Interactions between *Acanthaster planci* (Echinodermata, Asteroidea) and Scleractinian Corals at Kona, Hawai‘i

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ABSTRACT: Annual assessments of reef communities at Kona, Hawai‘i, from 1985 to 1995 determined that the corallivorous sea star *Acanthaster planci* preferred as prey the smaller colonies of *Pocillopora meandrina* over the far more abundant *Porites compressa* and *P. lobata*. This finding came from three distinct settings: a Reef-Top habitat, where large (>15 cm) colonies of *Pocillopora meandrina* were dominant; a Reef-Face/Boulder habitat, where living scleractinians—mainly an encrusting form of *Porites lobata*—covered <5% of the substrate; and a Coral-Rich habitat, where living scleractinians—mainly *Porites compressa* and a massive form of *P. lobata*—covered >95% of the substrate. Although a corallivore, *A. planci* was most numerous on the reef face and adjacent boulders, where corals were fewest. There it fed mainly on colonies of *P. meandrina*, even though this species represented <1% of the sparse coral coverage. Virtually all *P. meandrina* colonies in that habitat were <10 cm in diameter, and all seen eaten by *A. planci* there were <5 cm. The sea star was less numerous where corals were most abundant, and there it fed on species essentially in accordance with their relative abundance in the environment. A strong inverse relationship in occurrence between the sea star and small *P. meandrina* colonies on the reef face and adjacent boulders indicated that this favored prey was a limited resource and that sea-star predation prevented it from becoming established in that habitat.

Predation by the Indo-Pacific asteroid *Acanthaster planci* (L.) on scleractinian corals has been extensively documented, with attention directed mainly at large aggregations that have done great damage to established colonies (review by Moran 1986, Birkeland and Lucas 1990). Most of this information, however, has come from the western Pacific. Our experience has been that interactions between *A. planci* and reef corals in Hawai‘i vary somewhat from the standard perception. For example, we have not seen aggregations of more than 30 to 40 during >30 yr of study on Hawaiian reefs, and these have been rare. Although during 1970 Branham et al. (1971) observed an aggregation of about 20,000 on a reef off the Hawaiian island of Moloka‘i, the vast majority seen by us have been solitary. Furthermore, although the bleached-white skeletons typical of corals recently digested by *Acanthaster* have been common, we have never seen the extensive reef destruction attributed to this sea star elsewhere (e.g., by Chesher 1969).

Our understanding of relations between *A. planci* and scleractinians in Hawai‘i developed from study of one reef system over 11 yr. This occurred along the southern edge of Kealakekua Bay, on the island of Hawai‘i (Figure 1), where we monitored the reef communities during September of each year from 1985 to 1995. This report describes relationships between *A. planci* and corals on those reefs and discusses implications.

Habitats

The reef communities monitored in Kealakekua Bay represented three distinct habitats: a Reef-Top habitat, a Reef-Face/Boulder habitat, and a Coral-Rich habitat.

The Reef-Top habitat (Figure 2) is the surface of a shallow basaltic reef that extends offshore as the subtidal perimeter of Palemanō Point.
Most of this reef is under <3 m of water and is regularly swept by strong wave surge. Colonies of *Pocillopora meandrina* Dana up to 40 cm in diameter are prominent on the seaward sections of this reef, but only sparsely distributed on shoredward sections and elsewhere in the study area.

The Reef-Face/Boulder habitat (Figure 3) is the seaward face of the reef described above—a precipitous drop of 5 to 8 m—and the basaltic boulders adjacent to its base. Water depth over the boulders is 8–15 m. Scleractinian corals cover an estimated 2–5% of these basaltic surfaces, which otherwise are overgrown by a thin layer of algae and other organisms. (These habitat descriptions include estimates of coral coverage based on data presented in greater detail later in the report.) Virtually all of the scleractinians here are variously sized encrustations, with >95% being *Porites lobata* Dana and most of the rest being a mixture of *Montipora verrucosa* (Lamarck), *Leptastrea purpurea* Dana, and *Pavona varians* Verrill. Generally less prominent than any of these are small colonies of *Pocillopora meandrina* that vary in number from year to year but never compose more than a fraction of 1% of the coral cover.

The boulders northward from Palemano Point are increasingly covered with corals, and within relatively short distances the setting grades into the Coral-Rich habitat (Figure 4). There living scleractinians cover an estimated 80–90% of the substrate, which otherwise is mostly dead coral and patches of sand. Water depth is about 6–12 m over a gently sloping reef surface, then to about 25 m where the reef descends steeply to sand. Most of this reef is a broad field of *Porites compressa* Dana (60–80%) interspersed with large heads of a massive form of *Porites lobata* (20–40%). Other corals scattered over the reef include *Montipora verrucosa*, *Pavona varians*, and *Pocillopora meandrina*, which together represent <1% of the coral cover.

MATERIALS AND METHODS

The community assessments were based on visual counts and estimates made using scuba.
They included detailed examination of the biota within permanent 2 by 25 m transects and general surveys throughout the study area. There were four transects, all at depths from 8 to 12 m: two on boulders within 1–5 m of the reef face (Figure 3) and two on substrata largely overgrown by scleractinian corals (Figure 4). They were divided into segments, with each assessed separately. The two Reef-Face/Boulder transects were divided into ten 2 by 5 m segments, the two Coral-Rich transects into fourteen 2 by 3 m and two 2 by 4 m segments. (Segments of the Coral-Rich transects were smaller because the biota was more complex.) Difficulties in maintaining positions on the surge-swept reef top discouraged early attempts to establish permanent transects there, but the habitat was monitored by both standard and incidental observations.

The surveys recorded organisms and circumstances that were inadequately represented in the transects. They covered the environment to depths of about 25 m (where the reef confronted sand) within approximately 1 km northward from Palemanō Point (Figure 1). A total of 125.4 hr of these surveys was spent in the three habitats defined above: 20.6 on the reef top, 52.8 along the reef face and adjacent boulders, and 52.0 over reefs blanketed by corals. Unlike the transect assessments, which involved a standard set of procedures, the surveys remained flexible to accommodate unforeseen circumstances.

The relative abundance of scleractinian corals was among community features measured in the transects. First, we estimated the percentage of each transect segment that was covered by coral, then the percentage contribution of each coral species to that coverage. Generally the corals could not be enumerated, because most were highly irregular in shape and had indistinct margins, but *Pocillopora meandrina* was an exception. The colonies of this species were regular in structure, sharply defined, and readily counted. The highly visible *A. planci* was among organisms that could not be monitored effectively within the limited area of the transects, so estimates of its abundance came mainly from the surveys. We did not record the relatively few seen during the first 3 yr (1985–1987), but included the species in the annual assessments.
after it surged in abundance during 1988. To establish a basis for interannual and interhabitat comparisons, abundance data for *A. planci* are standardized as number counted per 10 min of search. Because the densities of organisms noted during the surveys were consistently low, it can be assumed that each 10 min of search involved a comparable area of reef surface. We also gained general impressions of relative sea-star abundance by remaining alert for them during other facets of the assessments, and these impressions never were inconsistent with the counts.

Some of the *A. planci* sighted during the surveys, randomly selected, were turned over to determine whether they were feeding and to identify the prey species. Those feeding were readily recognized because their stomachs had been everted to surround some or all of the coral colonies (as described by Brauer et al. 1970).

**RESULTS**

The major features of coral coverage are illustrated in the three habitat photos (Figures 2–4) and in the visual estimates from transects in the Reef-Face/Boulder and Coral-Rich habitats (Figure 5). These figures show that there was less coverage in the Reef-Face/Boulder setting than in either of the others, and Figure 5 shows that this coverage varied little from year to year. (The small interannual variation evident in Figure 5 may have been more in accuracy of the visual estimates than in differences in coral coverage.) Only the four dominant corals are distinguishable in these figures, however. Other corals noted in the habitat descriptions were small and always constituted <1% of the coverage. These cannot be discerned in the photos and are combined in Figure 5 as the virtually indistinguishable “Other” category.

The dominance of *Pocillopora meandrina* on the reef top is illustrated in Figure 2, but only the larger colonies can be distinguished effectively in that photo. The species was among forms enumerated in the Coral-Rich and Reef-Face/Boulder transects, with colonies of sizes down to <1 cm counted, but it was not more than a minor component of the coral coverage.
in either of those habitats. Furthermore, the few colonies noted in the Coral-Rich setting all exceeded 15 cm in diameter. Although we assume that there were some smaller colonies there as well, they could only have been rare.

In contrast, virtually all of the *P. meandrina* colonies present in the Reef-Face/Boulder setting were <10 cm in diameter; in fact, the vast majority were <5 cm. The only exceptions during the 11 yr of assessments were one of 15 cm from 1985 to 1987 and one of 13 cm in 1995. The sizes of colonies in transects of that habitat during 1995 are shown in Figure 6. The *P. meandrina* in that habitat also represented exceptions to the lack of interannual change evident in Figure 5. Thus, numbers recorded in the two transects there from 1985 to 1995 were 118, 68, 80, 26, 52, 9, 34, 53, 147, 268, and 382.

*A. planci* was like the smaller *P. meandrina* colonies (but unlike the more dominant corals) in being most abundant on the reef face and adjacent boulders, as well as varying in number from year to year (Figure 7). Its interannual pattern of abundance, however, was related inversely to that of the small *P. meandrina* colonies in the Reef-Face/Boulder habitat (Figure 8). All *A. planci* seen during these assessments were solitary, except during 1988—the year of greatest overall abundance. Sea stars counted in the Coral-Rich habitat that year included 35 individuals in a single aggregation.

Examination of the sea star’s feeding habits determined that its selection of prey differed between habitats. Of 33 individuals turned over and found to be feeding in the Reef-Face/Boulder habitat, 21 (63.6%) had attacked colonies of *Pocillopora meandrina (<5 cm in diameter), 10 (30.3%) were feeding on the encrusting form of *Porites Zobata,* and two (3.2%) on *Pavona varians.* Of 27 *A. planci* turned over and found to be feeding in the Coral-Rich habitat, 17 (63%) had attacked *Porites compressa,* seven (26%) the massive form of *P. lobata,* two (7.4%) were feeding on *Pocillopora meandrina (>15 cm in diameter), and 1 (3.6%) on *Pavona varians.* No record was kept of individuals turned over and
Figure 5. Species composition of coral coverage in transects representing the Coral-Rich and Reef-Face/Boulder habitat at Kona, 1985 to 1995. Other species of coral represented such a small proportion of the coverage in both habitats that they are represented on the graphs only as slight thickening in parts of the upper borders.

Figure 6. Size of Pocillopora meandrina colonies in transects of the Reef-Face/Boulder habitat during September 1995 ($n = 382$). Measurements are to nearest centimeter.

found to be not feeding, although in retrospect we realized that this would have been meaningful information.

The usual signs of A. planci predation were isolated concentrations of recently dead *P. meandrina* that occurred in areas of the Reef-Face/Boulder habitat where all other coral colonies, including those of *P. meandrina*, were untouched. These patches of dead coral, highly visible in their uniform stark-whiteness, may have represented bouts of intensive feeding followed by periods of nonfeeding, if not quiescence. This was indicated by observations during the 1996 assessment. Although these observations were made after the present paper had been submitted and accepted for publication, the following account has been inserted here.

The 1996 condition involving *A. planci* and corals was essentially unchanged from 1995,
except that a single *A. planci* was among organisms counted on a large boulder in one of the Reef-Face/Boulder transects. Despite the presence of this predator, there was no sign of seastar predation in the immediate area, including among the 35 *P. meandrina* colonies (1–15 mm, *x* = 4.0 mm in diameter) counted on this same boulder. Upon returning the next day, however, we found that 22 of the boulder’s *P. meandrina* colonies (2–12 mm, *x* = 5.1 mm in diameter) had been eaten, and the sea star was feeding on an additional colony (8 mm) at the base of an adjacent boulder. A photo taken at the time (Figure 9) shows at least 16 of these recently dead *P. meandrina* colonies, but not the *A. planci*, which was in the shadows at lower right. None of the boulder’s numerous encrusting corals (mostly *Porites lobata*) had been attacked, nor had any of the *P. meandrina* on adjacent boulders—except the one being eaten at the time of the observations. When we returned a day later, just one additional colony (5 mm) had been eaten, and the sea star was deep in the crevice seen at lower right in Figure 9 (where there were no stony corals). On our final visit the day after that, no more corals had been consumed and we were unable to find the sea star.

**DISCUSSION**

**Prey Preferences**

It seems anomalous that a corallivore like *A. planci* was most numerous in the habitat where corals were least abundant—especially because published reports (reviewed by Moran 1986) generally associate the species with coral-rich reefs. It also seems in conflict with the standard perception that *A. planci* favored the surge-swept reef face over relatively tranquil coral-rich settings nearby, because the species reportedly prefers sheltered environments (Moran 1986). These and other features of the sea star’s distribution on Kona reefs can be related to a feeding preference for small colonies of *Pocillopora*.
meandrina and to relative lack of interest in Porites spp.

In the Reef-Face/Boulder setting, where it was most abundant, A. planci fed mainly on small P. meandrina colonies that constituted <1% of a sparse coral coverage. And it consumed relatively little of the encrusting Porites lobata that constituted >95% of the same coverage. In its favored habitat, therefore, the sea star demonstrated both a strong preference for small Pocillopora and relative disinterest in Porites.

In the Coral-Rich setting, where it was less abundant, A. planci consumed coral species essentially in accordance with their relative abundance on the reef. In that habitat, therefore, it responded to P. meandrina’s scarcity in the environment by taking it as a minor prey. But all of these P. meandrina colonies were large, with both those noted on the reef and those consumed as prey being >15 cm in diameter. Although sea stars in that habitat fed mainly on Porites spp., these were so overwhelmingly dominant on the reef (Figures 4 and 5) that they could have been selected simply by default. That there were fewer A. planci on reefs essentially blanketed by Porites spp. suggests that these corals were relatively unattractive as prey.

It might have been predicted that A. planci would favor a species of Pocillopora over Porites spp. on Kona reefs, because reports from elsewhere have ranked Porites spp. among the sea star’s least-favored prey (e.g., Goreau et al. 1972, Ormond et al. 1976, Keesing 1990). Furthermore, Brauer et al. (1970) found that A. planci was attracted by extracts of Pocillopora and repelled by extracts of Porites.

Reasons why a corallivorous sea star might prefer pocilloporids over poritids as prey have been examined. Sonada and Paul (1973) considered the possibility that poritids are protected by a chemical defense, but concluded instead that protection comes simply from the absence
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FIGURE 9. Basalt boulder in one of the Reef-Face/Boulder transects during September 1996, with numerous recently
dead colonies of Pocillopora meandrina (stark white in hue), most <5 mm in diameter. Most of the visible encrustations
are Porites lobata, all of which appear healthy. The boulder is ca. 3 m in its greatest dimension.

of a chemical attractant. Their finding that pori­
tids are “chemically cryptic” would explain A. planci’s apparent disinterest in representatives
on Kona reefs. It would also explain why Bran­
ham et al. (1971) found that A. planci off Molo­
ka’i ignored Porites compressa in favor of the far
less abundant acroporid Montipora verrucosa.

Other possible reasons for selecting pocillo­
porids over poritids include their relative nutri­
tional value. An evaluation of barrier-reef corals
by Keesing (1990), for example, placed pocillo­
porids among those with the highest energy and
protein content, and poritids among those with
the lowest. Keesing also found that soft tissues
of the former are more superficially positioned
and therefore more accessible to sea-star diges­
tion. Finally, in considering why pocilloporids
were favored over poritids in Hawai’i by the
corallivorous sea star Culcita novaeguineae
Müller & Troeschel, Glynn and Krupp (1986)
noted in comparing Pocillopora damicornis (L.)
with Porites compressa that the former has
smaller, less-potent nematocysts, and, as Kees­
ing (1990) noted for congeners in the western
Pacific, its soft tissues are more accessible.

The preference that A. planci showed for Poc­
illopora meandrina on Kona reefs, however,
was directed at colonies <5 cm in diameter.
Colonies larger than 10 cm were seen under
attack just twice, and both were among the few
(all >15 cm in diameter) scattered about in the
Coral-Rich habitat. It is striking that we saw no
attacks on the many larger P. meandrina colonies
that dominated the reef top (Figure 1), even
though many of these were within a few meters
of smaller colonies consumed on the reef face.
A. planci occurred just occasionally on the reef top, feeding or not. We believe that this was because they have an aversion to strong water movement, as reported by Endean (1973). If so, the lack of attacks on reef-top P. meandrina may have been an incidental result of this aversion. In disagreement, Glynn (1976, 1981, 1985) argued that A. planci avoids the shallow, surge-swept reefs favored by Pocillopora because it can be grievously if not fatally injured by certain of the crustaceans and polychaetes that reside among the branches of the larger colonies. But having seen larger colonies under attack in the Coral-Rich habitat, we conclude that it is the sea star’s aversion to strong water movement that protects reef-top P. meandrina from these predators.

Although A. planci readily tolerated water movement in the Reef-Face/Boulder habitat, it experienced considerably less of it there. We can appreciate the distinction, because it was our own difficulty maintaining positions in the reef-top surge that prevented us from establishing transects in that habitat. Probably it is a question of how much water movement A. planci can tolerate in getting to preferred prey.

Preference for Small Colonies

Whatever influence water movement may have had on keeping A. planci away from P. meandrina on the reef top, it nevertheless appears that the sea star prefers to feed on smaller colonies. This preference has been reported from other regions and also when feeding on other corals. For example, Glynn (1976) reported that small colonies and fragments were the usual fare of A. planci feeding on Pocillopora spp. in the eastern Pacific; and Barham et al. (1973) found that A. planci in the Gulf of California attacked only the smaller colonies of Porites californica (the only common coral there), leaving larger colonies untouched.

It has been suggested that A. planci finds feeding on smaller colonies adaptive because it can cover these with its everted stomach and thus free its podia to attack surfaces free of nematocysts (Barham et al. 1973). This supposition was based on a study by Barnes et al. (1970), who showed that the sea star has a strong aversion to contact between its podia (but not its stomach) and coral nematocysts. We agree that avoiding nematocysts is likely to be important and suggest that this avoidance has influenced A. planci behavior and distribution far more than is generally recognized.

Other Influences on Prey Selection

Factors other than those already noted have been suggested to influence which corals are selected. Keesing (1990) concluded that A. planci should prefer branched corals (like P. meandrina) over encrusting forms because these present its everted stomach with more surface area. Such a preference would favor P. meandrina in the Reef-Face/Boulder setting, because the other corals there develop as encrustations. Among these others was Montipora verrucosa, which assumes a variety of forms (including branched) elsewhere (Maragos 1972) and, as noted by Branham et al. (1971), can be a preferred prey of A. planci.

Obviously availability can make many of the above considerations irrelevant. For example, Barham et al. (1973) found that A. planci in the Gulf of California fed exclusively on small encrustations of Porites—a form regularly passed over elsewhere—presumably because that was the only coral commonly available.

A Limited Resource

It was apparent that the smaller P. meandrina colonies on Kona reefs represented a limited resource. Although the sea stars present during at least most of our observations seemed to find a sufficient supply of the colonies in the Reef-Face/Boulder habitat, certainly many more of the sea stars could not have done so. Consider that virtually all of the predation evident in Figure 9 was the work of one sea star over 24 hr. So probably even the relatively few sea stars present during our assessments were stretching this resource to its limit. This is implicit in the tight, inverse relationship between the respective abundances of these two species in the Reef-Face/Boulder habitat (Figure 8).

If the trophic resources of that habitat cannot sustain large numbers of A. planci, as we surmise, then during years of exceptional abundance one would expect the increase in
population to be centered in the Coral-Rich habitat. Presumably a shortage of prey would make them less discriminating and more accepting of less-preferred prey, such as *Porites* spp. Furthermore, any aversion to coral nematocysts that may have kept them off expanses of living corals when other options were available probably are overridden by the need for more food.

*A. planci* could never be described as “exceptionally abundant” during our assessments, however. We assume that this accounts for some of the differences from circumstances reported elsewhere. Only during 1988 and 1990 were its numbers on Kona reefs appreciably above the “normal” range defined by Chesher (1969). Nonetheless, during the year of its greatest abundance (1988), there were almost as many in the Coral-Rich habitat as in the Reef-Face/Boulder habitat. Furthermore, the concentration of about 20,000 that Branham et al. (1971) observed off Moloka‘i—an exceptional abundance by any measure—was on a reef “... covered with a dense uniform growth of coral” (p. 1155).

Although numbers of *A. planci* on Kona reefs during this period were limited, evidently there were enough there to prevent *P. meandrina* from becoming established in the Reef-Face/Boulder setting. Based on the number present during each of the last 4 yr that had not been there the year before (Figure 8) and also on the 1995 size distribution (Figure 6), we conclude that the vast majority of *P. meandrina* colonies in that habitat were in their first or second year. It was apparent that *P. meandrina* colonies in this setting generally were eliminated within a few years after settlement, and our findings suggest that this was a result of sea-star predation.

**Regional Variations**

The Indo-Pacific distribution of *A. planci* is typical of species with evolutions centered in the Indo-Malayan region (Ekman 1953). Thus, one would expect the sea star to be particularly adapted to circumstances in the tropical western Pacific and less suited to conditions elsewhere. That is where the species is most abundant and also where its population explosions (with subsequent destruction of reefs—the basis of its notoriety) are centered (Moran 1986).

We suggest that *A. planci*’s preferences for prey on Kona reefs reflects its western-Pacific origin. Presumably its evolution involved selection of features suited for predation on the more abundant, readily eaten corals of that region. As a result, the major prey of extant representatives there are species of *Acropora* and, secondarily,
of *Pocillopora* (Moran 1986, Keesing 1990). It has been argued that individual *A. planci* in the western Pacific learn to prefer *Acropora* spp. because those are the most abundant of available prey (Moran 1986); however, we believe that the preference comes from a long evolution of adaptive morphological and behavioral features. That these features are less suited to feeding on *Porites* spp. is evident in the widespread reports of relative disinterest in these.

This heritage is evident in the selection of prey at Kona. The relative lack of interest in *Porites* spp. was particularly striking, considering the dominance of these corals on Kona reefs. (If prey preferences are learned [as we have already discussed], shouldn't Kona representatives have learned to prefer *Porites* spp.?) There are no *Acropora* spp. around the major Hawaiian Islands (Maragos 1972), so the western-Pacific preference for corals of that genus could not have been transferred to Kona. And the lone acroporid at our study site, *Montipora verrucosa*, was a minor presence that occurred only as apparently less-preferred encrustations. But a species of *Pocillopora*—*P. meandrina*—was both prominent in the environment and a preferred prey. Although this coral apparently found a refuge from *A. planci* on shallow, surge-swept reefs, its smaller colonies, at least, were highly vulnerable elsewhere.

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