

The influence of echinoderms on coral-reef communities

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Abstract -Certain species of echinoderms have broad-scale effects on entire coral-reef communities, more so than any other particular species of invertebrate or fish. The echinoderms with the most influence in coral-reef communities are generalists, adaptable to a variety of situations, with behavioral, distributional, and dietary plasticity. The concept of "niche" is not useful for influential species because the nature of their role is continuously changing, contingent upon factors such as predation pressure, recruitment success, and disease. The "niche" concept is more useful for specialists. More specialized echinoderms on coral reefs are "ornamental" because of morphological and physiological constraints, regardless of predation, recruitment and disease.

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1 INTRODUCTION

Each coral-reef community is unique. It differs from all other coral-reef communities, and it changes from its own previous state with time. Coral-reef communities are either in a state of 'recovery', with corals increasing in percent surface coverage in the benthic community or else the community is characterized by an extraordinary prevalence of certain species in the occupation of space. Whole-reef morphology can be explained partially on the basis of past geological processes and patterns of water movements; the distribution of individual species can be predicted on the basis of their 'niche dimensions'; but the coral-reef communities, the assemblages of organisms occupying the surfaces of the reef and moving over the reef, vary. Echinoderms are conspicuous invertebrates on coral reefs. Changes in abundances of certain species can have large-scale effects on reef community structure. To understand the variations in structure and function of coral-reef communities, it is necessary to understand the ecology of coral-reef echinoderms.

Echinoderms of particular species can have effects on coral-reef community structure and function through several trophic levels and on a geographic scale. A widespread mortality of a single species of echinoid on Caribbean reefs was directly followed by a several-fold increase in standing stock of benthic algae in Panama (Lessios *et al.* 1984a), Jamaica (Morrison 1984, T. Hughes *et al.* 1985), St Croix (Carpenter 1985a), and Curacao (Bak *et al.* 1984), and probably throughout the tropical western Atlantic (Lessios *et al.* 1984b). A second-order effect of echinoid mortality has been found in fish behavior (Hay & Taylor 1985) and is predicted for fish population structure (Hay & Taylor 1985) throughout the tropical western Atlantic. Likewise, increases in abundance of a single species of asteroid can bring about major changes in community structure of corals (reviewed in Endean 1973, 1976, Potts 1981, Moran 1986), second-order effects of increases in abundances of algae and decreases in abundances of corallivorous fishes (Sano *et al.* 1984, D. Williams 1986), and third-order effects of increases in abundances of herbivorous fishes (Wass 1987).

The coral-reef community is here considered to be the plants and animals associated with the shallow, hard-substrata in tropical regions occupied in part, or potentially occupied, by corals. The organisms occupying the sandy substrata bordering coral reefs or on reef flats are not considered unless they clearly influence the occupants of coral reefs.

Several reviews have considered coral-reef echinoderms from other perspectives. A.M. Clark (1976) emphasized zoogeographic aspects. Bakus (1973) reviewed biology and ecology of tropical holothuroids. Endean (1973), Potts (1981), and Moran (1986) reviewed the ecology of the asteroid *Acanthaster planci*. The books edited by Boolootian (1966) and by Jangoux & Lawrence (1982) contain a substantial amount of detailed information on coral-reef species, and the physiological, behavioral and ecological processes reviewed for echinoderms in general are mostly applicable to coral-reef echinoderms. Emson & Wilkie (1980) provide an extensive review of fission and autotomy in echinoderms. Glynn (in press) reviewed the effects on coral community structure of grazing and predation by animals of several phyla, including echinoderms. Keys to coral-reef echinoderms are given by A.M. Clark & Rowe (1971) and Guille *et al.* (1986) for identification of Indo-West Pacific coral-reef echinoderms, and by H.L. Clark (1933), Voss (1976) and Kaplan (1982) for Caribbean coral-reef echinoderms.

This review discusses the ecology of coral-reef echinoderms and their influence on variations in the structure and function of coral-reef communities. Particular attention is given to the question of why some species of echinoderms have greater influence on coral-reef communities than do others.

2 CRINOIDEA

2.1 Functional roles

Crinoids are the most conservative of coral-reef echinoderms; they have apparently always fed on plankton and particulate material in the water column as passive suspension-feeders throughout their evolutionary history (Rutman & Fishelson 1969, Meyer 1982). Crinoids have not been separated into groups on the basis of food type. The ecological categorization of coral-reef crinoids is made on the basis of their feeding time and attachment site (Meyer & Macurda 1980, Meyer 1982, Vai 1987). Crinoids are categorized into those that are exposed and feed mainly during the night, hiding under corals or in crevices during the day, and those that can be found at least partially exposed and feeding during the day or night. Within these temporal categories, coral-reef crinoids differ in terms of attachment site and feeding posture. Categories of attachment sites in order of increasing elevation are (1) within small cavities or caves within the reef (Fig. 1E), (2) with the oral disk hidden within a crevice or under a coral head and arms extended out into the water column (Fig. 1F), (3) perched on promontories such as outcrops or coral heads (Fig. 1B, C), and (4) perched on tall sponges or gorgonacean whips or fans (Fig. 1A).

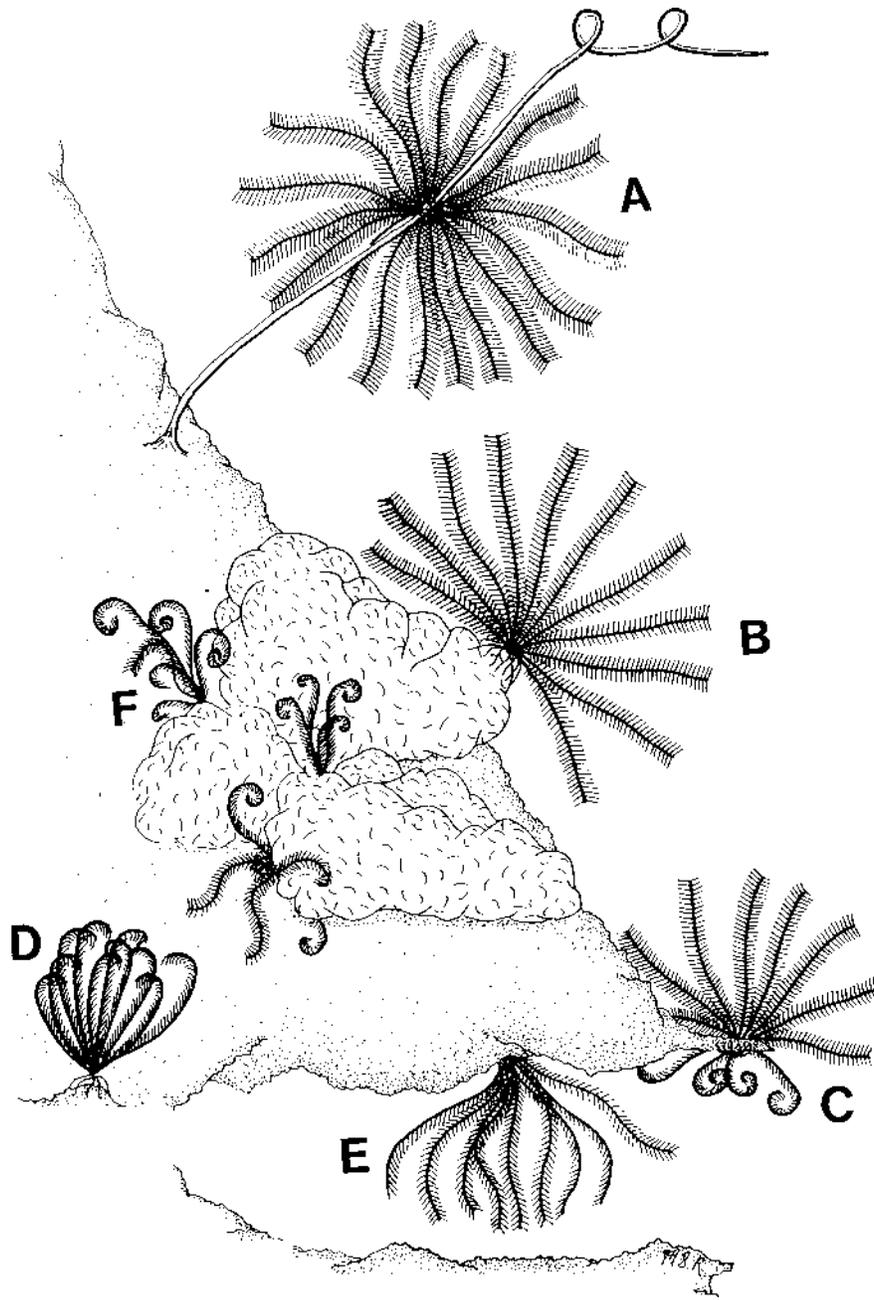


Figure 1. Diagrammatic representation of feeding-position postures of coral-reef crinoids. Adapted from Meyer (1982).

Behavioral categories of feeding posture and morphological categories of tube foot length and spacing are associated with categories of attachment site (Meyer 1973, 1982). The tube feet of cryptic crinoids that live within the reef infrastructure (Fig. 1E) or extend arms out from a crevice (Fig. 1F) are characteristically longer and more widely spaced than are those of crinoids generally found exposed in unidirectional currents (Meyer 1982). Crinoids that are generally found in a filtration fan posture have tube feet that are relatively shorter and more closely spaced.

Meyer (1979, 1982) interpreted the feeding posture, tube foot length and spacing in terms of the aerosol filtration theory of Rubenstein & Koehl (1977). The theory predicts the optimal size range of particles captured for a given mesh size in a given water flow velocity. An optimal set of morphological traits for one set of conditions is suboptimal for others and so niche diversification may be a result of morphological constraints. Nevertheless, the feeding postures and behavior of crinoids can vary with water-flow velocity (Meyer 1973, 1982) and when the hydrodynamic conditions are the same, their actual feeding behaviors may overlap more than might have been expected. Exposed crinoids in slack water or in multidirectional low velocity flow usually assume a meridional posture with tube feet extended (Fig. 1D).

Coral-reef crinoids tend to aggregate, presumably a result of being attracted to sites with features that are optimal for several species. D.L. Meyer (pers. comm. July 1986) has observed over 14 species of crinoids on one pinnacle of a reef near Lizard Island, Great Barrier Reef, on visits since his first in 1975.

2.2 Distribution

As passive suspension-feeders, crinoids are dependent on exogenous water movement to bring them food (Meyer 1982). Local distribution of crinoids largely results from availability of currents, shelter, proper topographic conditions for feeding and avoidance of wave impact and predators (Meyer 1973, 1982, 1985, Meyer & Macurda 1977, Meyer & Ausich 1983). Crinoids are dependent on habitat qualities. They have not been documented as expanding their distribution, diet, or behavioral repertoire in the regions where they are in great abundance to the extent that this has often been observed in some species of echinoids and asteroids. These constraints on distribution and behavior are probably important factors in determining the degree of influence crinoids have on the coral-reef community.

The large-scale distribution of crinoids is probably a result of both larval dispersal and nutrient availability. Coral-reef crinoids are characteristic of 'continental' regions of the Indo-West Pacific and Caribbean. The species richness decreases sharply across the oceanic regions of the Pacific from the west to east (Table 1). The fact that crinoids have the sharpest decline of any

9 Table 1. Numbers of species of shallow-water (< 60 m depth) echinoderms in the tropical Pacific. '0': has never been found in shallow water in the region. '-': a reasonably complete survey of the taxon was not found in the literature for the region. Numbers in parentheses are species endemic to the Panamic Faunal Province.

Region	East Indies	Philippines	New Caledonia	Palau	Guam	Marshall Islands	Hawaii	Society Islands	Line Islands	Eastern Pacific
References*	CR	CR	GLM	MM; M77	Y75; MM; RD; UOG	Y75; Y77; C52; EA	ED	M74	M74	BMSB SR
Crinoidea	91	55	28	21	6	6	0	0	0	0(0)
Asteroidea**	66	55	46	25	24	17	14	10	8	4(21)
Oreasteridae	12	10	7	3	4	2		1	-	0(2)
Ophidiasteridae	26	27	21	14	14	10	8	5	4	2(8)
Ophiuroidea	142	104	48	-	19	42	18		-	-(-)
Echinoidea (Regularia)***	43	33	21	-	13	17	13		-	0(11)
Holothuroidea	141	94	54	-	32	23	28		-	7(20)

*BMSB = Birkeland *et al.* (1975); C52 = A.H. Clark (1952); CR = A.H. Clark & Rowe (1971); EA = Devaney *et al.* 1987; ED = Eldredge & Devaney (unpubl.); GLM = Guille *et al.* (1986); M74 = L.M. Marsh (1974); M77 = L.M. Marsh (1977); MM = Meyer & Macurda (1980); RD = Rowe & Doty (1977); SR = Steinbeck & Ricketts (1941); UOG = University of Guam Marine Laboratory (1981); Y75 = Yamaguchi (1975); Y77 = Yamaguchi (1977b).

**Only coral-reef species are included; not Luidiidae, Astropectinidae, and Archasteridae from sand substrata. *Acanthaster ellisii* and *A. planci* are combined as one species.

****Diadema setosum* and *D. savignyi* are combined as one species.

group of coral-reef echinoderms in species richness from continental to oceanic regions suggests that they generally have a shorter larval life span than is typical of the other echinoderms groups (Table 1).

The shallow-water crinoids in the Caribbean do not demonstrate a similar gradient in species richness (Meyer *et al.* 1978). The Caribbean is interconnected by water currents (Wüst 1964). Nevertheless, crinoids are generally more abundant on continental margins even in the Caribbean (Meyer 1973, Meyer & Macurda 1976). This may be a result of increased productivity from upwelling or because terrestrial runoff is favorable for passive suspension- feeders (Meyer 1973, Meyer & Macurda 1976).

2.3 Mortality

Stalked crinoids disappeared from shallow seas in the late Cretaceous at the time durophagous teleosts were undergoing species radiation (Meyer & Ausich 1983). Most coral-reef echinoderms, even sedentary species, are motile to the extent of being able to withdraw into shelter to avoid strong wave impact or predation. Coral-reef crinoids that periodically feed in exposed positions are either nocturnal, toxic, or have their oral disk protected by a palisade of enlarged, rigid, spike-like proximal pinnules (Meyer 1972, 1973, 1985, Meyer & Macurda 1977).

Meyer & Ausich (1983) reported that seven specimens of the fish *Chrysophrys auratus* each had two to four fresh crinoids in their stomachs. Meyer (1985) reported that crinoids are found in the stomachs of representatives of ten families of fishes. Most predation is partial, which indicates that there is a constant pressure from predation on coral-reef crinoids. The nocturnal feeding behavior of the majority of coral-reef crinoids may result in part from the availability of demersal plankton at night, i.e. the crinoids may feed at night in part for the same reason that corals feed at night on plankton. However, the movement to protected locations during the day indicates a response to predation pressure.

2.4 Effects on coral-reef communities

Crinoids are absent from coral reefs in the eastern Indo-West Pacific region and from the Panamic faunal region (Table 1). There are 91 species in Indonesia, and night time densities averaging 18 individuals m⁻² have been found at Lizard Island, Great Barrier Reef (Vail 1987). No qualitative effect on coral-reef communities has been observed to result from the presence, abundance or absence of crinoids. Where crinoids are in abundance, one might anticipate direct effects on planktonic communities or second-order effects on fish and benthic communities by predation on larvae. Calculations could be made on possible quantitative effects (e.g. volume of water filtered,

amount of plankton and suspended particulate matter consumed, substratum occupied, contribution to community respiration, etc.) and they may be large. But even if quantitative effects are large, they may not have a qualitative or controlling effect on the coral-reef community. The only differences in coral-reef communities that can be clearly attributed to the abundance or absence of crinoids from personal observation and from the literature are the locations of the crinoids themselves. They take up substrata that might otherwise be occupied by other organisms at the specific location. The other organisms may be located a short distance elsewhere, but the character of the community has not changed except for the presence of the crinoids. Their qualitative influence may be mainly as 'ornaments' for the reef community. 'Ornaments' are organisms that are prevalent or conspicuous, and which may or may not process large amounts of materials in the ecosystem, but which do not have a qualitative or controlling effect on the system.

The decrease in numbers of crinoids from west to east across the Pacific involves many variables. It is improbable that interactions can be deduced by calculations of quantitative effects. Controlled field experiments are needed to determine the effects of crinoids. I predict that as passive suspension-feeders, crinoids are constrained by their dependence on favorable habitat characteristics, and by limitations on what they are capable of capturing as food. If a controlled experiment is undertaken, the effects of crinoids on the nature of coral-reef communities might be found to be less than expected considering the amount of space they occupy or the amounts of materials they process.

3 ASTEROIDEA

3.1 Functional roles

In contrast to the wide array of feeding methods used by asteroids of temperate regions (Mauzey *et al.* 1968, Sloan 1980, Jangoux 1982a), asteroids on coral reefs all extrude their stomachs over sessile or encrusting organisms, small motile invertebrates, and probably organic detrital material (Sloan 1980, Jangoux 1982a, Blake 1983). (*Luidia* spp., *Astropecten* spp., and *Archaster* spp. are tropical shallow-water species that often swallow prey whole, but they are found on sandy substrata, sometimes near reefs, but not on coral reefs). Thorough compilations of the published information on the diets of asteroids can be found in Sloan (1980) and Jangoux (1982a).

The feeding biology of coral-reef asteroids differs more often as a matter of size rather than species. Feeding is generally similar among species with the same size of stomachs, with differences in diet developing as sizes change with growth of the individual. Juveniles of most coral-reef asteroids have a

feeding biology similar to the ophidiasterids (Sloan 1980, Jangoux 1982a). Ophidiasterids (e.g. *Linckia*, *Ophidiaster*, *Leiaster*, and other genera are represented by Figure 2A; *Fromia*, *Nardoa*, *Neoferdina*, *Tamaria*, and other genera are represented by Figure 2C) are small, diverse, and ubiquitous members of the coral-reef community. At least 70 species occur in shallow waters of the Indo-West Pacific (A.M. Clark & Rowe 1971, Marsh 1974). They extrude their tiny stomachs over the substratum and browse the epibenthic film of organic detritus and microorganisms (Yamaguchi 1975, 1977a, Thomassin 1976, Sloan 1980, Jangoux 1982a). The substratum on which feeding takes place is often crustose coralline algae (Laxton 1974a) and a white spot can be seen occasionally in the coralline algae underneath the extruded stomach. Small encrusting sponges, bryozoans, and ascidians are sometimes browsed by the larger ophidiasterids (Yamaguchi 1975, various authors in Jangoux 1982a and Sloan 1980). Laxton (1974a) found 1 % of the *Linckia laevigata* feeding on small coral colonies on the Great Barrier Reef and Thomassin (1976) found *Nardoa variolata* consuming coral mucus at Madagascar.

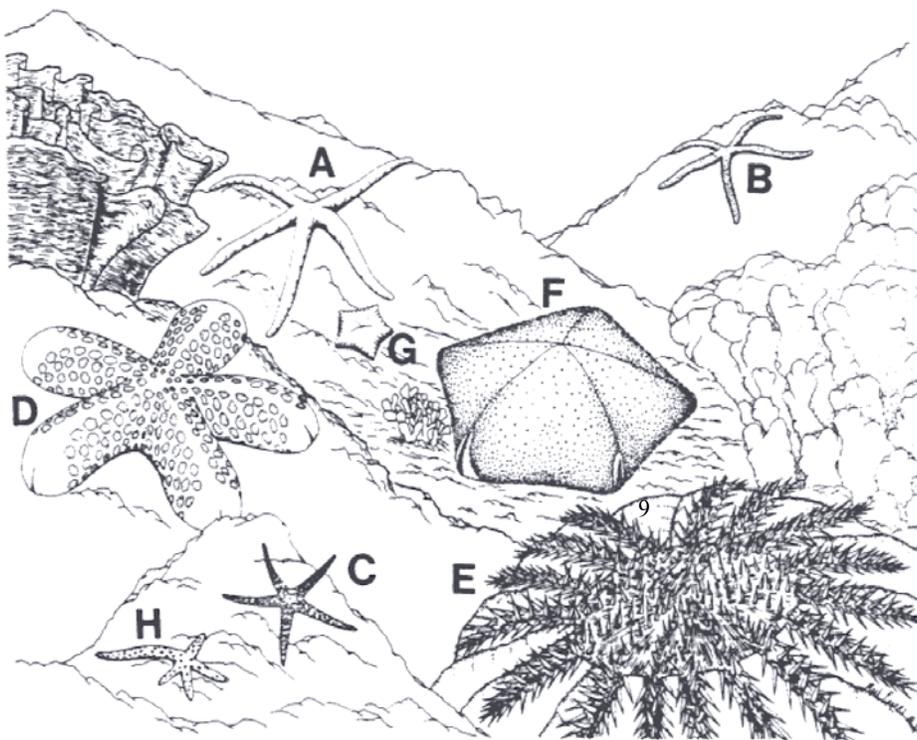


Figure 2. Diagrammatic representation of categories of coral-reef asteroids.

Echinasterids (Fig. 2B), asterinids, and juvenile *Culcita novaeguineae* (Fig. 20) also extrude their stomachs onto the substratum, apparently digesting the epibenthic film of organic detritus and microorganisms. As they grow, these asteroids take advantage of more opportunities to feed upon macroscopic prey, e.g. ascidians, bryozoans, and especially sponges.

Most oreasterids (Fig. 2D, F) can grow to considerably larger sizes than ophiasterids. With growth they become able to feed on larger colonies of animals such as colonial tube worms (*Salmacina* sp., cf. Olynn & Wellington 1983), ascidians, and especially sponges. Nevertheless, they can still extrude their stomachs over the substratum and apparently even large individuals often feed on microorganisms and organic detrital material.

At least nine species of asteroids occasionally prey upon living corals or feed on coral mucus in the Pacific (or at least ten if *Acanthaster ellisii* is separated from *A. planci*): *Culcita novaeguineae* (Endean 1971, 1976, Goreau *et al.* 1972, Glynn & Krupp 1986), *C. schmideliana* (Thomassin 1976), *Nidorellia armata* (Chesher 1972, Glynn & Wellington 1983), *Pharia pyramidata* (Dana & Wolfson 1970, Glynn & Wellington 1983), *Linckia laevigata* (Laxton 1974a, Thomassin 1976), *Nardoa variolata* and *Echinaster purpureus* (Thomassin 1976), *Asterina* sp. (Yamaguchi 1975), and *Acanthaster planci* (Goreau 1964, Pearson & Endean 1969, Branham *et al.* 1971, Goreau *et al.* 1972, Endean 1973, Branham 1973, Potts 1981, Moran 1986). Only *A. planci* and *Culcita* spp. are influential asteroid predators of Pacific corals. No asteroids are influential predators of corals in the Caribbean.

Acanthaster planci eats mainly hermatypic scleractinian corals and shows a marked preference for acroporids (*Acropora* and *Montipora*; Branham *et al.* 1971, Goreau *et al.* 1972), especially the tabular and branching forms of *Acropora* (Chesher 1969, Laxton 1974b, Nishihira & Yamazato 1974). Pocilloporids are eaten by *A. planci* when the colonies are not defended by crustacean symbionts (Glynn 1976, 1982b). Fungiids, poritids, faviids, and milleporids are not eaten frequently unless the preferred food species are scarce in the area. *Diploastrea heliopora* and *Coscinaraea* spp. are strongly avoided, but will be eaten when other corals are very scarce. *Turbinaria* spp. and *Tubastrea micrantha* may never be eaten.

Acanthaster planci has a very pliable and prehensile morphology. It is able to climb out to the tips of branching *Acropora* spp. (Plate 1). It has a large stomach which it can extrude over an area equivalent to that of its oral disk (Goreau 1964).

Although *Acanthaster planci* is a specialist in the sense that it has a definite preference for acroporids, it is a generalist in that it accepts a variety of foods depending upon availability and circumstances. When acroporids are scarce (and even if acroporids are common), *A. planci* can feed on other corals. When scleractinian corals are scarce, *A. planci* can feed on milleporids, alcyonaceans, actinians, and perhaps even sponges and molluscs (Potts

1981), although these less preferred foods may not have as much nutritional value for *A. planci*.

Even when corals are common, the feeding preferences of *Acanthaster planci* can be modified and the species of coral preyed upon can be influenced by a variety of factors other than feeding preference (Sloan 1980, Moran 1986). Moran (1986) listed factors which influence the prey taken by *Acanthaster planci*:

1. Nutritional state of the predator (Brauer *et al.* 1970), i.e. predators become less selective as they get hungrier (Ivlev 1961).
2. Release of chemical substances by damaged corals which attract *A. planci* to corals already being eaten (Brauer *et al.* 1970, Ormond *et al.* 1973, Collins 1974, Beach *et al.* 1975, Hanscomb *et al.* 1976).
3. Previous dietary experience (Collins 1975, Huxley 1976, Ormond *et al.* 1976).
4. Relative abundance and distribution of corals (Ormond *et al.* 1973).
5. Accessibility of corals (Barnes *et al.* 1970).
6. Morphology of corals (Chesher 1969, Ormond & Campbell 1974, Menge 1982).
7. Environmental conditions such as wave action (Endean 1973, Ormond *et al.* 1973) and topography of the habitat.
8. Release of defensive materials (e.g. nematocysts, mesenteric filaments) by corals (Barnes *et al.* 1970, Goreau *et al.* 1972).
9. The presence of crustaceans that are defensive symbionts of the coral (Glynn 1976, 1977, 1980, 1982b).
10. Relative nutritional value of the coral (Ormond *et al.* 1976).
11. Size and age of the asteroid.

Acanthaster planci has many options for choice and its diet may depend as much on food availability and other circumstances as on preference.

As typical of oreasterids, *Culcita novaeguineae* feeds on a broad range of encrusting prey such as algae, corals, bryozoans, and especially sponges. Within the corals, however, *C. novaeguineae* is relatively specialized in comparison with *A. planci*. *C. novaeguineae* has a rigid massive integument which does not allow it to climb out onto branches of *Acropora* spp. and it is less able to adhere to large hemispherical mounds like massive *Porites* spp. (Goreau *et al.* 1972). The ratio of the diameter of the extruded stomach during feeding to the total diameter of the *C. novaeguineae* is 0.41. The *C. novaeguineae* has a much larger biomass to support in relation to stomach surface, the size of the food-intake structure (a 'brontosaurus handicap', Fig. 3), because it has a massive hemispherical form (Fig. 2F) rather than a flaccid plate form like *A. planci* (Fig. 2E).

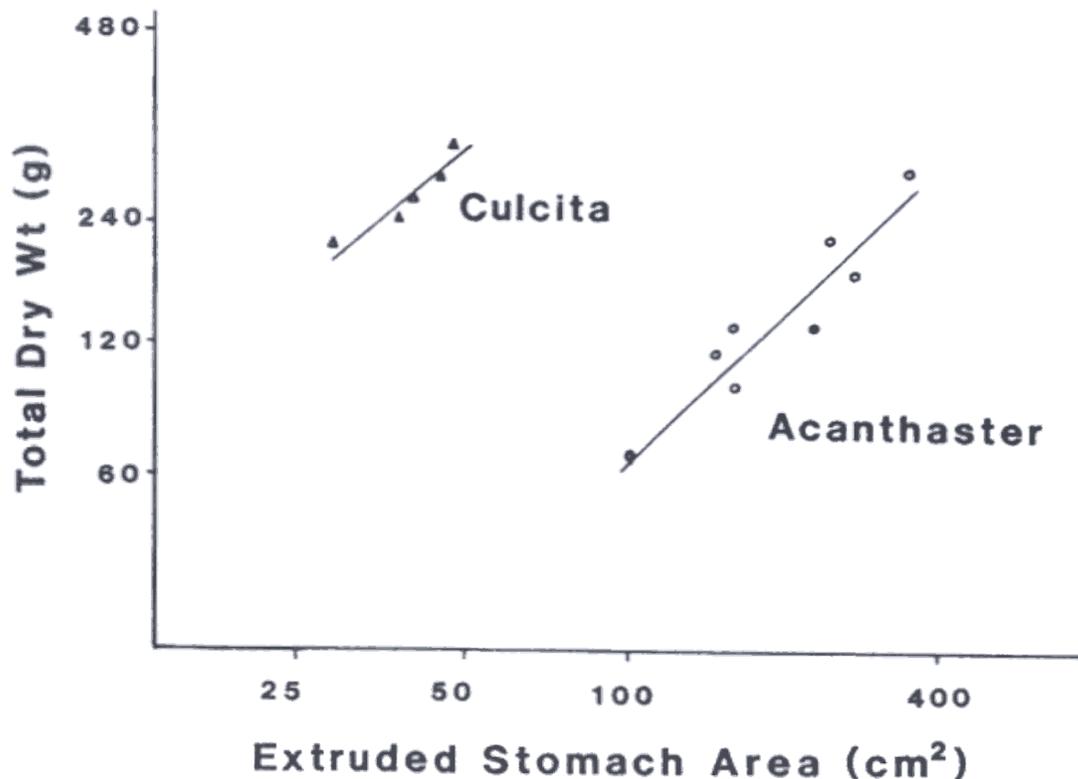


Figure 3. Relationship between total dry weight biomass and extruded stomach diameter of *Acanthaster planci* and *Culcita novaeguineae*.

The basic morphological characteristics of the families Acanthasteridae and Oreasteridae force *Acanthaster planci* and *Culcita novaeguineae* into different functional roles in the coral-reef community. *A. planci* is a generalized predator of hermatypic corals, with a preference for branching and tabular *Acropora* spp., but with the option of consuming corals from a wide variety of taxa and colony morphologies as circumstances require. *C. novaeguineae* will feed on sponges and other encrusting animals, as typical of oreasterids, but it shows a preference for small or encrusting scleractinians, especially pocilloporids and acroporids (Goreau *et al.* 1972, Glynn & Krupp 1986). *A. planci* is able to kill large or small coral colonies entirely. *C. novaeguineae* usually kills small corals (3 to 8 cm diameter) entirely, but only partially eats larger colonies (Glynn & Krupp 1986).

The extruded stomach of a two-year old *A. planci* would cover an area of about 160 cm²; the extruded stomach of a two-year old *C. novaeguineae* would cover about 64 cm². This allows *A. planci* to function more efficiently on coral reefs, at least as predators of corals, than do other large asteroides such as oreasterids. A typical *A. planci* probably consumes about 5 to 6 m² living coral per year (Pearson & Endean 1969, Dana & Wolfson 1970) while *C. novaeguineae* consumes about 0.9 to 1.0 m² per year (Glynn & Krupp 1986).

3.2 Distribution

The large-scale distributions of typical asteroids are affected by water -current patterns. The Caribbean is interconnected by water currents (Wust 1964) and the Caribbean asteroid fauna is relatively uniformly distributed; but there is a decrease in species-richness in asteroids from west to east across the Pacific (Table 1). Yamaguchi (1977b) pointed out that the larvae of ‘continental’ species of asteroids showed positive geotaxis and oceanic species showed negative geotaxis. The larvae of ‘continental’ species swam consistently close to the bottom in culture beakers when not disturbed and so only those near continental reefs may survive in nature. The larvae of more widely distributed species remained geonegative in culture beakers up to the stage near metamorphosis (Yamaguchi 1977b), and so they may have a better chance of being transported to oceanic islands in nature.

The location and timing of major events of asteroid-influence on coral reefs is related in several ways to current patterns. Primary outbreaks may be influenced by the cohesive transport of chemical nutrients, particulate organic matter, bacteria, or phytoplankton, and secondary outbreaks may be influenced by the cohesive transport of larvae. Primary outbreaks of *Acanthaster planci* on the Great Barrier Reef (GBR) may have occurred at Green Island because of the transport of nutrients from the Burdekin River 400 km to the south. Secondary outbreaks may have spread south from Green Island in subsequent years by transport of larvae (Kenchington 1977, Potts 1981, A.H. Williams *et al.* 1984, Moran 1986). Yamaguchi (1987) described pseudopopulations of *A. planci* in Japan and suggested that they were probably established by transport of larvae and maintained with abnormally warm water temperatures through fluctuations of the path of the Kuroshio Current.

3.3 Recruitment

The small coral-reef asteroid *Linckia multifora* is generally one of the more common asteroid species on Pacific reefs, yet it never undergoes population outbreaks like *Acanthaster planci* with which the population can quickly increase by as much as six orders of magnitude. It may be that autotomy is a more dependable method of recruitment (Rideout 1978), but spawning eggs that develop into planktotrophic larvae provides possibilities for an occasional tremendously successful recruitment. Fission and autotomy appear to be more prevalent among asteroids with small body sizes (Emson & Wilkie 1980). The number of eggs spawned increases with body size of asteroids (Conand 1985, Kettle & Lucas 1987).

Outbreaks of *Acanthaster planci* occur mainly on high islands and continental margins, but rarely on atolls (Birkeland 1982). The timings of the

outbreaks appear to be correlated with extra high levels of nutrient runoff which probably cause phytoplankton blooms. High concentrations of particulate organic material, microorganisms (e.g. bacteria) or phytoplankton may be necessary for a good rate of development and, indirectly, enhanced survival for *A. planci* larvae (Lucas 1982). Knowledge of current patterns along with location and timing of pulses of nutrient may be of predictive value for outbreaks of *A. planci*.

Olson (1987), to the contrary, found that *A. planci* larvae can successfully complete development through metamorphosis in plexiglass chambers in the natural environment (no phytoplankton bloom) of offshore coral reefs nearly as rapidly as with an enriched diet. Olson concluded that food resources for larvae are of little importance in explaining variation in larval recruitment of *A. planci*.

A large set of juvenile asteroids does not, however, necessarily result in a large adult population (Hancock 1958, Loosanoff 1964, Ebert 1983). Much mortality occurs during the long and vulnerable juvenile stage of asteroid life histories. Once having undergone metamorphosis, the first few meals of an asteroid are critical to its success (Birkeland 1974, Sloan 1980). Nauen (1978) found that asteroids may not grow for several months until a quality meal becomes available, at which time they begin to grow. The individual asteroid in "a cohort that obtains the first good meal may be several times larger than individuals that obtain later meals (Mead 1900), and its chances of survival far greater.

Acanthaster planci has traits which set it apart from the other coral-reef asteroids and which may give it an exceptional ability to break through the juvenile or 'ophidiasterid stage' in their life cycle. First, *A. planci* does not have the thick and rigid test that characterizes other coral-reef asteroids (Blake 1979, 1983). *A. planci* is rather elastic and pliable which allows it to crawl outland wrap itself around the pointed tips of branching corals (Fig. 3). It may be this plasticity of body form which gives the juvenile *A. planci* its early ability to attack coral polyps and to undertake adult feeding patterns early in life. *A. planci* is also rather flattened in a plate-like morphology with a large central disk and from 7 to 23 arms, usually 14 to 18. It has a large mouth aperture and it extrudes its stomach over a relatively large surface area. These morphological characteristics produce an asteroid that has a relatively large potential for food input per unit biomass (Fig. 3) which facilitates relatively rapid growth. *A. planci* as small as 8 to 10 mm diameter can transform from the juvenile to the adult feeding biology in about a one-month transition period beginning about four and a half to seven months after metamorphosis (Yamaguchi 1973a, 1974, Lucas & Jones 1976) and begin feeding on coral polyps. Once *A. planci* completes its transition to a corallivorous predator, its growth rate increases significantly (Lucas 1984) which facilitates its escape through the mortality risks of juvenile coral-reef asteroids. Within two years,

A. planci can grow to a total diameter of about 20 cm (Lucas 1984) or about 25 cm (Yamaguchi 1974). The extruded stomach area to biomass ratio may also contribute to the great fecundity of *A. planci*. Large *A. planci* can produce tens of millions of eggs each year (Conand 1985, Kettle & Lucas 1987).

Culcita novaeguineae transforms from a pentagonal flat juvenile to a cushion-form adult at about 9 cm diameter or an order of magnitude larger (Yamaguchi 1973b), and two years of age or about four times longer (Yamaguchi 1977c), than does *Acanthaster planci*. *Culcita novaeguineae* undergoes great morphological changes from juvenile to adult, but it nevertheless has a rather thick and rigid integument at both stages. *Linckia laevigata* may transform into an adult at about 5 cm in arm radius (Yamaguchi 1973b), also at about two years of age (Yamaguchi 1977a).

3.4 Origin of acanthasterids

Solasterids are asteroid with particularly strong influences on the subtidal marine communities in the northeastern coast of the temperate Pacific (Birkeland 1974, Birkeland *et al.* 1982). Acanthasterids are the only coral-reef asteroids with the effective predatory characteristics of solasterids: a pliable and prehensile body and arms, over a dozen arms, large size (often 30 cm total diameter), and a large mouth and extrusible stomach. Although the monogeneric family Acanthasteridae is considered closely associated with the Oreasteridae taxonomically (Blake 1979), the exceptional influence of *A. planci* on the coral-reef community is a result of its convergence with the Solasteridae in behavior, feeding morphology (Jangoux 1982b), and early transition to adult feeding patterns (Sloan 1980). The solasterid characteristic that may be the most important is the relatively rapid switch from the juvenile feeding pattern to adult (Sloan 1980). Other species of coral-reef asteroids retain the ophidiasterid-style feeding biology for a greater portion of their lives. With equal success in recruitment, a lower proportion of other coral-reef asteroids would successfully complete the juvenile stage because of the longer periods of time spent at greater risk because of small body size.

Solasterids are widely distributed in the Pacific from the shallow subtidal to several hundred meters depth (Fisher 1911, 1919), tending to the deeper portion of the range in the tropics. *Crossaster* spp., often cited as *Solaster* spp. (cf. Fisher 1919), resemble *Acanthaster brevispinus*. *Crossaster papposus*, for example, feeds on molluscs, including scallops (Mauzey *et al.* 1968, Birkeland 1974), assuming an arched posture when preying upon molluscs as does *A. brevispinus* (Lucas & Jones 1976). In Puget Sound, half the diet of *C. papposus* consists of pennatulid octocorals and actinians, showing a willingness to accept anthozoans. Other species of *Crossaster* occur in the Philippines and Indonesia, within the range of *A. brevispinus* (Fisher 1919). An asteroid such as *Crossaster* with a dozen or so prehensile

arms, a pliable body, a large central disk, a large extrusible stomach, and a propensity for feeding on anthozoans would seem preadapted to invade coral reefs for the abundant supply of large branching and massive anthozoan prey inaccessible to resident asteroids.

Acanthaster brevispinus has such behavioral and morphological similarities to the solasterids that it seems reasonable to suggest that *A. planci* arose in this manner. Lucas & Jones (1976) and Lucas et al. (1985) provide evidence that *A. planci* separated from *A. brevispinus* and invaded coral reefs fairly recently, since the closing of the Isthmus of Panama. However, a more detailed and thorough analysis of skeletal morphology of *A. planci* has led Blake (1979) to remove Acanthasteridae from the order Spinulosida (containing Solasteridae) and place it in the order Valvatida (near Oreasteridae). Blake (1979) proposed that the morphology of *Acanthaster* evolved as a direct in situ adaptation for exploitation of irregular coral surfaces rather than being a preadaptation inherited from a solasterid/*A. brevispinus*-type ancestor.

3.5 Mortality

The pliable, less rigid, morphology of *Acanthaster planci* probably makes it more vulnerable to predation by fishes than are other large asteroids on coral reefs (Blake 1983). *A. planci* is preyed upon by a variety of animals (Endean 1973, Moran 1986), although it is not necessarily the favored prey of any. It is plausible that predators are able to control populations of *A. planci* in certain regions (Glynn 1982a, b, 1984). Although adult *Culcita novaeguineae* may not be taken by fishes as frequently as are *A. planci*, *Charonia tritonis* shows no clear preference between the two species of large asteroids with the information available to date. One *C. tritonis* was kept supplied with four each of *A. planci*, *C. novaeguineae* and *Linckia laevigata* in a seawater tank at Guam. Over a six-month period, the triton consumed nine *A. planci*, eight *C. novaeguineae* and one *Linckia laevigata*, so adult oreasterids are not immune from predation. *Linckia* has a relatively high ratio of integument to gut and gonad, and may be of relatively little food value to predators. *A. planci* appeared able to move away more rapidly from the *C. tritonis* in the tank. A lack of a rigid calcareous integument for protection may be compensated in part by a greater motility, but this would not be effective for escape from fishes.

3.6 Effects on coral-reef communities

Acanthaster planci is the only coral-reef asteroid known to cause major second-order and third-order effects on coral-reef communities. The first-order effect of predation on corals is reduction in abundance and surface

cover of living corals. Pearson (1981) concluded that coral mortality from *A. planci* outbreaks was more extensive and severe than mortality from any other natural or man-made causes. A primary outbreak which began on the west coast of Okinawa in 1969, spread through the Ryukyus by a series of outbreaks and north to southern Shikoku and to Miyake Jima (140 km south of Tokyo), a range of over 1600 km. Yamaguchi (1986: 24) stated that 'it is safe to assume that most reefs in the Ryukyus have been devastated in the past 15 years'. A primary outbreak on the Great Barrier Reef (GBR) that apparently occurred at Green Island before 1962 spread by a series of subsequent outbreaks in a southerly direction to the Swain Reefs over the next ten years, a distance of nearly 1000 km. The outbreaks on the GBR were more patchily distributed than those in the Ryukyus. An outbreak on Guam in 1968 spread north along the northwestern coast and killed corals in a band 38 km long (Chesher 1969). Outbreaks also occurred in 1969-1972 at 21 of the 45 islands surveyed in Micronesia (Marsh & Tsuda 1973).

Acanthaster planci in large numbers can kill over 90% of the living corals over extensive areas, for example, over the 38 km band on northwestern Guam (Chesher 1969, Endean 1982). Percentage of coral mortality is variable. R.H. Randall (1973) found over 99% mortality of corals in deeper water (> 5 m), over 95% mortality on the reef front, and about 57% in shallow water. This is a typical pattern because *A. planci* on reefs exposed to high-energy wave action avoids shallow water and feeds most extensively in deeper water (Endean & Stablum 1973a, Colgan 1982). *A. planci* tends to aggregate while feeding and so intensity of feeding can be patchy. Preferred species such as acroporids are killed more extensively than are unpreferred species such as poritids, *Diploastrea heliopora*, and milleporids. Smaller coral colonies are fed on more intensively than are massive corals (Done 1985). However, the patchiness in coral predation that results from aggregation, feeding preference, and colony size varies with the population density. As *A. planci* becomes more densely distributed, the coral predation becomes more uniformly distributed in space, among prey species and across prey colony size categories.

In addition to abundance and surface cover of living corals, predation by *Acanthaster planci* also affects coral community structure: species composition, species diversity, and colony size distribution. These effects have been reviewed in detail by Goreau *et al.* (1972), Sloan (1980), Potts (1981), and Moran (1986). At moderate densities, predation is more intense on preferred prey species and on branching or tabular colonies which causes the shifts in community structure. At higher densities, predation is more uniformly distributed across potential prey species and colony sizes.

Four of the second-order effects of predation on corals by *Acanthaster planci* are:

1. an increase in surface cover by algae,

2. occasionally an increase in surface cover by other encrusting animals such as soft corals and the sponge *Terpios* sp.,
3. a decrease in topographic complexity of the reef community (in certain situations), and
4. a decrease in abundance of corallivores.

The increase in algal cover always results as the dead coral skeletons become covered by filamentous algae within a couple of weeks (Pearson & Endean 1969, Endean & Stablum 1973b, Belk & Belk 1975, Biggs & Emlinon 1977). Grazing by herbivorous fishes facilitates succession and the upright algae eventually decrease in abundance and crustose coralline algae increase. The timing and pattern of algal succession varies greatly between seasons and locations.

In a few instances, the decrease in scleractinian coral cover may be followed by an increase in cover by soft corals (Pearson & Endean 1969, Robinson 1971, Endean & Stablum 1973a, Nishihira & Yamazato 1974, Endean 1974, 1976) or *Terpios* sp. (Bryan 1973, Plucer-Rosario 1987). Whereas algae always cover dead coral surfaces quickly and then go through an algal succession, alcyonaceans and sponges only occasionally show a significant increase in surface cover. This increase takes place relatively slowly and, if alcyonaceans and *Terpios* sp. do cover the coral, they may occupy it for a long time. Whereas most colonizing algae generally are replaced in succession (facilitated by herbivorous fishes) and need disturbance to regain space, some algae such as *Turbinaria* sp. and *Sargassum* spp. and some sessile animals such as soft corals and sponges might be considered alternative stable states to a scleractinian coral community (Nishihira & Yamazato 1974). However, it has not been demonstrated that alcyonaceans can prevent scleractinians from reestablishing their populations (Garrett 1975).

Reefs on which branching *Acropora* spp. are prevalent will often collapse into rubble after the corals are killed by *Acanthaster planci* (Sano *et al.* 1987). This decrease in topographic complexity is not necessarily related to high-energy environments; the extensive *Acropora* spp. community along Ngell Channel in Palau was reduced to rubble although it was inside the barrier reef (pers. obs.). Hutchings (1986) suggested that the rates of bioerosion may increase following extensive coral mortality.

After devastation of a coral community by *Acanthaster planci*, the chaetodontid species that feed on coral or coral mucus become scarce (Sano *et al.* 1984, 1987, D; Williams 1986, Wass 1987). When the food supply is diminished, the effect on the fish community is soon evident.

One of the third-order effects on the coral-reef community by *Acanthaster planci* is the increase in carrying capacity of the reef for herbivorous reef fishes. As a result of *A. planci* predation on corals, algae colonize the newly opened substrata, and the herbivorous fish population may increase over a

period of years. This sequence occurred at American Samoa over a seven-year period following a major devastation of cover cover by *A. planci* (Table 2). During the seven years, the herbivorous fish population (counting only adults) increased from about 9% of the total fish population to about 44%. (The juvenile herbivorous fishes, but not juveniles of other fishes, were excluded from the calculations because the recruitment of herbivorous fishes, especially of *Ctenochaetus striatus*, was so large in 1985 that the counts of juvenile *Ctenochaetus striatus* would overwhelm the data for other categories of fishes.) The reduction in corallivorous fishes happened soon after diminution of their food supply, the coral population. The increase in herbivorous fishes, however, may have taken several years following the increase in algal cover. The success of larval recruitment apparently was not directly related to food supply for adults. D. Williams (1986) and Sano *et al.* (1987) did not observe the third-order effect of increases in herbivorous fish populations on the GBR and in the Ryukyus. This may be a result of reporting relatively short-term changes; a year of strong recruitment had not yet occurred.

It is heuristic to note that *Acanthaster planci* appears to be one of the causal agents for an increase in carrying capacity of the reef for schooling herbivorous fishes, but is probably not causal for the recruitment of schooling herbivorous fishes. The carrying capacity increased in American Samoa in late 1978 and strong recruitment occurred some time after 1979. A strong recruitment of herbivorous reef fishes occurred at all study sites in 1985, but adults had previously increased greatly only in areas affected by *A. planci* (Table 2). Whether or not third-order effects materialize may be contingent upon otherwise unrelated factors such as survival of larval fishes. Many higher-order effects of coral-reef echinoderms may be latent, depending on extrinsic events for them to become manifest.

The influence of *Acanthaster planci* provides insight into the controversy concerning the factors structuring coral-reef fish communities. Resource-limitation (Smith & Tyler 1972, Anderson *et al.* 1981) and recruitment-limitation (Sale & Dybdahl 1975, Doherty 1983) of fish populations actually may not be alternative factors in population regulation, but instead are probably two separate processes that act concurrently.

Other coral-reef asteroids which feed on corals, such as *Culcita novaeguineae*, may influence community structure by selectively feeding on small or encrusting colonies of certain species (Glynn & Krupp 1986). They could intercept coral recruitment. However, the other species of asteroids will never be as influential as *Acanthaster planci* during peak abundances. First, other asteroids will never reach such outbreak abundances (although they may be more common ordinarily) because morphological constraints lengthen the time spent in the relatively vulnerable juvenile stage (see Section 3.3). Second, other coral-reef asteroids have morphological constraints which

Table 2. Fish populations observed over 100 m² transects before and after predation of the coral community by *Acanthaster planci* in 1978. Values are numbers of individuals per 100 m². Original data in Wass 1987.

	Fagatele Bay (<i>Acanthaster planci</i> predation of the coral community in 1978)			Sita Bay (no major damage to the coral community by <i>A. planci</i> in recent years)			
	Before predation by <i>Acanthaster</i> 1978	After predation by <i>Acanthaster</i> 1985	% change	1978	1985	% change	
Corallivores	29	0	-100	28	17	-39	
Corallivore/herbivore	116	2	-98	81	70	-14	
Herbivore including recruits	36	372	+933	120	396	+230	
Adults only	26	92	+254	71	75	+6	
	Cape Larsen			<i>Acanthaster</i> outbreak		% change be- tween 1977 and 1985	
Sequence of dates	10.vi.77	14.vi.77	26.viii.77	1978	4.i.79	9.iv.85	
Corallivores	10	7	14		9	2	-86
Corallivore/herbivores	111	112	140		61	12	-91
Herbivores including recruits	73	83	101		92	460	+355
Adults only	36	36	56		65	134	+139
Adult herbivore							
% of entire fish fauna	9	9	12		20	44	

prevent them from feeding on large, finely-branched or massive colonies (see Section 3.1). No matter how abundant any of the other species become, most large coral colonies would be safe from total predation.

4 OPIUROIDEA

4.1 *Functional roles*

Warner (1982) divided ophiuroids into microphagous and predatory groups. Both groups are capable of feeding on material in the water column and on the substratum. The ophiocomids, amphiurids, ophiactids, and ophiotrichids (or ‘spiney-armed’ groups, Fig. 4A, B, C, D) have long arm-spines and long tube feet. They are generally microphagous and both deposit-feed (Fig. 4A) and suspension-feed (Fig. 4B). Suspension-feeding utilizes mucus in mucus- spine feeding, mucus-net feeding, and tube-foot filters. The ophiidermatids, ophiomyxids, and ophiolepids (Fig. 4F, G, H) have short arm-spines, short tube feet, and are more flexible and able to curl their arms. They are often predators and seize prey by arm-loop, whether on the substratum (Fig. 4F) or in the water column (Fig. 4G, H). They also deposit-feed by passing discrete food particles to their mouths by tube feet, sometimes taking larger particles and acting as carrion-feeders. Despite these characteristics of the two groupings, nearly all species employ more than one mechanism for capturing food and eat more than one kind of food. There is much dietary overlap between groups. Chartock (1983) did not distinguish among ophiocomids at Enewetak on the basis of diet; some were ecologically separated by microhabitat.

4.2 *Distribution*

The local distribution of ophiuroids is largely determined by crevice dimensions available (Chartock 1983, Sides 1985, Sides & Woodley 1985, Hendler & Littman 1986). On the geographic scale, ophiuroids decrease in species richness from west to east across the Pacific (Table 1).

4.3 *Mortality*

The cryptic and nocturnal behavior, and the importance of crevices of appropriate size, indicate the incessant pressure from predation on the life of coral-reef ophiuroids. A large percentage of regenerated arms indicate partial predation and that the pressure is incessant (Hendler & Miller 1984). Hendler (1984a) presents color-change and phototaxis in ophiuroids as adaptations to predation pressure. J.E. Randall (1967) listed 33 species of coral-reef fishes in the Caribbean that preyed upon ophiuroids, but ophiuroids made up over 10% of the diet in only 10 of the species.

4.4 Effects on coral-reef communities

Ophiuroids are prevalent on coral reefs throughout the world. As an indication of the magnitude of their predominance, Chartock (1983) found at Enewetak *Ophiocoma erinaceus* in densities between 150 and 15,000 per m² reef surface in the subtidal *Helionora coerulea* (blue coral) zone, and

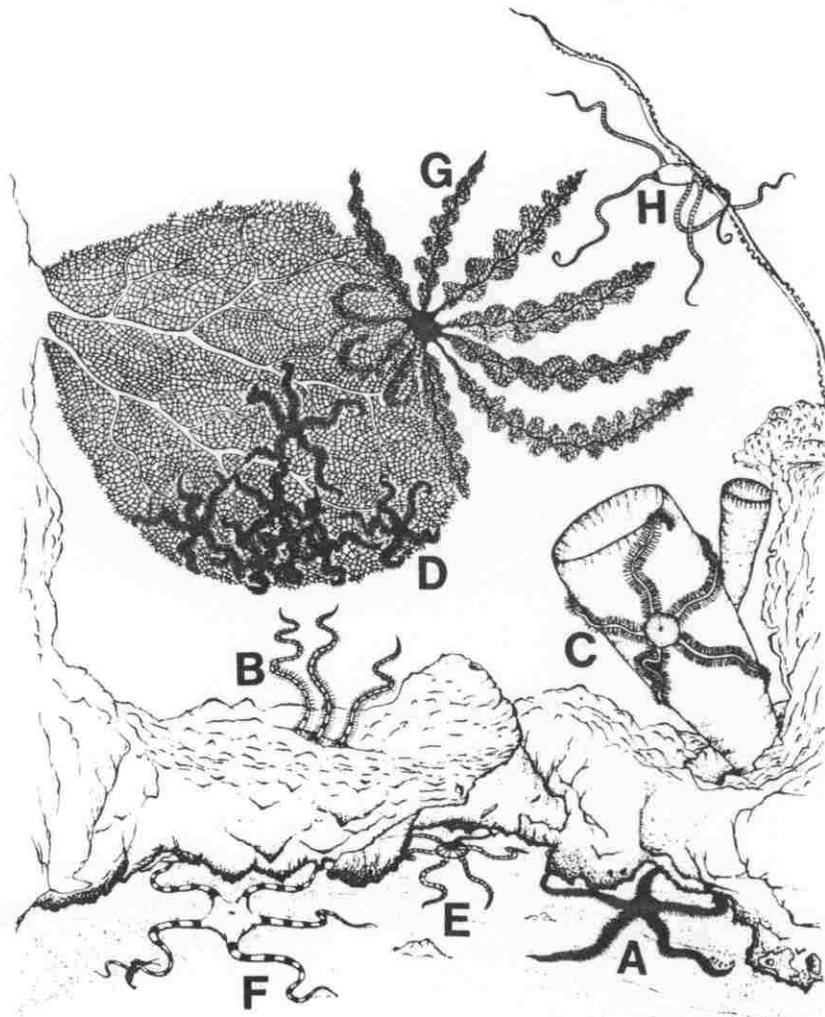


Figure 4. Diagrammatic representation of categories of feeding methods and feeding positions of coral-reef ophiuroids.

Ophiocoma anaglyptica in densities of 150 per m² (moist weight 240 g m⁻²) under reef conglomerate and coral slabs in the algal ridge. *Ophiocoma scolopendrina* was responsible for over 20% of the respiration of the crevice community among the intertidal beach rock (Chartock 1972).

In view of the abundance, biomass, and energy flow through the ophiuroid populations on coral reefs, one would assume they are influential in the coral-reef community. This has not been documented. Fricke (1966) calculated that an average individual basketstar (*Astroboa nuda*) would filter 86 m³ of water during an eight-hour period, but it is not known whether this significantly reduces larval survival of any other populations. Hendler (1984b) documented the cleaning of the inhalent surface of sponges by the feeding of ophiuroids, but he acknowledged that sponges were surviving without ophiuroids and the degree to which feeding efficiency and growth of the sponge benefit from the feeding activities of ophiuroids has not been determined. Sides (1985) demonstrated that some ophiuroids can alter crevice dimensions under coral slabs by shifting sand to the degree that the distribution of other species is altered; but this may only result in a redistribution of animals rather than a qualitative change in the community. Many fishes prey upon ophiuroids, but there is no evidence that any of the fish populations would show a measurable effect if ophiuroids were absent. Ophiuroids may prey upon recruits of other coral-reef animals and prevent or reduce the establishment of other species, but I have found no evidence for this in the literature: The influence of ophiuroids on coral-reef communities has yet to be tested.

5 ECHINOIDEA

5.1 Functional roles

Regular echinoids on, or immediately adjacent to, coral reefs may be categorized into seven morphological life-forms, each with characteristic habits: long-spined, large, motile diadematids (Fig. 5A); long-spined, small, sedentary, hole-dwelling *Echinostrephus* spp. (Fig. 5C); short-spined, large, motile toxopneustids, temnopleurids and others which usually attach debris to their upper surface (Fig. 5B); short-spined, small, generally sedentary *Echinometra* spp. which often dwell in holes or grooves in the reef (Fig. 5D); omnivorous cidarids with bare, rough, blunt primary spines (Fig. 5E); herbivorous *Heterocentrotus* spp. with smooth blunt primary spines (Fig. 5F); and the limpet-like *Colobocentrotus* (Fig. 5G).

Regular echinoids have the broadest diets of any of the groups of echinoderms on coral reefs. Echinoids are opportunistic, promiscuous, generalized

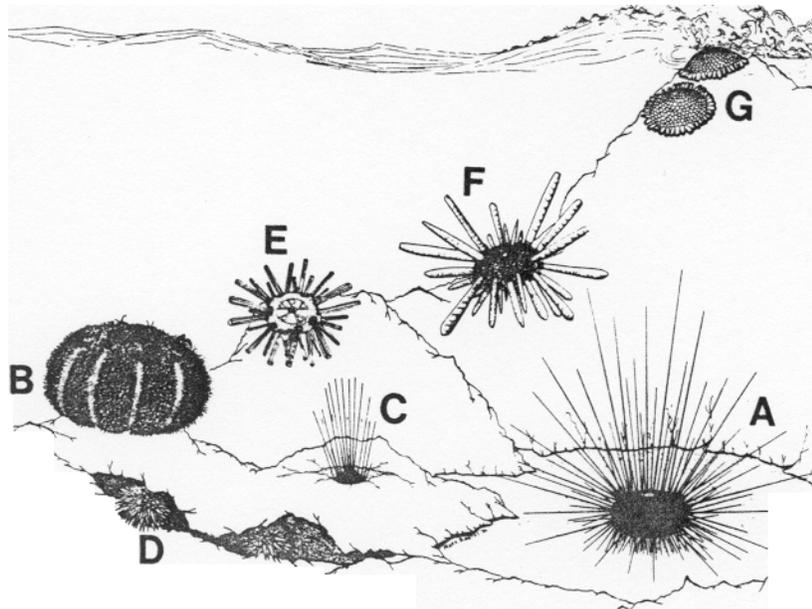


Figure 5. Diagrammatic representation of categories of coral-reef echinoids.

feeders, whose diets are typically determined to a large degree by what is available at the time and place at which the feeding is observed (Lawrence 1975, De Ridder & Lawrence 1982). Although coral-reef echinoids may possess feeding preferences that are demonstrated within controlled conditions in laboratory aquaria (Hay 1984a), and preferences are sometimes inferred by comparisons of relative proportions of food in the diet at a given location with the proportions of those food species at the study site (Atkinson *et al.* 1973), the choice of diet is made from the materials available in the habitat. Availability of materials influences the diet as much as does the choice among the available materials (J.E. Randall *et al.* 1964). Diets vary with season (Carpenter 1981), microhabitat (Atkinson *et al.* 1973), habitat (Lewis 1964, J.E. Randall *et al.* 1964), location, season, age or size of echinoid (Lawrence 1975, De Ridder & Lawrence 1982), and even between periods a few days apart at the same location (Dix 1970). The diets of many coral-reef echinoids include animal and plant material attached to the subs-

trawns, plants within the substratum, and drift algae (Lawrence 1975, De Ridder & Lawrence 1982). Although the diets of most echinoids are largely influenced by which foods are available, some differences in general tendencies in food choice can be discerned among the seven life-form categories of coral-reef echinoids.

Diadematids on coral reefs tend to be herbivorous (Lewis 1964, J.E. Randall *et al.* 1964, Dart 1972, Atkinson *et al.* 1973, Lawrence 1975, Hawkins 1981), although they also take up bottom material (sand, silt, calcareous substratum) along with boring algae, foraminiferans, and encrusting animals such as corals, and bryozoans (Mortensen 1940). While algal production decreases during the winter season in the Caribbean, up to 25% of the diet of *Diadema antillarum* at certain localities is made up of living scleractinian corals (Carpenter 1981).

Herring (1972) listed corals as occasionally predominant food items in the diets of the diadematids *Diadema setosum*, *Echinothrix catamaris*, and *Astropyga radiata* at Zanzibar. However, no mention was made of whether this implies skeletal material or living coral tissue and since the data were listed between algae and mud and silt, and separate from other animal materials, I will interpret this to mean that 'coral' indicates grazing of algae on dead coral substrata.

Diadema antillarum shows a strong preference for algal turf (dense stands of filamentous algae). When algal turf is abundant, *D. antillarum* will tend not to eat macroalgae, crustose algae or living coral tissue (Carpenter 1981). When algal turf is sparse, *D. antillarum* accepts them as alternate foods. The preference hierarchy among algal species as food is generally similar between *D. antillarum* and fishes (Hay 1984a). *D. antillarum* forages over a smaller range (ca. 0.5-1 m²) in comparison with schooling herbivorous fishes (ca. 1 ha). The greater motility of fishes allows them to determine their diet more by choice than by availability in comparison to echinoids.

Hawkins (1981) found that *Diadema antillarum* feeds on crustose coral-line algae with greater absorption efficiency than it does with filamentous endolithic or epipelagic algae. When algal turf is sparse, crustose coralline algae serve as nutritional support for *D. antillarum*. Hawkins (1981) suggested that the relatively fast growth of juvenile *D. antillarum* (Lewis 1966, Bauer 1976) may be partially a result of greater access of small individuals to crustose algae in small crevices. The fast growth of juveniles is probably an important factor in survival of the hazards such as predation which are generally more intense on small individuals.

A major factor leading to the success of diadematids in coral reef communities is their broad 'niche'. *Diadema antillarum* inhabits coral reefs, mangrove roots, seagrass beds, and sand flats (J.E. Randall *et al.* 1964). Diadematids may grow faster or attain a larger size on certain preferred diets than on others, but they will not starve to death in nature because of their basically

generalized diets, at least once they have reached their postlarval stage in their life cycle. As generalists, coral-reef herbivorous echinoids are able to thrive under a wide variety of circumstances, including those circumstances in which schooling herbivorous reef fishes cannot exist. In the coral communities of the northern Gulf of Thailand, rich terrestrial nutrient input from river drainage and direct runoff supports a rich phytoplankton-based food- web, as evidenced by the abundance of suspension-feeding bivalves, barnacles, ascidians, massive sponges (Tsuchiya & Lirdwitayapakit 1986, Tsuchiya *et al.* 1986) and planktivorous fishes (Menasveta *et al.* 1986). Algae are very sparse (Tsuchiya & Lirdwitayapakit 1986, Tsuchiya *et al.* 1986). Under conditions of massive input of nutrients, the pre-emption of nutrients and light by phytoplankton inhibits the growth of benthic algae, except in very shallow water (Birkeland 1987). Eighty-five species of hermatypic corals were present, 21 of which were acroporids (Sakai *et al.* 1986) which suggests that algae were not inhibited by pollutants. Corals generally grow slower than algae, but are relatively generalized in terms of trophic options (Muscatine & Porter 1977).

Of 31 families of reef fishes observed in the northern Gulf of Thailand, not a single schooling herbivorous species representing the Scaridae, Acanthuridae, Siganidae, or Kyphosidae was seen (Menasveta *et al.* 1986). *Diadema* spp., in contrast, were extraordinarily abundant with as many as 28 to 38 individuals m⁻² (Tsuchiya & Lirdwitayapakit 1986, Tsuchiya *et al.* 1986). Their diet consisted mostly of detrital material, sediment and diatoms. Scarids and other herbivorous fishes may be specialists on plant material and may not be able to do as well for long periods on alternate foods when benthic algae are not available. It is likely that *Diadema* spp. graze benthic algae whenever it is available, but are able to sustain themselves on alternate foods. Specialists run the risk of being outcompeted by generalists such as diadematid echinoids even if, as specialists, they are more efficient at utilizing their resources (Brooks & Dodson 1965, Birkeland 1974, Buss & Jackson 1981).

Although four families of schooling herbivorous fishes were absent in the northern Gulf of Thailand, territorial herbivorous pomacentrids, *Stegastes apicalis*, were able to maintain a resource of rich algal vegetation by defending it from *Diadema* spp. (Kamura & Choonhabandit 1986). Although generalists will win in exploitative competition, specialists might persist by means of interference competition.

Shallow-water toxopneustids, the short-spined motile echinoids, such as *Tripneustes* spp., *Toxopneustes* spp., and *Lytechinus* spp., are most often found on the sandy substrata of reef flats and lagoons, but they move into coral communities on patch reefs and back reefs of lagoons. Toxopneustids have a greater tendency to be herbivorous and detritivorous than do the diadematids. *Tripneustes gratilla* (Pacific and Indian Oceans) may occasionally have calcium carbonate in its stomach (Herring 1972), but its diet

consists mainly of plant material (Mukai & Nojima 1985). Likewise, *Tripneustes ventricasus* (Atlantic) also appears to be largely herbivorous (Lewis 1958, Moore & McPherson 1965, Stevenson & Ufret 1966).

The most important difference in feeding style between toxopneustids and diadematids is that the former are generally browsers (biting off exposed plant material and ingesting loose bottom material) and the latter are generally grazers (scraping or abrading the hard substratum as they take encrusting or boring plants or animals, removing upright algae down to the substratum, and taking rhizomes of seagrasses). This standard distinction between browsing and grazing made by Hiatt & Strasburg (1960), Jones (1968), Ogden (1977), Ogden & Lobel (1978), Steneck & Watling (1982), Steneck (1983a, b), Hatcher (1983), Glynn & Wellington (1983), Foster (1987), and Glynn (in press) is important. Individual prey may regenerate after being browsed. Geological effects of grazing are direct.

The short-spined *Echinametra* spp. are often relatively sedentary, living in burrows in the reef substratum or among branches within colonies of *Pacillapara*, *Acrapara* and other branching corals. They are usually found with algal and carbonate material in their guts (Doty & Morrison 1954, Stevenson & Ufret 1966, McLean 1967, McPherson 1969). They often graze boring blue-green algae and, in doing so, erode the reef substratum. At times of strong wave action, drift algae can be an important part of their diet (Russo 1980).

As with *Diadema* spp., *Echinametra* spp. have a broad repertoire and can change their behavior patterns to adjust to a variety of circumstances. In the northwestern Gulf of Arabia, *E. mathaei* is larger than usual, not sedentary, is only occasionally found in cracks or crevices, and generally moves about the open surface of dead corals, grazing the exposed algae by day and by night (Downing & El-Zahr 1987). Individual *E. mathaei* in the northwestern Gulf of Arabia produce bioerosion at a rate an order of magnitude greater than do individual *E. mathaei* at Enewetak (Downing & El-Zahr in 1987). McClanahan & Muthiga (1988) also found populations (534 g m^{-2}) of large (4 cm diameter) *E. mathaei*, with 93% living outside their burrows, grazing $3.8 \text{ kg m}^{-2} \text{ yr}^{-1}$ from the substratum of the reef at Kenya.

Eucidaris spp., and cidaroids in general, tend to graze encrusting organisms, especially animals (McPherson 1968a, b, Lawrence 1975, Glynn *et al.* 1979, Glynn & Wellington 1983). Laboratory experiments showed that *Eucidaris tribuloides* prefer the sponge *Cliona lampa* over algae and seagrass (McPherson 1968a). Laboratory experiments with animal and plant homogenates showed that *E. tribuloides* prefer models mixed with animal material over those prepared with plant material (McClintock *et al.* 1982).

Eucidaris spp. on coral reefs, including *E. thouarsii* on continental shelf reefs, are generally located beneath rocks, slabs of dead coral, or in crevices during daylight hours. They wedge themselves into crevices and holes in the

reef so securely that they usually cannot be removed without breaking their spines or test. At night they will sometimes, but not usually, move out into the open to feed on encrusting animals and plants. They are relatively sedentary compared to diadematids and appear not to move far. *Eucidaris thouarsii* in the Galapagos Islands, on the other hand, are larger, live out in the open and forage for food by day and by night. In the Galapagos, the diet is largely scleractinian coral and crustose coralline algae (Glynn *et al.* 1979, Glynn & Wellington 1983). Like *Echinometra mathaei*, the functional role of *Eucidaris thouarsii* varies with circumstances.

Heterocentrotus spp. and *Colobocentrotus* spp. are generally herbivorous and are most often found in areas of reef exposed to strong wave action and water turbulence (Weber 1969, Dart 1972, Ebert 1971, 1982). *Heterocentrotus* spp. generally feed on filamentous or fleshy algae, the 'algal lawn' (Dart 1972). *Colobocentrotus* spp. appear to feed mainly on crustose coral-line algae. *Heterocentrotus* spp. are usually found in shallow subtidal areas of strong wave surge while *Colobocentrotus* spp. are usually found in the splash zone or the upper intertidal region.

The Aristotle's lantern is an efficient general tool for biting, grasping, catching and scraping (De Ridder & Lawrence 1982). This must be a major factor in the success of echinoids in feeding on such a variety of materials, taking advantage of whatever is available. Ebert (1980) discovered that starving *Diadema* spp. and *Strongylocentrotus purpuratus* allocated more of their resources to growth of the jaws of Aristotle's lantern when food was less available than when well fed. Black *et al.* (1982, 1984) found that *Echinometra mathaei* varied the relative size of Aristotle's lantern within twelve months in a manner consistent with food shortage; as *E. mathaei* population densities increased, the relative size of the lantern also increased. This is another aspect of the phenotypic plasticity of echinoids that contribute to their success as generalists in grazing and/or browsing.

Juvenile echinoids may be limited by size when attempting to browse macroscopic algae or encrusting animals. Because of this, juvenile regular echinoids on coral reefs may tend to be detritivores or grazers of encrusting algae until they become large enough to be successful as grazers of macroalgae. Protein requirements may be a general problem that echinoids face on coral reefs when feeding solely on plant material. Numerous examples can be found of regular echinoids feeding predominantly on animal material (Lawrence 1975, De Ridder & Lawrence 1982). *Eucidaris* spp., and cidaroids in general, eat animal material. Cidaroids are similar to the form from which extant regular echinoids evolved. McClintock *et al.* (1982) showed in laboratory experiments that *Echinometra lucunter*, *Lytechinus variegatus*, and *Eucidaris tribuloides* showed a feeding response to animal food as great as, or greater than, to plant food. Although *Eucidaris* spp. seem to feed on animals regularly in nature, other echinoids such as *Diadema antillarum*

appear to feed on corals mainly when algal standing stock is down (Carpenter 1981).

Sessile, hole-dwelling coral-reef echinoids usually live in habitats characterized by high wave energy. Motile echinoids in more protected habitats generally forage nocturnally and stay sequestered in crevices or under ledges during the day. Herbivorous fishes forage during the day and motile regular echinoids forage at night. In areas in which predators of echinoids are scarce or in which echinoids are especially abundant, the motile echinoids will forage in the daytime.

5.2 Distribution

5.2.1 Habitat and local distribution

General trends in the distribution of coral-reef echinoids can be described, but exceptions are prevalent. It is easier to differentiate echinoids on the basis of morphological adaptations to their habitat than on the basis of specialization for feeding. Diadematids are nearly ubiquitous in coral reefs, although usually uncommon in Oceania. *Diadema antillarum* of the tropical Atlantic lives among corals, rocks, and mangrove roots, and can be found on seagrass beds and sand flats (J.E. Randall *et al.* 1964). Its depth distribution extends from low tide to about 400 m (J.E. Randall *et al.* 1964), although population density generally decreases with depth (Bak *et al.* 1984, Bauer 1980). *Diadema* spp. in the Indo-West Pacific are generally more tightly concentrated into a band of 0-4 m depth on reef margins, moving into the intertidal only at high tide (Herring 1972, Tsuchiya & Lirdwitayapsit 1986, Tsuchiya *et al.* 1986). Oiadematids are generally associated with cavities, ledges, crevices or small overhangs for shelter from predation (Carpenter 1984), although *Diadema* spp. can be found in aggregations on sand flats and in seagrass beds away from shelter (Pearse & Arch 1969). Diadematids are typically more abundant in sheltered backreef habitats than in areas directly exposed to wave impact (Foster 1987).

Toxopneustids, stomopneustids and temnopleurids are also widely distributed, but they have a greater tendency to be found in areas of rubble and sand rather than near large surfaces and unbroken solid substrata. Representatives of these families have relatively thin tests (Ebert 1982) and are generally located away from heavy wave impact.

Unlike the more motile echinoids, the echinometrids have relatively thick tests (Ebert 1982) and tend to occur where the water currents or surf are strong. *Colobocentrotus* spp. live in the intertidal or supratidal splash zones. *Colobocentrotus* spp. are rarely submerged, but nearly always wet from splash. *Heterocentrotus* spp. also live in high-energy, open coast surf zones, but in the shallow subtidal region (Weber 1969, Ebert 1982). The sedentary *Echinostrephus* spp. are found in holes in exposed hard substrata. *Echinome-*

Table 3. Population densities of diadematids in different geographic regions. Da = *Diadema antillarum*, Dp = *D. paucispinum*, Dspp = *D. setosum* and *D. savignyi*, Ed = *Echinothrix diadema*, Espp = *E. diadema* and *E. calamaris* (expansion of compilations by Bauer 1980 and Hay 1984a).

Location	Habitat	Species	Population density (individuals m ⁻²)	Reference
Caribbean -where most experimental field studies of effects of echinoids have been carried out				
St Croix	patch reef	Da	5-10	Ogden <i>et al.</i> 1973, Sammarco <i>et al.</i> 1974, Carpenter 1985a, 1986
Discovery Bay, Jamaica	patch reef	Da	6-73	Sammarco 1980 A.H. Williams 1981, Lawrence & Sammarco 1982
Caribbean -heavily fished reefs				
Teague Bay, St Croix	fore reef	Da	16	Hay 1984a
Coki Point, St Thomas	fore reef	Da	5	Hay 1984a
Caracol Bay, Haiti	fore reef	Da	20	Hay 1984a
Knight Bay, St Croix	patch reef	Da	9	Hay 1984a
Caribbean -lightly fished reefs				
Carrie Bow Cay, Belize	fore reef	Da	0.05-4.3	Lewis & Wainwright, 1985
	back reef	Da	0.13	Hay 1984a
Lighthouse, Belize	fore reef	Da	<1	Hay 1984a
	patch reef	Da	8	Hay 1984a
Media Luna, Honduras	fore reef	Da	0.6	Hay 1984a
Becerro, Honduras	fore reef	Da	<1	Hay 1984a
Salt River, St Croix	fore reef	Da	0.2	Hay 1984a
Eleuthera, Bahamas	patch reef	Da	<1	Hay 1984a
San Blas Islands, Panama	patch reef	Da	1-5	Foster 1987
Caribbean -undocumented degree of fishing pressure				
Depth<7m				
Florida Keys	coral community	Da	1.0-4.2	Bauer 1980

Table 3 (cont).

Location	Habitat	Species	Population density (individuals m ⁻²)	Reference
	<i>Thalassia</i> bed	Da	2.0-2.6	Bauer 1980
Bahmas	patch reef	Da	2.9	Bauer 1980
Cozumel	intertidal coral community	Da	25.8	Bauer 1980
Grand Cayman	coral-sponge community	Da	2.6-12.7	Bauer 1980
Puerto Rico	intertidal rock	Da	13.8	Bauer 1980
St John	coral reef community	Da	9.8-13.8	Bauer 1980
St Thomas	intertidal coral community	Da	14.3	Bauer 1980
St Croix	intertidal	Da	4.5-7.8	Bauer 1980
Antigua	offshore reef	Da	3.9	Bauer 1980
Curacao	fore reef	Da	0.26-12	<i>Baketa/1984</i>
	reef flat	Da	6.6	Bauer 1980
Tobago	fore reef	Da	0.04	Bauer 1980
	reef flat	Da	2.4	Bauer 1980
Barbados	shallower water of flinging reef	Da	23	C. Hawkins, cited in Steam & Scoffin 1977
Depth>7m				
Bermuda	patch reef	Da	0.6	Bauer 1980
Florida Keys	coral community	Da	0.1-1.4	Bauer 1980
Cozumel	offshore reef	Da	9.1	Bauer 1980
Grand Cayman	coral community	Da	1.7	Bauer 1980
Great Dog Island, BVI	coral community	Da	1.4	Bauer 1980
Barbados	coral	Da	3.0	Bauer 1980
Indo-West Pacific shelf				
Sichang Island, Gulf of Thailand	intertidal	Dspp	4 -38	Tsuchiya & Lirdwitayapsit 1986
	subtidal	Dspp	12-28	<i>Tsuchiyaetal.1986</i>

Table 3 (cont).

Location	Habitat	Species	Population density (individuals m ⁻²)	Reference
West Sabath	fringing reef	Dspp	‘very abundant in patches of 20 to 30’	Mathias & Langham 1978
	reef flat	Dspp	‘large numbers... packed into groups of 20 to 30’	Mathias & Langham 1978
Bunaken Island, Sulawesi*	reef flat	Dspp	1.7-3.1	Birkeland unpubl.
Montupore Island, Papua New Guinea*	reef flat	Espp	0.02-0.12	Birkeland unpubl.
		Dspp	7-17	
Egyptian Red Sea (12 sites)	reef crest	Espp	0	Birkeland unpubl.
		Dspp	0.18	
Diani, Kenya	fringing reef	Espp	0.46	Messiha-Hanna & Ormond 1982
		Dspp	0.8-4.4	
Mazizini Bay, Zanibar		Dspp	0.03	McClanahan & Muthiga 1988
Micronesia		Dspp	0.1-6.7	Herring 1972
Arakabesan Island, Palau	reef flat	Dspp	0.034	R.H. Randall <i>et al.</i> 1978
	fore reef	Dspp	0.050	R.H. Randall <i>et al.</i> 1978
	fore reef	Ed	0.006	R.H. Randall <i>et al.</i> 1978
Malakal Island, Palau			0**	Birkeland <i>et al.</i> 1976
Kayangel Atoll			0***	Birkeland <i>et al.</i> 1976
Balabat, Yap			0****	Tsuda <i>et al.</i> 1978
Ulithi Atoll	reef flat	Dspp	0.030	Tsuda <i>et al.</i> 1978
Agana Bay, Guam	reef flat	Dspp	0.01	R.H. Randall 1978
	reef flat	Ed	0.001	R.H. Randall 1978
	reef flat	Dspp	0.001	R.H. Randall 1978
Tumon Bay, Guam	reef flat	Ed	0.0035	R.H. Randall 1978
	reef flat	Dspp	0.005	
Yling Bay, Guam	reef flat	Ed	0.10	R.H. Randall 1978
	reef flat	Dspp	0.005	R.H. Randall 1978
Agat Bay, Guam	reef flat	Dspp	0.005	R.H. Randall 1978
	reef flat	Ed	0.003	R.H. Randall 1978
French Polynesia Raiatea	fringing reef	Dspp	0.34	J.C. Bauer (pers. comm.)

Table 3 (cont).

Location	Habitat	Species	Population density (individuals m ⁻²)	Reference
Tau Tau Island (near Tahaa)	<i>Acropora</i> coral community	Dspp	0.47	J.C. Bauer (pers. comm.)
Bora Bora	<i>Acropora-Porites</i> coral communities		0*****	J.C. Bauer (pers. comm.)
Great Barrier Reef				
nearshore	backreef		0.76	Sammarco 1985
mid-shelf	backreef		0.06	Sammarco 1985
outer shelf	backreef		0	Sammarco 1985
Hawaii				
Kapalus Bay, Maui	shallow, rocky substratum with heavy wave action	Dp	6.18	J.C. Bauer (pers. comm.)
Kona Coast, Hawaii	<i>Porites</i> spp., rocky substratum, 10 m depth	Dp	0.85	J.C. Bauer (pers. comm.)
		Espp	0.10	J.C. Bauer (pers. comm.)
	fore reef, 0-21 m depth	Dp	0.03	Ebert 1971
	fore reef 0-21 m depth	Espp	0.001 to 0.009	Ebert 1971

*Random transects were taken on reefs with diadematids common and not on reefs where

no diadematids were seen. **No echinoids were found in 1020 m² of coral reef area apparently appropriate for diadematids, although seven species of asteroids, five species of holothuroids, and eleven species of crinoids were present. ***Only a few

Echinometra

mathaei and no diadematids on the fore reef and lagoonal reef on all sides of the atoll.

****No echinoids were found in 1300 m² of area about half coral community and half seagrass, apparently appropriate for diadematids; six species of asteroids and eleven species of holothuroids were present. *****No *Diadema* were observed in large areas with ideal conditions (J.C. Bauer, pers. Comm.).

tra spp. are usually found under rocks or in crevices, cavities, burrows, or grooves in the reef. The sedentary *Echinostrephus* spp. and relatively sedentary *Echinometra* spp. often rely on water motion to transport drift algae.

Echinometra mathaei can also be found exposed in large numbers, grazing the surface of dead corals (Downing & El-Zahr 1987, McClanahan & Muthiga 1988).

Cidarids are widely, and usually sparsely, dispersed. On coral reefs, *Eucidaris* spp., *Chondrocidaris* spp. and *Prionocidaris* spp. generally stay hidden under rocks or tightly braced in holes or crevices during the day, and come out to forage only at night, if at all. However, *Eucidaris tribuloides* can also be found in seagrass beds associated with coral rubble (Florida; Kier & Grant 1965) and *E. thouarsii* can also be found exposed in large numbers on the surfaces of corals in broad daylight (Galapagos; Glynn & Wellington 1983).

In general, echinometrids have thick tests and are found most abundantly in high-energy habitats (Ebert 1982); the other regular echinoids avoid strong surf conditions. However, Ebert (1971) found *Heterocentrotus mammillatus* had higher relative weight values and higher population densities in protected regions than in exposed regions. Furthermore, he found that the densities of *Echinothrix* spp. were less well correlated than *H. mammillatus* to wave exposure. Even though the population densities of *Echinothrix* spp. decrease as wave exposure increases, the combined weight of all individuals of *Echinothrix* spp. tended to be greater relative to the weights of other echinoids as a group in areas of exposure to strong surf. Ebert also found no consistent pattern regarding the distribution of *Tripneustes gratilla* in terms of wave action, although the densest population was within an area highly protected from wave action. Each species of coral-reef echinoid may do best under particular conditions of wave-stress or water motion, but diadematids, *Tripneustes* spp., and *Echinometra* spp. can live well under a broad range of suboptimal conditions of water movement.

The population densities of coral-reef echinoids as a group generally decrease with depth, beginning at the low tide level (e.g. Table 3 in this paper and Figures 6 to 8 in Ebert 1971). *Colobocentrotus* spp. are generally found in the intertidal or supratidal splash zone. Echinometrids and diadematids particularly tend to be found in shallow water, while cidarids, temnopleurids, and *Asthenosoma* spp. tend to be found at greater depths. The concentration of diadematids in shallower depths often appears to be more pronounced in the Indo-West Pacific than in the Caribbean. Deterring factors such as wave-stress and food availability are often distributed along a depth gradient (Ebert 1971).

Rate of biomass accumulation in the benthos decreases with depth on coral reefs (Birkeland 1977), so presumably food production relevant to echinoids decreases with depth. Echinoids tend to aggregate on food supply (Kitching

& Ebling 1961, Vadas *et al.* 1986). Although the abundance of echinoids is probably not affected by food supply (Ebert 1968, Carpenter 1986), the distribution of echinoids may be affected. If wave-stress, predation-pressure, substratum-type, competition from the other herbivores and other factors are not overriding food availability, then coral-reef echinoids may tend to aggregate in shallow water.

Ebert (1971) concluded that chance was an important factor in the distribution of coral-reef echinoids in Hawaii. The local distributions of *Echinothrix* spp. and *Tripneustes gratilla* did not appear to be associated with physical or biological factors. *Heterocentrotus mammillatus* had apparently been predominant on the Kona Coast of Hawaii and generally uncommon on other Hawaiian Islands throughout recorded time, yet the range of conditions where they were common on the Kona Coast appeared to encompass many areas where they were scarce on other islands.

The thick tests of *Colobocentrotus* spp. and *Heterocentrotus* spp. allow them to withstand the stress of wave impact, but as Ebert (1982) points out, these same species do not do well in aquaria or areas of calmer water motion. Ebert hypothesized that physiological stress, perhaps respiratory stress, associated with decreased water motion set a lower limit to their distribution. Although adapted to an extreme tolerance of wave-impact, *Colobocentrotus* spp. and *Heterocentrotus trigonarius* may have lost the ability to tolerate low water motion (Ebert 1982).

5.2.2 Geographic distribution

Populations of diadematids are generally about two orders of magnitude more dense in the Caribbean and in continental shelf regions of the Indo-West Pacific than in Oceania (Table 3). The species do not decrease along the west-east gradient to the extent that crinoids do (Table 1). It is abundance rather than the number of species of regular echinoids that is the more striking gradient in Oceania.

One source of apparent differences between regions may be a problem of differences in sampling techniques of different investigators. Nevertheless, Brauer's (1980) estimates of echinoid density are greater than those of others in the same region by one order of magnitude while the population densities of echinoids in Oceania are generally two orders of magnitude less than in the Caribbean or continental shelf regions. I believe this geographic trend is real despite probable problems of nonstandardized sampling.

Hay (1984a, b) suggests that the high abundance of *Diadema antillarum* in the Caribbean (Table 3) is a result of low predation pressure. The sites at which the majority of field studies have been made on the effects of *D. antillarum* on the coral-reef community are all regarded as overfished (Ogden *et al.* 1973, Carpenter 1984). The echinoids may have been exceptionally abundant at these sites because overfishing of predators of *D.*

antillarum lowers the predation pressure and overfishing of herbivorous fishes might lower the competitive pressures. Carpenter (1986), however, noted that fishing at Buck Island National Monument very near the St Croix study sites has been controlled for decades, yet the densities of echinoids there are nevertheless 67% of the densities in the overfished areas. Foster (1987) found *D. antillarum* in a relatively pristine area on the Caribbean coast of Panama to have population densities typical of Caribbean areas and two or three orders of magnitude greater than populations in Oceania (Table 3). It appears that there are two levels of differences in abundances of diadematids. First, Caribbean or 'continental' Indo-West Pacific reefs tend to have denser populations of diadematids than do oceanic reefs. Added to this, reefs that are overexploited for fishes tend to have denser populations.

At least two additional hypotheses must be considered as possible explanations for the geographic patterns in coral-reef echinoid abundances. The first involves larval recruitment. Although food-limitation probably does not affect the numbers of adult echinoids (Ebert 1968, Carpenter 1986), it may affect the success of recruitment. Larvae of coral-reef regular echinoids may be planktotrophic and therefore may be favored by an abundance of phytoplankton, bacteria, or particulate organic material which, in turn, are favored by nutrient input from a variety of sources in continental regions (Birkeland 1984). The geographic pattern of diadematid abundance (Table 2) is similar to the pattern of abundance of boring bivalves which is, in turn, related to geographic patterns of primary productivity (Highsmith 1980). Even with Oceania, the big island of Hawaii appears to have a greater density of coral-reef echinoids than do the smaller high islands of Micronesia, and atolls appear to have the lowest densities of all (Table 3). Sammarco (1985) called attention to the relatively low population densities of echinoids on the Great Barrier Reef as compared to the Caribbean. Within the Great Barrier Reef, diadematids occurred predominantly near the coast of Australia and were essentially absent on offshore reefs (Table 3), a pattern consistent with the hypothesis of nutrient input from large land masses.

R.J. Moore (pers. comm.) noted that echinoids (as well as asteroids, bivalves, sponges, pelagic fishes, manta rays and seabirds) are more abundant in the regions of the Red Sea that are characterized by higher concentrations of phytoplankton in the water column. He found abundances of *Diadema* spp. on reefs in relatively phytoplankton-rich waters of the Farasan Archipelago to be 1.3 m⁻² and the average densities of *Diadema* spp. on reefs in oligotrophic waters near Jeddah to be 0.2 m⁻². He suggested that the increase in echinoid and asteroid abundances were caused by increased survival of planktotrophic larvae as a result of more food material in the water column. The data presented in Table 3 and the patterns noted in the preceding paragraph are consistent with this hypothesis.

The second additional hypothesis is that recruitment of regular echinoids,

perhaps through survival of juveniles, is favored by a decrease of living coral and an increase in surface cover by algae. Bauer (1980) observed in his survey of population densities of *Diadema antillarum* around the western Atlantic, that population densities generally increased in association with sewage outfalls where filamentous algae generally proliferate. The numbers of diadematids in Jakarta Bay were very great and numbers in the outer islands of the Pulau Seribu Chain, which extend northward from the bay, were very small, inversely related to the distribution of corals (J.R.E. Harger pers. comm.). The few incidents in Oceania in which diadematids and *Echinometra mathaei* have become exceptionally abundant have apparently followed or have been associated with a presumed increase in algal abundance following outbreaks of *Acanthaster planci*. Palauan fishermen describe an increase in abundance of echinoids following an outbreak of *Acanthaster planci* which took place in Palau just prior to 1940 (Birkeland 1981). A similar pattern was observed at Saipan, Micronesia (Tsuda *et al.* 1970) and at Huahine-Nui, French Polynesia (Randall & Amesbury 1987).

No information is available that can be used to consider the importance of current patterns in determining the population density of echinoids through larval retention or distribution.

Humans tend to settle in greater numbers in nutrient-rich areas (continental margins and large islands) than on small oceanic islands and atolls. There-fore, the overfishing and nutrient input from pollution caused by human activities, and the decrease in living corals and increase in algal cover caused by outbreaks of *Acanthaster planci*, may be found along the same geographic gradient in nutrient richness as is the abundance of diadematids. A careful study of echinoid abundance needs to be done in which the nature of the land mass is not confounded with human activities such as overfishing in order to determine why regular coral-reef echinoids are distributed as they are.

The west to east decline in species richness across the Pacific and the separate group of species in the eastern Pacific (Table 1) suggest that larval dispersal and speciation are major factors in species richness within a region.

5.3 Recruitment

The abundance and effects of adult echinoids are more stable than are those of herbivorous fishes or microherbivores which vary seasonally (Carpenter 1986). Prior to the echinoid disease of 1983, the adult populations of *Diadema antillarum* at St Croix had been stable for over twelve years (Carpenter 1986). At Rio Bravo, Jamaica, the abundance of *D. antillarum* did not vary between 1977 and 1983 (T.P. Hughes *et al.* 1985). In contrast to the stability of adult populations, recruitment is erratic and infrequent for coral-reef echinoids. Relatively rapid return of echinoids following their removal is

by migration. Ogden *et al.* (1973) removed over 7,000 *Diadema antillarum* from a small patch reef. There was no recruitment from 1973 to at least 1977 (Ogden & Lobel 1978). Only about half the original number had returned during the next ten to eleven years while the control reef still had approximately its original number (Hay & Taylor 1985). J.A. Marsh *et al.* (1977) noted that an extensive settlement of *Diadema* spp. and *Echinothrix diadema* occurred in 1973 and the year-class prevailed for several years. Erratic and infrequent recruitment is characteristic of regular echinoids in general, not just of species on coral reefs (Ebert 1983). Moore & Lopez (1972) reported that *Lytechinus variegatus* had successful recruitment in five of six successive years, then had no successful recruitment in the subsequent ten years. Camp *et al.* (1973) reported an outbreak of *L. variegatus* that was apparently a result of successful recruitment as evidenced by nearly all of them being of one year class. Ebert (1983) found one successfully strong recruitment in a population of *Strongylocentrotus purpuratus* in a twenty-year period. The size distribution still reflects the one heavy recruitment.

The mass mortality of *Diadema antillarum* in 1983 virtually eliminated the breeding stock of the populations at numerous localities. Recovery of the populations may be facilitated by parthenogenesis according to Bak *et al.* (1984) who found gonads of *D. antillarum* with blastulae. It will be difficult to actually assess whether recruitment is relatively poor after the breeding stock has declined because successful recruitment is ordinarily so erratic and because we do not have an adequate baseline for comparisons. T.P. Hughes *et al.* (1987) documented no significant increase in recruitment of *D. antillarum*, *Echinometra viridis*, *Lytechinus williamsi*, *Eucidaris tribuloides*, *Tripneustes ventricosus*, or herbivorous reef-fishes over three years following the mass mortality. As discussed at the end of Section 3.6, an increase in carrying capacity of a habitat is latent until a strong recruitment also occurs. Muthiga & McClanahan (1988) acknowledged a release of predation pressure and larval recruitment as alternative explanations for the increase in abundance of *Echinometra mathaei* in a region of the coast of Kenya subjected to intense human influences. The explanations may be complementary, rather than alternative.

5.4 Mortality

Predation is a primary cause of regional differences in patterns of abundance, distribution, and behavior within species of coral-reef echinoids. Coral-reef echinoids are preyed upon by numerous species of predators. J.E. Randall (1967) found 34 species of Caribbean reef fishes with echinoid material in their stomachs. Echinoids made up over 10% of the diets of 16 reef-fish species (plectognaths, labrids, pomadasyids, and sparids) and the principal component of the diets of six of the species (*Haemulon macrostomum* -87 %;

Balistes vetula -73%; *Anisotremus surinamensis* -54%; *Calamus bajonado* -45%; *Diodon hystrix* -35%; *Canthidermis sufflamen* -25%). The most frequent prey were *Diadema antillarum*, but *Echinometra lucunter*, *E. viridis*, *Eucidaris tribuloides*, *Lytechinus variegatus*, and *Tripneustes ventricosus* were also taken. Toadfish also prey upon coral-reef echinoids (Hoffman & Robertson 1983), primarily on *D. antillarum*. Echinoid density is significantly lower near toadfish holes and these areas support unusually dense stands of algae (Hay 1985).

Coral-reef echinoids are also preyed upon by crustaceans (J.E. Randall *et al.* 1964), gastropods (J.E. Randall *et al.* 1964, Moore 1966, McPherson 1968b, Snyder & Snyder 1970, Ogden *et al.* 1973), and birds (Moore *et al.* 1963).

The regional intensity of predation by fishes is the most likely explanation for differences in size distribution, abundance, and foraging behaviors of echinoid species which have different functional roles on coral reefs in different regions, e.g. *Eucidaris thouarsii* (Glynn *et al.* 1979) and *Echinometra mathaei* (Downing & El-Zahr 1987, McClanahan & Muthiga 1988). Local variation in predation pressure can influence the foraging behavior, homing fidelity, and degree of selectiveness of crevice quality by *Diadema antillarum* (Carpenter 1984).

Annual, seasonal, and irregular fluctuations in sea levels cause local mass mortality and temporary local changes in echinoid distribution and abundances (Glynn 1968, Hendler 1977, Hay 1981a, b, c, Hay *et al.* 1983, Cubit 1985). Mass mortalities on a local scale can be brought about in shallow water by low tides of extreme duration in midday or by water dilution associated with heavy rainfall. Year-to-year changes in sea levels affect the extent and severity of tidal exposures and, thereby, the long-term patterns of distributions of echinoids on reef flats (Cubit 1985).

Water-borne pathogens appear to be the mortality factor that brings about the greatest fluctuations in time of population densities over the greatest areas (Lessios *et al.* 1984a, b). Diadematids occasionally undergo mass mortalities on a geographic scale. These mortalities have occurred sequentially across large regions, indicating that water-borne pathogens are involved. In August 1981, a mass mortality of *Echinothrix calamaris* occurred on the west coast of Hawaii. By December 1981, *E. calamaris* were dying at Molokai, Maui, Oahu and Kauai (the late D.M. Devaney, B.P. Bishop Museum; M.G. Hadfield, Kewalo Marine Laboratory; J.A. Brock, Aquaculture Development Program, Honolulu, pers. comm.). The symptoms of dying echinoids were drooping spines, spines falling out, and degeneration and sloughing of the epithelium from the test (J.A. Brock pers. comm.). Another diadematid, *Diadema paucispinum*, was also affected at Hawaii (the Big Island), but other types of echinoids (*Tripneustes gratilla*, *Heterocentrotus mammillatus*, and *Echinometra mathaei*) were not affected (J.A. Brock pers. comm.).

A similar mass mortality of a diadematid was noted two years later in the Caribbean at the Galeta Marine Laboratory, near the entrance of the Panama Canal, in mid-January 1983 (Lessios *et al.* 1984a). The symptoms of affected diadematids (Bak *et al.* 1984, Lessios *et al.* 1984a) appeared to be the same as those at Hawaii. By early April, the mortality had spread to the San Blas Islands, about 120 km to the east, where the *Diadema antillarum* populations were reduced by over 90% (Lessios *et al.* 1984a). One year later, by February 1984, the mortality of *D. antillarum* had spread throughout the Caribbean and to Bermuda. The mass mortalities of *D. antillarum* occurring at Jamaica ('more than 98%' or 'close to 100%' mortality) in July 1983 were documented by Morrison (1984) and Hughes *et al.* (1985), at St Croix (99% mortality) in February 1984 by Carpenter (1985a), and at Curacao (98-100% mortality) October 1983 by Bak *et al.* (1984).

Lessios *et al.* (1984b) documented the sequence of this mortality and described the probable role of currents in the distribution of the pathogen. The simplest interpretation of the sequence of mortalities in space and time (cf. Lessios *et al.* 1984b) would involve two points of origin in the Caribbean, one near the entrance to the Panama Canal in mid-January and another at Barbados in late September. It is noteworthy that the only successful establishment of a species of coral-reef fish from the Indo-West Pacific into the Caribbean also occurred at the Caribbean entrance to the Panama Canal and at Barbados (Springer & Gomon 1975). Perhaps the 1983 pathogen was introduced to the Caribbean in the ballasts of ships at the Panama Canal and at Barbados. It is also interesting that the first outbreak at Curacao was first observed in the harbor in early October. The mortality started at Barbados in late September upstream from any other affected locality. From Panama and Barbados, the spread of the disease is consistent with the major current patterns.

Lessios *et al.* (1984a, b) give indirect evidence which support the hypothesis that the cause of the mortality was a pathogen. First, it was species-specific, affecting only *Diadema antillarum* and none of the other six species of regular echinoids that coexist with it. Second, potency of the mortality factor was not diluted or dissipated as it spread from Panama to Bermuda. Third, the factor in some places travelled in directions other than that of the prevailing current, apparently travelling long distances in open water, then spreading by shore eddies in a direction opposite that of the main offshore current. Fourth, no abnormal changes in water temperature, tidal levels, rainfall or salinity were observed to be associated with the mortality (Lessios *et al.* 1984a). Fifth, the spread of the mortalities downstream on a local scale (1 km d⁻¹ [Bak *et al.* 1984] to 3.6 km d⁻¹ [T.P; Hughes *et al.* 1985]) was too slow for a water-borne chemical pollutant.

A few recovering adults appeared on reefs in the San Blas and at Jamaica about a month after the mass mortality (Lessios *et al.* 1984a). Lessios *et al.*

(1984a) speculated that sick individuals unable to move within crevices may have had a slightly better chance of survival from fish predation than debilitated individuals in exposed locations. Survivors may emerge from crevices after having recovered enough to be motile.

Sources of mortality can have synergistic effects. Temporary debilitation of echinoids by a pathogen while outside a crevice could lead to susceptibility to predation by fishes during daylight hours while those immobilized within crevices may not move from their crevice until they recover enough to regain their motility and by this time they may forage mainly at night and may be able to defend themselves. Sick *D. antillarum* are preyed upon by scarids, labrids and pomacentrids (Lessios *et al.* 1984a). Furthermore, as most *Diadema antillarum* die from the pathogen, those species of predator that have echinoids as a major component of their diets may provide increased predation pressure on the surviving *D. antillarum* and on other species of echinoids and other prey.

It is too early to know whether the *Diadema antillarum* will soon return to population densities similar to those prior to the mortality. Bak (1985), T.P. Hughes *et al.* (1985, 1987), and de Ruyter van Steveninck & Bak (1986) observed low recruitment rates following the mass mortality. Recovery may be slow because of the scarcity of unaffected localities that may serve as sources of larvae. If areas that serve as sources of larvae could be identified, the pattern of recovery at affected sites might provide a useful indication of degree and pattern of successful larval dispersal.

In December 1984, *Astropyga magnifica* were found dead in shallow water (0.6 to 1.2 m) on the northwest coast of Puerto Rico (L.B. Williams *et al.* 1986). The symptoms of dying *A. magnifica* were very similar to those of *Diadema antillarum* during its mass mortality in 1983. However, the mortality of *A. magnifica* was apparently confined to shallow water. *A. magnifica* in deeper water (21 m) were apparently not affected.

Food-resource limitation of adult coral-reef echinoids may influence the mean size of individuals (Carpenter 1981), but there is no evidence that food limitation causes mortality in echinoids.

5.5 Competition

Echinoids win against fishes in exploitative competition (Hay & Taylor 1985). Fishes win against echinoids in interference competition (Kaufman 1977, A.H. Williams 1978, 1980, 1981, Sammarco & Williams 1982). Diadematids win in exploitative competition with herbivorous fishes because diadematids are generalists and capable of survival in the absence of macroalgae by subsistence on alternative food sources (live coral, organic detrital material, diatoms). Furthermore, echinoids can survive for months without food, probably longer than herbivorous fishes. Fishes have an

immediate (within five days) functional response (increased grazing activity) when *Diadema antillarum* is removed, whether the removal is experimental or by natural causes (Hay & Taylor 1985). Fishes have not yet increased total population size following the mass mortality of *D. antillarum* in the Caribbean, but this may take years if the survival of larval fishes is a separate conditional factor from the carrying capacity of the habitat for adult fishes (see Section 3.6).

In some coral communities in the northern Gulf of Thailand, *Diadema* spp. are extraordinarily abundant and schooling herbivorous fishes (scarids, acanthurids, kyphosids, siganids) are absent (see Section 5.1).

Damselfishes actively defend their territories from coral-reef echinoids (Kaufman 1977, A.H. Williams 1978, 1979, 1980, 1981, Sammarco & Williams 1982). Whether an organism is a generalist or specialist is important when exploitative competition is involved. The probable outcome of interference competition must be considered on a case by case basis, accompanying the mechanisms of physical removal or aggression.

Intraspecific exploitative competition can affect the mean size of individual echinoids and, presumably, their egg production (Ebert 1968, Carpenter 1981). Echinoids do not die of exploitative competition (Ebert 1968, Carpenter 1981), but their local distribution can change (Carpenter 1981).

As population density increases, *Diadema antillarum* on coral-reefs tend to disperse or spread out by decreasing their homing fidelity to their shelter (Carpenter 1981). However, on sand-bottom or reef flats without shelters, echinoids tend to aggregate (Pearse & Arch 1969).

Evidence for interspecific exploitative competition has been implied by the observation that the removal of *Diadema antillarum* from a small patch reef at St Croix (Ogden *et al.* 1973) was followed by the immigration of *Tripneustes ventricosus* onto the reef (Ogden & Lobel 1978). The mass-mortality of *D. antillarum* on the reef flats in the San Blas Islands was followed by an immigration of *Echinometra viridis* onto the vacated area (Lessios *et al.* 1984a). The experimental removal of *D. antillarum* from coral patches also resulted in immigration of *E. viridis* (A.H. Williams 1981). These movements might be evidence of amensalism rather than competition. *T. ventricosus* is usually found in stands of algae. The change in habitat rather than increased food supply following the decrease in *D. antillarum* may have brought about the immigration of *T. ventricosus*.

McClanahan & Muthiga (1988) report that when predation pressure from fishes was reduced, *Echinometra mathaei* became abundant and grazed the algae outside their burrows. In this event, they suggested, *E. mathaei* may feed closer than diadematids to the substratum and may pre-empt the food source, thus winning out in exploitative competition.

Interference competition has not been observed in motile coral-reef echinoids. They tend to aggregate in exposed situations. Sedentary, groove--

dwelling *Echinometra lucunter* shows interference competition in defense of its burrow and, perhaps, in defense of its field of interception of drift algae (Grunbaum *et al.* 1978). Tsuchiya & Nishihira (1985) documented the existence of two types of *Echinometra mathaei* which differ in their ability to compete for territory.

5.6 Effects on coral-reef communities

Grazing by echinoids has major biological and geological effects on coral-reef communities (Lawrence 1975, Lawrence & Sammarco 1982). The qualitative and quantitative nature of these influences vary greatly among taxa of echinoids, among geographic regions, and among local sites. Direct biological effects include an alteration of the abundance, distribution, and community structure of plants and animals, as well as an increase in rate of primary productivity per unit biomass. Direct geological effects include sediment production, erosion of carbonate rock and, in certain cases, limitation of coral reef growth. Second-order biological effects include alteration of foraging behavior of herbivorous fishes and, possibly, alteration of the abundances of herbivorous fishes and invertebrates and a change in community trophic structure. Second-order geological effects may be the toppling of coral heads through weakening of their basal structures, loosening of sediments, and facilitating the influences of wave action.

5.6.1 Effects on biomass of algae

The decrease in biomass of benthic algae resulting from grazing by regular echinoids has been documented extensively for both temperate and tropical habitats (reviewed by Lawrence 1975, Lawrence & Sammarco 1982). The addition of *Diadema antillarum* has been shown in field experiments to reduce the biomass of the algal turf on Caribbean reefs (Carpenter 1986). The removal of *D. antillarum* in field experiments resulted in greatly increased algal biomass (Ogden *et al.* 1973, Sammarco *et al.* 1974, Sammarco 1982a).

The influence of grazing by echinoids on algal biomass varies with exposure to wave action, season, depth, predation-pressure and other factors. Foster (1987) demonstrated that on the shallow (< 3 m) reef front, feeding by *Diadema antillarum* was inhibited even during generally calm periods because of occasional waves generated by light winds. In backreef areas, decalcified dry weight algal biomass was only a third the a real density as on the reef front because water movement was not enough to inhibit *D. antillarum* grazing even during periods of heavy wave impact. In habitats between the reef front and the backreef, the degree of reduction of algal biomass by *D. antillarum* varied seasonally. In periods of calm weather, the mean size of grazed area surrounding *D. antillarum* would increase from 757 to 1704 cm². During extensive periods of rough weather, the *D. antillarum* would remain

sheltered in crevices, the algal biomass would increase and the grazed area would become overgrown with algae.

The grazing pattern of *Diadema antillarum* changes with season also as a result of differences in productivity. Carpenter (1981) found that algal turf was fed on preferentially, but as productivity of the algal turf decreased during the winter and the algal turf became less abundant, alternate foods such as macroalgae, crustose coralline algae, and living corals would be taken. A seasonal shift in diet probably results in a seasonal variance in impact of *D. antillarum* among the prey.

The effects of the 1983 mass mortality of *Diadema antillarum* were found to vary with depth, probably as the result of an interaction of release from grazing pressure and benthic productivity. The algal standing stock in Curacao increased to a higher 'new equilibrium' level at 3 m depth than at 15 and 27 m (de Ruyter van Steveninck & Bak 1986). A similar pattern was observed at Jamaica (T.P. Hughes *et al.* 1987). Likewise, the decrease in diadematids was followed by an increase in algal cover and in grazing intensity of fishes in shallow (5 to 10 m depth) water but not in deeper (below 15 m) water at Jamaica (Morrison 1984). Conversely, the decrease in occupation of space by corals occurred in shallow, but not deep (27 m), water (de Ruyter van Steveninck & Bak 1987, Hughes *et al.* 1987). This is probably because the growth rate of benthic algae is strongly influenced by levels of light. Algae can overgrow juvenile corals in shallow water, but corals can maintain their space in deeper waters (Birkeland 1977).

Although the effects of the mass mortality of *Diadema antillarum* are similar at different locations around the Caribbean at shallow depths, the effects vary between locations at greater depths. For example, Morrison (1984) reported no changes in the deeper reef community at Jamaica. The degree of concentration of effects of *D. antillarum* in shallow depths may be particularly a result of degree of aggregation of *D. antillarum* in shallow depths, the relative abundance of herbivorous fishes, water turbidity, distribution and prevalence of crustose coralline algae, corals and bare space, all of which vary between locations. The smallest increase in algal cover was documented at 15 m depth because the grazing pressure of herbivorous fishes were important at this depth and *D. antillarum* were relatively rare there even before the mass mortality (de Ruyter van Steveninck & Bak 1987).

An impression from the literature is that herbivorous fishes have the major impact on algal biomass in the tropical Pacific (Hatcher 1982), while echinoids have the major influence in the Caribbean (Carpenter 1986, Foster 1987). We might be cautioned by the local variation in the influence of *Diadema antillarum* described in the previous paragraphs to consider that the relative influence of diadematids and herbivorous fishes probably vary locally, on a scale of tens of meters. The relative scarcity of diadematids in Oceania as compared to the Caribbean (Table 3), however, suggests that the

relative importance of herbivorous fishes in Oceania and echinoids in the Caribbean is a real trend.

Mean algal biomass showed a significant increase when *Diadema antillarum* were excluded from areas at St Croix (Carpenter 1985a) and Panama (Foster 1987), but herbivorous fishes were allowed to graze the areas. The biomass of algal turfs grazed by herbivorous fishes was two to four times greater than the biomass of turfs grazed by *D. antillarum*. When *D. antillarum* were allowed to graze an area but fish were excluded, the algal biomass did not differ significantly from areas in which both *D. antillarum* and fishes were allowed to graze (Carpenter 1985a). These results indicate that *D. antillarum* has a major influence on algal standing stock on coral reefs at St Croix and Panama, while herbivorous fishes had a negligible influence on biomass of algae (Carpenter 1985a, Foster 1987).

There is often a negative log-linear relationship between density of *D. antillarum* and algal cover in both natural areas and in field experiments (Sammarco 1980, Carpenter 1981). Carpenter (1986) tested the effects of various combinations of microherbivores (amphipods, syllid polychaetes, and gastropods such as limpets and *Cerithium literatum*), *Diadema antillarum*, and herbivorous fishes on the biomass of algae on the coral reef. Areas subjected to grazing by *D. antillarum*, whether in combination with herbivorous fishes and/or with herbivorous microinvertebrates, always had the least algal biomass.

However, the relationship between the density of *Diadema antillarum* and algal biomass is not consistent within the Caribbean. J.E. Randall *et al.* (1964) enclosed 16 *D. antillarum* per 0.84 m² at St John, US Virgin Islands, yet these echinoids did not control the growth of algae. That *D. antillarum* ate well was evidenced by their growth. Twenty-two years later, three years after the mass mortality of *D. antillarum*, Don Levitan (cited in T.P. Hughes *et al.* 1987) found that herbivorous fishes were able to control the abundance of algae. Likewise, Wanders (1977) found that the rate of grazing by fish alone could prevent upright algae from overgrowing encrusting algae at Curacao although the density of *D. antillarum* at Curacao was high (Table 3). Vine (1974), Tribble (1981), Hay (1981b), Hay *et al.* (1983) and Lewis & Wainwright (1986) also found that the grazing pressure of echinoids in the Caribbean was very small in comparison with that of herbivorous fishes.

Ogden *et al.* (1973) gave a caveat on the general applicability of their conclusion as to the magnitude of influence of echinoids on reefs near St Croix because they recognized that the reefs at St Croix were overfished. The study site of J.E. Randall *et al.* (1964) was in a national park and presumably had some fishing regulation. Hay (1984b, c) suggested that field experiments at St Croix and at Jamaica were in areas which had unusually high population densities of *Diadema antillarum* (Table 3) resulting from overfishing of predators and competitors of *D. antillarum*. Nevertheless, Foster's (1987)

study site was in the San Blas Islands, an area not overfished, and *D. antillarum* was still the most influential grazer, and the effects of herbivorous fishes were essentially negligible.

The mass mortality of *Diadema antillarum* across the tropical western Atlantic in 1983 resulted in changes in the community structure of coral reefs that were remarkably similar in shallow water (3 to 7 m depth) at each documented site. With the decrease in abundance of *D. antillarum* there was an immediate increase in algal standing stock, a change in species composition towards 'new equilibrium' in algal standing stock at each site investigated. The 'new equilibrium' in algal biomass at St Croix was at an increase of 413% over the previous level of algal biomass under the influence of grazing by *Diadema* (Carpenter 1985a). The 'new equilibrium' at Jamaica appeared to reach a plateau at 500% increase in algal biomass (Hughes *et al.* 1985); at Curacao, it was at about 145% (de Ruyter van Steveninck & Bak 1987). In each of the cases, the 'new equilibrium' occurred in two to three months and was maintained for at least eight to ten months. A recent report by Hughes *et al.* (1987), however, indicates that the algal biomass and surface cover continued to increase and the living coral cover continued to decrease in certain areas over the following three years.

The similarities among Caribbean locations in the responses of the algal communities to the decreases in abundances of *D. antillarum* are not a result of seasonal changes. The sequence of changes began at Jamaica in July 1983, at Curacao in October 1983, and at St Croix in February 1984. In each sequence the fleshy and filamentous algae began increasing immediately. The mass-mortality was so extensive that no areas were observed for changes in the reef community that might have occurred even though *D. antillarum* remained abundant. Nevertheless, the number of locations and seasons of occurrence, along with the background of information from previous controlled field experiments and knowledge of the natural history of the system makes it quite reasonable to interpret the changes in the reef community as being the result of the decrease in grazing pressure from *D. antillarum* rather than a peculiarity of the time or place (Carpenter 1985a).

In controlled experiments (Carpenter 1985a), *Diadema antillarum* were reintroduced into the area by use of inclusion cages. Although the 'new equilibrium' persisted in the general area, the algal biomass decreased to one-third its original size where *D. antillarum* was introduced. This experiment supports the interpretation that the increase in algal biomass resulted from the mass mortality of *D. antillarum*.

The reason that the uniformity of changes in standing stock of algae, community structure of algae, and feeding intensity of fishes across locations and seasonal replicates seems remarkable is that previous field experiments have demonstrated such widely varying results between sites and between times. For example, after the *Diadema antillarum* were effectively removed

by mass-mortality, the grazing intensity by herbivorous fishes increased by 60% (Morrison 1984) to 380% (Carpenter 1985a), yet the herbivorous fishes were still unable to lower the 'new equilibrium' of algal biomass. Herbivorous fishes appeared to have had the major influence on algal communities at St John (J.E. Randall *et al.* 1964) while *D. antillarum* had the major influence at St Croix. The similarity among sites in effects of the 1983 mass mortality may be a result of most before-and-after studies having been undertaken in areas overfished by man and having had extraordinarily dense populations of *D. antillarum* before the mortality. A more complete survey may show that the effects of the 1983 mass mortality are actually more variable than is indicated in the literature.

5.6.2 Effects on algal community structure

Algal turfs in areas grazed by *Diadema antillarum* are predominantly composed of filamentous forms. Fleshy algae are sparse and generally present as tiny recruits only. Before the 1983 mass mortality of *D. antillarum*, the filamentous algal turfs at St Croix were generally 1 to 3 mm in height (Carpenter 1985a). Following the mass-mortality of *D. antillarum* at St Croix, the algal turf grew to a mean height of 7 mm within seven months and fleshy algae (e.g. *Dictyota* sp. and *Laurencia obtusa*) became more prevalent. *Sargassum* sp. and *Turbinaria turbinata* grew to over 30 cm tall in some areas (Carpenter 1985a).

The changes in community structure following the 1983 mass mortality of *Diadema antillarum* were remarkably similar at different sites and seasons. Fleshy macroalgae increased in abundance in all cases. The reef surface cover by fleshy macroalgae quadrupled (7% cover increased to 27% cover) while the cover by filamentous algae tripled (17 to 45%) within four months after the mortality of *D. antillarum* (July) at Jamaica (Morrison 1984, Liddell & Ohlhorst 1986). *Lobophora variegata* and *Dictyota divaricata* were among the fleshy algae that increased at Jamaica (Morrison 1984, Liddell & Ohlhorst 1986); *Dictyota* sp., *Laurencia obtusa*, and *Acanthophora spicifera* became more common in February at St Croix (Carpenter 1985a); *Lobophora variegata* and *Dictyota* spp. increased in surface cover in October at Curacao (de Ruyter van Steveninck & Bak 1987).

Fleshy algae, such as *Lobophora variegata*, *Dictyota divaricata*, and *Caulerpa racemosa*, which increased in abundance following the mass mortality of *Diadema antillarum*, are distasteful to herbivorous fishes but are not avoided by *D. antillarum* (Morrison 1984). At high densities, the *D. antillarum* appears to prevent succession and the dominance of fleshy macroalgae because of its generalized diet and high rate of feeding. The selective feeding by schooling herbivorous fishes may facilitate succession and favor the establishment by distasteful fleshy algae (Birkeland *et al.* 1985).

This similarity in change in community structure towards an increase in proportion of fleshy macroalgae at all sites documented following the 1983 mass mortality of *Diadema antillarum* is remarkable in view of the usual variance in the outcome of succession. Macroalgal dominance did not increase on the Great Barrier Reef even after treatment periods of nearly six months (Hatcher & Larkum 1983). The outcome of grazing by any particular species is usually contingent in part on season, depth, other herbivores and other factors and their interactions. The uniformity of algal response following the mass-mortality of *D. antillarum* in 1983 is noteworthy because it occurred at different seasons and at different localities. Perhaps some of the uniformity was brought about by a similarity among areas in being heavily overfished by man and having extraordinarily dense populations of *D. antillarum* before the mass-mortality (Hay 1984b). The effects of these usually dense populations of *D. antillarum* may overwhelm the influence of the other factors so they account for a relatively large portion of the variance and the effects of other factors are still there but difficult to distinguish.

Crustose coralline algae probably require the continuous removal of filamentous and fleshy algae by herbivores in order to exist (Steneck 1982, 1983a, Steneck & Watling 1982). This exposed cover of crustose coralline algae decreased on the coral reefs at Curacao as the cover by filamentous and fleshy algae increased following the mass-mortality of *Diadema antillarum* (de Ruyter van Steveninck & Bak 1987). This same decrease in cover by crustose coralline algae occurred after the experimental removal of *D. antillarum* at St Croix (Carpenter 1986).

Coral-reef echinoids have feeding preferences which influence their effect on the benthic community most strongly when the echinoids are at low or medium population densities in regards to their food supply. Echinoids become more generalised as their food supply becomes less available. In most situations, herbivorous fishes can be more selective than echinoids because they can move over a larger area more rapidly and are visually discriminating. This relatively selective grazing over a broad area by herbivorous fishes facilitates succession while the intense generalized grazing of abundant echinoids sets back succession within their foraging ranges.

When at intermediate levels of population density, selective feeding by *D. antillarum* results in a shift in algal community structure, the nonpreferred species become relatively prevalent and the preferred species become more scarce (Sammarco *et al.* 1974, Ogden & Lobe 1978). If the competitively superior algal species recruits readily, the greatest algal diversity will occur at intermediate levels of grazing intensity (Paine & Vadas 1969, Carpenter 1981, Lawrence & Sammarco 1982). If the competitively superior algal species are not the preferred prey species or if no obvious competitive dominant occurs, the algal diversity will decline with increasing grazing pressure.

5.6.3 Effects on distribution of marine plants

Many of the studies on the influence of grazing pressure on the distribution of algae on coral reefs and on seagrass near coral reefs have been concerned mainly with the influence of herbivorous fishes, but the influence of grazing by coral-reef echinoids has also been documented. *Diadema antillarum* eliminates or greatly reduces the density of *Thalassia testudinum* near coral reefs, thereby creating a halo in seagrass beds bordering coral reefs (Ogden *et al.* 1973). In the northern Gulf of Thailand, where schooling herbivorous fishes (scarids, acanthurids and siganids) were absent (Menasveta *et al.* 1986) and where *Diadema* spp. (*Diadema setosum* and *D. savignyi*) were exceedingly abundant, short filamentous algae were limited to rock crevices, to shells of the bivalve *Arca ventricosa*, in depressions in the coral *Porites lutea*, and to territories guarded from *Diadema* spp. by damselfishes (Tsuchiya *et al.* 1986).

The successes of macroalgae and sessile animals in becoming established on a coral reef depends upon their reaching a size that is large enough for their defenses to be effective. Many macroalgae have structural and/or chemical defenses and may be avoided when large enough to be discriminated from other algae in the turf by herbivores (Norris & Fenical 1982, Littler *et al.* 1983, Paul & Hay 1987). Likewise, when small corals and other sessile organisms are large enough to be discerned by grazers, they are often not accepted. Some herbivorous fishes in the Caribbean consistently avoid biting coral recruits as small as 2.5 mm diameter (Birkeland 1977). Diadematids, and probably coral-reef echinoids in general, graze the substratum in a less discriminating manner and coral recruits are often grazed either incidentally or as a portion of a generalized diet.

Algae with defensive chemicals, such as *Chlorodesmis* sp. and *Halymenia* are found in widely separated clumps or turfs. The size and frequency of these clumps or tufts must depend on the probability of a recruit reaching the critical size before being grazed. This depends in part upon the abundance of recruits and upon the growth rate of the sessile organism at the site. It must also depend upon the frequency with which an herbivore is likely to graze a particular spot, its food selectivity, and its ability to discriminate among prey. Herbivorous fishes and echinoids differ in these aspects. Diadematids generally have more varied diets, are apparently less able to discern such items as small corals, tend to forage over a smaller range, and tend to graze the same spot close to their shelter more frequently than do schooling herbivorous fishes. These differences in grazing patterns lead to differences in patterns of algal distribution, when areas with differences among the relative abundances of herbivorous fishes and diadematid echinoids are compared. At Micronesian atolls where schooling herbivorous fishes are abundant and diadematid echinoids are scarce, algae are found in widely scattered tufts of individuals that were able to reach a size at which their defenses could be recognised (pers. observ.).

5.6.4 Effects on rates of primary productivity

Grazing stimulates primary production in forests (Matson & Addy 1975), in grasslands (Dyer & Bokhari 1976, McNaughton 1979), in seagrass beds (Greenway 1974), and in the plankton (Porter 1976). Wanders (1977), Brawley & Adey (1977), Ogden & Lobel (1978), and Montgomery (1980) concluded that grazing by herbivorous fishes increases reef productivity. The explanations given for the increase in productivity per unit biomass of algae in that when heavily grazed, algae are kept in their exponential growth phase, turnover is increased, self-shading and competition between algae are reduced, succession is set back, the predominance of rapidly growing (early successional) species of algae is favored, and nutrients are recycled.

Reef surfaces within the foraging area of *Diadema antillarum* are typically occupied by multispecific turfs of filamentous algae, single-celled algae, and crustose forms (Carpenter 1985a). There is no canopy of fleshy macroalgae in areas intensely grazed by echinoids. Under these conditions, the small filamentous and single-celled algae are the most productive per unit biomass of the algae (J.A. Marsh 1976, Wanders 1976, de Ruyter van Steveninck & Breeman 1981, Adey & Steneck 1985, Carpenter 1985b, 1986).

An assessment of the various categories of herbivores on the coral reef, showed that grazing intensity was greatest by *Diadema antillarum* and resulted in low biomass of highly productive algae (Carpenter 1986). The filamentous algae in areas grazed by *D. antillarum* in all cases showed greater rates of primary productivity than did the algal turf in areas without *D. antillarum*. Although there was significantly less algal biomass in the areas grazed by *D. antillarum*, the net primary production per unit area was not significantly less because of the greater rate of production (Carpenter 1985a, 1986).

Within five days following the mass-mortality of *Diadema antillarum* at St Croix, the productivity per unit biomass of the algal turf decreased by 61 % and the productivity per unit area decreased by 37% (Carpenter 1985a). As *D. antillarum* remained scarce, the biomass of the algal turf increased. As the biomass increased, the productivity per unit area increased but the productivity per unit biomass remained at low levels. Thus at St Croix, *D. antillarum*, not the herbivorous fishes, controlled the productivity and biomass of algae.

By selective grazing, herbivorous fishes appear to facilitate succession (Birkeland *et al.* 1985); by generalized grazing, coral reef echinoids appear to continually set back succession. The Caribbean and Indo-West Pacific shelf reefs have a greater density of echinoids in shallow water than do reefs in Oceania (Table 2). Carpenter (1986) hypothesizes that areas in which diadematids are rare or absent would show similar rates of algal productivity per unit area of substratum, but less algal productivity per unit biomass, than would otherwise comparable areas where diadematids are abundant.

5.6.5 Second-order biological effects on the coral reef community

Corals are preyed upon by a variety of diadematids and echinometrids (Herring 1972, Bak & van Eys 1975, Carpenter 1981, Sammarco 1980, 1982a, b), but probably only during times of low algal productivity (Carpenter 1981). Nevertheless, diadematids and echinometrids affect the composition of the coral community directly and indirectly. At low densities of echinoids, coral recruits are most often surrounded or overgrown by algae and smothered in the sediment trapped by the algal baffles. At intermediate densities of diadematids, much of the algae is grazed. Although coral recruits are also grazed incidentally, the survival of coral recruits is actually greater under these conditions because the additional recruits that have not succumbed to algal overgrowth are more numerous than the additional recruits that were incidentally grazed by *D. antillarum* (Dart 1972, Sammarco 1980). When diadematids become very abundant, both the algae and the coral recruits may be overgrazed (Schuhmacher 1974, Sammarco 1980).

Hughes *et al.* (1987) documented the continuous decrease in coral cover over a three-year period as algal cover increased following the 1983 mass mortality of *Diadema antillarum*. These observations imply that even adult coral colonies benefit from the grazing of algae by echinoids.

Echinometra mathaei makes burrows in the substratum that are cleared of macroalgae. These areas are relatively favorable for coral recruitment because the coral recruits are free of competition with algae (Birkeland & Randall 1982). Topographic complexity becomes more important for coral recruitment along a tropical to temperate gradient (Birkeland & Randall 1982). As herbivorous fishes become less abundant, the prevalence of fleshy algae increases, and a greater proportion of successful coral recruits are found in burrows of *E. mathaei*.

Eucidaris thouarsii directly grazes corals on Galapagos reefs at a rate high enough to reduce reef growth (Glynn *et al.* 1979, Glynn & Wellington 1983). Following mass mortality of pocilloporids in the Galapagos during the 1982/83 El Nino, the bioerosion of the reefs by grazing affected the reef framework (P.W. Glynn pers. comm.). In areas in which *Diadema antillarum* is extraordinarily abundant, the amount of food available for herbivorous fishes is greatly reduced. Herbivorous damselfishes guard territories from diadematids in both the Caribbean and Indo-West Pacific. The mass mortality of *D. antillarum* resulted in an increase in grazing intensity by herbivorous reef fishes at Jamaica (Morrison 1984) and at St Croix (Carpenter 1985a). The inability of fishes to lower the increased standing stock of algae may have been partially influenced by differences in selectivity and feeding preferences between fishes and *D. antillarum* (Morrison 1984).

Grazing by *Diadema* spp. may have an indirect effect (amensalism) on microherbivores (amphipods, small gastropods, syllids and other herbivo-

Table 4. Rates of bioerosion of coral-reefs substrain by echinoids and scarids.

Grazer	Location	Rate of bioerosion by grazing (g/individual/day)	Rate of sediment production (kg/m ² /yr)	Reference
<i>Diadema antillarum</i>	St Croix	0.52	4.6	Ogden 1977
<i>Diadema antillarum</i>	Barbados	0.42	9.7	Hunter 1977
<i>Diadema antillarum</i>	Barbados	0.25	5.9	Stearn & Scoffin 1977
<i>Diadema antillarum</i>	Barbados	0.23	5.3	Scoffin <i>et al.</i> 1980
<i>Diadema antillarum</i>	Curacao	0.24	2.9	Bak <i>et al.</i> 1984
<i>Echinometra lucunter</i>	St Croix	0.12	3.9	Ogden 1977
<i>Echinometra lucunter</i>	Barbados	0.07		McLean 1967
<i>Echinometra mathaei</i>	Enewetak	0.1-0.2	0.008-0.26	Russo 1980
<i>Echinometra mathaei</i>	Gulf of Arabia	0.5		Shinn (in Hughes & Keji 1973)
<i>Echinometra mathaei</i>	Kuwait	0.9-1.4	9.9-15.3	Downing & El-Zahr 1987
<i>Echinometra mathaei</i>	Kenya	0.5	3.8	McClanahan & Muthiga 1988
<i>Echinostrephus aciculatus</i>	Enewetak	0.2-0.4	0.04-0.07	Russo 1980
<i>Eucidaris thouarsii</i>	Galapagos	0.18	1.9	Glynn & Wellington 1983
scarids	Saipan		0.04-0.06	Cloud 1959
scarids	Bermuda		0.23	Bardach 1961
scarids	Bermuda		0.21	Gygi 1975
scarids	Curacao		0.23	Bak <i>et al.</i> 1984
<i>Scarus croicensis</i>	St Croix		0.49	Ogden 1977
<i>Sparisoma virde</i>	Barbados		0.04	Stearn & Scoffin 1977
<i>Sparisoma virde</i>	Barbados		0.04-0.17	Frydl & Stearn 1978
<i>Sparisoma virde</i>	Barbados		0.03	Scoffin <i>et al.</i> 1980

rous polychaetes) and other microinvertebrates. By grazing the algal turf, *Diadema* spp. remove the microhabitat for a variety of microherbivores (Bailey-Brock *et al.* 1980).

5.6.6 Effects on coral reef geomorphology

Echinoids are considered the ‘prime architects of the coral reef ecosystem’ (Ogden 1977). *Diadema antillarum* is responsible for eroding more calcium carbonate from the Caribbean coral-reef framework than is any other species (Ogden 1977, Steam & Scoffin 1977, Scoffin *et al.* 1980). More than 90% of the bioerosion of coral-reef framework in the Caribbean is by echinoids (Table 4). When released from predation-pressure, *Echinometra mathaei* forages like *D. antillarum* and effects an even greater rate of bioerosion (cf. Kuwait in Table 4). The grooves and holes made by echinoids contribute greatly to the topographic complexity of the coral reef.

R.H. Randall & Amesbury (1987) reported dense populations of *Echinometra mathaei* at Huahine Nui, French Polynesia, where 53 *E. mathaei* in a single colony of *Pocillopora eydouxi* was not exceptional. They described the stages of bioerosion of massive *Porites* sp. by *E. mathaei* as: ‘ 1) initial infestation of the coral colony where the polypoid surface has been killed, 2) continued evacuation which enlarges and deepens initial infested areas along with continued upward growth of polypoid areas which tends to produce a hillocky colony surface, 3) coalescence of evacuated areas forming isolated living pillars scattered over the original colony surface, 4) formation of knobs by evacuation of basal pillar regions and growth and enlargement on upper living pillar regions, 5) collapse of isolated knobs by continued basal excavation or physical breakage (may result in asexual propagation of the colony), 6) continued excavation of the remaining colony (commonly with no living polypoid surface area remaining) producing a honeycombed structure, and 7) continued evacuation and eventual collapse of the honeycombed mass to rubble’.

Based on published estimates of rates of bioerosion by *D. antillarum* and on rates of accretion by corals and coralline algae, Bak *et al.* (1984) calculated that following the great decrease in abundance of *D. antillarum*, the reefs should be accreting at eight times their previous value. However, Bak *et al.* (1984) pointed out the dangers of this deductive reasoning. The interactions in coral-reef systems are complex and it is unlikely that all can be foreseen. While the annihilation of *Diadema antillarum* may reduce the rate of reef bioerosion by an eight-fold factor, the decreased abundance of *D. antillarum* may also allow the build-up of a much larger standing stock of fleshy algae. This may, in turn, inhibit coral recruitment and growth.

5.6.7 Secondary geological effects

The bioerosion of the bases of corals by grazing activities of coral-reef

echinoids weakens coral colonies and makes them more susceptible to being toppled by wave action (cf. Fig. 2 in Ogden 1977 and Figs. 3 and 4 in Messiha-Hanna & Ormond 1982). Ogden 1977 noted the 'reef surface is literally dropping away from the coral bases'.

6 HOLOTHUROIDEA

6.1 *Functional roles*

All holothuroids collect food with buccal tentacles (Massin 1982a). Nearly all aspidochirotetes are deposit feeders and are segregated more on the basis of microhabitat distribution (Fig. 6A, B, C) than by the type of food selected (Sloan 1979, Sloan & von Bodungen 1980, Lawrence 1980, Massin 1982a). *Actinopyga mauritiana* (Fig. 6A) is solidly constructed and is distinctive in being found in high-energy microhabitats on coral reefs, feeding on diatoms growing on the surface of the surge channels (J. Lawrence, pers. comm.). Most aspidochirote holothuroids are found in low-energy habitats because they feed on sedimentary deposits.

Aspidochirote holothuroids generally are not selective for particle size (Yamanouchi 1939, Bonham & Held 1963, Bakus 1968, Sloan & von Bodungen 1980, Hammond 1982), but appear to be selective for organic matter content (Webb *et al.* 1977, Hammond 1983), especially for bacteria (Moriarty 1982), although bacteria are not a major component of the diet simply because bacteria comprise a small portion of the organic matter in the sediment (Moriarty 1982, Hammond 1983). High density patches of holothuroids are positively associated with relatively high organic content of sediments on sandy patches on reef flats, and negatively associated with regions of strong currents (Webb *et al.* 1977), wave action (Massin & Doumen 1986), and anaerobic sediments (Yamanouchi 1939). Some aspidochirotetes act as suspension-feeders (Lawrence & Kafri 1979, Sloan 1979).

Dendrochirote holothuroids (Fig. 60) are most often suspension-feeders, ingesting diatoms and particulate organic matter (Massin 1982a). Dendrochirotetes are prevalent on hard-substratum communities in temperate regions, but are generally scarce on tropical reefs (Pawson 1970, Bakus 1973). Exceptions occur; dendrochirotetes were very abundant in a community of hermatypic corals at southeast Taiwan near upwelling, although the coral community was not a true coral reef (pers. obs.). Dendrochirotetes are probably rare in clear-water coral-reef habitats because of the low concentrations of plankton and organic matter in the water column. It would be interesting to determine whether dendrochirote holothuroids will use their tentacles to take up sediment from substrata surrounding their burrows when long periods of insufficient food occurs in the water column (Massin 1982a).

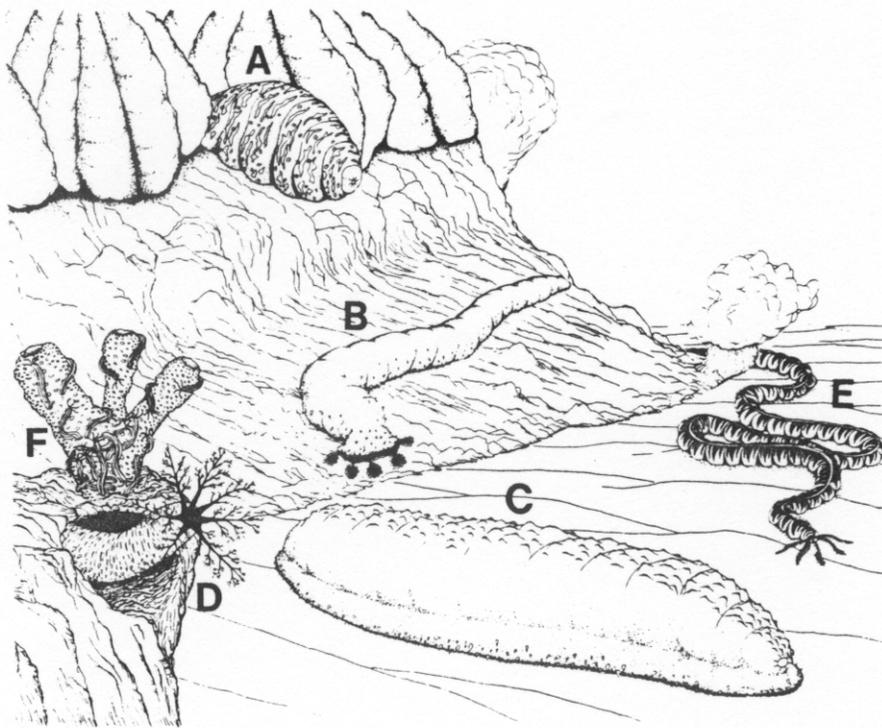


Figure 6. Diagrammatic representation of categories of coral-reef holothuroids.

Apodid holothuroids (Fig. 6E) tend to forage nocturnally as deposit feeders. *Synaptula lamperti* (Fig. 6F) feeds on organic exudates from sponges (Hammond & Wilkinson 1985). Although aspidochirotates such as *Bohadschia graeffei* (Fig. 6B) often occur on large sponges, working their tentacles over the surface of the sponge, they are most likely removing sediment from the sponge surface in the manner of *Ophiothrix* (Hendler 1984b) and not feeding on sponge exudates.

6.2 Mortality

Holothuroids form the basis of food-webs in temperate regions (Birkeland *et al.* 1982). On coral reefs, predation pressure has selected for toxicity in holothuroids {Bakus 1968,1973,1974,1981, Bakus & Green 1974}. *Charonia variegatus* generally preys upon echinoderms, including holothuroids (Parrish 1972). Holothuroids are a main item in the diet of *Tonna perdix* (Kropp 1983). A variety of crustaceans occasionally prey upon holothuroids

(Kropp 1983). Coral-reef holothuroids have a variety of escape and defense mechanisms (Bakus 1968, Kropp 1983).

6.3 *Effects on coral-reef communities*

There is very little information on 'genuine' coral-community holothuroids (Bakus 1973), so species inhabiting sandy substrata on nearby reef flats will also be considered. The abundances of aspidochirote holothuroids on some reef flats (5 to 35 m⁻², see Fig. 1 in Bakus 1973) and the amount of sediment passed by some tropical holothuroids (about 80 g dry weight day⁻¹ per median-sized individual: Mayer 1917, Yamanouchi 1939, Webb *et al.* 1977) are impressive. With these figures in mind, the hypothetical impact of deposit-feeders on community structure by incidental consumption of invertebrate recruits and microfauna (Dayton & Hessler 1972) might be even more applicable to the reef flat than to the abyssal benthos. However, meiofauna made up a small portion (ca. 1% available carbon) of the diets of holothuroid specimens taken from a Jamaican lagoon, and meiofauna ingested were a lower portion of the diets than they were of the available sediment (Hammond 1983). Diatoms were a major organic resource in the available sediments, but only a small portion of the diatoms ingested was assimilated (Hammond 1983). From the data available, it appears that non-living detrital material is the major source of nutrient for reef-flat aspidochirotetes. There is no substantive evidence that holothuroids are a controlling factor for reef-flat meiofauna or invertebrate recruitment on coral reefs.

Coral reefs are widely recognized as being very productive, often surrounded by oligotrophic seas (Sargent & Austin 1969, Kohn & Helfrich 1957), so recycling of nutrients is an important characteristic of the eco-system. Sander (1981) described 'benthic-pelagic coupling' as a mechanism of nutrient regeneration and Rhoads (1973) suggested that deposit-feeders can recycle or transfer nutrient-rich organic matter as fecal material to the degree that growth of suspension-feeders is enhanced. Massin (1980) found that the feces of a temperate holothuroid had consistently higher organic content than did the available sediment. Sloan & von Bodungen (1980) suggested that holothuroid feces are a potentially enriched food source for the benthos. Hammond (1983), however, found the organic content of tropical holothuroid feces to be similar to the surrounding sediment, there was no measurable enrichment of feces by bacterial growth 24 hours after the feces were deposited, and feces did not maintain their integrity beyond 24 hours. Enrichment of the environment by holothuroids near coral-reefs does not appear to be of ecological significance (Hammond 1983).

The reworking of sediments and the changing of grain size of ingested particles by mechanical (grinding) or chemical (dissolution) action has been studied extensively for tropical deposit-feeding holothuroids. Hammond

(1981) found that the amount of dissolution of calcium carbonate was a measurable, but ecologically insignificant, portion (2% or less) of the annual carbonate fixation on reef flats. Yamanouchi (1939) also found that change in size of ingested particles by holothuroids to be of no ecological significance.

True coral-reef holothuroids such as *Actinopyga mauritiana* are usually not in dense populations. Holothuroids on reef flats are often in dense populations, but studies have not indicated their ecological impact. To my knowledge, there has not been a controlled field experiment yet attempted to determine the influence of holothuroids on coral-reef or nearby sand flats (Massin 1982b).

7 DISCUSSION

Species of echinoderms most influential in coral-reef ecosystems are characteristically generalists, adaptable to a variety of situations, and with behavioral, distributional, and dietary plasticity. They are capable of exploiting a variety of environments and their diets result as much from food availability as from feeding preference. Their functional roles in coral-reef communities change greatly as their environmental situations change. It is difficult to try to use the 'niche' paradigm for influential coral-reef echinoderms. A 'niche' could always be described with a large number of qualifiers and dimensions, but this is ponderous and tautological. A paradigm based on contingency paths would be more useful.

Some primary conditions for a contingency (conditional) diagram are predation pressure, recruitment success, and disease. Long-term geographic differences within a species concerning behavior patterns, average size of individuals, diet, abundance, and functional role in the community may be related to predation pressure. *Eucidaris thouarsii* is more abundant, larger in size on the average, and forages openly on corals and crustose coralline algae by day and by night in the Galapagos because of reduced predation pressure from fishes in the Galapagos (Glynn & Wellington 1983).

Echinometra mathaei is more abundant, larger in size on the average, and forages openly on algal turf by day and by night at some localities in the northern Gulf of Arabia and on the coast of Kenya because of reduced predation pressure from fishes (N. Downing pers. comm., McClanahan & Muthiga 1988). The influence of grazing by *Diadema antillarum* may be exceptionally great at certain locations on Caribbean reefs in historical times because overfishing by humans may have lowered the predation pressure on *D. antillarum* (Hay 1984b, c).

Coral-reef echinoderms are preyed upon by a polyphyletic list of predators. The pervasive importance of predation pressure on coral-reef echinoderms can be observed in their nocturnal foraging behavior, homing behav-

ior, and morphological (spines, pedicellariae, tough integument) and chemical (toxins) defense mechanisms. Individuals forage during the day and decrease their homing fidelity when predation pressure per individual is reduced (either the predators decrease in abundance or the prey become much more common).

Sloan (1980) and Menge (1982) concluded that the factors that made asteroids influential in benthic communities was their flexibility or pliability in foraging behavior, food selection, general morphology, digestive system, and body size. While this is characteristic of asteroids of temperate regions, *Acanthaster planci* is the only asteroid with these traits on coral reefs. The foraging biologies of coral-reef asteroids are generally severely constrained by their rigid calcareous integument, compelled by the intense predation pressure on echinoderms on coral reefs (Blake 1983). This is why *A. planci* is the only coral-reef asteroid that influences the community on a scale comparable to asteroids in temperate regions.

Although predation pressure can often be cited as the conditional factor responsible for long-term differences on a geographic scale or an evolutionary scale in the ecological role of a species, successful recruitment is more likely the contingency factor for abrupt increases in local abundance. There is no known mechanism by which a release of predation-pressure on adults could allow a local population increase of several orders of magnitude during one year for *Acanthaster planci*. With millions of eggs released per individual, an increase of a tenth of a percent in larval or recently metamorphosed juvenile survival would allow a thousand-fold increase in recruitment success (Birkeland 1982, Lucas 1986).

Vagaries of nutrient pulses, current patterns, and larval survival are major factors leading to the variability in recruitment success that characterizes broadcasting echinoderms. After successful larval recruitment, however, a population must survive the postlarval phase in the life-history before an outbreak of adults will occur. *Diadema* and *Acanthaster* are characterized by rapid growth through the juvenile phase of their life-cycle, a factor that is important in determining their abundances. Although the larval biology of *Culcita* is similar to that of *Acanthaster*, *Culcita* takes a much longer period to acquire the adult morphology and feeding behavior. This extends the time it spends in the more vulnerable juvenile stage. Even with equivalent success in larval recruitment, *Culcita* would never reach the abundance of *Acanthaster* during outbreaks.

Increases in population size on a scale too large to be accounted for by redistribution (immigration) must involve reproductive recruitment success, even if the population build-up is allowed by a decrease in predation-pressure or an increase in carrying capacity of the habitat (cf. end of Section 3.6). The basis of attributing the large differences in echinoid abundances mainly to release of predation-pressure rather than increased recruitment success alone

is the build-up of population size over several years (e.g. a five-fold increase in biomass of *E. mathaei* over a fifteen-year period [McClanahan & Muthiga 1988]) or the maintenance of high population densities over several decades or longer (e.g. *Eucidaris thouarsii* in the Galapagos or *Diadema antillarum* in the Caribbean prior to the mass mortality of 1983). The basis of attributing large differences in *Acanthaster planci* abundances mainly to recruitment success through survival of larvae and juveniles is the abrupt increase of population density of 4 to 6 orders of magnitude. Predators are overwhelmed by this magnitude of population increase.

Disease is a most effective factor in mortality when populations are dense. Water is an effective medium for transport, and disease has been influential in large-scale changes in marine communities. Scheibling (1984) suggested that echinoid disease might be a toggle-switch for large-scale oscillations between two alternative stable states of the northwestern Atlantic coastal benthos: kelp beds or barren grounds. This could also be the case for the Caribbean.

Not only are the functional roles or 'niches' of echinoderm species on coral reefs influenced largely by the above contingencies, but the reactions of the reef communities are also influenced by the local conditions. For example, on the north coast of Tutuila (American Samoa), wave impact is a contingency for both the behavior of the predator (*Acanthaster planci* moves onto shallow reef-flats in areas protected from waves, but avoids shallow water in high-energy regions) and the response of the prey (*Acropora* spp. reinvade the reef front by fragmentation, tumbling from the refuge in the surf zone, and reattachment on the reef front in high-energy regions, but *Acropora* spp. reinvade mainly by recruitment of planulae in protected areas) (Birkeland & Randall 1979). Massive colonies of *Pavona* and *Gardineroseris*, ordinarily protected from predation by *A. planci* on eastern Pacific reefs by a surrounding community of live *Pocillopora* and their protective symbiotic crustaceans, become accessible to *A. planci* after an El Nino event kills the *Pocillopora* (Glynn 1985a, b). Foster (1967) documented the effects of *Diadema antillarum* on the algal community as being contingent upon seasonal and spatial changes in wave impact.

While the abundance, behavior, functional role, average individual size, and even morphology of influential species of coral-reef echinoderms change with contingency, factors such as predation-pressure, recruitment success, and disease, coral-reef echinoderms which are not so influential are less plastic and more specialized. It is these less influential species for which the 'niche' paradigm might be applicable. It is because of morphological or physiological constraints that the less influential species are specialized and, when a potential competitive interaction exists, more vulnerable to exploitative competitive pressure. *Colobocentrotus* and *Heterocentrotus* have specialized morphologies and probably physiologies that restrict them to specific

areas of the coral reefs (Ebert 1982). *Diadema*, *Echinometra* and *Eucidaris*, in contrast, can function in a variety of circumstances and their influences will be much greater if conditions allow for a large population increase. Similarly, the morphology of *Culcita* restricts its behavior and feeding. It will not have as important a role in determining community structure as will *Acanthaster*, even if equally abundant.

Atlantic and Pacific reef communities have so many fundamental differences that it is difficult to generalize about the role of echinoderms in coral-reef communities other than to state that the influential species are generalists. Nine species of asteroids in the Pacific feed on living corals or coral mucus, and *Acanthaster planci* has a major effect on reef community structure when it becomes abundant. No Atlantic asteroids feed on corals or are known to have a major effect on community structure. Conversely, diadematis appear to have a much greater effect on community structure and processes in the Caribbean and continental-shelf Pacific than in Oceania.

The tropical Atlantic and tropical Pacific are very different in species richness of echinoderms. More than 1100 shallow-water (upper 60 m depth) species of echinoderms occur in the Indo-West Pacific faunal region and only about 150 comparable species occur in the West Indian (Caribbean) faunal region (A.M. Clark 1976). The eastern tropical Pacific (Panamic) shallow-water echinoderm fauna is richer than the western Atlantic shallow-water echinoderm fauna, with 27 species of echinoids (including both regular and irregular echinoids) in the eastern Pacific and 24 species in the western Atlantic (Chesher 1972). About 37 shallow-water asteroid species (including sand-bottom families such as Luidiidae and Astropectinidae) occur in the eastern Pacific compared to about 18 species in the tropical western Atlantic (Chesher 1972). Most echinoid genera in the shallow waters of the eastern Pacific originated in the Caribbean region before the rise of the Isthmus of Panama (Mayr 1954). In contrast, all but three of the asteroid genera appear to be more closely related to Indo-West Pacific asteroids (Chesher 1972).

Another notable difference between the oceans is the relative uniformity of dispersion of the coral-reef echinoderm fauna around the Caribbean in comparison to the sharp decrease in numbers of taxa on a west to east gradient in the tropical Pacific (Table 1). The gradient in species richness in the tropical Pacific provides a 'natural experiment'. Although physical and biological factors change along the same gradient, two conclusions can be made: 1) larval dispersal is an important factor in community structure and 2) some species are more influential in the dynamics and structure of the communities than are others. This gradient in species richness indicates that speciation and dispersion probably have more effect on species richness of coral-reef echinoderms than does competition.

To restate this conclusion from the reverse perspective, the coral communities at the two ends of the gradient in the tropical Pacific appear to operate in

similar ways. When abundant, *Acanthaster planci* is a major disruptive factor in patterns of occupation of space, whether in Malaysia or Tahiti, and *Diadema* spp. and *Echinometra mathaei* are major factors in bioerosion. However, the community structure of reefs in regions with many species of crinoids (East Indies) seems similar to those in regions in which crinoids are absent (e.g. Tahiti, Tuamotus, Line Islands, Hawaii). I have not detected a major differences in the functioning of these reefs that could be attributable to the presence or absence of crinoids. Ophiasterids also may not have a controlling effect on coral-reef community structure. Although crinoids or ophiasterids process a substantial amount of organic matter and energy through their population when they are abundant, this does not demonstrate a qualitative effect on other species or on the coral-reef community as a whole. On the other hand, *Acanthaster planci* is an exceptionally influential species, and the absence of this single species in the Caribbean brings about some fundamental differences in the dynamics of Atlantic and Pacific reefs which extend through several trophic levels.

In addition to Atlantic-Pacific differences, there are fundamental differences between continental-shelf reefs and oceanic reefs. Because of differences in population density, generalizations regarding echinoids may be valid for either shelf reefs or for oceanic reefs (Table 3), but not necessarily for both.

At insular Caribbean St Croix, *Diadema antillarum* is the most important agent of herbivory and the effect of herbivorous reef fishes on the coral-reef community is considerably less, so fishes might be disregarded (Carpenter 1986). The same pattern has been documented at continental Caribbean Panama (Foster 1987). In contrast, Hatcher (1982) considered mainly herbivorous fishes and some herbivorous invertebrates as important at One Tree Island on the Great Barrier Reef, and disregarded echinoids, presumably because of their scarcity. Carpenter (1986) pointed out that an annual average of 97% of the backreef/reef crest algal turf production at St Croix entered the animal community through the herbivores while Hatcher (1982) reported that about 50% of algal production entered the animal community through herbivores on the Great Barrier Reef. In both cases the remainder was processed by detritivores or decomposers. The differences between the proportions of benthic algal production entering the foodweb through herbivores at St Croix and One Tree Reef results from the differences in the foraging patterns of the more important grazers. The echinoids were abundant at St Croix and therefore grazed intensely in a generalized manner. The schooling herbivorous fishes were abundant at One Tree Reef and foraged over a wide range and generally fed more selectively than did echinoids. The intense, generalized grazing by echinoids within a relatively small home range produces a high rate of turnover, a low standing stock of algal turf, and an increased rate of algal production per unit biomass (Carpenter 1986). The

selective, albeit intense, grazing by schooling herbivorous fishes facilitates succession of benthic algae (Birkeland *et al.* 1985). This produces a standing stock of morphologically tough or chemically defended algae that is not directly consumed by herbivores but which eventually goes through the detritivores or decomposer food web. It would be of interest to determine the ratio of echinoid to herbivorous fish densities at which the nature of the coral-reef food web makes the switch from a system in which the algal production enters the food web mainly through herbivores to one in which the algal production enters mainly through decomposers.

Echinoids may also be a major factor determining whether the reef is accreting or eroding. Two large scale events may have recently changed the progress of reef development in opposite ways in two geographic regions. Under previous conditions in the Galapagos, grazing of living corals by *Eucidaris thouarsii* was sufficient to limit reef growth (Glynn *et al.* 1979, Glynn & Wellington 1983). With the death of a major portion of the corals in the Galapagos during the El Nino of 1982-1983, the net bioerosion of reefs by *E. thouarsii* has probably increased greatly (P.W Glynn pers. comm.). Conversely, the mass mortality of *Diadema antillarum* may result in an eight-fold increase in net accretion (Bak *et al.* 1984) in the Caribbean (cf. Section 5.6.6).

An increasing rate of sea-level rise over the next century has been predicted (Hoffman *et al.* 1983, Cubitt 1985). Echinoderms could be a critical component involved in the effect of this change on coral-reef communities. On continental margins, near large rivers of high islands, and in regions of upwelling, scleractinian corals are at a disadvantage to sessile heterotrophs and algae because of the ability of the latter to have a greater and more rapid response to a pulse of nutrients through an increase in rate of growth (Birkeland 1977, 1987). *Acanthaster planci*, diadematids, *Echinometra* spp. and *Eucidaris thouarsii* can be deleterious to scleractinian coral communities when abundant and they appear to be most abundant in areas with pulses of nutrient input (Birkeland 1982), continental margins (Table 3), or regions of high biological production (Wooster & Hedgepeth 1966).

Abundant diadematids are inimical to coral recruitment (Sammarco 1980), while schooling herbivorous fishes are often beneficial (Birkeland 1977). Diadematids are generally more prevalent in the Caribbean and on continental shelf reefs (Table 3), and schooling herbivorous fishes are relatively more influential on atolls. As a consequence, coral reefs may have a larger net accretion rate on atolls than on continental shelves or on large high islands because of less competition for space with sessile heterotrophs, because of reduction of competitive pressure from algae by herbivorous fishes which avoid damaging coral recruits, and because of lower densities of *Acanthaster planci* and echinoids which are detrimental to corals when abundant. However, coral reefs on atolls can only grow upwards as the sea-level rises;

their future depends upon their abilities to grow fast enough. Corals on high islands and on the margins of continents can recruit upward onto inland substrata as the sea-level rises.

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