

## Some Ecological Consequences of Coral-Crustacean Guard Mutualisms in the Indian and Pacific Oceans

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### Abstract

Several reef-building coral species, members of the families Pocilloporidae and Acroporidae (Scleractinia: Astrocoeniina), harbor on their branches obligate xanthid crab and alpheid shrimp symbionts that protect their coral hosts against sea star predators (*Acanthaster planci*), and thus reduce predator-related mortality. The crustacean guards repel *Acanthaster* by pinching (crabs) or pinching and snapping (shrimps) at the attacking predator. In the Gulf of Oman, the intensity of coral host defense by different crustacean guards was taxon specific and similar to that reported in the Pacific Ocean (Panama, Guam, Samoa) with corals and associated guards ranked in ascending order of defense:

Coral hosts:	<i>Acropora</i>	<	<i>Stylophora</i>	<	<i>Pocillopora</i>
Crab guards:	<i>Tetralia</i>		<i>Trapezia</i> (1 sp.)		<i>Trapezia</i> (2 spp.)
Shrimp guard:	rare		<i>Alpheus</i>		<i>Alpheus</i>

These increasing levels of defense were positively correlated with resistance to sea star predation: (a) *Acropora* was generally a preferred coral prey taxon, (b) *Stylophora* was neutral (neither preferred nor avoided), (c) *Pocillopora* assumed a neutral position in coral communities with few preferred prey species, and (d) *Pocillopora* was strongly avoided in communities of high coral diversity. That is, prey choice was dependent, in part, on the relative abundances of preferred and nonpreferred prey species. In Panama, coral species present in habitats frequented by *Acanthaster* demonstrated significantly smaller colony sizes and higher proportions of dead colonies than comparable corals present in habitats without *Acanthaster*. However, reef patches surrounded by guarded *Pocillopora*, and thus free of *Acanthaster* predation, served as refugia for large, living colonies of otherwise preferred corals.

An outbreak of *Acanthaster* in Oman (1978–80) resulted in differential coral reef mortality with nearly total devastation of *Acropora* reefs and only minor damage to *Pocillopora* reefs. Pacific and Indian Ocean coral communities containing resistant pocilloporid corals suffer relatively low mortality during periods of sea star predation, due to coral/crustacean guard symbiotic interactions.

Keywords: coral-crustacean mutualism, host protection, *Acanthaster* feeding preferences, coral community structure, Pacific, Indian Ocean comparison

## 1. Introduction

Students of symbiosis often are interested in more general extensions of their studies, to considerations of how specific intimate associations might affect population and community processes (Addicott, 1986). Or alternatively, what would the biotic world be like without particular symbioses (Janzen, 1985). Without the presence of coral-algal symbioses coral reefs would probably be nonexistent, or at best only pale reflections of extant reefs. If certain symbioses are essential for the development of coral reefs, then do there exist other symbioses that influence the structure (relative abundances of coral species) of reef coral communities? In this paper, I examine the effects that an influential group of symbioses, coral-crustacean guard mutualisms, have on coral populations and coral communities.

Crustacean guards (xanthid crabs and an alpheid shrimp) are obligate mutualists that reside on the branches of pocilloporid and acroporid corals, and which defend their coral hosts against sea star corallivores such as *Acanthaster planci* (Linnaeus) and *Culcita novaeguineae* Muller and Troschel (Glynn, 1983a; Glynn and Krupp, 1986). Some studies in the western and eastern Pacific suggest that pocilloporid-crustacean guard symbioses can have an effect on coral community structure: (1) defended corals experience relatively high rates of survival and have high relative abundances in areas of intense predation (Randall, 1973; Colgan, in press; Glynn et al., 1982), (2) an avoidance of defended corals may depress local species diversity through the survival of few species (Glynn, 1976, 1983a), and (3) continuous tracts of defended coral prevent sea star predators from entering centrally-located patches of undefended coral prey (Glynn, 1985). Here I explore further the coral-crustacean guard symbiosis from the perspective of an interoceanic comparison between field studies conducted in Oman and Panama. Some notable similarities in guard defensive behavior, predator responses and community-level effects are discussed.

## 2. Study Areas and Methods

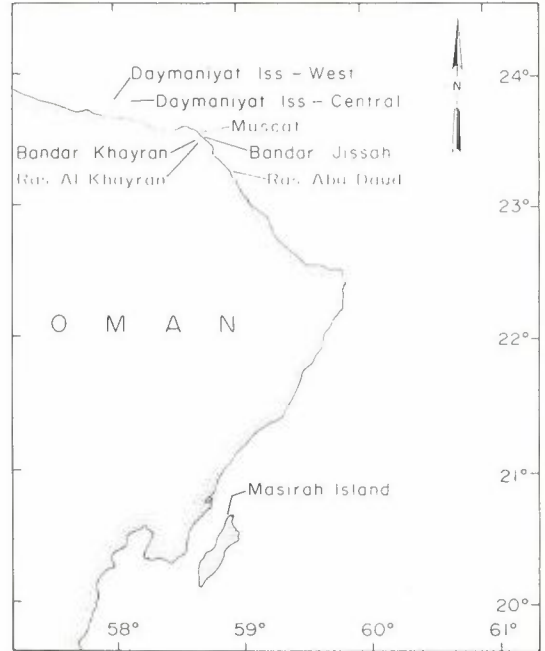
Observations in Oman (Fig. 1) were made from 20 September to 25 October 1982. Field work in Panama (Fig. 1) has been conducted continuously from January 1980 to August 1986, however, all observations on live coral abundances were made prior to significant coral mortality related to the 1982-1983 El Niño warming event (Glynn, 1984).

Voucher specimens of Omani corals were collected for identification by specialists. Panamanian coral species were identified according to Wells (in Glynn and Wellington, 1983). Corals sampled for crustacean guard composition were enclosed in plastic bags and dislodged *in situ*. Of the rich assemblage of crustaceans present, only the crustacean guards were considered in this study. These specimens were chilled (to prevent autotomy), preserved in 70% ethanol with glycerin, sorted in the laboratory, and sent to specialists for identification. Crab size is measured as the maximum carapace width and shrimp size by the carapace length (from posterior border to base of rostral spine).

Coral colony volume, determined in the study of crustacean guard densities, was estimated from linear measurements of the length, width and height of colonies. Coral colony size represents the longest growth axis, which was determined from either maximum colony height or radius dimensions. The percentage of live polypal surface was estimated visually, and if this was equal to or greater than 50% the colonies were scored as live, and dead if less than 50% live surface area. The areas selected for coral size measurements were those where local coral abundances were highest, and all colonies present were measured. On reefs where *Acanthaster* was present, areas were designated as protected if surrounded by stands of live *Pocillopora*  $\geq 5$  m in width (*Acanthaster* was never observed in these areas) and unprotected if not encircled by *Pocillopora* and thus exposed to predation by *Acanthaster*.

Crustacean guard defensive interactions were quantified by simulating predatory attacks with live *Acanthaster*, ranging in size from 14 × 28 cm (maximum disc diameter × maximum body diameter) to 21 × 39 cm. Relatively large coral colonies, 15-30 cm diameter, were selected as potential prey. *Acanthaster* was placed about 5 cm from the edge of a test colony and then moved slowly toward the coral until 2-5 arms overlapped the peripheral branches by 3-4 cm. Each test sea star was employed in 10 trials and then exchanged for a fresh one. Ten consecutive trials with each of two species of *Acropora*, and one species each of *Pocillopora* and *Stylophora* (both genera

A



B

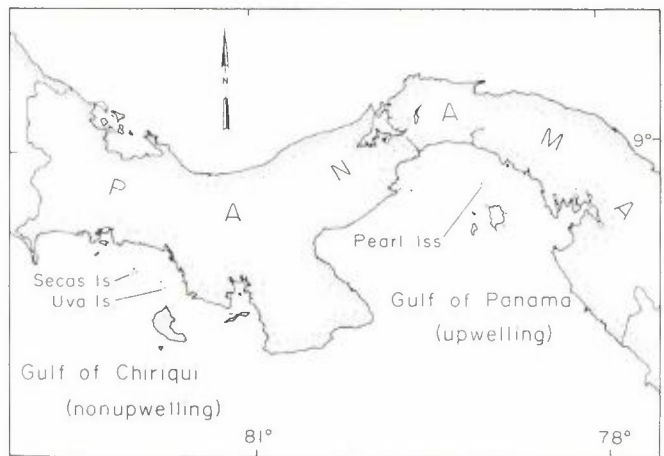


Figure 1. Location of study areas in Oman (A) and Panama (B).

members of the Pocilloporidae) (total = 40) failed to demonstrate significant changes in crustacean (crab and shrimp guards combined) defensive behavior with repeated use of test sea stars ( $p > 0.05$ , in 4 one-sample runs tests). The aggressive responses were recorded on a slate over 3 min periods. Each aggressive encounter (a score of 1) involved direct physical contact between crab and sea star (i.e. pinching, clipping, stroking, jerking, and pushing). Shrimp aggression involved direct encounters (snapping in contact, pinching), and also indirect encounters (snapping at a distance) since these activities alone generally elicited a response from sea stars (arm lifting and rapid dismounting). Non-contact activities by crabs, e.g. startle displays, lurching and shivering movements, were noted but not scored as effective repellent behaviors. See Glynn (1983a) for further details on methodology.

Seven sites in the Gulf of Oman (Fig. 1), where *Acanthaster* was feeding, were sampled to determine the proportions of different coral species eaten. Each sample consisted of 5,  $1/4 \text{ m}^2$  quadrats, with 16 uniformly-spaced points (crossed nylon lines), that were employed to quantify coral cover (prey availability). A quadrat was centered on a feeding *Acanthaster* which was then removed, and all items directly beneath the points (total  $n = 80$ ,  $5 \times 16$ ) were tallied. Four quadrats were then aligned contiguous to each side of the first quadrat, thus forming a cross pattern that encompassed  $1.25 \text{ m}^2$  of bottom area. All potential coelenterate prey were recorded, including the alcyonaceans and zoanthids that were occasionally observed being eaten by *Acanthaster*. Only freshly-killed coelenterates (bearing white, usually circular lesions) near feeding sea stars were assumed to have been eaten by *Acanthaster*. The total reef area sampled at each site ranged from about 1,000 to 2,500  $\text{m}^2$ , and *Acanthaster* densities were estimated by counting the sea stars in measured plots. According to local divers, an *Acanthaster* outbreak occurred in the Gulf of Oman during 1978–80. Several hundreds of sea stars per hectare were observed feeding on reef corals in the Daymaniyat Islands. Live coral cover observed in this study (1982) was probably greatly influenced by this earlier predation event.

Both the median and mean were calculated for samples with high numbers of zeros. Due to incomplete information on distributions and small sample sizes, nonparametric statistical tests were generally employed in this study. Chi-square tests of significance (employing Yate's correction in  $2 \times 2$  tables) were used to assess patterns of prey preference and avoidance.

### 3. Results

#### A. Coral-crustacean guard symbioses (Oman)

The predominant crustacean guard in acroporid corals in Oman was *Tetralia cavimana* Heller, which was present in colonies of *Acropora pharaonis* (Edwards and Haime) (Table 1), *Acropora nasuta* (Dana) and *Acropora cytherea* (Dana). While large numbers of the crab were usually associated with acroporid corals (median = 12 crabs per colony in *A. pharaonis*) this guard was relatively small (Table 2) and timid with respect to host colony defense (Table 3). The guards only scored median defensive responses of 0 and 3 in *A. cytherea* and *A. pharaonis* respectively, and a high frequency of corals were not defended (Table 3). Most crabs near an attacking *Acanthaster* were aroused quickly (i.e. quickened their movements), but soon retreated into the coral host. Some crabs, however, performed startle displays, slashed with their chelae and shivered, with all activities directed towards sea stars. A few large *T. cavimana* on *A. pharaonis* defended their hosts vigorously by pinching both the tube feet and spines of *Acanthaster*. *Trapezia cymodoce* was found in 2 colonies of *Acropora* (Table 1) and occasionally alpheid shrimp, possibly *Alpheus lottini* Guerin (only snapping was heard), also were involved in colony defense (Table 3).

The two pocilloporid species hosted *Trapezia* guards with two crab species associated with *Pocillopora damicornis* and usually only one crab species with *Stylophora pistillata* (Table 1). Wolodarsky (1979) found three species of *Trapezia* associated with *S. pistillata* in the northern Gulf of Eilat (Red Sea), but usually only a single species pair was present on any given colony. *Alpheus lottini* was also present on all pocilloporid colonies sampled, usually at one pair per colony. *Pocillopora* colonies usually contained a second species of *Trapezia*, *Trapezia tigrina* Eydoux and Souleyet, and exhibited a higher median density of crustacean guards (Md, median = 8/colony) than did *Stylophora* (Md = 4/colony). Due to the small numbers of colonies censused (n = 6 colonies/species), a rigorous comparison of guard densities in different host species is not possible here. But, field observations also suggested that *Stylophora* contained fewer guards than *Pocillopora* among corals of comparable size. It should be noted that *T. tigrina*, readily identified in the field due to its distinctive spotting, was observed defending some *Stylophora* colonies. *T. tigrina* was consistently more aggressive in thwarting *Acanthaster* than was *T. cymodoce* in both pocilloporid species. Total median guard attacks among host species, which were 1 and 3 in *Acropora*, 14.5 in *Stylophora*, and 23 in *Pocillopora* (Table 3), were highly significantly dif-

Table 1. Crustacean guard species composition and abundances (median number and range per colony) in three coral host species censused in Oman

Coral host species	Number of colonies sampled	Colony volume (cm)	Median (range) of crustaceans/colony				Total
			<i>Trapezia cymodoce</i>	<i>Trapezia tigrina</i>	<i>Tetraia caesiama</i>	<i>Alpheus lottini</i>	
<i>Acropora pharaonis</i> <sup>1</sup>	6	13,100(3,100-35,000)	0(0-1)	none	12(2-20)	none	12(2-20)
<i>Stylophora pistillata</i> <sup>2</sup>	6	9,400(1,300-21,800)	2(2-2)	0(0-2)	none	2(2-2)	4(4-6)
<i>Pocillopora damicornis</i> <sup>3</sup>	6	6,800(3,060-12,800)	3(2-5)	2(2-3)	none	2(2-6)	8(6-11)

<sup>1</sup> One colony collected at Bandar Khayran, 28 September 1982; 5 colonies from Bandar Jissah, 15 October 1982.

<sup>2</sup> All colonies collected at Bandar Khayran, 28 September 1982.

<sup>3</sup> All colonies collected at Muscat, 28 September 1982.

Table 2. Crustacean guard sizes (median and range per collection) in three coral host species censused in Oman

Coral host species <sup>2</sup>	Crustacean size measurements (cm) <sup>1</sup>							
	<i>Trapezia cymodoce</i>	n	<i>Trapezia tigrina</i>	n	<i>Tetraia caesiama</i>	n	<i>Alpheus lottini</i>	n
<i>Acropora pharaonis</i>	0.70(0.40-1.00)	2	none	-	0.51(0.29-1.41)	66	none	-
<i>Stylophora pistillata</i>	1.22(1.11-1.35)	6	1.42(0.96-1.89)	2	none	-	2.14(2.00-2.35)	6
<i>Pocillopora damicornis</i>	0.88(0.41-1.27)	19	1.37(0.37-1.55)	13	none	-	2.10(0.80-2.61)	16

<sup>1</sup> Crab sizes are maximum carapace widths, shrimp sizes are carapace lengths (excluding rostrum).

<sup>2</sup> Collection sites same as listed in Table 1.

Table 3. Frequency of crustacean guard defensive responses (number per 3 min) directed toward simulated *Acanthaster* attacks on four coral host species, Oman

Coral host	Number of simulated attacks	Number of Attacks						Colonies not defended			
		<i>Trapezia</i> spp.		<i>Tetraota caesiama</i>		Alpheids		Total Md	Total $\bar{x}$	No.	%
		Md	$\bar{x}$	Md	$\bar{x}$	Md	$\bar{x}$				
<i>Acropora cytherea</i>	10	none	0.7	0	0.7	1	3.1	1.1	3.8	5	50.0
<i>Acropora pharoonis</i>	11	none	4.5	3	4.5	0	0.3	3	4.8	4	36.4
<i>Stylophora pistillata</i>	20	7.5	11.6	none	none	4.5	6.2	14.5	17.9	4	20.0
<i>Pocillopora damicornis</i>	33	8	11.6	none	none	7	10.2	23	21.7	3	9.1

<sup>1</sup> Vertical lines connect similar median values (*a posteriori* MCP,  $\alpha = 0.20$ )

Table 4. Amounts of coral consumed in communities of *Acropora-Monitipora* and *Porites-Pocillopora*

Coral Community	Site	Percent coral cover		Coral sampled (points)		Coral eaten/ <i>Acanthaster</i> density <sup>1</sup>	
		total	% eaten	total	% eaten	total	% eaten
<i>Acropora/Monitipora</i>	Bandar Jissah	60.7	37.5	3,103	1,164	37.5	13.9
	Ras al Khayran	75.2	21.6	602	130	21.6	4.2
	Central Daymaniyat	26.9	12.4	323	40	12.4	0.4
	Ras abu Daud	31.8	12.8	483	62	12.8	3.3
<i>Porites/Pocillopora</i>	Bandar Khayran	31.5	6.7	252	17	6.7	0.6
	West Daymaniyat	44.7	8.6	393	34	8.6	1.1
	Muscat	80.0	2.8	640	18	2.8	0.6

<sup>1</sup> Ratio of coral eaten (points) per *Acanthaster* population density (individuals/ha.).



ferent ( $p < 0.001$ , Kruskal-Wallis test). The number of attacks in acroporid corals was significantly lower than in pocilloporid coral hosts (*a posteriori*, multiple comparisons procedure, MCP).

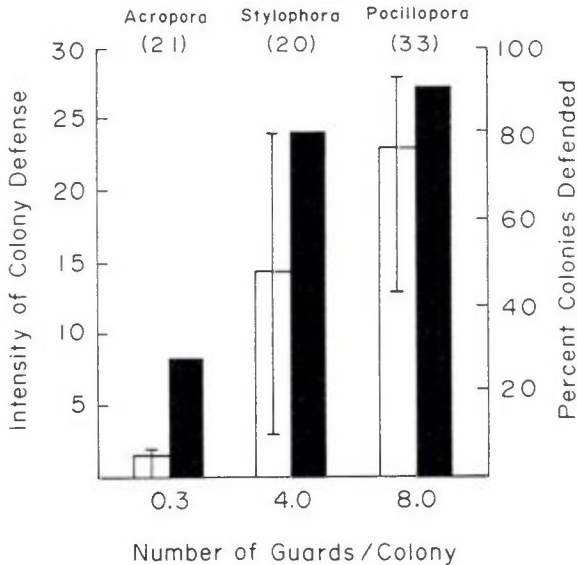


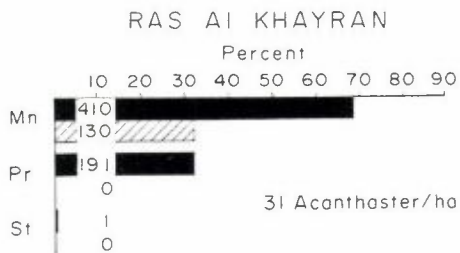
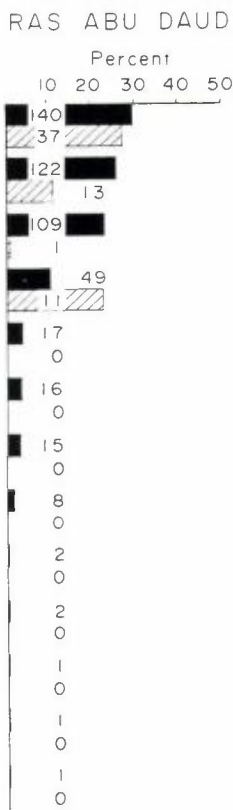
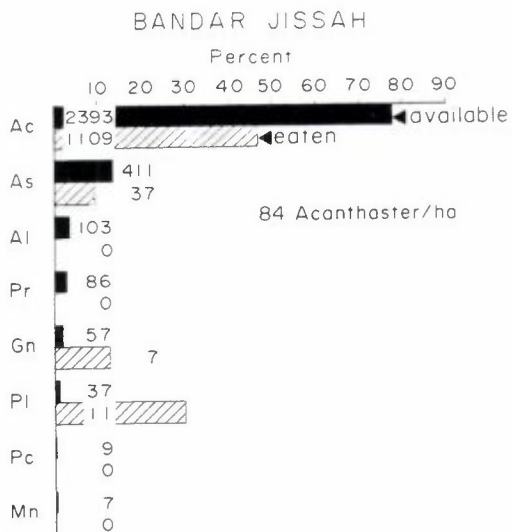
Figure 2. Median intensity of colony defense (left-hand open bars) and percentage of colonies defended (right-hand occluded bars) in relation to number of aggressive guards per colony among three coral host taxa. Vertical lines denote 0.95 confidence limits of median. Number of crustacean guards per colony is indicated by the mean for *Acropora* and by the median for *Stylophora* and *Pocillopora*. Six corals per genus were censused. Intensity of colony defense was measured as the number of defensive encounters during a 3 min period. Sample sizes for intensity and frequency of colony defense are noted in parentheses.

Some tentative relationships between crustacean guard densities, frequency of colonies defended, and intensity of colony defense are summarized for three coral host taxa in Fig. 2. Frequency and intensity of colony defense seem to be host specific and functions of the number of *Trapezia* spp. and *A. lottini* guards per colony. Aggressive guards were uncommon on acroporid corals which were infrequently (28.6%) and weakly ( $\bar{x} = 1.6$  interactions/3 min) defended. *Pocillopora* exhibited a high density of aggressive guards and was frequently (90.9%) and strongly ( $Md = 23$  interactions/3 min) defended.

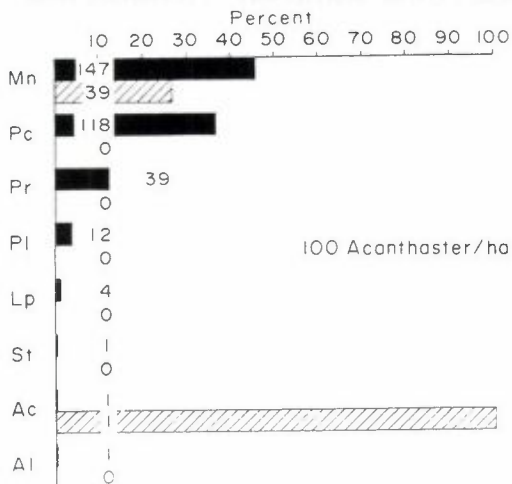
### B. Coral mortality and *Acanthaster* feeding behavior (Oman)

Differential coral species mortality was evident in the Gulf of Oman where *Acanthaster* was present and feeding: (1) heavy predation on *Acropora* and *Montipora* corals (both members of family Acroporidae) occurred at sites where these genera were relatively abundant (Fig. 3), (2) zero to light predation on *Porites* and *Pocillopora* occurred where these corals were community subdominants (Fig. 3), and (3) light to moderate predation of *Porites* and *Pocillopora* occurred where these corals were abundant (Fig. 4). Higher proportions of available coral were eaten in *Acropora-Montipora* dominated communities (12.4–37.5%) than in *Porites-Pocillopora* dominated communities (2.8–8.6%) (Table 4). However, the amount of coral consumed was not a simple function of overall prey availability (total percent coral cover) or predator population densities. For example, predation was heavy at Ras al Khayran (21.6% eaten) and light at Muscat (2.8% eaten), two sites of nearly equal coral abundance (75.2% and 80.0% cover respectively). And the proportion of coral eaten per *Acanthaster* present was only 0.4 (40 eaten/100 *Acanthaster*) in the central Daymaniyat Islands where *Acanthaster* density was high, for example, and 1.1 (34 eaten/32 *Acanthaster*) in the western Daymaniyat Islands where *Acanthaster* was only moderately abundant (Table 4).

Figure 3. Percent availability of corals, alcyonaceans and zoanthids (darkened bars, total coelenterate prey = 100%) at four sites with foraging *Acanthaster* present, Gulf of Oman. Corresponding percentages of each taxon eaten by *Acanthaster* (cross hatched bars) are also shown. Number of sample points are indicated for each taxon and densities of *Acanthaster* are noted at each site. Ac - *Acropora cytherea* (Dana) predominant, *Acropora pharaonis* (Edwards and Haime), *Acropora nasuta* (Dana); Al - unidentified alcyonaceans; An - *Acanthastrea echinata* (Dana); As - *Astreopora myriophthalma* (Lamarck); Fv - *Favites* sp. cf. *F. spinosa* (Klunzinger), *Favites* sp. cf. *pentagona* (Esper); Gn - *Goniopora savignyi* Dana; Lp - *Leptastrea transversa* Klunzinger; Mn - *Montipora effusa* (Dana) predominant, *Montipora tuberculosa* (Lamarck), *Montipora scutata* Bernard, *Montipora venosa*; Pc - *Pocillopora damicornis* (Linnaeus); Pl - *Platygyra rustica* Dana predominant, *Platygyra lamellina* (Ehrenberg), *Platygyra sinensis* (Milne-Edwards and Haime); Pr - *Porites lobata* Dana predominant, *Porites andrewsi* Vaughan, *Porites columnaris* Klunzinger, *Porites cocosensis* Wells, *Porites solida* (Forsk.); Ps - *Psammocora contigua* (Esper); St - *Stylophora pistillata* (Esper) predominant, *Stylophora subseriata* (Ehrenberg); Zn - unidentified zoanthids.



DAYMANIYAT ISLANDS (CENTRAL)



19 Acanthaster/ha

PREY TAXA

- Ac Acropora
- Al Alcyonacea
- An Acanthastrea
- As Astreopora
- Fv Favites
- Gn Goniopora
- Lp Leptastrea
- Mn Montipora
- Pc Pocillopora
- Pl Platygyra
- Pr Porites
- Ps Psammocora
- St Stylophora
- Zn Zoantheida

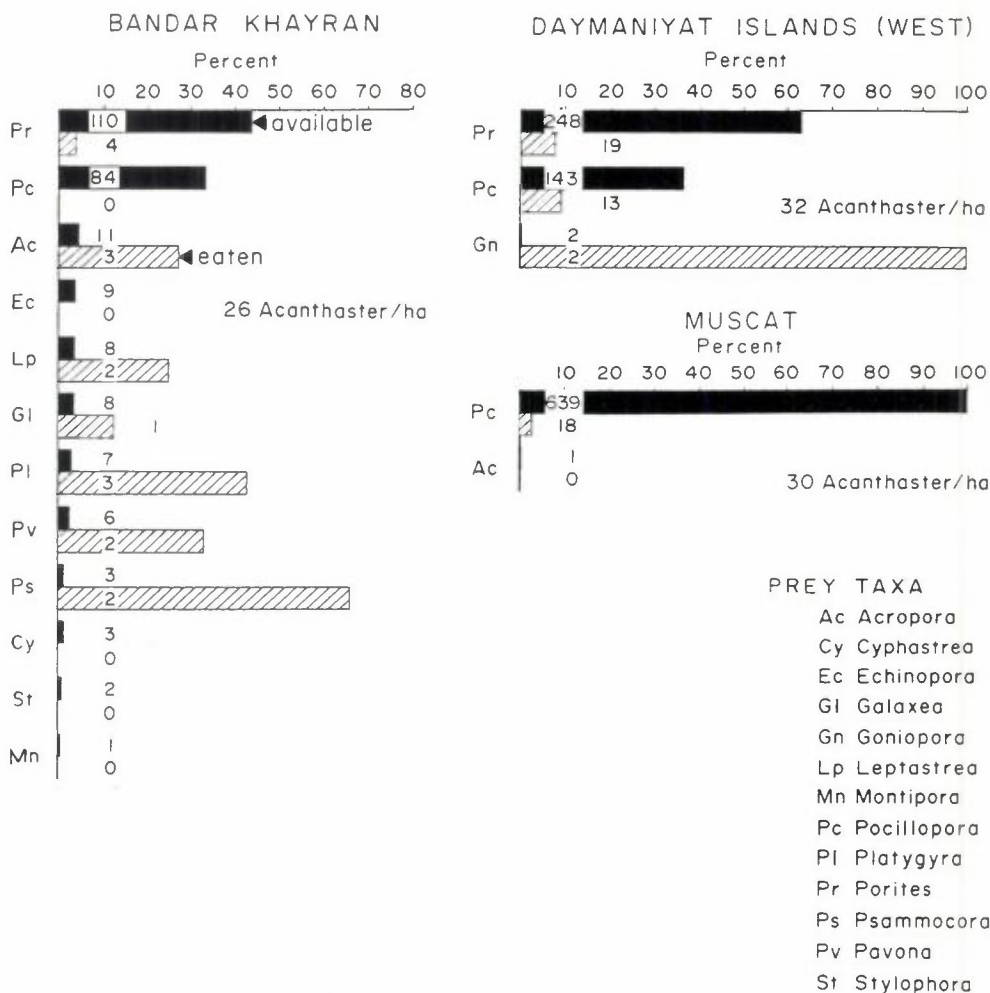


Figure 4. Percent availability of corals (darkened bars, total coral prey = 100%) at three sites with foraging *Acanthaster* present, Gulf of Oman. Corresponding percentages of each taxon eaten by *Acanthaster* (cross hatched bars) are also shown. Number of sample points are indicated for each taxon and densities of *Acanthaster* are noted for each site. Prey taxa identities as in Fig. 3, and Cy - *Cyphastrea microphthalmia* (Lamarck); Ec - *Echinopora lamellosa* (Esper); Gl - *Galaxea astreata* (Lamarck); Pv - *Pavona frondifera* Lamarck.

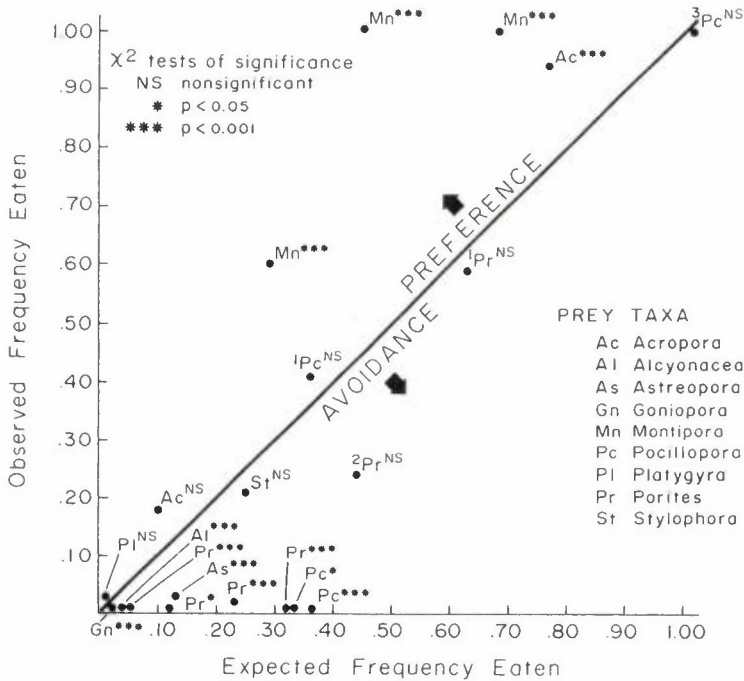


Figure 5. Scatterplot of the frequency of corals found eaten during surveys in relation to expected frequency eaten (based on relative abundances). Only corals with  $n \geq 37$  sample points per site are included in this analysis. Chi-square significance levels are noted for each taxon (right superscript). In some cases, sampling sites are identified by left superscripts: 1, western Daymaniyat Islands; 2, Bandar Khayran; 3, Muscat.

A consistent pattern of prey preferences was evident for *Acropora* and *Montipora* with a higher proportion of these genera consumed than expected (significant in 4 of 5 cases) based on their relative abundances (Fig. 5). *Porites* and *Pocillopora* were significantly avoided when present as community subdominants. However, these genera were neither avoided nor preferred prey items (neutral prey) in coral communities of which they were predominant members ( $^1Pr^{NS}$ ,  $^2Pr^{NS}$ ,  $^1Pc^{NS}$ ,  $^3Pc^{NS}$ , Fig. 5).

### C. Coral colony sizes and vitality (Panama)

Summarized here are data from Panama on colony size and the frequency of live colonies in 8 coral species that showed a negative correlation (inverse relationship) with the occurrence of *Acanthaster planci*. Six coral species demonstrated significantly smaller colony sizes where *Acanthaster* was present than

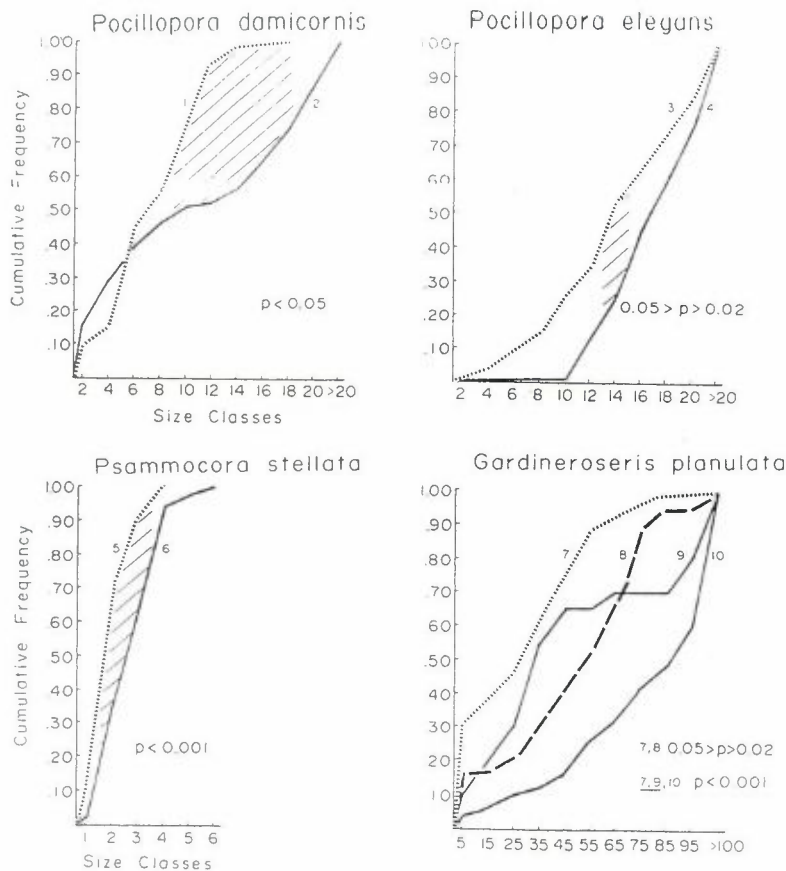


Figure 6. Cumulative frequency distributions of coral colony sizes under different conditions of exposure to *Acanthaster* predation, Pacific coast of Panama. Size-class midpoints (growth axes, cm) are indicated. Key to curves: *Pocillopora damicornis*: 1 - Uva Island ( $n = 89$  colonies), unprotected from *Acanthaster*, median = 7 cm; 2 - Pearl Islands ( $n = 87$ ), *Acanthaster* absent, median = 9 cm; regions of significantly different colony sizes are denoted by cross hatching (Kolmogorov-Smirnov test,  $p < 0.05$ ). *Pocillopora elegans*: 3 - Uva Island ( $n = 56$ ), unprotected, median = 14 cm; 4 - Pearl Islands ( $n = 40$ ), *Acanthaster* absent, median = 17 cm; Kolmogorov-Smirnov test ( $0.05 > p > 0.02$ , cross hatching). *Psammocora stellata*: 5 - Uva Island ( $n = 114$ ), unprotected, median = 2 cm; 6 - Pearl Islands ( $n = 140$ ), *Acanthaster* absent, median = 3 cm; Kolmogorov-Smirnov test ( $p < 0.001$ , cross hatching). *Gardineroseris planulata*: 7 - Uva Island ( $n = 132$ ), unprotected, median = 32 cm; 8 - Uva Island ( $n = 32$ ), protected from *Acanthaster*, median = 61 cm; 9 - Secas Island ( $n = 20$ ), *Acanthaster* absent, median = 39 cm; 10 - Pearl Islands ( $n = 50$ ), *Acanthaster* absent, median = 92 cm; Uva Island colony size significantly smaller at unprotected compared with protected site, Kolmogorov-Smirnov test ( $0.05 > p > 0.02$ , for colonies 25-65 cm in size, curves 7, 8); median colony size larger in Pearl Islands than at Uva (unprotected) or Secas Islands, Kruskal-Wallis test,  $p < 0.001$ , a posteriori multiple comparison procedure (MCP),  $\alpha = 0.15$ , curves 7,9, 10 (Daniel, 1978).

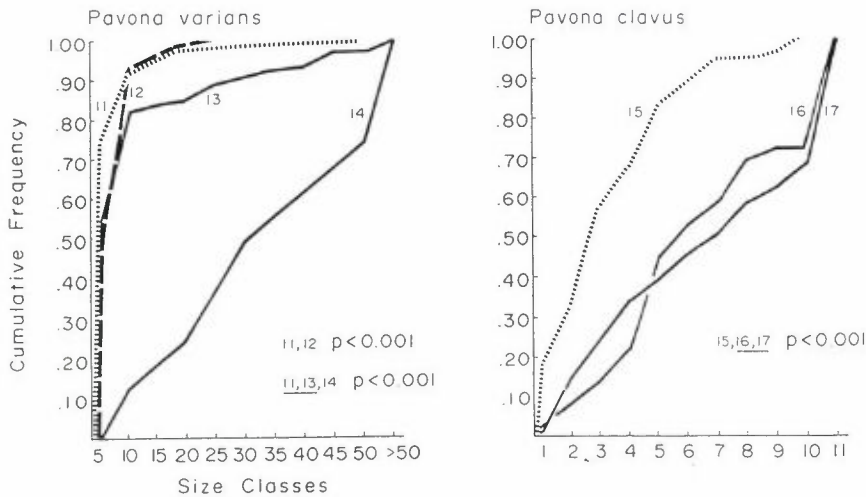


Figure 7. Cumulative frequency distributions of coral colony sizes under different conditions of exposure to *Acanthaster* predation, Pacific coast of Panama. Size-class midpoints (growth axes, cm) are indicated. Key to curves: *Pavona varians*: 11 - Uva Island (n = 203), unprotected, median = 3 cm; 12 - Uva Island (n = 82), protected, median = 6 cm; 13 - Pearl Islands (n = 107), *Acanthaster* absent, median = 5 cm; 14 - Secas Island (n = 16), *Acanthaster* absent, median = 32 cm; Uva Island colony sizes significantly smaller at unprotected compared with protected site, Kolmogorov-Smirnov test ( $p < 0.001$ , for colonies 3 cm in size, curves 11, 12); median colony size larger in Secas Island than at Uva (unprotected) or Pearl Islands (Kruskal-Wallis test,  $p < 0.001$ , MCP,  $\alpha = 0.15$ , curves 11, 13, 14). *Pavona clavus*: 15 - Uva Island (n = 77), unprotected, median = 28 cm; 16 - Pearl Islands (n = 36), *Acanthaster* absent, median = 58 cm; 17 - Secas Island (n = 79), *Acanthaster* absent, median = 70 cm; Uva Island median colony size significantly smaller than in Pearl and Secas Islands (Kruskal-Wallis test,  $p < 0.001$ , MCP,  $\alpha = 0.15$ ).

in habitats without the corallivore (Figs. 6 and 7). In two coral species for which *Acanthaster* shows a strong feeding preference (*Gardineroseris planulata* and *Pavona varians*), this test of size frequency was made at a single site, i.e. in habitats exposed to predation (curves 7 and 11, Figs. 6 and 7) and in habitats surrounded by live *Pocillopora* spp. with their crustacean guard symbionts (curves 8 and 12, Figs. 6 and 7). Since *Acanthaster* does not traverse continuous stands of live *Pocillopora* spp. (Barnes et al., 1970; Glynn, 1985), nonpocilloporid corals encircled by *Pocillopora* are rarely attacked by the sea star. Colony sizes within refugia were significantly larger than those outside at sites where the two coral species are exposed to predation.

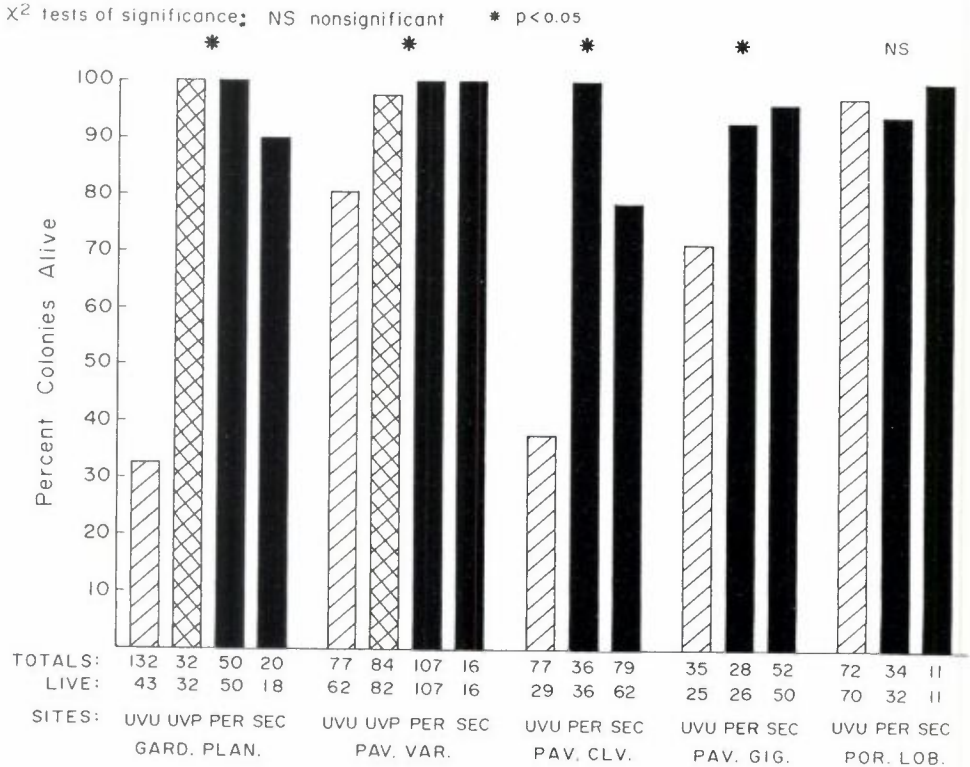


Figure 8. Proportion of live coral colonies present in reef areas under different conditions of exposure to *Acanthaster* predation, Pacific coast of Panama. Five coral species were examined and respective sample sizes (and number alive) are indicated for each locality: UVU - Uva Island reef, unprotected from *Acanthaster*; UVP - Uva Island reef, protected; PER - Pearl Islands, *Acanthaster* absent; SEC - Secas Island, *Acanthaster* absent. There were significant differences among sites in all species except for *Porites lobata*. Chi-square statistics and associated probabilities for each species are: *Gardineroseris planulata* ( $X^2 = 104.4$ ,  $p < 0.001$ ); *Pavona varians* ( $X^2 = 34.69$ ,  $p < 0.001$ ); *Pavona clavus* ( $X^2 = 51.69$ ,  $p < 0.001$ ); *Pavona gigantea* ( $X^2 = 12.84$ ,  $p < 0.01$ ), *Porites lobata* ( $X^2 = 1.104$ ,  $0.70 > p > 0.50$ ).

In 4 of 5 coral species, the frequency of dead colonies in habitats exposed to *Acanthaster* predation (UVU, Uva unprotected, Fig. 8) was significantly higher ( $p < 0.05$ ,  $X^2$  test) than at sites without the corallivore (PER, Pearl Islands; SEC, Secas Islands) or in pocilloporid refugia on a reef where *Acanthaster* has probably been moderately abundant (10-30 inds/ha, Glynn, in prep.) for several hundreds of years (UVP, Uva protected). The exception to this trend, *Porites lobata*, had high frequencies of live colonies at all 3 sites examined. This species is generally avoided by *Acanthaster*, especially in communities with alternative coral prey (Glynn, 1983a; Colgan, in press; Oman, present study).



#### 4. Discussion

Observations in Oman document the occurrence of the coral-crustacean guard mutualism on coral reefs in the Indian Ocean. The symbionts involved in these mutualisms differ from those in the Pacific only at the species level. The defended pocilloporid corals in Oman were *P. damicornis*, *S. pistillata* and *S. subseriata*. *S. pistillata* also is defended in the Gulf of Eilat (Wolodarsky, 1979) and *S. subseriata* is reported here as a guarded host for the first time. Of the two crab guards on pocilloporid corals, *T. cymodoce* also defends pocilloporids in Guam, Samoa, and Eilat, but *T. tigrina* represents a new guard species (Glynn, 1983a). *A. lottini*, the shrimp guard, is an ubiquitous symbiont of pocilloporid corals, known to defend its host in various areas across the Pacific Ocean — eastern Pacific, Hawaii, Samoa, Guam (Glynn, 1983a; Glynn and Krupp, 1986) — and now in Oman. All three of the acroporid host species in Oman, namely *A. cytherea*, *A. pharaonis* and *A. nasuta*, are now recognized as weakly defended corals. *T. cavimana*, the acroporid crab guard in Oman, is the second known guard species in this genus; *T. glaberrima* is known to defend at least three acroporid species in Guam (Glynn, 1983a).

The defensive behaviors of Omani *Trapezia* and *Alpheus* were similar to those reported by Glynn (1983a), and involved noncontact displays (startle, shivering, lurching in *Trapezia*; snapping in *Alpheus*) and contact aggression (mounting, pushing, striking, pinching, clipping, jerking, resisting retreat in *Trapezia*; snapping, pinching in *Alpheus*). *Tetralia cavimana* behaved more aggressively than *T. glaberrima*. Some large individuals of *T. cavimana* defended *A. pharaonis* vigorously; the crabs approached attacking sea stars without hesitation and pinched spines and tube feet briskly.

The intensity of colony defense for all crustacean guards in Oman was within the range of values reported for pocilloporid and acroporid corals in the Pacific. Among localities with *Acanthaster*, where corals are generally well guarded, the strongest median host defense in the Pacific for *P. damicornis* (Panama,  $n = 16$ ) was 29.5 interac./3 min (Glynn, 1983a), compared with 23 interac./3 min ( $n = 33$ ) in Oman ( $p < 0.02$ , Mann-Whitney U test, MWU-test). The strongest defense reported for *S. mordax* (Guam, Glynn, 1983a), 31.5 interac./3 min ( $n = 45$ ) was similar to that for *S. pistillata* in Oman, 40 interac./3 min ( $n = 20$ ) ( $p > 0.05$ , MWU-test). Median colony defense in acroporid corals, reported for only one Pacific locality (Guam, Glynn, 1983a), was 0 interac./3 min (3 species, total of 8 interactions in 30 observations); this was significantly lower than the guard defense observed in

Oman, 3 interac./3 min (2 species, total  $n = 21$ ) ( $p < 0.03$ , MWU-test). The frequency of colony defense for the above species and localities was similar (with  $p > 0.05$ ,  $X^2$  test, for the 3 comparisons). If further study establishes a causal connection between crustacean guard aggression and frequency of predation (i.e. defensive threshold a function of predator attack rate), then it may be surmised that *Acanthaster* is often relatively abundant in the Gulf of Oman.

Central to the question of the origin of guard aggressive behavior are the nature and strength of the selective forces that acted on the coral-crustacean guard mutualism as it evolved. It may be inferred that initially a loose, facultative association developed between corals and crustaceans with the latter seeking shelter and trophic resources (Patton, 1976) and the former benefitting from the cleansing activities of the crustaceans (Glynn, 1983b). Under increasing competition, and dependency upon the coral host, crustacean symbionts would have evolved intra- and interspecific aggressive and appeasement behaviors. In time, the crustacean's aggressive repertoire would be suited (preadapted) to defend the coral host against predators as well as competitors. If this scheme is correct, then acroporid guards (*Tetralia* spp.) would appear to be just entering the third phase of repelling corallivores. There even exists the possibility that crabs may cooperate in colony defense with shrimp; the snapping may serve as an alert signal of an imminent threat to resident crabs (Vannini, 1985). Coral hosts could also have evolved mechanisms that influence crustacean densities, e.g. increasing their number by offering more resources (trophic or shelter) if selection strongly favored increased protection or decreasing their number if crustacean-induced damage became serious at high densities.

Some interoceanic similarities of the coral-crustacean guard mutualism are apparent at the ecological level. Pocilloporid corals are strongly defended and show relatively high survivorship even after severe predation by *Acanthaster*. Acroporid corals often have numerous crab guards, but are weakly defended and suffer high mortality from *Acanthaster* predation. In general, *Acanthaster* avoids pocilloporid corals when other coral prey are available. And in communities where pocilloporid corals are predominant, forming continuous, juxtaposed colonies, *Acanthaster* occurs on the edges of such tracts, and commonly feeds on broken coral branches that contain relatively few crustacean guards. Thus, pocilloporid reefs are apparently resistant to sea star predation, even at outbreak densities.

Besides individual host colony defense, guarded pocilloporid corals may also extend protection to unguarded, nonpocilloporid corals in three ways. (1) As noted above, densely packed, continuous stands of *Pocillopora* spp. are not traversed by *Acanthaster* and when such stands encircle other corals they prevent the entry of predators (Glynn, 1985). (2) Some shade-tolerant poritid and pavonid corals use the dead, understory branches of *Pocillopora* as settlement substrates and thus benefit from the protection of the coral-crustacean guard canopy. (3) Corals immediately surrounding guarded colonies are also sometimes protected by their proximity to coral guards, resulting in a narrow halo (band) of uneaten colonies (Colgan, in press).

Site specific differences in *Acanthaster* predation help to explain coral colony size differences in Panama. Corals in the Gulf of Chiriqui, which are preyed upon frequently by *Acanthaster*, tend to be more youthful and smaller than corals in the Gulf of Panama, an area from which *Acanthaster* is absent (Glynn, 1974). It is also possible that coral colony size differences could be due to other factors (besides predation) related to the localities sampled. For example, it could be argued that upwelling, or some associated factor, in the Pearl Islands favors coral longevity (large colony sizes) compared with the Uva and Secas sites in the Gulf of Chiriqui where upwelling is infrequent (Glynn et al., 1972; Glynn, 1977; Dana, 1975). However, the 3-site comparisons for *Gardineroseris planulata*, *Pavona varians* and *P. clavus* are not consistent with this argument. While colony size in *G. planulata* was largest in the Pearl Islands, the largest colonies of *P. varians* occurred in the Secas Islands, and of *P. clavus* in the Pearl and Secas Islands (Kruskal-Wallis test,  $p < 0.001$ , MCP,  $\alpha = 0.15$  in all 3 comparisons). Additionally, this argument fails to explain the larger colony sizes found within guarded coral refugia (see above).

Coral community structure may also be influenced indirectly by predation. For example, at Masirah Island (south coast of Oman, Fig. 1), an upwelling environment without *Acanthaster*, pocilloporid corals were present and formed small patch reefs on the leeward (north) island shore. However, *Montipora* corals, a group preferred by *Acanthaster* (Branham et al., 1971, and this study), were also abundant. *Montipora foliosa* (Pallas), an erect and spreading foliaceous species, formed large tracts that monopolized much of the substrate in this area. Competitive overtopping was observed in numerous instances, with *M. foliosa* excluding entire colonies of *Pocillopora damicornis*. This kind of competitive advantage, observed in rapidly-growing and spreading corals (Stimpson, 1985), was not seen in the Gulf of Oman

where *Acanthaster* was abundant. It is possible that frequent predation by *Acanthaster* on the preferred *Montipora* corals seldom allows this potentially superior competitor to reach sufficiently high population densities to interfere with the growth of *Pocillopora*. Another case reported at Gorgona Island (Pacific coast of Colombia), in reef communities without *Acanthaster*, involved an increase in the relative abundance of unprotected, nonpocilloporid corals (Glynn et al., 1982). The absence of predaceous sea stars presumably has allowed unprotected (preferred) corals to persist, resulting in an increase in local species diversity. Finally, if Birkeland's (1982) hypothesis is correct, namely that *Acanthaster* outbreaks are caused by wet, typhoon-induced nutrient runoff on high islands (by increasing larval food supply and survival), then coral prey preferred by *Acanthaster* would be expected to suffer bouts of massive mortality in such areas. Randall (1973) and Colgan (in press) provide evidence of severe *Acanthaster* predation on preferred coral prey and low mortality on guarded corals at Guam following *Acanthaster* outbreaks. Corals preferred by *Acanthaster* steadily increased in abundance during the recovery of the coral community after the severe predation event. Such conditions might favor higher relative abundances of guarded corals in high island reefs than in atoll coral communities.

## 5. Conclusions

If we consider some of the possible consequences of Janzen's (1985) question — the appearance of the biotic world without symbioses — in the context of Indo-Pacific coral reef communities without crustacean guards, we may find: (a) lower biomass and diversity of coral-associated crustaceans owing to the absence of guards; (b) less frequent disturbance to corals by predators hunting for crustaceans (this could result in reduced coral breakage and less frequent asexual propagation); (c) low relative abundances of pocilloporid corals where *Acanthaster* is abundant; (d) pocilloporid reefs present only in upwelling environments where *Acanthaster* is absent; (e) fewer corals surviving *Acanthaster* outbreaks because of absence of guarded coral refugia (e.g. pocilloporid encirclements and halos).

In this paper, several patterns of coral community structure have been related to predation and to the degree of protection offered to corals by crustacean guard symbionts. While some studies have indicated that guarded corals experience a high survivorship under intense predation, it must be emphasized that this is only one of several possible kinds of protection. Other coral taxa may escape predation by the production of noxious secondary

metabolites, potent nematocyst defenses (Brauer et al., 1970; Ormond et al., 1976; Thomason and Brown, 1986 [three "super-aggressive" Indo-Pacific corals with high numbers of nematocysts per polyp, namely *Fungia*, *Galaxea*, and *Goniopora* are rarely eaten by *Acanthaster* when other prey are available]), extrusion of mesenterial filaments, colony form and location in habitats inaccessible to *Acanthaster* (Goreau et al., 1972). Further, other important processes affecting coral community structure include supply of larvae, settlement and recruitment success, competition, and numerous forms of physical and biotic disturbance. An urgent area of research is to identify and quantify these various effects, and to determine their relative importance in controlling coral community structure and development.

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