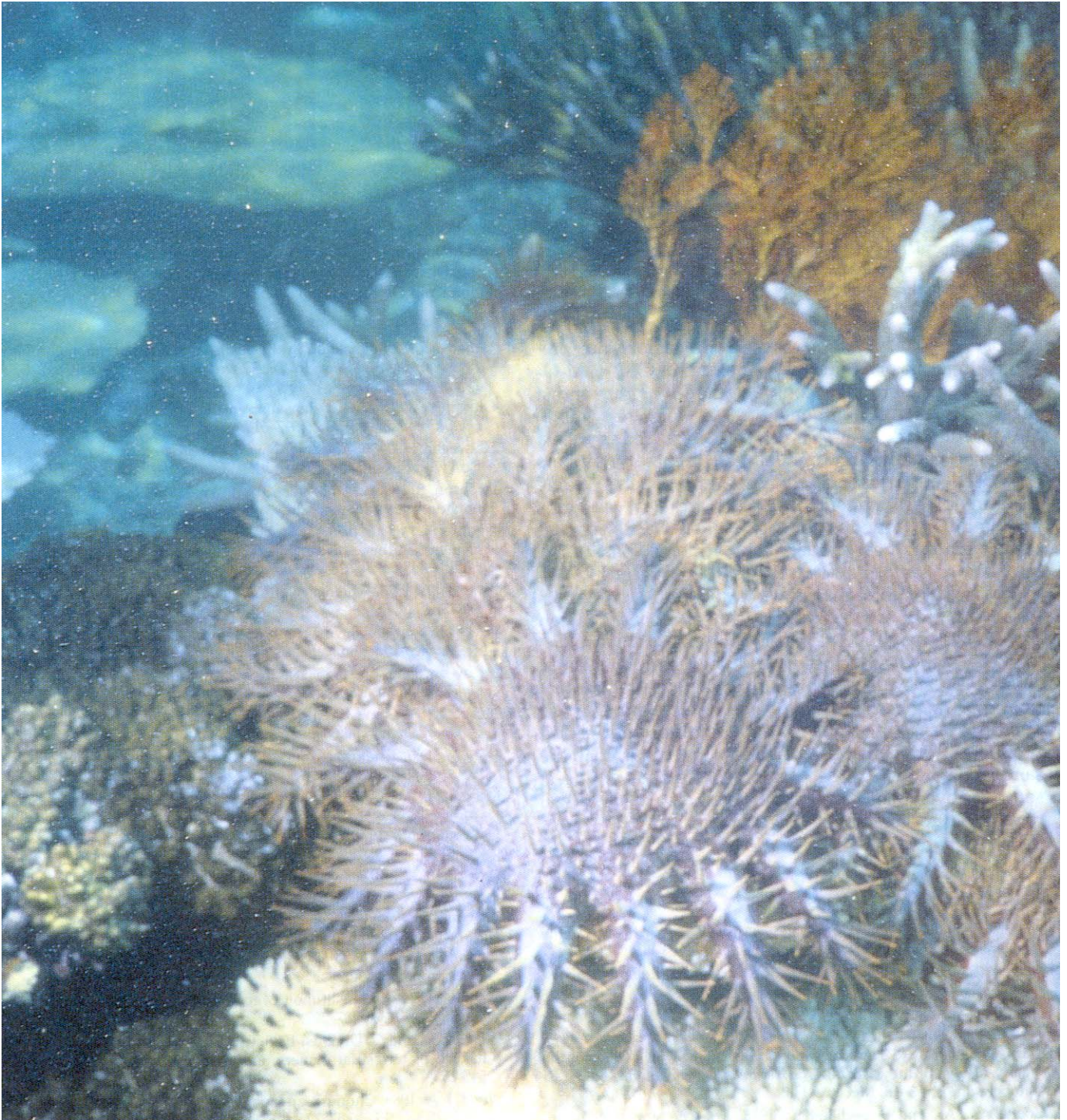
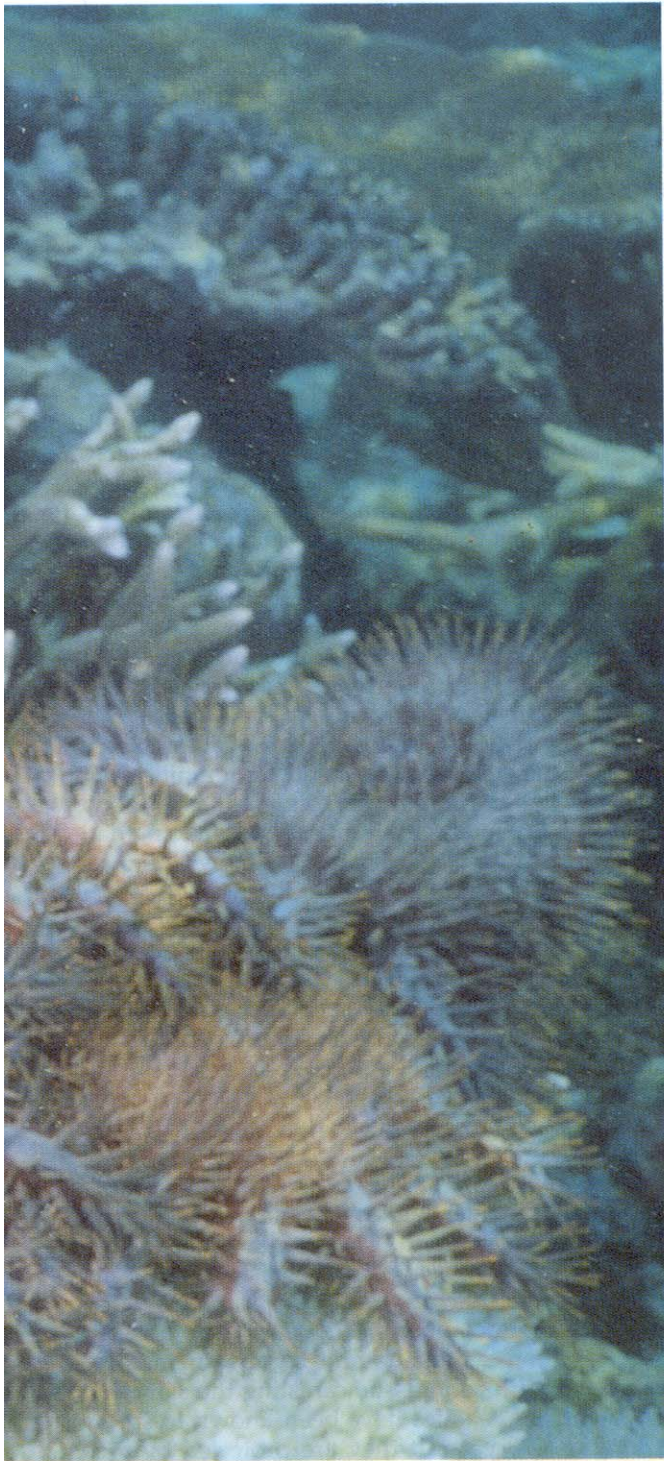


The Faustian Traits of The Crown-of-Thorns Starfish

Charles Birkeland



The crown-of-thorns starfish, *Acanthaster planci*, is one of the most influential species in the diverse biotic communities that make up tropical reefs. Although nine or ten species of starfish in the Pacific occasionally feed on coral or coral mucus, the crown-of-thorns starfish affects the reef community to a far greater extent than do any of these. In a short period of time, *A. planci* can alter the composition of a coral reef over large areas. An individual crown-of-thorns starfish digests an average of about 5 to 6 m² of coral surface per year (Pearson and Endean 1969; Dana and Wolfson 1970). An outbreak of *A. planci* may consist of tens of thousands to millions of



individuals, capable of devouring from 0.5 to 5 or 6 km² of living coral tissue in a single year (Fig. 1).

The impact of the crown-of-thorns starfish has been dramatic (Fig. 2). Between late 1968 and early 1969 it killed over 90% of the coral along 38 km of coastline in northwestern Guam (Chesher 1969). Extensive mortality also occurred at 21 of 45 islands surveyed in Micronesia in the period from 1969 to 1972 (Marsh and Tsuda 1973). Commenting on the situation in the northwestern Pacific, Yamaguchi has stated that "it is safe to assume that most reefs in the Ryukyus have been devastated in the past 15 years" (1986, p. 24). In the southwestern Pacific, an outbreak on the Great Barrier Reef that apparently began in the vicinity of Green Island before 1962 spread southward in a series of subsequent outbreaks over the next ten years, traveling hundreds of kilometers (Kenchington 1977). In recent surveys covering hundreds of reefs in the Great Barrier system, about 28% were found to be affected to varying degrees by *A. planci* (Zann and Eager 1987).

The ecological effects of these incursions are complex. When corals are eaten by the crown-of-thorns

Structural traits otherwise found only in temperate starfish have produced a fast-growing, voracious, but relatively fragile tropical predator

starfish, they are replaced initially by algae (Fig. 3). This change is occasionally followed by an increase in sessile animals other than reef-building corals, such as alcyonacean soft corals or *Terpios* sponges (Pearson and Endean 1969; Bryan 1973; Nishihira and Yamazato 1974). In some cases, coral communities composed predominately of branching *Acropora* corals have collapsed into rubble several months after predation by *A. planci*, demonstrating the major effect of the crown-of-thorns starfish on reef topography (Sano et al. 1987).

As algae invade the space vacated by living coral tissue killed by *A. planci*, the food supply of herbivorous fishes increases and that of coral-eating fishes decreases. Thus a decrease in the density of populations of coral-eating fishes usually follows an outbreak of *A. planci* (Bouchon-Navaro et al. 1985; Williams 1986; Sano et al. 1987; Wass 1987). An increase in the population densities of herbivorous fishes occurs sometimes, but not always. At American Samoa, Wass (1987) found that herbivorous fishes increased from about 9 to 44% of the reef-fish population when the corals were killed by *A. planci*. At Moorea in French Polynesia the butterfly fish *Chaetodon*

Figure 1. A phalanx of crown-of-thorns starfish grazes on a coral reef off the coast of Palau. *Acanthaster planci* feeds by extruding its stomach over the surface of the reef and digesting the coral externally. Rapid growth and a high ratio of stomach surface area to total biomass make *A. planci* a formidable predator in the coral-reef community. Crown-of-thorns starfish tend to feed in tight aggregations, often, as here, piled several layers deep; chemicals released when corals are damaged attract more *A. planci* to the scene. (Unless otherwise noted, all photos are by the author.)

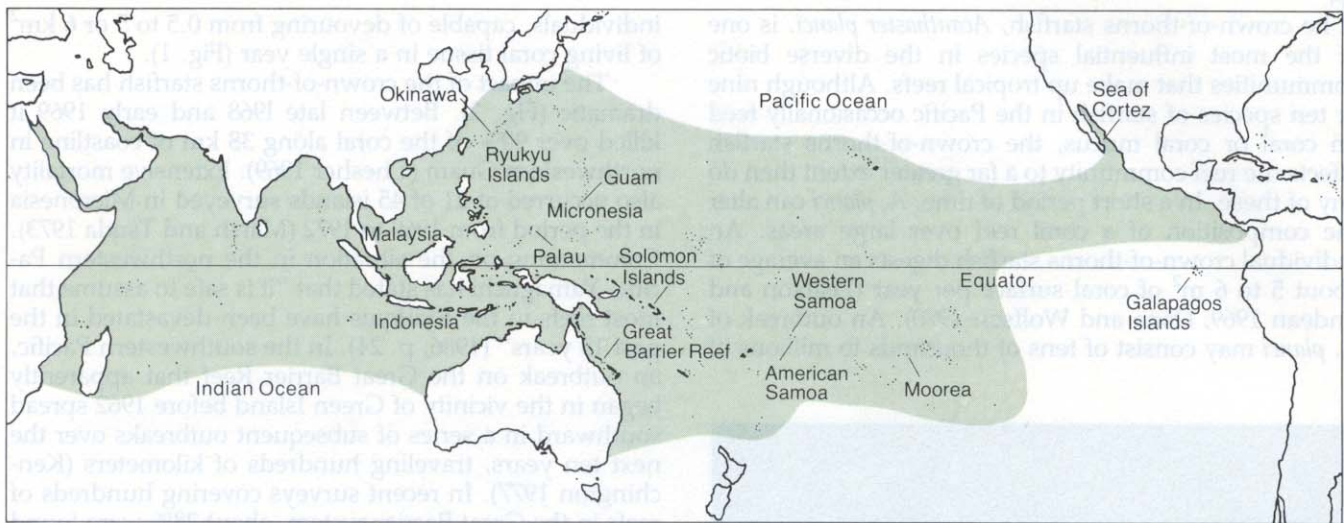


Figure 2. The crown-of-thorns starfish is found throughout the tropical Pacific and Indian oceans in the shaded area; it is not present in the Galapagos Islands or in the waters south of Panama. *A. planci* is thought to have evolved in the area of Malaysia and Indonesia, perhaps when the archipelago was partitioned into isolated seas during the recent glacial periods. It may then have spread rapidly across the Indo-Pacific, taking advantage of the vast food resource offered by the coral reefs. The ability of *A. planci* to extend its range is seen in modern outbreaks, which are sometimes followed by a series of secondary outbreaks hundreds of kilometers downstream along major water currents. (After Zann and Eager 1987.)

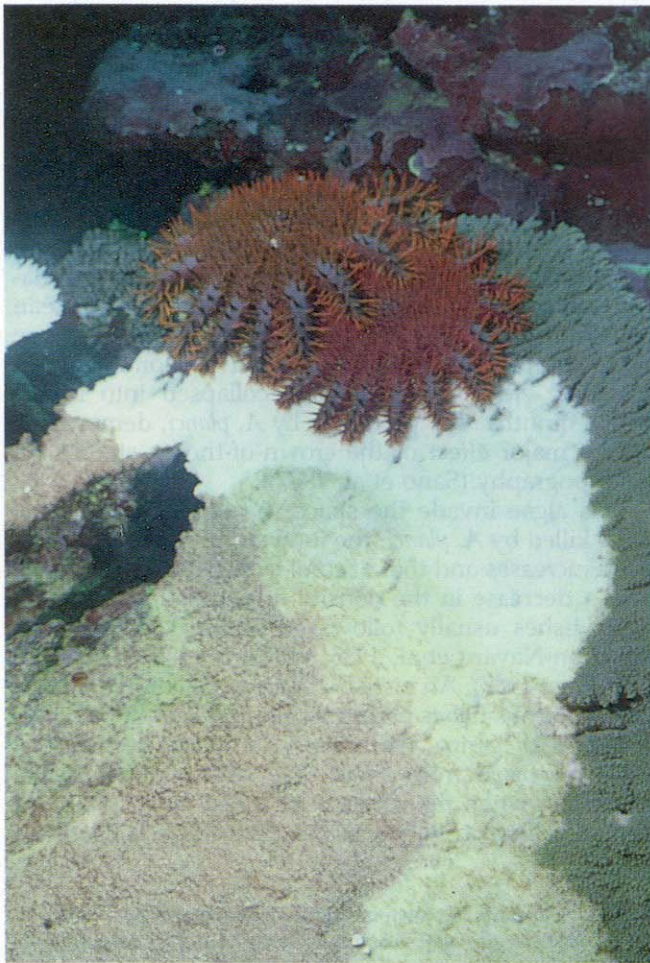


Figure 3. The ecological effects of the crown-of-thorns starfish are visible in this view of two starfish feeding on tabletop *Acropora*. The green area at the right indicates living coral tissue. Coral skeleton recently cleaned of living tissue by *A. planci* is white. Increasingly darker shades of gray at the left show algal succession on the coral skeleton.

citrinellus, an algae-eater, also increased in abundance, replacing two coral-eating species (Bouchon-Navaro et al. 1985).

However, increases in herbivorous fish populations were not observed following outbreaks of *A. planci* on the Great Barrier Reef and at Okinawa (Williams 1986; Sano et al. 1987). Although the removal of a food resource often leads to a decrease in a population that consumes it, an increase in the carrying capacity of a community does not necessarily result in an increase in population. Such increases depend also on the increased survival of larval recruits. It is likely that other factors independent of carrying capacity interfered with the recruitment of herbivorous fishes during the years studied.

The crown-of-thorns starfish can have a major influence on the structure of coral communities even at densities lower than those classified as an outbreak (Glynn 1976). Coral communities exposed to predation in the eastern tropical Pacific are generally dominated by branching pocilloporid corals (Glynn 1976). In similar areas where *A. planci* is absent, massive agariciid and poritid corals are most prominent (Birkeland et al. 1975; Glynn and Wellington 1983). Certain species of crabs and shrimps that live among the branches of pocilloporid corals drive away the crown-of-thorns starfish by nipping at its tube feet and spines. *A. planci* readily accepts pocilloporid corals as prey when they are unprotected, but larger colonies are usually defended by these crustacean symbionts.

The repulsion of the crown-of-thorns starfish by crustacean defenders effectively shifts its feeding preference from pocilloporid to agariciid corals. However, dense stands of *Pocillopora* can act as refuges for massive agariciid corals (Glynn 1976). *A. planci* will not move across a continuous band of *Pocillopora* both because of the crustacean symbionts and because nematocysts in the pocilloporid coral tissue can sting the starfish's tube feet. Agariciid colonies have been known to survive for as long as 190 years if they are protected by a contin-

uous surrounding band of *Pocillopora* colonies (Glynn 1985).

When many of the pocilloporid colonies on the Pacific coast of Panama were killed by the elevated water temperatures produced by the El Niño of 1982–83, this barrier to predation by *A. planci* was eliminated. The agariciid corals were not as strongly affected by the rise in water temperature, but they were eaten by the crown-of-thorns starfish after the high temperatures had killed the *Pocillopora*. The extent of agariciid mortality on this occasion indicates that *A. planci* is a powerful factor in shaping reef structure even at relatively low densities.

One modern approach to ecology is to concentrate on ecological processes and to avoid referring to individual species as much as possible (Mann 1982). However, some species have such distinct, controlling effects on communities that they cannot be averaged into trophic levels or rate processes. Their natural histories must be taken into account if the ecological system is to be understood.

Why outbreaks occur

Population increases of 5 to 6 orders of magnitude have been observed in the crown-of-thorns starfish within a single year (Birkeland 1982). No mechanism directly affecting adult starfish has yet been discovered that could account for increases of such magnitude and abruptness. Factors affecting larval *A. planci*, however, are plausible causes. An individual can produce as many as 65 million eggs each spawning season (Kettle and Lucas 1987). Thus a small improvement in the rate of larval survival would result in a tremendous increase in numbers. The distribution of outbreaks following an initial event indicates that *A. planci* spreads over hundreds of kilometers downstream along major water currents (Kenchington 1977; Yamaguchi 1986). This pattern suggests that larval survival and distribution are probably key factors in determining the time and place of outbreaks.

Evidence from a variety of sources indicates that nutrients—phytoplankton and perhaps bacteria and organic detritus—are an important element in larval survival. Records of previous outbreaks indicate a strong correlation with heavy rainfall, which facilitates terrestrial runoff (Birkeland 1982). Outbreaks usually occur in the coastal waters of high islands or along continental shelves,

where runoff from the land can release a pulse of nutrients; they rarely occur at atolls in intermediate locations. Such nutrient pulses are often associated with phytoplankton blooms. The spawning season of *A. planci* coincides with the beginning of the rainy season on both sides of the equator—the time phytoplankton blooms are most likely to occur. In controlled laboratory experiments, Lucas (1982) has shown that *A. planci* larvae survived on particular species of phytoplankton only when these nutrients occurred at densities characteristic of a phytoplankton bloom.

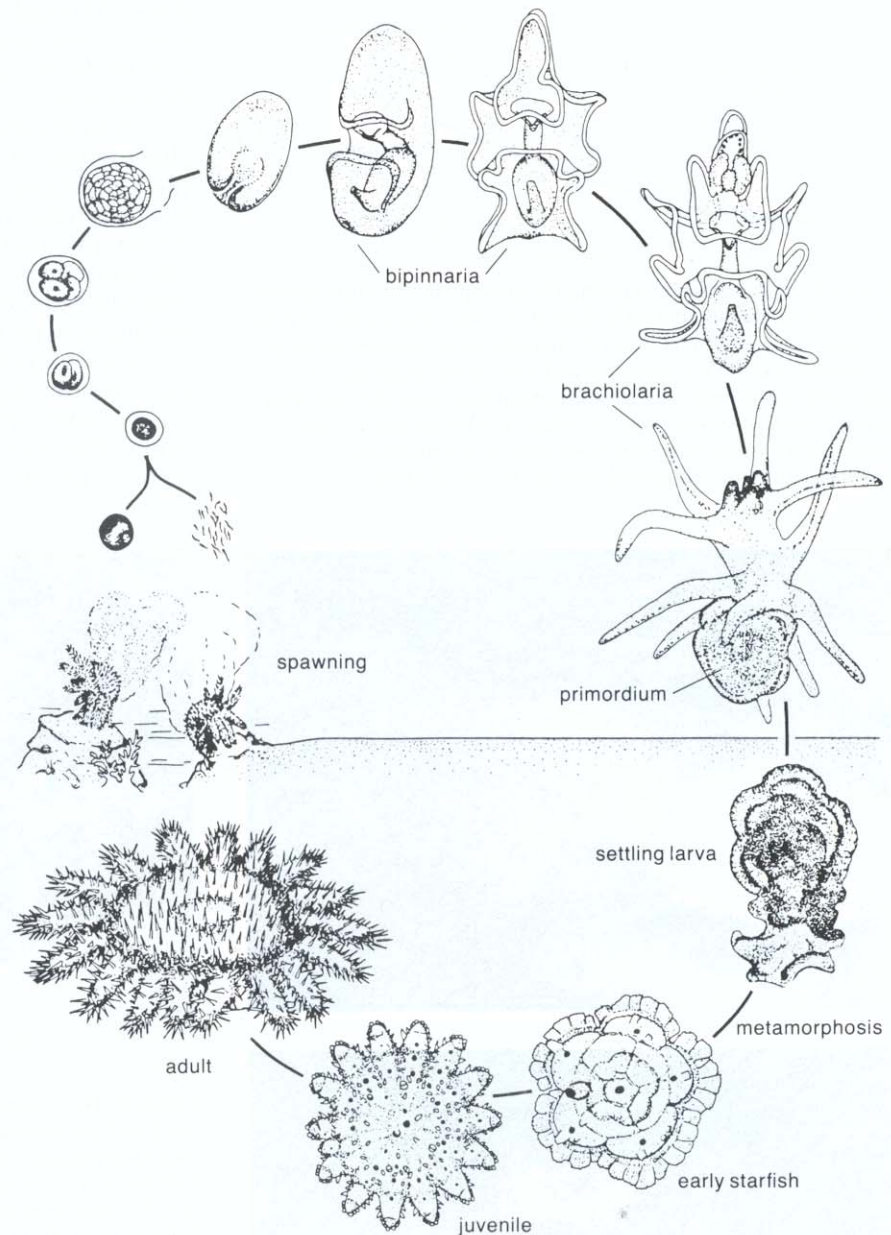


Figure 4. The life cycle of the crown-of-thorns starfish is distinguished by a larval stage lasting two to three weeks followed by rapid growth through the vulnerable juvenile stage. The primordium of the larva in the late brachiolaria phase is the early form of the small starfish. The settling larva attaches itself to the ocean floor by means of the brachiolar arms and a small adhesive disk located between the arms. The primordium then absorbs the larval body and grows into a small starfish, which crawls away. The newly metamorphosed starfish has five arms, but over the next few months the juvenile acquires a new arm every nine or ten days. The average adult *A. planci* has from 14 to 18 arms, although some individuals may have as few as 8 or as many as 21. (Drawing © Australian Institute of Marine Science.)

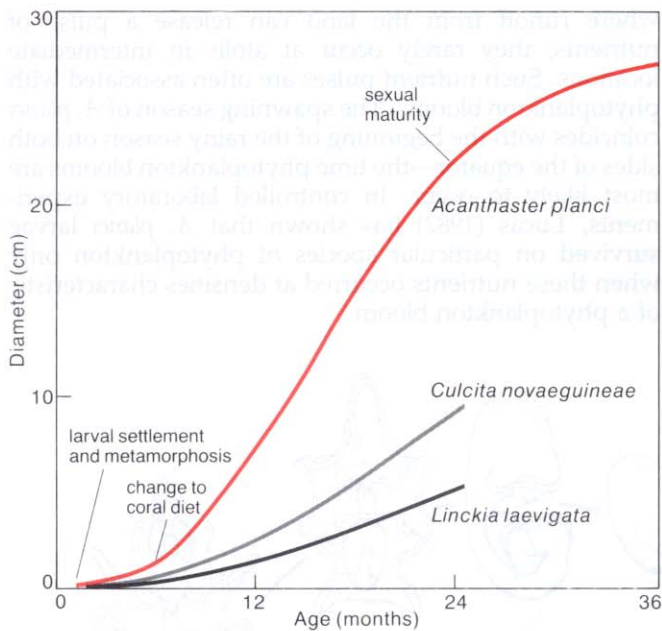


Figure 5. In this graph comparing the growth rates of three species of coral-reef starfish, the early shift of *A. planci* from a juvenile diet of algae to an adult diet of coral coincides with a conspicuous spurt in growth. *Culcita novaeguineae* and *Linckia laevigata* do not change to adult form until they are about two years old, and their growth is much slower. Once *A. planci* reaches sexual maturity, some energy is diverted from body growth to reproductive products, and thus the growth rate slows considerably.

By devising a way to raise larvae in chambers near a coral reef both in ambient seawater and in seawater enriched with phytoplankton, Olson (1987) demonstrated that they could survive in concentrations of nutrients normal for coral reefs—that is, in the absence of phytoplankton blooms. This suggests that the diversity of nutrients in natural seawater may enhance the development of larvae, as opposed to the controlled monocultures of food used in the laboratory. However, the mean length of time required for larvae to reach a late stage of development was about 9% less for enriched seawater than for natural seawater—12.6 as compared to 13.8 days. Although this difference was statistically significant, Olson concluded that it was not large enough to explain the abrupt escalation of population that occurs in an outbreak.

A large variation in recruitment from year to year is characteristic of coral-reef animals whose larvae feed on phytoplankton. The larval biology of some tropical starfish is similar to that of *A. planci* (Fig. 4; Yamaguchi 1973a). But starfish with nearly identical larval histories can have very different rates of recruitment due to characteristics of the juveniles and events following metamorphosis (Birkeland 1974).

Crown-of-thorns starfish as small as 8 to 10 mm in diameter can change from the juvenile mode of feeding on encrusting algae to the adult mode of preying upon corals. This transition begins from 4½ to 7 months after metamorphosis and takes about a month (Yamaguchi

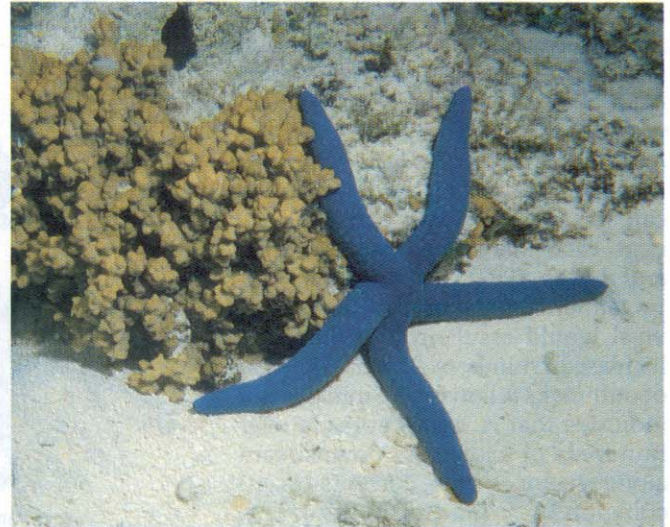


Figure 6. The crown-of-thorns starfish contrasts sharply with other coral-reef asteroids not only in growth rate but in structure. With its disk-shaped body and multiple prehensile arms, *A. planci* (upper left) has a large surface area compared to other tropical forms. Adults range from 25 to 40 cm in diameter, although they can be as large as 60 to 70 cm. The stomach covers an area about the size of the central disk—approximately half the total diameter. *C. novaeguineae* (lower left) is typical of the heavy, robust reef starfish of the family Oreasteridae. Its thick, calcareous skeleton is probably a good defense against predation by most fish, but limits the prey available to it. The brightly colored *L. laevigata* (above) is a typical member of the Ophidiasteridae, a family of reef starfish with finger-like arms and a small central disk. *L. laevigata* is not preyed on by most fishes, perhaps because of the high ratio of extremely thick skeleton to digestible tissue. (Photos of *C. novaeguineae* and *L. laevigata* courtesy of R. F. Myers.)

1973a, 1974; Lucas and Jones 1976; Lucas 1984). Once the juvenile switches to an adult diet of corals, its rate of growth increases significantly (Lucas 1984; Zann et al. 1987). An individual can grow to a diameter of 20 to 25 cm in about two years (Lucas 1984; Yamaguchi 1974). At the time it reaches sexual maturity, *A. planci* is several times larger than most other starfish species at the same stage of development (Fig. 5; Lawrence 1987).

By contrast, *Culcita novaeguineae*, another starfish that feeds on corals, changes from a flat, pentagonal juvenile to a cushion-form adult at a diameter of about 9 cm—ten times the width and about eighty times the surface area of *A. planci* when it makes the transition from juvenile to adult diet (Fig. 6; Yamaguchi 1973b). *C. novaeguineae* makes the change to adult form at about two years of age, or about four times the age of *A. planci* at its changeover (Yamaguchi 1977a). Another common asteroid of coral reefs, *Linckia laevigata*, may make the shift to adult form at a diameter of about 5 cm, when it is approximately two years old (Yamaguchi 1973b, 1977b).

The growth of juvenile *A. planci* may be slower if corals are not readily available (Lucas 1984; Zann et al. 1987). If a dense larval population occurs where corals are scarce, growth and survival rates might not be much better than those of other coral reef starfish. In areas where corals are common, however, dense recruitment of *A. planci* larvae might result in an outbreak because of the rapid switch to a diet of corals. In other asteroid species, an individual that first obtains a good meal has been observed to grow several times larger than other individuals in the same group that obtained meals later, and its chances of survival are greater (Mead 1900). Nauen (1978) found that starfish may not grow for several months until they come upon a good meal, after which they begin to grow.

The crown-of-thorns starfish has an exceptionally large area of food intake—the extruded stomach—in relation to the biomass it supports (Fig. 7; Birkeland, in press). This high ratio between the ability to take in food and total biomass is probably an important factor in its relatively rapid growth. Other large coral reef starfish have a much greater biomass to support in relation to the size of their feeding apparatus—what might be called a “brontosaurus handicap.” All juvenile asteroids remain concealed until they reach adult size, whether or not they have attained reproductive maturity. The rapid growth of *A. planci* through the especially vulnerable juvenile stage increases its chances of survival after metamorphosis.

Structure and success

In the shallow waters of temperate regions starfish have a controlling influence on benthic communities (Menge 1982), but most of the diverse array of asteroids on coral reefs have a negligible effect on their communities. The large stomach surface of *A. planci* allows it to consume coral tissue at five or six times the rate of *C. novaeguineae*, the next most important asteroid predator of corals (Glynn and Krupp 1986). But a more crucial characteristic that sets *A. planci* apart from other coral-reef starfish is its thin, pliable form. Other large starfish that evolved on coral reefs developed thick, calcareous bodies. *A. planci*

has a body form that is large, multi-armed, elastic, and prehensile—traits that are common in influential species in temperate regions but which are found in no other starfish on coral reefs. The flaccid, disklike structure of *A. planci* not only makes it the most efficient of the coral-reef asteroids in rapid growth, allowing it to pass quickly through the hazardous juvenile stage, but also permits it to prey upon large coral colonies that are inaccessible to other starfish (Fig. 8).

Starfish with a thick, calcareous structure are unable to climb onto branching coral colonies and are also less able to adhere to large hemispherical corals. Asteroids such as *C. novaeguineae* can kill only small colonies 3 to 8 cm in diameter, and can only partially eat larger colonies (Glynn and Krupp 1986). Both the recovery of a coral reef and the structure of the future community are profoundly affected by whether all large corals are killed or only nonbranching or small branching colonies. Thus even if other coral-reef starfish occurred in the enormous numbers found in *A. planci* outbreaks, they would not affect the reef communities to the same extent.

The evolution of *A. planci* and its affinity with temperate forms may provide some insights into the appearance of the structural traits that make it such a successful predator of coral. On the basis of cross-fertilization, rearing, and electrophoretic studies, Lucas and his co-workers have concluded that *A. planci* and *A. brevispinus* are recently separated sibling species, with the mollusc-eating *A. brevispinus* being the archetype (Lucas and Jones 1976; Lucas et al. 1985). They hypothesize that the ancestor of *A. planci* found a vast food resource in the coral reefs and spread rapidly across the Indo-Pacific.

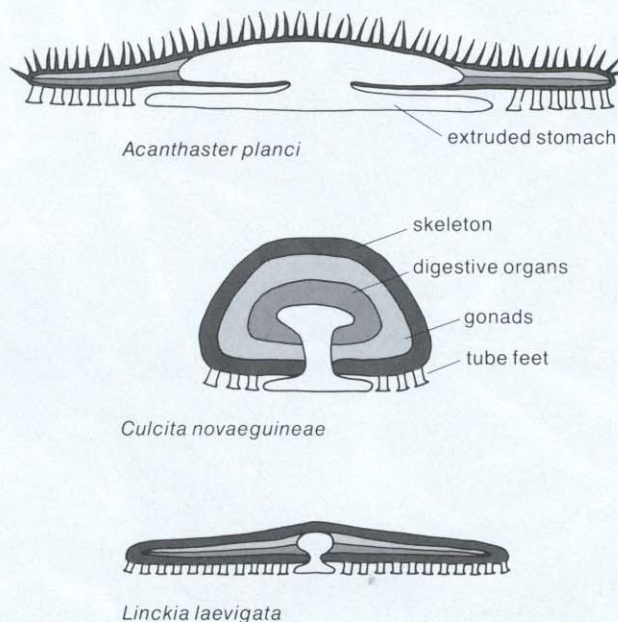


Figure 7. A schematic diagram shows the relative stomach area and skeletal thickness of three coral-reef starfish. The ratio of extruded stomach to biomass is over seven times greater in *A. planci* than in *C. novaeguineae*; the stomach area of *C. novaeguineae* in turn exceeds the small intake area of *L. laevigata*, which corresponds to its small central disk. The thickness of the calcareous skeleton—greater in *C. novaeguineae* and *L. laevigata*, least in *A. planci*—enhances resistance to predators but limits mobility and thus access to some coral prey.

The ability of *A. planci* to extend its distribution in this way can be seen in the spreading of secondary outbreaks over hundreds of kilometers within a few years (Kenchington 1977; Yamaguchi 1986). Since *A. planci* is found from the Sea of Cortez to the Pacific coast of Panama, and since no evidence of acanthasterids has been found in the Caribbean, this sequence of events probably took place within the last three million years, after the rise of the Isthmus of Panama.

Lucas and his colleagues further suggest that the

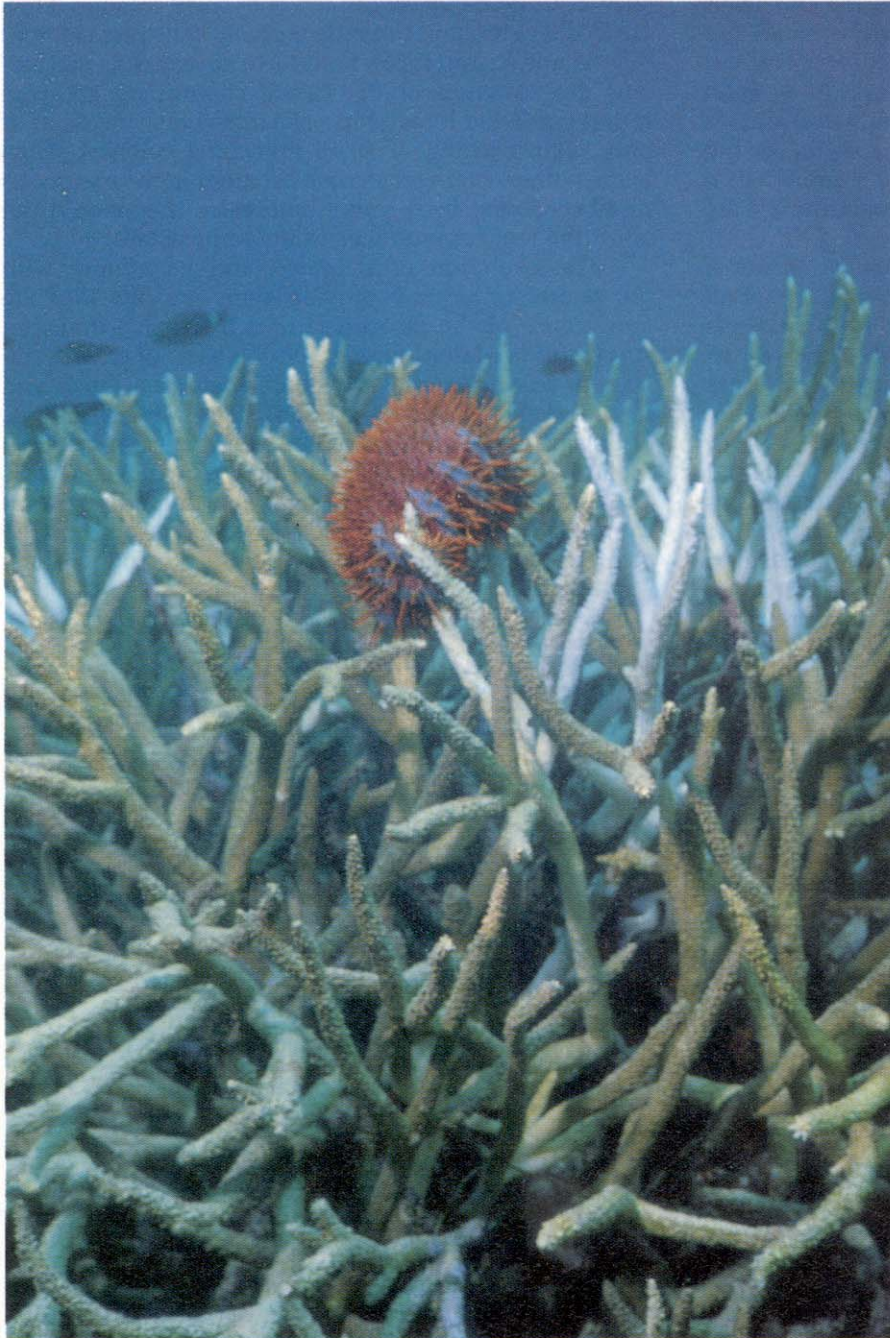


Figure 8. The pliable, prehensile form of the crown-of-thorns starfish allows it to feed on branching corals and adhere to large massive corals that are unavailable to rigid, thick-bodied oreasterids and ophiasterids. Here a single *A. planci* clings to the branches of an *Acropora nobilis* coral in the waters off American Samoa. The crown-of-thorns can feed on almost any species of coral, while other tropical starfish are limited to small or encrusting coral colonies.

separation of *A. planci* and *A. brevispinus* might have occurred in the region of Malaysia and Indonesia, because this archipelago was partitioned into isolated seas during the recent glacial periods (Potts 1983). Both of the sibling species exist in this region, and the split could have occurred when their ranges were partitioned into isolated pockets during the Pleistocene epoch.

The family Acanthasteridae, which consists of a single genus, bears a strong resemblance to the Solasteridae, which are similar in ecology, behavior, feeding structure, and early transition from juvenile to adult feeding patterns. The two families have traditionally been placed next to each other in taxonomic arrangements on the basis of morphology. Immunological studies have supported this association, although one researcher has recently placed Acanthasteridae near the Oreasteridae because of certain skeletal characteristics (Mochizuki and Hori 1980; Blake 1979).

Like *A. planci*, solasterids are magnificent predators because of their large stomachs, pliable bodies, and multiple prehensile arms. They have been a major influence in subtidal habitats in the temperate Pacific (Mauzey et al. 1968; Birkeland 1974; Sloan 1980; Menge 1982; Birkeland et al. 1982). Solasterids are cosmopolitan in distribution and are generally found on both sandy and rocky substrata, although they occur in deeper waters in the tropics. Species in the genus *Crossaster* resemble *A. brevispinus* and are found in deeper waters in the Philippines and Indonesia, within the geographic ranges of *A. brevispinus* and *A. planci*. Both acanthasterids and *Crossaster* species are absent from the tropical western Atlantic.

Similarities of diet and feeding methods are also suggestive. *Crossaster papposus*, a northern species, feeds on molluscs and anthozoans—a group including sea pens, anemones, and soft corals—in addition to a variety of other taxa (Sloan 1980). When it feeds on molluscs it assumes the arched position used by *A. brevispinus*. Half the diet of *C. papposus* in the Puget Sound region consists of an octocoral, *Ptilosarcus gurneyi*, showing a propensity for this kind of prey (Mauzey et al. 1968; Birkeland 1974).

Since a thick, calcareous skeleton restricts prey to small or encrusting coral colonies, and since the thicker skeleton and smaller ratio of stomach to biomass lead to slower growth and a longer period at a vulnerable size, why do most large asteroids on coral

reefs have these apparently disadvantageous traits? Blake has theorized (1983) that coral-reef starfish evolved under intense pressure from strong-jawed fishes that prey on shelled invertebrates, a factor much less important for starfish in temperate benthic communities. Juvenile oreasterids and adults of other coral-reef starfish are under continuous pressure from predators and generally remain hidden. But in spite of the fact that adult oreasterids often display bite marks, they appear to be protected by their thick calcareous skeletons and no kills have been observed. Unsuccessful predation is a stronger selective force for a defensive trait than either successful predation or absence of predation (Vermeij 1982). Perhaps because of the large ratio of calcareous to digestible matter, *L. laevigata*, *L. guildingii*, and other relatively large ophiasterids do not appear to be the favored prey of fish.

By contrast, both *A. brevispinus* and *A. planci* depend on spines for defense. As compared to its sibling species, *A. planci* has developed longer spines which are toxic; it is the only known venomous starfish in the world (Halstead 1978). Nevertheless, the toxic spines appear to be a less effective deterrent than the thick calcareous skeletons of other coral-reef starfish that live in exposed locations. *A. planci* is eaten by a variety of predators,

The traits that provide for quick success may also increase the likelihood of an early demise

although it is not known to be the preferred prey of any fish (Endean 1973; Moran 1986). During the daylight hours individuals are often found on the undersides of overhanging coral plates or in other concealed locations, especially when the population is not abundant; they are probably hiding from visual predators such as fish. When sparse, *A. planci* forages in the open primarily at night, but when it is abundant enough to overwhelm its predators it forages both day and night. Predation by the shrimp *Hymenocera picta* and the marine worm *Pherecardia striata* appears to have kept the crown-of-thorns starfish at relatively low levels of density on the Pacific coast of Panama (Glynn 1984).

The structural basis of the exceptional influence of *A. planci*—an elastic, disklike form with multiple prehensile arms combined with a large ratio of stomach to biomass—has developed often in temperate Pacific regions. It is found not only in *Crossaster* but in such genera as *Pycnopodia*, *Solaster*, and the multi-armed *Heliaster*, which is most commonly found in the Galapagos Islands and the Sea of Cortez, where the pressure of predators on echinoderms is less than in other regions of the eastern Pacific (Glynn and Wellington 1983; Lucas et al. 1985). Intense predation by fish has probably been a major factor in preventing these traits from developing in coral-reef starfish (Blake 1983). Thus the general form from which *A. planci* originated must have evolved in other habitats. The rapid dissemination of the crown-of-thorns starfish across the Indo-Pacific appears to be analogous to the expansion of an introduced species—

except that in this case the species originated in the center of the region. *A. planci* is an “introduced” form in that it came equipped with a structure that would not have evolved under the intense pressure of predation by fishes on a coral reef.

Faustian traits

As *A. planci* grows larger, achieving a thousand-fold increase in linear dimension and a ten-million-fold increase in biomass (Kettle and Lucas 1987), the morphological traits which were beneficial for a small asteroid can become detrimental. Lucas (1984) has determined that the increase in biomass with growth exceeds the rate of food intake by an exponential factor of 0.32. As the individual increases in size, more of the caloric content and dry-weight biomass of the body is apportioned to the gonads, less to the body wall (Kettle and Lucas 1987). Larger individuals have less ossification of body wall and become more flattened, pliable, and fragile in construction. Thus the elastic, disklike structure may represent a Faustian bargain for *A. planci*, allowing it quick growth in the early years but resulting in a loss of integrity and strength in later life.

In exchange for access to a broad range of coral prey unavailable to other starfish, a large ratio of food intake to biomass, and rapid growth through the juvenile stage with a better chance of survival and greater population density, *A. planci* is relatively susceptible to predation in comparison to other large coral-reef starfish such as oreasterids. As the crown-of-thorns starfish grows larger it becomes more fragile and thus more susceptible to damage by wave action or exposure to air. Large *A. planci* tend to lose structural integrity when lifted from the water. Dense populations may also overexploit their food supply, which may contribute to the abrupt disappearance of some outbreak populations. Thus the traits that provide for quick success may also increase the likelihood of an early demise. The thousands of *A. planci* involved in an outbreak generally disappear within a year or so.

Scientists and managers sometimes wish to determine the “normal” density of *A. planci* in a given region in order to establish a scale for monitoring or a target for management plans. In some areas affected by terrestrial runoff—for example, high islands in the Caroline Islands or the region of the Great Barrier Reef influenced by the Burdekin River—the abundance of *A. planci* fluctuates widely. The factors of high fecundity, transport of larvae by water currents, rapid growth to adult size, and relatively short persistence of dense populations would seem to make it meaningless to attempt to define normal density. It is probably more meaningful to determine the sequence of events that lead to outbreaks than to obtain a quantitative estimate of the normal population for the coast of a high island or a continental shelf.

In view of the extensive mortality of corals when the crown-of-thorns starfish reaches high population densi-

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ties, the public has become understandably worried about outbreaks. The Australian government has allocated some three million Australian dollars (about \$2,460,000 in American dollars) to the study of the ecology of the starfish and the development of techniques for its management. In 1969 the US Department of the Interior provided \$215,000 for a survey of *A. planci* populations around Micronesia. American Samoa invested \$75,000 in the removal of nearly half a million *A. planci* from the shallow coastal waters of the main island in 1978, and Japan spent more than 600 million yen (about \$2,400,000) to remove over 13 million *A. planci* from the Ryukyu Islands between 1970 and 1983 (Yamaguchi 1986). No other tropical starfish has caused such widespread concern.

The question of how far back in time outbreaks have occurred is germane, but it is difficult to obtain solid information. Core sampling and radiocarbon dating of sediments on the Great Barrier Reef, along with the distribution and density of *A. planci* skeletal elements in the sediments, suggest that outbreaks have been taking place there for thousands of years (Walbran and Henderson 1988). Older fishermen on such Pacific islands as Samoa, the Solomons, New Ireland, Pohnpei, and Palau remember various brief periods decades ago when the crown-of-thorns starfish was so abundant that it was unsafe to walk on the reefs at night; at such times they had to alter their fishing schedule temporarily (Birkeland 1981; Flanigan and Lamberts 1981).

However, the outbreaks recalled by the fishermen occurred at intervals of several decades—two or three times a century. Outbreaks appear to be more frequent now, and they are sometimes chronic. For example, no outbreaks are remembered on Guam before the 1950s, but there was a major outbreak in late 1967 and a smaller one in 1979. The second outbreak has perpetuated itself for a decade and is still with us. Similarly, *A. planci* has become a chronic problem in the Ryukyu Islands, beginning in 1969 and continuing to the present (Yamaguchi 1986).

Crown-of-thorn outbreaks are not the only tropical marine phenomenon that has increased in frequency during the past two decades. Red tides, dinoflagellate blooms, and paralytic shellfish poisoning have been increasing at a geometric rate in the western Pacific since 1975 (Macleán 1984; Holmes and Catherine 1985). The clearing of land for agricultural and urban use has also accelerated in the past twenty years, increasing the runoff of nutrients and sediments in coastal regions. If phytoplankton blooms increase the development rate and hence the larval survival of *A. planci*, then it is plausible that *A. planci* outbreaks might be related in part to increased coastal development in southeast Asia and the western Pacific.

Large-scale efforts to control outbreaks, like attempts to control red tides, the warming of the climate, and the rising sea level, are probably not feasible or at least exorbitantly expensive. The problem will recur unless the causes are acted on, and thus the greatest effort at this time should be put into probing causes. We may discover that reducing the frequency and magnitude of outbreaks is a more complex task than we now realize, requiring careful management of developing coastal lands.

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