Oecologia (Berl.) 47, 287–290 (1980)

Oecologia

Defense by Symbiotic Crustacea of Host Corals Elicited by Chemical Cues from Predator

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Summary. Observations and experiments carried out on a coral reef off the Pacific coast of Panamá demonstrated that shrimp (*Alpheus lottini*) and crab (*Trapezia* spp.) symbionts that protect their host coral (*Pocillopora elegans*) can detect an approaching sea star predator (*Acanthaster planci*) by chemical cues. Simulated feeding attacks by *Acanthaster* in sealed transparent bags elicited only 0.5 defensive responses (snipping at spines and tube feet, jerking the sea star, and snapping) per 3 min; defensive behavior increased significantly to 4 and 5 responses, respectively, for *Acanthaster* in perforated bags and for *Acanthaster* in direct contact with coral. Neutralized (boiled) *Acanthaster* elicited only 3 defensive interactions per 3 min compared with 12 interactions for live *Acanthaster*. Simulated feeding attacks by *Oreaster*, a non-corallivorous sea star, elicited only 0.5 defensive responses per 3 min, whereas *Oreaster* introduced with "*Acanthaster* water" increased the level of defensive responses to 7. These results suggest that chemical, and to a lesser extent visual (physical presence and movements of sea star), cues stimulate the defensive behavior of the symbiotic crustaceans. The ability to detect a predator at a distance is probably advantageous because in responding only to an actual threat it minimizes the time the defending symbionts spend in an exposed position on the terminal branches of the host coral and because it alerts the crustaceans to sea stars feeding at night.

Introduction

Feeding preferences of the crown-of-thorns sea star *Acanthaster planci* (Linnaeus) influence the differential survival of reef-building corals (Barnes et al. 1970; Branham et al. 1971; Goreau et al. 1972; Laxton 1974; Glynn 1976; Ormond et al. 1976). Some coral species are preyed upon relatively little because of their colony form, their habitat (accessibility), their production of noxious substances, their potent nematocysts, and mutualistic crustaceans that defend them from attack. *Acanthaster* attempting to mount and feed on corals in the family Pocilloporidae (*Pocillopora, Seriatopora, Stylophora*) are often repelled by crabs that snip spines and tube feet and jerk the attacking sea star to and fro, and by shrimp that snap at and occasionally snip the sea star's spines (Pearson and Endean 1969; Weber and Woodhead 1970; Glynn 1976). These crustaceans are obligate symbionts of pocilloporid corals and feed primarily on the host coral's mucus (Knudsen 1967; Patton 1974).

I have found that *Acanthaster* approaching potential prey in the direction of the current elicit the defensive response of the crustaceans before actually contacting the colony, suggesting that a kairomone or chemical danger signal (Whittaker and Feeny 1971; Kittredge et al. 1974) could be alerting the crustaceans to the threat of an approaching predator. I report here field experiments which demonstrate that some chemical substance(s) diffusing from *Acanthaster* stimulates defensive behavior in the crustacean symbionts of *Pocillopora elegans* Dana.

Materials and Methods

The animals examined in this study were: a) *Acanthaster planci*, a corallivore; b) *Pocillopora elegans*, a coral prey of *Acanthaster;* c) the crustacean symbionts of the host coral. The identity of *A. planci* in the eastern Pacific region was confirmed in Glynn (1974). *Pocillopora elegans* was selected as a prey test species because it occurred abundantly with *Acanthaster*, it was easily identified under water, and its widely-spaced branches permitted a view of the interactions between *Acanthaster* and the crustacean symbionts. The crustacean symbionts of *P. elegans* were an alpheid shrimp, *Alpheus lottini* Guérin, and four species of xanthid crabs in the genus *Trapezia*. According to Castro (in press), the crabs were *Trapezia corallina* Gerstaecker, *Trapezia digitalis* Latreille, *Trapezia ferruginea* Latreille and *Trapezia formosa* Smith. The relatively small and secretive *T. formosa* may not be important in defending coral. The defensive responses of the crustaceans were also tested against *Oreaster occidentalis* Verrill, a large (20–25 cm, arm tip to arm tip) sea star that feeds chiefly on sponges.

All observations were made at Uva Island (Glynn 1973, 1976), Gulf of Chiriquí, Panamá (10–16 January 1980) during daylight hours (0700–1800). *Acanthaster* feeds on corals during the day and night in Panamá (Glynn 1976). The population density of *Acanthaster* in the study area was 4–7 individ. per 1,000 m^2. Interactions between the crustaceans and *Acanthaster* were observed under water (≤ 10 m depth), using scuba, at a distance of ~ 40 cm and by moving around the colony when necessary; all observable events and their duration were recorded on a slate. The sizes of the *Acanthaster* (21–33 cm, arm tip to arm tip) and coral colonies (528–1,248 cm^2, length by width) were selected so as not to differ appreciably among themselves. Because the numbers and sizes (and possibly aggression) of *Trapezia* increase with increasing coral host size (Abele and Patton 1976; Castro in press), large colonies are probably more effectively defended than small colonies. *Alpheus lottini* has an area-independent population size, usually with a single male-female pair per coral colony (Abele and Patton 1976).

To quantify the usual defensive behavior of the crustacean symbionts, eight *Acanthaster*, were placed on different colonies of *Pocillopora elegans*. The sea stars were placed directly on the top-center of the colonies and the defensive activities of the crustaceans observed until the sea star had abandoned (no longer in contact) the coral. One *Trapezia* bout usually consists of a crab moving peripherally along a coral branch and clipping tube feet or spines, usually 1 to 3) or grasping a spine and vigorously jerking the sea star up and down (usually for 2 to 5 s).

0029-8549/80/0047/0287/$01.00

An *Alpheus* bout normally involved a shrimp moving peripherally and snapping (each snap was scored as 1), sometimes snapping with the cheliped in contact with the sea star and occasionally clipping the tube feet or spines.

To test the response of the crustaceans to an attacking *Acanthaster* in the absence of a possible chemical cue, sea stars were placed inside clear, 6 liter, polyethylene bags that could be sealed tightly. These were placed on top of *Pocillopora* colonies. Six holes 3-cm in diameter were then cut into the side of each bag (the surface resting against the coral). In the last treatment the sea stars were removed from the bags and placed directly on the top-center of the coral. The interactions in each trial were observed for 3 min. This time interval was selected because it was found that a) several defensive bouts occurred over this duration, b) it was not necessary to reposition the dismounting sea star, and c) its brevity permitted sufficient replication. Each coral colony was subjected to the three treatments consecutively (employing the same sea star) in the order: a) sealed bag, b) perforated bag, and c) direct contact. The bags were large enough to permit movement of the sea stars. About 3 min elapsed between treatments during the transfer of sea stars from bag to bag and then directly onto the coral. The order of the three treatments here, and those involving the sea stars *Oreaster* and *Acanthaster* (see below), each eliciting a stronger response, was employed in order to avoid a possible bias due to some lingering substance(s). A time-dependent response was not apparent over the duration of the observations.

The defensive behavior of the symbiotic crustaceans was also tested with a dead *Acanthaster* that had been boiled for 5 min and washed

Table 1. Defensive behavior of crustacean symbionts toward *Acanthaster* in direct contact with host coral

Sea star no.	Sea star size (cm)[a]	Coral host size (l.xw., cm^2)	No. of agonistic responses			Dismounting time (min)
			Trapezia[b]	*Alpheus*	Total	
1	21	528	0	12	12	1′55″
2	26	616	7	2	9	4′10″
3	23	960	5	1	6	3′10″
4	25	1,200	19	6	25	8′+[d]
5	22	1,248	2	16	18	4′30″
6	33	924	5	18	23	3′45″
7	26	1,230	11	13	24	7′10″
8	25	1,000[c]	3	3	6	2′25″
Median	25	980	5	9	15	3′58″

[a] Greatest overall length (arm tip to arm tip) measured in relaxed state in near-horizontal position

[b] *T. corallina* Gerstaecker, *T. digitalis* Latreille, *T. ferruginea* Latreille and *T. formosa* Smith

[c] Estimated

[d] Observation terminated after 8 min

Table 2. The defensive responses of coral crustacean symbionts to three different degrees of exposure to *Acanthaster*

Sea star no.	*Acanthaster* in sealed bag			*Acanthaster* in perforated bag			*Acanthaster* in direct contact		
	Trapezia	*Alpheus*	Total	*Trapezia*	*Alpheus*	Total	*Trapezia*	*Alpheus*	Total
1	[a]	[a]	0	[b]	2	2	5	1	6
2	0	0	0	[a, b]	0	0	2	0	2
3	0	0	0	1[b]	3	4	1	4	5
4	[a]	2	2	2[b]	12	14	14	15	29
5	0	2	2	4	0	4	3	1	4
6	[a]	1	1	1	9	10	1	4	5
Median	0	0.5	0.5	1.0	2.5	4	2.5	2.5	5

[a] Crustacean symbiont aroused

[b] Crab displayed by directing extended chelipeds toward the sea star

Table 3. The defensive responses of coral crustacean symbionts to *Oreaster*, *Oreaster* with water from *Acanthaster*, and *Acanthaster*

Sea star no.	*Oreaster*[c]			*Oreaster* with *Acanthaster* water[d]			*Acanthaster*		
	Trapezia	*Alpheus*	Total	*Trapezia*	*Alpheus*	Total	*Trapezia*	*Alpheus*	Total
1	[b]	0	0	–	–	–	1	0	1
2	[a]	[a]	0	–	–	–	8	9	17
3	[b]	1	1	–	–	–	3	5	8
4	[a]	0	0	4	2	6	6	6	12
5	4	0	4	5	2	7	5	9	14
6	2	4	6	5	12	17	5	20	25
Median	0	0	0.5	5	2	7	5	8	13

[a] Crustacean symbiont aroused

[b] Crab displayed by directing extended chelipeds toward the sea star

[c] Pulled over surface of coral at same speed *Acanthaster* dismounted

[d] Obtained from 6 liters of sea water in which the sea star was confined for at least 10 min; about 300 ml of this water was squirted gently onto the coral colony every minute during the 3 min observation period.

thoroughly before use. Each of six trials involved two 3-min observation periods. The same dead sea star was first placed on the summit of a coral colony and slowly pulled over the surface to simulate the movement of a live animal; then a different live *Acanthaster* was similarly placed on each coral.

I next tested the crustacean response to a sea star (*Oreaster occidentalis*) that does not feed on live coral. First, *Oreaster* alone was placed onto *Pocillopora,* then it was placed on the coral and perfused, using a hypodermic syringe, with water, in which an *Acanthaster* had been maintained for at least 10 min. Finally, I placed live *Acanthaster* alone on the coral. Each coral colony was subjected to the treatments consecutively in the order (for sea stars 1–3): a) *Oreaster,* b) *Acanthaster;* (for sea stars 4–6): a) *Oreaster,* b) *Oreaster* with *Acanthaster* water, and c) *Acanthaster.* About 3 min elapsed between treatments.

Results

The intensity of the defensive behavior of each crustacean species, and all combined, was not correlated significantly with the size of the coral host or the size of the sea stars (Kendall partial rank correlation, $p > 0.05$, Table 1). The median number of responses of *Trapezia* spp. and *Alpheus lottini* were five and nine per colony, of respectively, with a total median defensive response 15 events per 3 min *Acanthaster* assault. Median dismounting time was about 4 min (3 min 58 s), and individual dismounting times increased significantly in proportion to the defensive response ($\tau = 0.58$, $p \sim 0.03$, Kendall rank correlation coefficient). Delay often occurred because the crustaceans disturbed the sea star's forward locomotion and because *Trapezia* gripped or jerked the sea star, impeding its retreat.

Increasing levels of agonism were evident in *Trapezia,* in *Alpheus* and all the crustaceans combined (totals) for all three treatments (Table 2), which represented increasing degrees of exposure to *Acanthaster* ($p \ll 0.0001$ for the three tests, Friedman 2-way anova). The combined (total) median defensive response toward the isolated (bagged) *Acanthaster* was only 0.5 interactions per 3 min. The combined (total) median defensive responses increased to 4 and 5 interactions per 3 min, respectively, for *Acanthaster* in the perforated bag and in direct contact. These higher levels of agonism are not significantly different from each other ($p > 0.05$, Wilcoxon paired-sample test), indicating that the presence of the perforated bag had little or no effect on the defensive responses of the crustaceans.

Dead (boiled) *Acanthaster* pulled slowly over the surface of the coral elicited very little defensive behavior compared with live sea stars (Fig. 1). In every trial, the responses of *Trapezia* and *Alpheus* were greater for live than for dead sea stars ($p < 0.05$, Wilcoxon paired-sample test). The combined median defensive responses for dead and live *Acanthaster* were 3 and 12 interactions per 3 min, respectively ($p < 0.05$). These results suggest that the chemical agent(s) is thermolabile. However, since the boiled *Acanthaster* water was not tested there still remains the possibility that an active substance was extracted into the solution by boiling, leaving little extra to diffuse from the surface of the sea star.

The reaction of the crustaceans to *Oreaster* showed a graded response with the defensive interactions increasing in proportion to the exposure to *Acanthaster* (Table 3). Responses for *Trapezia* and *Alpheus* separately, and their combined activities of 4, 7 and 14 interactions per 3 min respectively (sea stars 4–6), all differed significantly among treatments ($p \ll 0.03$, Friedman 2-way anova, $n = 3$). The crustaceans were also aroused when 50 ml of *Acanthaster* water alone was injected between the branches of coral colonies. A comparison of live *Oreaster* and dead *Acanthaster* (both pulled over the coral at same speed) indicates a similarly low defensive response toward the two sea stars after neutralization (by boiling) of the active agent(s) from *Acanthaster* ($p \sim 0.16$, Mann-Whitney U test). While there was considerable variability in the combined levels of defensive responses among the different experiments, the median total response toward *Acanthaster* in direct contact with coral following enclosure in bags was 5 defensive interactions per 3 min (Table 2), compared with 12 (Figure 1) and 13 (Table 3) observed in the other experiments – these differences were not statistically significant ($p \sim 0.10$, Kruskal-Wallis anova).

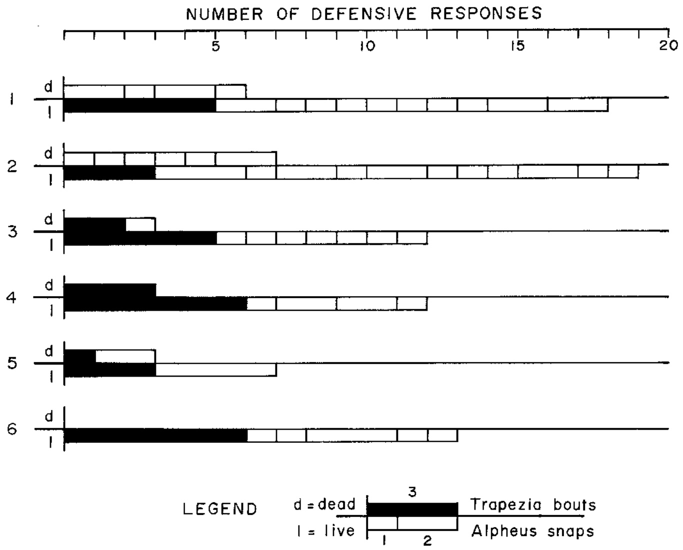

Fig. 1. Defensive responses of *Trapezia* and *Alpheus* toward dead *(boiled)* and live *Acanthaster.* The frequency of *Alpheus* snaps per bout is indicated by the length of each open horizontal bar; the total frequency of *Trapezia* bouts is indicated by the length of each occluded bar (*see legend*)

Discussion

Examples of mutualistic interactions involving host protection are numerous, e.g. ants defending acacia trees from caterpillars (Janzen 1966), damselfish protecting sea anemones from foraging fishes (Mariscal 1970; Fricke 1974), and alpheid shrimp defending sea anemones from worms (Smith 1977). Several cases have been described in which potential prey are alerted to the proximity of predators through chemical agents (Bullock 1953; Feder 1963; Mauzey et al. 1968; Mackie and Grant 1974; Dayton 1975). The olfactory recognition of sea star predators is clearly a feasible and adaptive phenomenon. The only other reported instance of a symbiont protecting its host from an asteroid predator involves a temperate commensal polychaete that may defend a keyhole limpet by biting the tubefeet of a sea star (Dimock and Dimock 1969). It is not clear, however, that a kairomone elicits the defensive response in the latter case or if the worm reacts to the defensive mantle response of the limpet.

The present study represents the first documented case of crustaceans responding defensively to the chemical agents of a sea star. Rainbow (1974) described the importance of olfactory cues in the detection of sea stars by the painted shrimp *Hymenocera.* Unlike the crustacean symbionts that keep *Acanthaster* away from their coral host, *Hymenocera* is a predator that specializes on sea stars (Glynn 1977).

Margolin (1964) has shown that the mantle response of a limpet can be stimulated by a sea star predator at a distance and also by "sea star water" (water that had contained the sea star). Boiled "sea star water" did not evoke the mantle response. This result is similar to that of the present study which showed a significantly diminished defensive response for boiled *Acanthaster* involved in a simulated attack. However, some crustacean symbionts of *Pocillopora* were aroused into a defensive behavior by the presence and movement of neutralized *Acanthaster*. Some defensive activity also occurred when *Acanthaster* was pulled over coral in a sealed bag. These results suggest that the crustaceans are weakly stimulated by visual cues (combination of physical presence and movement) and strongly stimulated by chemical cues. Mackie and Grant (1974) claim that saponins – water soluble, surface-active substances that form a soapy foam in high dilution – are the active substances in sea stars in all cases studied.

The sensitivity of the crustacean symbionts to a chemical cue signaling the approach of a predator would appear to have a clear selective advantage. First, the crustacean symbionts would need to move peripherally onto the terminal branches, exposing themselves to fish predators, only when their host is threatened, and secondly, a specific response to a kairomone would allow detection of a predatory threat at night when *Acanthaster* also forages. It is conceivable that *Acanthaster* may also benefit in revealing its presence. By the early recognition that a colony is defended by highly agonistic crustaceans, the sea star minimizes the loss of time and energy in fruitless preliminary feeding activities and avoids injury by not mounting defended corals.

Acknowledgments. This research was supported by the Smithsonian Tropical Research Institute. I thank I. Rubinoff for his encouragement, R. Highsmith, M.C. Stouder and A. Velarde for assistance in the field, and L.G. Abele, P. Castro and R.B. Manning for identification of the crustacean symbionts. Helpful comments were offered by D.P. Abbott, P. Castro, R. Highsmith, G.M. Wellington and an anonymous reviewer.

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Received June 20, 1980