Symbiosis, 10 (1991) 123–134
Balaban, Philadelphia/Rehovot

The Effect of Anemone Size and Hermit Crab Behavior on the Distribution of *Calliactis tricolor* (Le Sueur) on Snail Shells

WILLIAM R. BROOKS
Florida Atlantic University, Department of Biological Sciences
Boca Raton, FL, USA
Tel. (407) 3673320, FAX (407) 3672749

Received March 16, 1990; Accepted September 2, 1990

Abstract

The purpose of this study was to analyze the distribution of symbiotic sea anemones by size on snail shells of hermit crabs and to determine whether these patterns are the result of anemone or crab behavior. The distribution in the field of the anemone *Calliactis tricolor* on the shells of the hermit crab *Dardanus venosus* was recorded. Tests were also done in which crabs were given simultaneous access to a large and small anemone. The crab's transfer behavior and positions of transferred anemones on the shell were recorded. Analysis of field data showed little correlation between crab/shell size and the number of anemones, but anemones were nonrandomly distributed on the shells. Additionally, large anemones were found more commonly on top of the shell, while small anemones usually bordered the shell aperture. Choice tests showed crabs had preference for large anemones. Small anemones were frequently eaten. There was also a significant difference in the transfer behavior of the crabs with the two size classes of anemones. The chelipeds and pereiopods were rarely turned beyond 45° of vertical when transferring small anemones, but were frequently parallel to the substratum when transferring large anemones. These postural changes resulted in large and small anemones being placed in similar patterns to field distributions. Once transferred, anemone movement on the shell was negligible; individuals occupied the same positions after 1 week. Therefore, the field distributional patterns are most likely the result of the crab's activities.

Keywords: anemone, *Calliactis tricolor*, *Dardanus venosus*, hermit crab, symbiosis

0334-5114/91 /$03.50

1. Introduction

Hermit crabs can have a variety of organisms living on or inside the gastropod shells which the crabs occupy. Common examples include sea anemones of the genus *Calliactis*, which are found almost exclusively on snail shells. In the laboratory, these symbioses can be initiated by the active participation of both the hermit crab and the anemone (for review, see Ross, 1983; Brooks and Mariscal, 1986b). It is not known, however, how these associations are initiated in the field. In some localities anemones are extremely abundant, with crabs sometimes having their shells almost covered with *Calliactis*. Given the small size of individual shells and total surface areas of all available shells in many habitats, space for these anemones is limited. Additionally, competition between organisms (e.g., hydroids versus slipper shells and anemones) for space on the shell can be intense (Karlson, 1978, 1981; Brooks and Mariscal, 1986a). Only a few studies, however, have concentrated on analyzing the distribution of these symbiotic anemones on the restricted space of snail shells.

Balasch et al. (1977) found that *Calliactis parasitica* (Couch) was nonrandomly distributed on shells of freshly-collected *Dardanus arrosor* (Herbst) hermit crabs. In the laboratory, this same crab placed anemones in similar patterns to the field distributions. They suggested these placement patterns adjusted the shell's balance and maximized protection from predators but provided no experimental evidence for such conclusions. These two hypotheses were supported, however, with work on the hermit crab *Pagurus pollicaris* Say. This crab placed *C. tricolor* (Le Sueur) nonrandomly on snail shells for balance and reduced predation (Brooks, 1989). In balance trials, where weights were attached to either side of the shell, crabs placed large anemones in positions furthest from the weight. Small anemones (presumably with less biomass) were placed more randomly in these same trials. In another study (Cutress and Ross, 1969), *C. tricolor* and *Sagartiomorphe guttata* (Verrill) (a small, infrequent symbiont) were commonly placed by the hermit crab *Dardanus venosus* (Milne-Edwards) on the shell's inner lip. This crab placed most large anemones on the outside of the shell (specific positions were not given). These last two studies suggest a possible sized-based difference in resource value of these symbiotic anemones to hermit crabs.

The purpose of the present study was to look at causes of distribution patterns of symbiotic sea anemones on snail shells occupied by *D. venosus*. Specifically, three major questions were addressed. First, are anemone distribution patterns in the field the result of anemone activities (e.g., settlement or movement on the shell) or the hermit crab's behavior? Second, does the hermit crab select anemones based on size and place them in different patterns

on the shell? Finally, what behavioral modifications does the hermit crab use to place anemones in different areas on the shell?

2. Materials and Methods

Field sampling

The hermit crab *Dardanus venosus* and the anemone *Calliactis tricolor* were collected bimonthly from December 1988 to December 1989 in the Florida Keys (in fish traps at 30 m depth) most often in *Fasciolaria hunteria* Perry, *F. tulipa* (L.) and *Pleuroploca gigantea* (Kiener) shells and less commonly in *Tonna maculosa* (Dill.), *Busycon contrarium* (Conrad), and *B. spiratum* (Lam.) shells. The animals were housed in outdoor, running seawater tanks at the Florida Keys Regional Marine Laboratory, Long Key, FL. The crabs were fed flaked fish food and frozen squid. The anemones were fed live brine shrimp. Cephalothorax lengths were not used to determine hermit crab size because of the risk of injury to the crab during the necessary shell removal. Instead, major manus width (MMW) was measured with calipers to the nearest 0.1 mm while the crab was still in the shell. Pedal disc diameter (PDD) of anemones was also measured with calipers to the nearest 0.1 mm. The number of *Calliactis* on each shell was recorded for analysis of correlation between crab size (which was positively correlated to shell size for each gastropod species) and the number of anemones.

The distribution of *Calliactis* on shells of *D. venosus* was analyzed by using the same nine shell zones used by Brooks (1988, see Fig. 1, p. 111) and Balasch et al. (1977, see Fig. 2, p. 40). All zones were estimated to be of equal area ($\pm 5\%$) by using geometric equations (see Brooks, 1988). On each shell, the zone occupied by each anemone was recorded. Each anemone was measured (PDD) and then removed from the shell. If an anemone was partially in two zones, the zone with greatest coverage was counted. A coin toss would determine the zone when an anemone was covering two zones equally. Only *Calliactis* on *F. hunteria, F. tulipa*, and *P. gigantea* shells were analyzed for distribution patterns because these shells were most abundant and had similar shapes (all are members of the family Fasciolariidae and are spindle-shaped, with high, pointed spires).

Distribution patterns were analyzed using chi-square analysis on 3×3 contingency tables with each cell representing a zone on the shell and the null hypothesis that each zone would have an equal probability of being occupied. The data were analyzed three ways: (1) all anemones; (2) anemones ≤ 2.0 cm PDD; and (3) anemones > 2.1 cm PDD. A heterogeneity chi-square test was

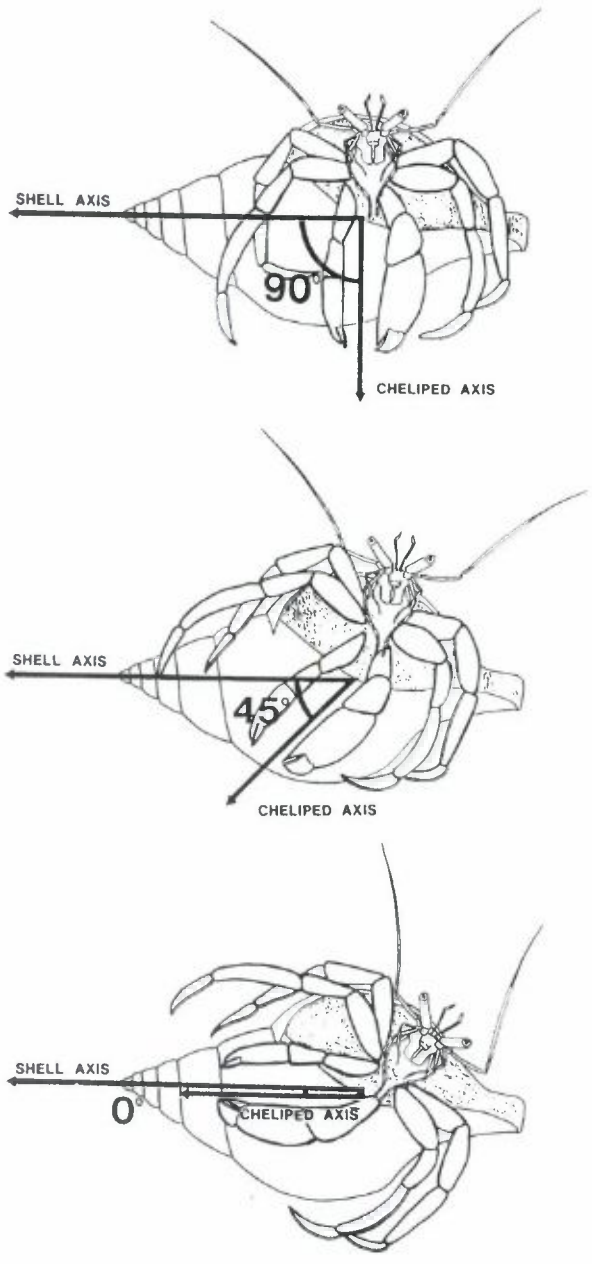

Figure 1. Diagrams showing the categories of cheliped and pereiopod orientation for the hermit crab *Dardanus venosus* during the transfer of *Calliactis tricolor* anemones to shells. Left twists by the crab were scored in the same manner.

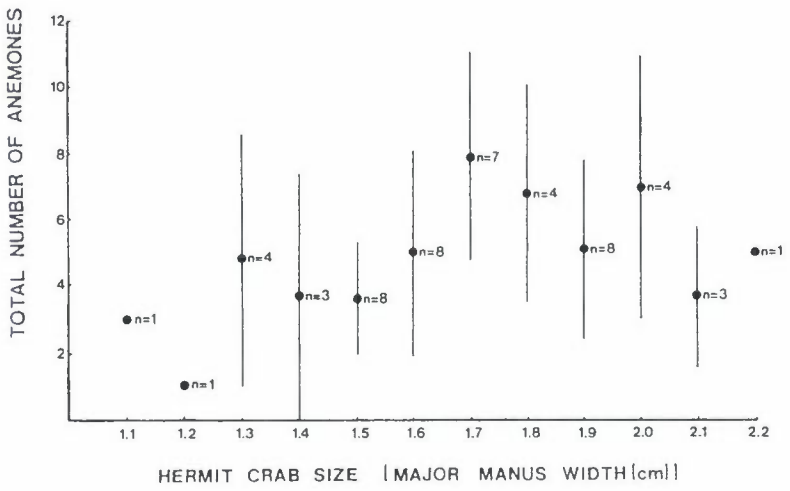

Figure 2. Scatterplot showing the mean number (±SD) of *Calliactis tricolor* on shells versus the size of the hermit crab *Dardanus venosus*. Sample sizes for each size class are given.

used to determine if group 1 (all anemones) represented a homogeneous data set.

Anemone placement in laboratory trials

Within 2 weeks of collection, hermit crabs and anemones were transported back to labs with closed-system aquaria at Florida Atlantic University for behavioral tests. The crabs (which previously had their anemones removed) were kept separate from the anemones until tested. Two *Calliactis*, one $\leq$ 1 cm PDD and the other $\geq$ 2 cm PDD, were allowed to attach (6–8 cm apart) to the glass bottom of a 9.5 l aquarium. A single *D. venosus*, in either a bare *Fasciolaria* sp. or *Pleuroploca gigantea* shell, was added to the aquarium and observed for up to 45 min. Observations were concluded earlier if both anemones were transferred (or consumed) prior to the end of the period.

During these 45 min trials, the orientation of the crab's chelipeds and pereiopods during anemone transfers was recorded to determine what behavioral modifications are used to place anemones in different positions on the shell. Specifically, three categories of positions were designated: (1) appendages closest to 90° from the shell axis (i.e., horizontal); (2) 45° left or right from the shell axis; and (3) 0° left or right from the shell axis (Fig. 1). A crab was scored in only one of these three categories per anemone based on the predominant orientation of the appendages during the transfer. Chi-square

tests were used to determine the predominant orientation for each size class of anemone. A heterogeneity chi-square test was used to determine orientation differences between size classes of anemones.

The positions (zones) on the shell of any transferred small and large anemones were recorded. Distribution patterns of the two groups of anemones were analyzed in the same manner as the field data, but two sets of chi-square tests per anemone class were done here. One analysis used the null hypothesis that each zone would have equal likelihood of being occupied, while the second analysis used field patterns for each size class for expected values.

All crabs from the trials above which had transferred anemones were kept in their 9.5 l aquaria and observed for one week to see whether anemone positions on the shell changed.

3. Results

Field data

A total of 57 *D. venosus* were collected with an average of 5.1 (SD=3.3) *C. tricolor* per shell. Some crabs had as many as 13 anemones while others (9%) had none. An analysis of those crabs with anemones showed little correlation (Spearman's $r_s = 0.27$, NS) between crab size and the number of anemones (Fig. 2).

Table 1 shows that 235 anemones from 52 *D. venosus* were nonrandomly distributed among the nine shell zones. Most anemones were in zones in columns 2 and 3 (33 and 42%, respectively) and rows 2 and 3 (37 and 34%, respectively). Four of the crabs had a single *Calliactis* outside of all zones in the columella groove or canal. Additionally, seven crabs had a single *Sagartiomorphe guttata*, which was located either in zones G and H or the columella groove.

Table 1.

Row on shell	Column on shell			Total
	1	2	3	
1	12	19	36	67
2	31	23	33	87
3	16	35	30	81
Total	59	77	99	235

Chi-square = 23.9, 4 d.f., $P < 0.001$

Figure 3 shows three-dimensionally the data from Table 1 as well as data of the two size classes of anemones. A heterogeneity chi-square of 44.5 (4 d.f.,

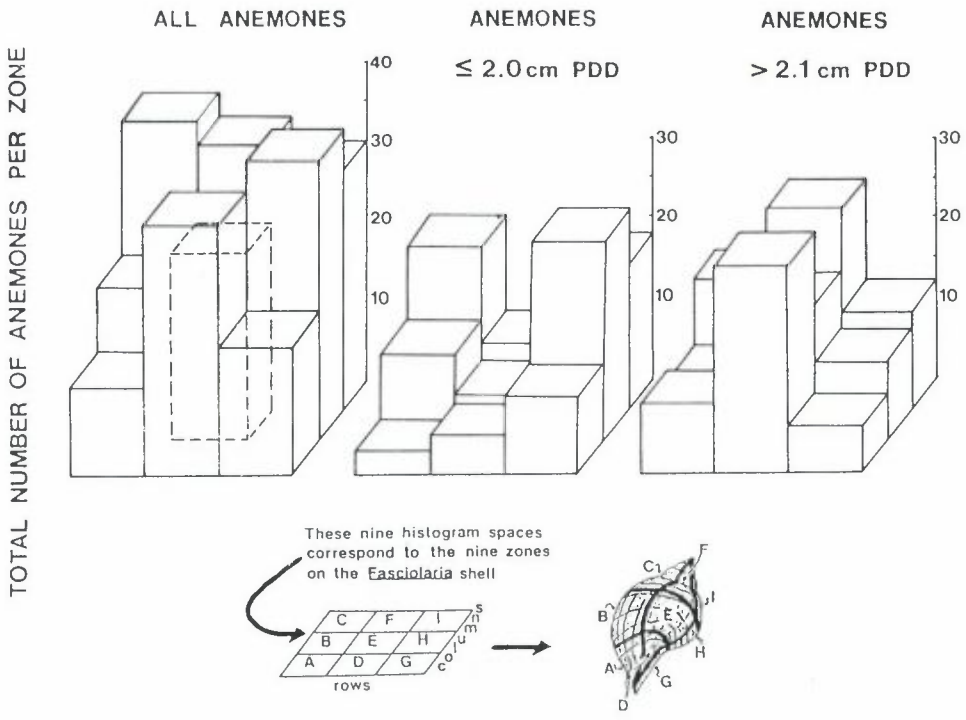

Figure 3. Histograms showing the total number of *Calliactis tricolor* per zone on the snail shells of freshly-collected *Dardanus venosus* for all anemones and small and large anemones in the field.

$P < 0.001$) shows that anemones $\leq$ 2.0 cm PDD were distributed on shells in significantly different patterns from anemones > 2.1 cm PDD, and thus Table 1 is not a homogeneous data set. Most small anemones were in zones in columns 2 and 3 (40 and 43%, respectively) and rows 1 and 3 (32 and 50%, respectively). All *S. guttata* and those *Calliactis* found in the columella groove were $\leq$ 2.0 cm PDD. Most large anemones were found in columns 1 and 3 (32 and 41%, respectively) and row 2 (52%).

Laboratory placement patterns

D. venosus transferred 36 of 67 (54%) small *Calliactis*. Four were not picked up, and the remaining 27 were eaten. The crabs transferred 68 of 79 (86%) large anemones (which is significantly more than small anemones, chi-square

= 18.5, 2 d.f., $P < 0.001$). The remaining 11 were neither transferred nor eaten. In 83% of the trials in which transfers were made, the large anemone was contacted and transferred first.

The placement patterns for small and large anemones are shown in Fig. 4. Because of low numbers in some of the nine zones, all chi-square analyses

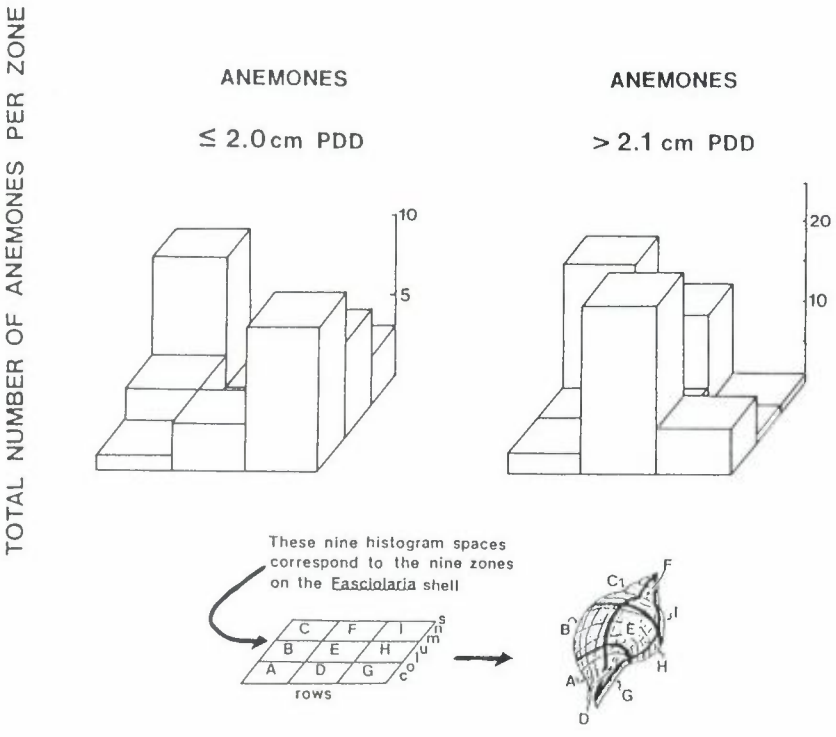

Figure 4. Histograms showing the total number of small and large *Calliactis tricolor* placed in the nine zones on the snail shell by *Dardanus venosus* in the laboratory.

were done on column and row totals. Small anemones were placed randomly in columns (chi-square = 0.5, 2 d.f., N.S.), but this placement differed significantly from field distributions where most small anemones were found in columns 2 and 3 (chi-square = 9.5, 2 d.f., $P < 0.01$). Small anemones were placed nonrandomly with 36% in row 1 and 50% in row 3 (chi-square = 7.2, 2 d.f., $P < 0.05$), which was not different from field patterns (chi-square = 0.6, 2 d.f., N.S.).

Large anemones were placed nonrandomly in columns with 1 and 3 having 90% of the anemones (chi-square = 16.2, 2 d.f., $P < 0.001$), which was significantly higher than the 73% for the field distribution (chi-square = 10.6, 2 d.f.,

$P < 0.005$). Large anemones were placed nonrandomly in rows with 53% in row 2 (chi-square = 17.4, 2 d.f., $P < 0.001$), which was not different from field distributions (chi-square = 5.4, 2 d.f., N.S.).

No small or large anemones were placed in the columella groove.

Anemones that had been transferred to shells in the above trials did not move from their original zones during 1 week of observations.

Transfer behavior

Table 2 shows that *D. venosus* used significantly different orientations to transfer small and large *Calliactis*. The crab's chelipeds and pereiopods were parallel to the shell axis only 8% of the time when transferring small anemones. With large anemones, however, the crab's appendages were parallel to the shell axis 74% of the time. *D. venosus* turned to the right during transfers 54% of the time with small anemones and 62% with large ones (chi-square = 0.8, 1 d.f., N.S.).

4. Discussion

Because shell supplies for crabs are limited in many soft-bottomed, benthic communities (Childress, 1972; Vance, 1972; Spight, 1977; Brooks, 1984), *Calliactis* must maximize its use of this resource. Finding *D. venosus* with up to 13 anemones on a single shell supports this conclusion. If anemone settlement was the major factor determining the abundance of anemones on snail shells, then one might expect a positive relationship between available settlement area (i.e., shell size) and number of anemones. The present data, however, do not support this hypothesis. Those larger *D. venosus*, which were in larger shells, did not carry significantly more anemones than smaller crabs.

Table 2. Orientation data of chelipeds and pereiopods of *Dardanus venosus* relative to the substratum during the transfer of small and large *Calliactis tricolor* anemones to shells. PDD = Pedal disc diameter

Anemone size	Position of appendages relative to shell axis		
	90°	45°	0°
≤ 2.0 cm PDD	8	25	3
> 2.1 cm PDD	0	18	50

Heterogeneity chi-square = 27.9, 2 d.f., $P < 0.001$

Settlement by planulae (which have been found for *C. polypus* Forskal by C. Cutress, pers. comm.) might still be responsible for the initial appearance of *Calliactis* in these associations, but transfers between hermit crabs (see Ross, 1979) could subsequently redistribute the anemones. Additionally, Cutress and Ross (1969) found that some *D. venosus* were "active" transferrers of anemones whereas other individuals were not. The crab's size (and sex and shell type) was unrelated to these differences. Some crabs (of various sizes) were unresponsive to anemones in the present study, as well. Perhaps large *D. venosus* initially have more anemones settle on their shells, but those that are "inactive" might subsequently lose them to "active" crabs of all sizes. Although *C. tricolor* can transfer itself to shells, it is unlikely to do so unless detached (Cutress and Ross, 1969; Cutress et al., 1970; Brooks, 1986a). Therefore, the observed abundance of *C. tricolor* on shells of *D. venosus* is most likely the result of the crab's behavior.

Overall, *C. tricolor* were found nonrandomly distributed on shells of freshly-collected *D. venosus*. These patterns were similar to the findings of Balasch et al. (1977), with most anemones in rows 2 or 3 and columns 1 or 3. There were some discrepancies involving specific zones, but these could be related to differences in crab (*D. venosus* versus *D. arrosor*), anemone (*C. tricolor* versus *C. parasitica*), or shell (fasciolariid versus muricid shells) species studied. An analysis of the distribution of these same *C. tricolor* by size, however, showed that small anemones were found in positions closest to the shell aperture while large ones were primarily on top of the shell. Although it is unknown whether anemone settlement would result in these same nonrandom patterns, movement of individual *C. tricolor* on shells was minimal in the present study. Therefore, if crabs place anemones in similar patterns in the laboratory, it is likely that field distributions are primarily the result of these activities (see Balasch et al., 1977).

Similarities between laboratory placement patterns and field distributions indicate *D. venosus* is primarily responsible for distributions of small and large *C. tricolor* on freshly-collected shells. For example, placement of both sizes of anemones in rows was almost identical to their respective field patterns. The dexterity of the chelipeds and pereiopods resulted in the crab's ability to place anemones in any of the nine shell zones. Consistent differences in orientation of these appendages with small and large anemones were observed and resulted in these different spatial patterns. Although some *Sagartiomorphe* and *Calliactis* were found in the columella groove, no anemones were placed in this position in laboratory trials; therefore, it is unclear how these anemones get in this area in the field.

It is also unclear why placement patterns for the two sizes of anemones

were different, but protection and balance may be important factors. Perhaps *D. venosus* placed small anemones adjacent to the shell aperture (zones in row 1 and 3) to maximize protection against octopus predators and large, bulky anemones on top of the shell for balance (see Brooks, 1988, 1989).

Large anemones were usually contacted and transferred first, and more large anemones were transferred than small ones. Additionally, small anemones were frequently eaten. These results suggest a preference for large anemones. The basis for this preference is unclear, but protection might again be a factor. Hermit crabs can increase the level of protection by adding more anemones to their shells (Brooks, 1988). Perhaps a single, large anemone is a more effective deterrent than even several smaller ones.

The phenomenon of crabs consuming their *Calliactis* has been reported before for individuals of *D. arrosor* that had become inactive towards anemones after 4–5 months in aquaria (Balasch and Mengual, 1974), but most *D. venosus* in the present trials were still very active. Frequently, the small anemone was eaten only after the large anemone had been transferred to the shell. This would suggest the resource value of a small anemone is diminished by the possession of a large one.

Although information about the life history and role of *C. tricolor* in these associations is incomplete, the present study provides data that suggest the abundance and spatial arrangement of these anemones on snail shells are primarily the result of the crab's activities.

Acknowledgements

I thank T. Conner, T. Gwaltney, M.B. Mihalik, D. Reichert, and J. Swanson for assistance in collecting specimens, E. Barham and T. Gwaltney for reviewing the manuscript, and the Florida Keys Regional Marine Laboratory for providing research space. This work was supported by grants from the National Science Foundation (BSR – 8711455) and the Florida Endowment Fund for Higher Education.

REFERENCES

Balasch, J. and Mengual, V. 1974. The behavior of *Dardanus arrosor* in association with *Calliactis parasitica* in artificial habitat. *Mar. Behav. Physiol.* **5:** 251–260.

Balasch, J., Cuadras, J., and Alonso, G. 1977. Distribution of *Calliactis parasitica* on gastropod shells inhabited by *Dardanus arrosor*. *Mar. Behav. Physiol.* **2:** 37–44.

Brooks, W.R. 1984. Hermit crab-cnidarian associations in the northern Gulf of Mexico. Ph.D. dissertation, Florida State University. 120 pp.

Brooks, W.R. 1988. The influence of the location and abundance of the sea anemone *Calliactis tricolor* (Le Sueur) [*Sic*] in protecting hermit crabs from octopus predators. *J. Exp. Mar. Biol. Ecol.* **116:** 15–21.

Brooks, W.R. 1989. Hermit crabs alter sea anemone placement patterns for shell balance and reduced predation. *J. Exp. Mar. Biol. Ecol.* **132:** 109–121.

Brooks, W.R. and Mariscal, R.N. 1986a. Interspecific competition for space by hydroids and a sea anemone living on gastropod shells inhabited by hermit crabs. *Mar. Ecol. Prog. Ser.* **28:** 241–244.

Brooks, W.R. and Mariscal, R.N. 1986b. Population variation and behavioral changes in two pagurids in association with the sea anemone *Calliactis tricolor* (Lesueur). *J. Exp. Mar. Biol. Ecol.* **103:** 275–289.

Childress, J.R. 1972. Behavioral ecology and fitness theory in a tropical hermit crab. *Ecology* **53:** 960–964.

Cutress, C.E. and Ross, D.M. 1969. The sea anemone *Calliactis tricolor* and its association with the hermit crab *Dardanus venosus. J. Zool.* **158:** 225–242.

Cutress, C.E., Ross, D.M., and Sutton, L. 1970. The association of *Calliactis tricolor* with its pagurid, calappid, and majid partners in the Caribbean. *Can. J. Zool.* **48:** 371–376.

Karlson, R. 1978. Predation and space utilization in a marine epifaunal community. *J. Exp. Mar. Biol. Ecol.* **31:** 225–239.

Karlson, R.H. 1981. A simulation study of growth inhibition and predator resistance in *Hydractinia echinata. Ecol. Model.* **13:** 29–47.

Ross, D.M. 1979. A behavior pattern in *Pagurus bernhardus* L. towards its symbiotic actinian *Calliactis parasitica* (Couch). *J. Mar. Biol. Assoc. U.K.* **59:** 623–630.

Ross, D.M. 1983. Symbiotic relations. In: *The Biology of the Crustacea.* F.J. Vernberg and W.B. Vernberg, eds. Vol. 7. Academic Press, New York, pp. 163–212.

Spight, T.M. 1977. Availability and use of shells by intertidal hermit crabs. *Biol. Bull.* **152:** 120–133.

Vance, R.R. 1972. The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* **53:** 1074–1083.