

Protection of Symbiotic Cnidarians by Their Hermit Crab Hosts: Evidence for Mutualism

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Abstract

Symbioses involving sea anemones (*Calliactis* sp.) and hydroids (*Hydractinia* sp. or *Podocoryne* sp.) living with hermit crabs usually have been classified as mutualisms (i.e., both partners benefit). Several benefits have been reported for the crabs, but none has been demonstrated for the cnidarians. This paper examines the ability of two species of hermit crab (from different geographical regions) to protect their cnidarian symbionts from predation. Experiments demonstrated that *Pagurus pollicaris* provided protection for anemones and hydroids against sea stars (*Echinaster spinulosus*), while *Dardanus venosus* protected *Calliactis* from fireworms (*Hermodice carunculata*). These results provide the first evidence that these symbioses are mutualistic.

Keywords: anemones, *Calliactis*, *Dardanus*, hermit crabs, *Hermodice*, hydroids, *Pagurus*, predation, symbiosis

1. Introduction

Why do sea anemones and hydroids associate symbiotically with hermit crabs? Selection pressures should favor the development of symbiotic associations if at least one partner's fitness is enhanced (Boucher et al., 1982; Ahmadjian and Paracer, 1986); the effect on the other partner's fitness can

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vary. If it is harmed, the association is parasitic; if it is unaffected, it is commensalistic; if it also benefits, it is mutualistic (Ahmadjian and Paracer, 1986). Symbioses between cnidarians and hermit crabs are common and have been generally regarded as associations beneficial to both species, that is mutualisms (for review, see Hazlett, 1981; Ross, 1983).

Previous studies have demonstrated that hermit crabs are protected from their predators by the sting of the cnidarians, which repels attacking crabs and octopuses (Ross, 1971; Brooks and Mariscal, 1985). No comparable data exist, however, to show whether benefits accrue to anemones and hydroids as a consequence of their association with hermit crabs.

This paper examines the ability of hermit crabs to protect their symbiotic sea anemones and hydroids. Predation trials were done in the laboratory with two species of hermit crab from different geographical areas. The sea star *Echinaster spinulosus* was used as a predator in trials with the hermit crab *Pagurus pollicaris*, while the polychaete fireworm *Hermodice carunculata* was the predator in trials with the hermit crab *Dardanus venosus*.

2. Materials and Methods

Collection and maintenance

Pagurus pollicaris was collected in *Polinices duplicatus* shells from St. Joseph Bay, Florida, in the northeastern Gulf of Mexico at depths of < 2 m. About 20% of all crabs were found with either anemones (*Calliactis tricolor*) or hydroids (*Hydractinia echinata* or *Podocornye selenia*). The anemone and hydroid were rarely found on the same shell (probably because of aggressive interactions between the cnidarians; Brooks and Mariscal, 1986a). Sympatric sea stars (*Echinaster spinulosus*) were also collected. Hermit crabs (with their cnidarians) and sea stars were kept separately in 38 l closed-system aquaria at Auburn University, Montgomery, Alabama, for 8–10 d before being used in experiments. Hermit crabs and cnidarians were fed on alternate days with flaked fish food and adult brine shrimp. Sea stars were fed small chunks of squid on each of the first 3–5 d, but were not fed within 5 d of the start of a trial to standardize satiation levels among individuals.

Dardanus venosus was collected in *Fasciolaria hunteria* or *F. tulipa* shells in the Florida Keys. Most of the crabs had several to many *C. tricolor* on their shells. Hydroids were not found on the shells. Fireworms (*Hermodice carunculata*) were also collected in the Florida Keys. Hermit crabs (and anemones) and fireworms were kept separately in outdoor, running seawater tanks at the Florida Keys Marine Laboratory, Long Key, Florida, for one week prior to being transported to 38 l closed-system aquaria at Florida Atlantic University

where all trials were performed. Hermit crabs and anemones were fed as described above. Fireworms were fed pieces of shrimp, squid, or live anemones (*Bartholomea* sp.) every 2 d while being housed at these two locations, but were not fed within 5 d of the start of a trial. No fireworms were held for more than 2 weeks before being used in experiments.

General predation behavior

The behavioral responses of the sea stars and fireworms toward the cnidarians were recorded by placing a single predator in a 9.5 l aquarium with a *Calliactis* that had been removed from its shell or a hydroid on a vacated shell (fireworms were not paired with hydroids).

Experimental protocol

Sea star predation trials

The following experiments were done to test the effectiveness of *P. pollicaris* and their shells in protecting cnidarians from sea stars. In the first set of trials, an individual sea star was given access to a *C. tricolor* in a 9.5 l aquarium for 3 hr under each of the following conditions: (1) *C. tricolor* attached to the gastropod shell occupied by a hermit crab, (2) *C. tricolor* attached to an unoccupied gastropod shell (see Brooks, 1988, for hermit crab removal technique), and (3) *C. tricolor* attached to the aquarium substratum. Twenty replicates of each condition were run. The number of trials in which an attack (i.e., the mouth of the sea star contacting the anemone) occurred was recorded.

In the second set of trials the protocol described above was used for the hydroid (either *Hydractinia* or *Podocoryne*), except for condition #3 (because the hydroid could not be removed intact from the snail shell).

Individual sea stars and crabs with their cnidarians were used only once in these trials.

Chi-square tests were used to analyze the data from each set of trials. The null hypothesis was that sea star attacks would occur with equal frequency, regardless of trial conditions.

Fireworm predation trials

The same three trial conditions were used to determine the effectiveness of *D. venosus* and their shells in protecting *Calliactis* from fireworms. Six replicates of each trial condition were run. Because of limited numbers of fireworms collected, a repeated measures design was employed, involving six previously untested worms. The sequences in which the six worms were placed

under the three conditions was not completely random. Each of the worms was tested last with the hermit crab present because preliminary observations showed that injury to the fireworm was likely. Randomization of trials one and two was employed by a coin toss. All trials began by 0900. Observations were made hourly during the first 8 hr. Trials were run overnight to include nocturnal periods, but hourly observations were not made during this time. Differences in survival times (up to 24 hr) for the anemones for each condition were analyzed using the Kruskal-Wallis ANOVA test.

3. Results

Sea star section

General predation behavior

Seven sea stars were observed individually during interactions with a *C. tri-color* attached to the substratum. All seven sea stars eventually consumed the anemone.

An attack usually began after one of the arms of the sea star contacted the anemone. If this initial contact was with the anemone's tentacles, the sea star would curl its arm up and backward. The anemone's tentacles would retract in a typical cnidarian prey-capture response (Brooks and Mariscal, 1986a). The sea star typically moved 2–4 cm away from the anemone after initial contact with the anemone. Within 2–3 min (but in one case, up to 45 min), the sea star re-approached the anemone with two of its arms spread out on the substratum; after contacting the anemone, it pressed its oral surface and mouth against the column of the anemone (Fig. 1). Eventually, the anemone was pushed over so that its column axis was parallel to the substratum. The sea star then began digesting the column first, and eventually the tentacles. Within 4–5 hr, the anemone was completely consumed.

Nine sea stars were observed in trials with an empty hydroid-colonized shell. In eight of these trials, the sea star attacked the colony after initial contact. Upon initial contact, the arm of the sea star curled back, but to a lesser degree than with the anemone. The polyps of the hydroid also retracted after being contacted. The sea star remained in the same position near the shell for 10 min or less, then positioned its oral surface on top of a portion of the colony. It remained there for up to 1 hr before moving to a different portion of the colony. In the previously grazed area, all that remained of the colony was the non-living hydrorhizal plate. The sea star could not position its oral surface over all areas of the shell, and thus some sections of the colony were not grazed. After 3–4 hr of feeding, the sea star usually left the shell.

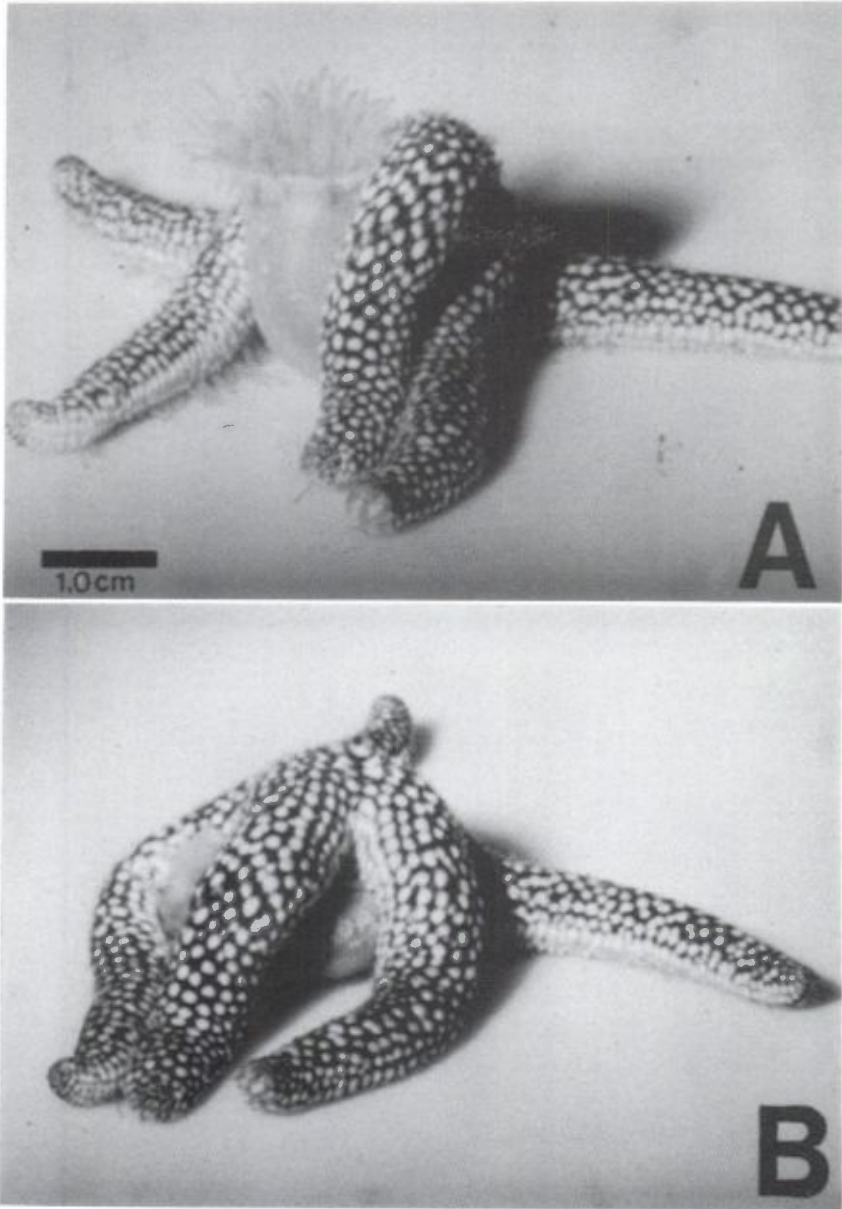


Figure 1. The sea star *Echinaster spinulosus* attacking (A) and consuming (B) the anemone *Calliactis tricolor*. Digestion of all tissues usually occurred within 4-5 hr.

Predation experiments with Pagurus pollicaris

When this crab was present, the number of sea star attacks on *C. tricolor* was reduced significantly. Attacks were frequent on anemones on empty shells or the substratum. Similar results were obtained with the hydroid prey, where significantly fewer attacks occurred in the presence of a hermit crab. A summary of all trial results is given in Table 1.

Fireworm section

General predation behavior

Five fireworms were observed during interactions with *C. tricolor* attached to the substratum. Four of the worms attacked and consumed the anemones. Attacks were not initiated until after the head region of the worm contacted the anemone. If tentacles were contacted, the worm would move its head back momentarily, and the tentacles would retract. Within 30 sec, however, the worm re-positioned its head and mouth on top of the anemone (the tentacles were fully retracted again), everted its buccal region, and began predigestion (Fig. 2).

Predation experiments with Dardanus venosus

None of the *C. tricolor* on shells with *D. venosus* was consumed during the 24 hr trials. Anemones on unoccupied shells survived ($X \pm SD$) 7.2 ± 2.9 hr, which was similar to the survival time of 7.5 ± 2.5 hr for anemones on the aquarium substratum. Anemones survived significantly longer, however, in the presence of the crab (Kruskal-Wallis $H = 45$, $P < 0.01$).

Table 1. The number of trials ($N = 20$ /trial) with sea star attacks on anemones (*Calliactis tricolor*) and hydroids (either *Hydractinia echinata* or *Podocornye selenae*). Experimental conditions: (1) cnidarian on gastropod shell occupied by the hermit crab *Pagurus pollicaris*, (2) cnidarian on unoccupied shell, (3) *C. tricolor* on the aquarium substratum (* hydroids could not be removed intact from shells).

cnidarian prey	Number of sea star attacks in trials:			X^2	p
	1 on shell occupied by crab	2 on shell without crab	3 on aquarium substratum		
Anemones	1	19	20	17.2	< 0.001
Hydroids	2	18	*	11.3	< 0.001

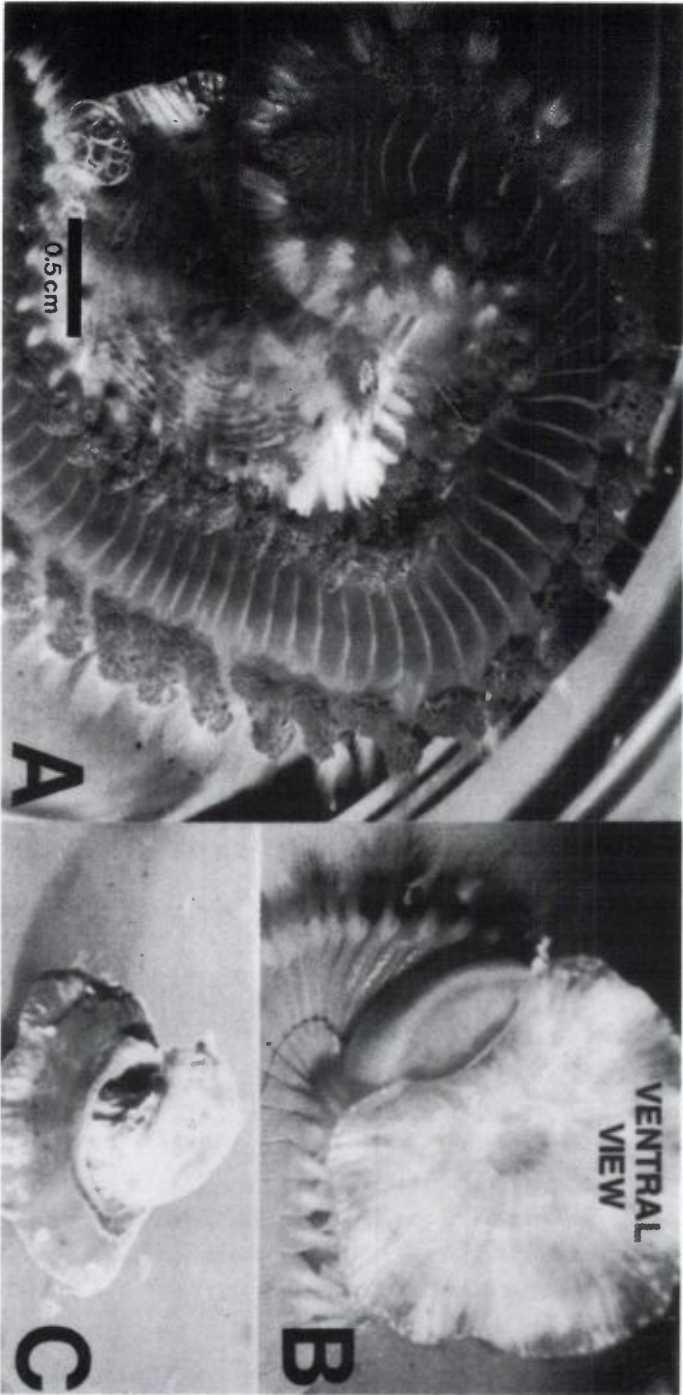


Figure 2. The fireworm *Hermodice carunculata* attacking the *Calliactis tricolor* (A). In B, a portion of the worm's everted buccal region, which releases digestive enzymes, can be seen from a ventral view. In C, the tentacles and oral disc of the anemone have been partially dissolved and were consumed by the fireworm within 15 min. Complete digestion occurs within 1-2 hr.

Four crabs attacked the worm, ripping its body into pieces and eventually eating it. Two crabs avoided the worm after initial contact, which prevented the worms from attacking the anemones.

4. Discussion

Documentation of benefits to partners

Several benefits to hermit crabs have been reported. For example, some sea anemones (genus *Adamsia*; Faurot, 1910; genus *Stylobates*; Dunn et al., 1980; Dunn and Liberman, 1983; Fautin, 1987) apparently find the shells occupied by juvenile hermit crabs attractive. They settle on these substrates and secrete a chitinous shell (carcinoecium) as the crab grows. Another unidentified anemone uses its pedal disc to directly envelop the abdomen of its hermit crab (*Munidopagurus* sp.) (Provenzano, 1971; Ross, 1983). In these examples, the hermit crab might benefit because the anemone's shell or pedal disc lessens or eliminates the need for the crab to change snail shells. Schifjsma (1935) and Jensen (1970) suggested that symbiotic hydroids (*Hydractinia* sp.) might benefit crabs in the same way, because the shell secreted by these hydroids extends the lip of the mollusk shell with perisarc material, increasing the shell's internal volume.

Some cnidarians are known to provide protection for hermit crabs. *Calliactis* anemones and *Hydractinia* hydroids deter predatory crabs (Grant and Pontier, 1973; McLean and Mariscal, 1973; Brooks and Mariscal, 1985) and octopuses (Ross, 1971; Balasch and Mengual, 1974; Ross and Boletzky, 1979; McLean, 1983; Brooks and Mariscal, 1985; Brooks, 1988).

Benefits to the cnidarians have not yet been demonstrated. One suggestion is that transported cnidarians have greater access to food (Ross, 1974). Christensen (1967) found that 90% of the *Hydractinia* diet consisted of benthic organisms. The colony fed as the crab dragged its shell along the substratum. No studies, however, have compared feeding or growth rates of transported versus non-transported anemones.

Predation on cnidarians

The cnidarian nematocyst is an effective structure for feeding and defense. Nonetheless, some animals consume cnidarians regularly. The list includes amphipods and pycnogonids (Van-Praet, 1985), annelids (Lizama and Blanquet, 1975; Witman, 1988; Vreeland and Lasker, 1989), nudibranchs (Harris, 1971; Greenwood and Mariscal, 1984), asteroids (Milligan, 1916; Glynn, 1974, 1980, 1987), fishes (Webb, 1973; Ottaway, 1977; Ates, 1989; Godwin and Fautin,

in press), and reptiles, birds, and mammals (Ates, 1991). Many cnidarians, including symbiotic sea anemones and hydroids, are primarily sessile and thus susceptible to predation. In fact, Milligan (1916) reported the sea star *Solaster papposus* could consume the symbiotic anemone *Sagartia*(=*Calliactis parasitica*).

Host protection

This study demonstrates for the first time that cnidarians can benefit from associations with hermit crabs by receiving protection. Sea stars and fireworms were observed consuming symbiotic cnidarians in the laboratory. Sea stars appeared to have been stung during initial contacts with the cnidarians, but nematocyst discharge did not prevent the subsequent consumption of *C. tricolor* and *H. echinata*. Some sea star species can do considerable damage to populations of cnidarians (e.g., *Acanthaster*: Glynn, 1974). Therefore, based on these laboratory trials, *E. spinulosus* could be an important predator in St. Joseph Bay, Florida, if these cnidarians were found commonly on stationary substrates.

Pagurus pollicaris provided protection for both species of cnidarians by moving away from the sea star. Thus, by simply being more mobile than predators, the crab contributes to the survival of these sedentary cnidarians. The non-symbiotic anemone *Stomphia coccinea* has developed a quick escape response to avoid predation by asteroids. It releases its pedal discs from the substrate and "swims" away after being touched (Yentsch and Pierce, 1955) or exposed to chemical effluent from the sea star (Elliot et al., 1989). Anemones in general can release their pedal discs or even crawl, but these movements are usually very slow. Sometimes it takes hours for anemones to move several centimeters (Brooks, 1991). *Calliactis tricolor* had very little time to move away after the initial contact by the sea star, and likely would have been consumed in all of the trials without a hermit crab to carry it.

Hydractinia colonies are sessile and therefore cannot escape sea star grazing unless the hermit crab moves away. Grazing can damage, but not necessarily kill the colony. Assuming sea star attacks were infrequent, ungrazed portions of the hydroid might survive and reestablish the colony through normal growth (McFadden et al., 1984).

Fireworms are voracious predators on corals (Glynn, 1974; Sebens, 1982; Witman, 1988; Vreeland and Lasker, 1989), zoanthids (Sebens, 1982; Karlson, 1983) and sea anemones (Lizama and Blanquet, 1975). Fireworms readily consumed *Calliactis* under laboratory conditions, and could also be important predators in the Florida Keys if these anemones were found other than on snail

shells occupied by hermit crabs. The initial reaction of the worm upon contact with the anemone suggested that nematocyst discharge occurred, but at best had little deterring effect on the worm.

Dardanus venosus provided 100% protection for symbiotic *Calliactis* from fireworm predation, either by eating the worm or by moving away. Although fireworms possess numerous poisonous setae, 4 of 6 *D. venosus* seems unaffected. They began consuming the worm immediately. The two crabs that moved away from the fireworm may have been satiated, repelled by the setae, or both.

This study shows that hermit crabs can protect their symbiotic cnidarians through movement and predation in the laboratory. Although field experiments are lacking, these results provide valuable clues as to why some cnidarians associate with hermit crabs. Predator avoidance could explain why both are found almost exclusively on hermit-crab-occupied gastropod shells in the field. These cnidarians can survive for months on other surfaces in the lab where predators are absent (Ross and Boletzky, 1979; Brooks and Mariscal, 1986b). *Hydractinia* has been found in the field on other substrata in areas where it is resistant to local sources of predation (Karlson, 1981). Under other circumstances, however, predation appears to have been a critical selection pressure for both of the cnidarians and the hermit crabs in the evolution and development of these mutualistic associations.

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