) demonstrated that in the absence of grazing by *D. antillarum*, the algal community on a patch reef became dominated by macroalgae and that halos into the seagrass bed surrounding the reef disappeared. Results from manipulative experiments with algal turf substrata exposed to different combinations of reef herbivores indicated that grazing by *D. antillarum* reduced algal biomass and increased rates of biomass-specific primary productivity of algal turfs. These experiments indicated further that *D. antillarum* removes an average of 97% of algal turf biomass produced over a year (Carpenter, 1986).

The effects of grazing by *Diadema antillarum* are not confined to the algal community. Due to both the direct effects of grazing on settled coral spat and indirect effects of modifying competitive interactions between algae and corals, Sammarco (1980) found that grazing by *D. antillarum* controlled the survivorship and abundance of newly settled corals. At high population densities of *D. antillarum*, intense grazing led to the mortality of juvenile corals, while in the absence of sea urchin grazing, corals were overgrown by algae. As a result, at intermediate population densities of sea urchins, grazing was a regulating force controlling the relative abundances of corals and algae on the reef.

In addition to effects on sessile organisms, *Diadema antillarum* may affect the abundances of other herbivorous species, presumably as a result of exploitative competition for limited algal resources. Results of field experiments in Jamaica suggested that *D. antillarum* outcompeted another echinoid, *Echinometra viridis*, in areas not dominated by a territorial damselfish (Williams, 1981). Abundances of *E. viridis* increased when the damselfish excluded *D. antillarum*. Hay and Taylor (1985) demonstrated that the abundances of herbivorous fishes increased in reef areas from which *D. antillarum* had been removed. Because of the short-term nature of these experiments, they concluded that fishes from neighboring areas of the reef migrated into the sea urchin removal areas to exploit increased algal resources and that this was evidence for prior exploitative competition between the herbivore groups.

Prior to 1983, much of what was known about the effects of *Diadema antillarum* on components of coral reef communities was based on manipulative field experiments. In 1983-84, a natural experiment (unreplicated) occurred throughout range of *D. antillarum* in the western Atlantic. Beginning in Panama in January 1983, a mass mortality of *D. antillarum* occurred throughout the Caribbean, Gulf of Mexico, the Bahamas, and Bermuda (Lessios et al., 1984). Averaged over all sites where data were
available, 93% of the individuals died and in many locations 100% mortality was common (Lessios, 1988). The only known populations that were not affected by the mass mortality were in the eastern Atlantic. No other species were affected. The cause of the mortality remains unknown, but given the direction and timing of the spread of mortality between populations, a species-specific water-borne pathogen is suspected (Lessios et al., 1984; for a review see Lessios, 1988). Recently, Phinney et al. (2001) used images obtained from remote sensing to estimate benthic changes associated with the mortality of *D. antillarum* to reevaluate the hypothesis that a pathogen distributed via surface currents was responsible for the epizootic. They concluded that for some locations (Gulf of Mexico, Bermuda) that progression of the mass mortality was consistent with movements of surface currents, however, for sites in the eastern Caribbean (Barbados, Curaçao, Virgin Islands) that patterns of infection were not consistent with surface current patterns. Whether other vectors for the suspected pathogen, such as transport in ballast water, were operating remains speculative.

Regardless of the cause, the mass mortality of *Diadema antillarum* provided a unique opportunity to evaluate the importance of a single species to the coral reef community and allowed the testing of hypotheses regarding the effects of grazing on benthic community structure and function, as well as hypotheses about the competitive relationships between *D. antillarum* and other species. The effects of sea urchin removal were immediate and significant. In St. Croix, algal biomass increased by 27% five days after the mortality and continued to increase to 400-500% of premortality levels (Carpenter, 1985; 1990a). A similar pattern was observed in Jamaica where algal cover increased from 31% to 50% within two weeks and increased further to 65% cover after one year (Liddell and Ohlhorst, 1986). Algal biomass also increased on the reefs of Curaçao (de Ruyter van Steveninck et al., 1986) and slight increases were observed on some reefs in Panama (Lessios, 1988).

The species composition of the algal community changed on many affected reefs from algal turfs comprised of many filamentous species (Hackney et al., 1989) and crustose corallines, to a community dominated by macroalgal species such as *Lobophora variegata*, *Sargassum* spp., and *Turbinaria turbinata* (Lessios, 1988). The increases in algal abundance occurred at the expense of other reef components since many of the macroalgal species are capable of abrasion and overgrowth of other benthic components (Figure 2). Cover of crustose corallines, clionid sponges, live coral, zoanthids, and encrusting gorgonians decreased at several reef locations (Lessios, 1988).

Consistent with previous experimental results, rates of algal primary productivity decreased immediately following the mass mortality and increased thereafter as algal biomass increased (Carpenter, 1985; 1990a). At some sites, the longer-term increased rates of algal biomass production, rather than entering the trophic web via grazing, resulted in increased algal standing crop and export of algae from the reef community as detritus (Carpenter, 1990a).

Increased grazing by herbivorous fishes (mostly acanthurids and scarids), as measured by the number of fish bites, was observed at one reef location, suggesting that the increase in algae following the removal of *Diadema antillarum* resulted in an immediate functional response by herbivorous fishes (Carpenter, 1985). Similarly,
Figure 9-??: Diagrammatic representation of the transitions of the coral reef community from one state to another as a result of the removal of Diadema antillarum by mass mortality. It is unclear if a transition from a macroalgal dominated community to a coral/algal turf community can occur or what events might facilitate this transition.

increased fish grazing was observed on reefs in Jamaica (Morrison, 1984). These observations support the hypothesis that sea urchins and herbivorous fishes were competing prior to the mass mortality. However, increased grazing by herbivorous fishes was not sufficient to compensate for the removal of sea urchins, and algal biomass continued to increase and species composition changed until many reef areas were dominated by macroalgal species (Lessios, 1988).

The longer-term impacts (several years) of the removal of Diadema antillarum on many coral reef communities were a reduction in the cover of live coral and other sessile invertebrates and a shift to a reef community dominated by macroalgae (Birkeland, 1989a). The direction of the changes in reef communities throughout the western Atlantic following the mass mortality were consistent, however the magnitudes of the changes were correlated with the previous population densities of D. antillarum (Lessios, 1988). Changes in reef community structure at reef locations where sea urchins were rare were minimal, lending support to the hypothesis that changes in community structure elsewhere were the direct result of the removal of D. antillarum and not due to other physical or biological factors. Long-term increases in the population sizes of herbivorous fishes have been reported from two locations where data were available prior to the mass mortality. Both in St. Croix (Carpenter, 1990b) and Panama (Robertson, 1991), increased abundance of acanthurids and scarids resulted from the removal of a major competitor. It is not known if the increase in population sizes of primary consumers at these sites has led to an increase in secondary consumers. No changes have been observed in the populations of fishes that preyed previously on
D. antillarum, as they have switched to feeding on other prey species (Lessios, 1988; 1995).

There has been some evidence to suggest that other echinoid species may have responded to the removal of D. antillarum. In Jamaica, Woodley et al. (1999) and Moses and Bonem (2001) documented an increase in the abundance of Tripneustes ventricosus on the shallow forereef, a habitat where they previously were rare or absent. Haley and Solandt (2001) suggested that it was an increase in populations of T. ventricosus that may have facilitated the return of D. antillarum in this habitat, however, similar patterns have not been reported elsewhere.

Recruitment of Diadema antillarum for 15 years following the mass mortality was minimal or nonexistent on most reefs in the western Atlantic where data have been collected (Lessios, 1995). The only site where high recruitment of juveniles was reported during this period was for Barbados (Hunte and Younglao, 1988). The most likely explanation of the lack of recruitment at most sites during this period was the lack of larvae available to settle which could be a function of decreased production of larvae or increased larval mortality in the plankton. Because there appears to be a minimum population size required to effect successful fertilization in D. antillarum (Levitan, 1988), it is likely that the lack of recruitment is due to reproductive failure for most populations and a drastic reduction in the abundance of larvae produced (Lessios, 1995), although size distributions of populations from some locations in the Florida Keys suggest that post-settlement mortality may also play a role in the continued low population densities (Chiappone et al. 2002).

Since the late 1990s, reported abundances have varied for different locations in the Caribbean. Abundances in 1997-98 at locations throughout the Caribbean (Jamaica, Barbados, Belize, Grand Cayman, Cuba) were uniformly low (<0.01 individuals/m²) (Williams and Polunin, 2001). Large-scale surveys conducted in the Florida Keys in 1999 and 2000 revealed mean abundances of <0.05 individuals/m² over all reefs surveyed (Chiappone et al. 2002). However, during the same sampling period, mean abundances of up to 0.33 individuals/m² were found on reefs in the Dry Tortugas (Chiappone et al. 2001). Surveys during the late 1990’s at Glover’s Reef, Belize found very few D. antillarum with abundances < 0.001 individuals/m² (McClanahan and Muthiga, 1998). In the southeastern Caribbean (Tobago Cays, St. Vincent), mean densities on shallow reefs were only 0.05 individuals/m² (surveys in 1999, Deschamps et al., 2003). Surveys on patch reefs and backreef habitats in St. Croix, U.S. Virgin Islands by Miller et al. (2003) found densities from 0.2 to 0.5 individuals/m². In the western Caribbean, reported densities between 1999 and 2003 from sites in Costa Rica ranged from 0.3 to 0.7 individuals/m² (Alvarado et al. 2004). Overall, data from these locations indicated very little recovery of populations of D. antillarum.

While these population densities are far lower than those common prior to the mass mortality, some reefs along the north coast of Jamaica began to have increasing abundances of Diadema antillarum in the late 1990’s (Aronson and Precht 2000). By 2000, densities at shallow forereef depths on five reefs in the vicinity of Discovery Bay averaged 5 individuals/m² and size-frequency distributions suggested that recruitment was occurring (Edmunds and Carpenter 2001). Furthermore, benthic community structure of these shallow reefs was
significantly different than in areas where sea urchins were rare, with the community dominated by algal turfs and crustose coralline algae, similar to that present before the mass mortality (Carpenter 1981). Importantly, abundances of juvenile corals also were significantly higher in the sea urchin zones. After nearly 2 decades of limited recruitment of juvenile corals, the return to near historical abundances of D. antillarum and coral recruits (Figure 3) suggest the potential for recovery of coral populations on these reefs. To date, many shallow reefs in the western Atlantic (although not all) still are dominated by macroalgae with low cover of live coral (Gardner et al. 2003). As populations recover throughout the Caribbean, the reverse predictions of the effects of grazing by D. antillarum on coral reef communities can be tested once again.
The abundance of diademid echinoids associated with coral reefs varies greatly within the Pacific Ocean and between the Pacific and western Atlantic (Bauer, 1980; Birkeland, 1989a). Previous explanations of the disparity in abundances between the western Atlantic and Pacific have been based largely on the argument that *D. antillarum* abundances increased in Caribbean as a result of the removal of predators by overfishing (Hay, 1984; Levitan, 1992; Jackson et al. 2001). With the recent demonstration that populations of *D. antillarum* have been large historically, well before any anthropogenic effects could have influenced their numbers (Lessios et al. 2001), other explanations must be sought. Perhaps the most parsimonious relates to the higher diversity of herbivores on Pacific reefs that might lead to increased competition for algal resources and keep the abundances of diademid echinoids in check. On reefs in the western Atlantic, lower herbivore diversity may have allowed *D. antillarum* to competitively dominate the guild.

Several other explanations have been proposed, including higher abundances of echinoid predators in the Pacific and the dependence of echinoid larvae on abundant phytoplankton for successful recruitment. The latter might explain the higher abundances of diadematis on inshore reefs of the GBR and the larger, high islands of...
the Pacific and their generally low abundances on offshore reefs of the GBR and other coral reefs in the Pacific. An additional hypothesis that might explain the distribution and abundance of diadematids that has not received serious attention is that their abundance is related to the abundance of their prey, mainly algal turfs (Birkeland, 1989a). In general, Pacific reefs have higher coverage of live corals than reefs in the western Atlantic. Similarly, inshore reefs and reefs surrounding high islands are subject to increased physical stresses and disturbances that decrease the cover of live coral, resulting in higher coverage of algae that can support a larger biomass of invertebrate herbivores. Recruitment of diadematids has been demonstrated to be greater under conditions where algal turfs are present (Bak, 1985), so that a combination of settlement cues and subsequent increased survivorship might explain the higher abundances of diadematids on these reefs.

As with Acanthaster planci populations, it is likely that a combination of factors underlies the distribution and abundance of diadematid echinoids. For example, the abundances of Diadema spp. and Echinothrix spp. on some reefs in Palau were high enough previously to be harvested by humans (Birkeland, personal communication). The echinoids probably were over-fished, removing the major herbivores. These reefs have also been devastated by A. planci outbreaks and are now dominated by algae and diadematids are rare. This suggests that larval supply is not sufficient to repopulate these reefs and that a combination of predation (by humans), lack of recruitment, and disturbance by A. planci have caused a phase shift in the coral reef community.

9.3 DISPROPORTIONATE EFFECTS OF SOME INVERTEBRATE SPECIES

While the diversity and abundance of invertebrate predators and grazers associated with coral reefs is high, it is striking that a few species have such disproportionate effects on coral reef community structure and function. These species are capable of changing the reef environment as a result of their direct effects and the cascade of indirect effects that are initiated by their activities. The aggregate effect of this influence can be to shift the balance of processes, causing the reef to move from one state to another. As a result, these species are located ecologically in a position to mediate processes that involve the life and death of coral reefs. An important question is why these species have the capability to alter significantly what has been regarded historically as a stable biological community?

Although the invertebrate species discussed previously that have disproportionate impacts on coral reefs are all echinoderms, and therefore have some morphological similarities, other characteristics of these species must result in their important influence on reef communities. One attribute they share is the capability of rapidly attaining and maintaining large population sizes. Acanthaster planci, Diadema antillarum, Euclidaris thouarsii, and Echinometra mathaei all exhibit very high fecundity and the potential for producing extremely high numbers of larvae. Behaviors such as formation of spawning aggregations probably facilitates fertilization success and increases the number of larvae produced (Levitan, 1988; Karlson and Levitan, 1989). High recruitment into existing populations and establishment of new populations may be dependent on environmental conditions that promote phytoplankton abundance and contribute to increased larval survivorship, as proposed for both A. planci and diadematid echinoids (Birkeland,
1989a). Such conditions are more likely for reef habitats near continents and large islands where nutrient run-off is higher and often seasonal. This adds a stochastic factor that controls, in part, the population sizes of these species, and together with the longevity of adults influences whether population sizes oscillate or are more stable through time.

_Acanthaster planci_ and _Diadema antillarum_ both settle cryptically and exhibit very rapid growth of juveniles, minimizing predation on their early stages, attaining sexual maturity at an early age, and therefore contributing further to rapid increases in population size. However, much of the success of these species may be dependent on the high degree of both morphological and dietary plasticity that they exhibit (Birkeland, 1989a; 1989b). _A. planci_ are unique among the seastars associated with reefs in having a reduced skeleton and a pliable body form that allows them access to a wide range of coral colony shapes. While they exhibit distinct preferences for some species of corals, under a variety of conditions they will readily eat other prey, effectively making them a generalist able to subsist in environments where the abundances of some prey species vary (Birkeland, 1989a). As an early juvenile, _A. planci_ feed primarily on crustose coralline algae which are abundant in the microhabitats where they settle. Later, they switch to a diet of corals, which are more abundant and have higher nutritional quality. Similarly, _D. antillarum_ will forage on a variety of prey, preferably filamentous algal turfs, but will feed on most algal species and even corals, when conditions require it. Furthermore, _D. antillarum_ allocates energy to growth of the test and feeding apparatus that allows them to forage effectively even when algal abundance is reduced (Ebert, 1980; Levitan, 1991). _Eucidaris thouarsii_ and _Echinometra mathaei_ also have general diets that include a variety of prey species.

On many coral reefs, predation does not appear to control the population sizes of _Acanthaster planci_ or _Diadema antillarum_. This is a result of the rarity of predators in some locations, and morphologies and/or behaviors that reduce the effects of predation in general. Spines and/or toxins are used by these species to deter predators, while diel behaviors reduce the risk of predation. While a correlation exists between human fishing pressure, predator abundance, and _D. antillarum_ abundance, this is confounded with environmental conditions that promote high recruitment of echinoid larvae, such that a clear-cut conclusion that predation controls populations sizes of _D. antillarum_ is not possible. Additionally, evidence that populations of _D. antillarum_ have been large historically in the western Atlantic (Lessios et al. 2001) suggests that the relatively recent reduction in predation as a result of overfishing of echinoid predators does not explain the relatively high abundances across reefs in the region. However, it does appear that population sizes of _Echinometra mathaei_ are controlled by predation in some locations (McClanahan and Muthiga, 1989). For _Acanthaster planci_, it is unlikely that a reduction in predator abundance could result in the rapid population explosions that have been observed.

When population sizes of these important invertebrate species become large, the direct effects of their feeding are to reduce the abundance of their prey; corals in the case of _Acanthaster planci_ and _Eucidaris thouarsii_, and algae in the case of _Diadema antillarum_ and _Echinometra mathaei_. Because these species are the main agents of biological disturbance in their respective coral reef communities, the effects of their feeding are community-wide. Feeding activities by _E. thouarsii_ and _E. mathaei_, have
effects that are important locally, but do not result in a new type of community. Drastic reduction in live coral cover by A. planci leads to changes in community structure as other sessile organisms occupy the opened space. Changes in benthic community structure lead to other second and third order effects. However, high population densities of A. planci are not sustainable and recovery of the reef occurs over a time scale of 10-15 years as corals settle, grow, and outcompete other benthic organisms. Grazing by D. antillarum mediates competitive interactions between the coral and algal components of the reef and the effects of grazing on the reef community are density-dependent (Sammaroo, 1980). When D. antillarum is extremely abundant, juvenile corals are grazed, live coral cover may be reduced and increased bioerosion of the reef occurs (Glynn, Chapter IV). However, a transition to another community state does not occur. In the absence of D. antillarum, algae outcompete corals and the reef is transformed into an algal-dominated community. It is unclear whether this transition is reversible over the short-term or represents an alternate stable state (Knowlton, 1992).

While the vast majority of invertebrate predators and grazers have minor effects on coral communities, a few species exert important, community-wide effects on the reef. These species tend to be fecund, fast growing, generalists that exhibit both morphological and dietary plasticity and their populations often are not controlled by predation. Their effects on the reef community are substantial and their presence or absence can result in transitions between different community types. As a result, these invertebrate species are involved in a complex of processes that determine the state of the coral reef and the trajectory of its development over time.

Acknowledgements
I would like to thank Chuck Birkeland for his useful comments and his tremendous patience during the preparation of this chapter. I also owe a debt of gratitude to S. Longmore, C. Zilberberg, and H. Carpenter for their assistance with the references. I appreciate the support of the University of Puerto Rico Sea Grant Program and the National Science Foundation for some of my work with coral reef herbivores.

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