11-2008

Distributional Ecology of the anemone shrimp Periclimenes rathbunae associating with the sea anemone Stichodactyla helianthus at Tobago

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Abstract

We studied the distributional ecology of the anemone shrimp *Periclimenes rathbunae* associating with the anemone *Stichodactyla helianthus* in Tobago, West Indies. The shrimps occupied 83.1% of the anemones (n = 83), with mean densities of 2.8 shrimps per anemone in the population and 3.4 shrimps per occupied anemone, and up to 11 inhabiting a single anemone. Shrimp density was significantly correlated with anemone size. Because the density of shrimps was not significantly correlated with the distance to the nearest neighboring anemone or the number of anemones in a cluster, colonization appears to be related to chance or some unknown factor rather than degree of isolation. The significantly negative correlation between density and mean size class of shrimps suggests that adult shrimps may limit juveniles from colonizing an anemone. The high frequency of cohabitation between *P. rathbunae* and other decapod crustaceans, coupled with the lack of correlation between density of *P. rathbunae* and the number of individuals or species of other decapod crustaceans, suggests that the density of *P. rathbunae* was unaffected by interspecific competition.

Key words: distributional ecology, *Periclimenes rathbunae,* shrimp-anemone association, *Stichodactyla helianthus,* Tobago.

Introduction

Decapod crustaceans form symbiotic relationships with a variety of invertebrate hosts, including cnidarians (Bruce, 1976a, b; Ross, 1983). The association between anemone shrimps of the genus *Periclimenes* and a variety of anemones is especially well known. Some species of shrimp are generalists, associating with a variety of anemone species, whereas others are specialists associating with only one species (Bruce 1976a, b; Spotte *et al.,* 1991). The shrimps are generally thought to benefit from the association without benefitting or harming the anemones (Bruce 1976a, b; Ross, 1983). However, a few species of shrimps have been reported to feed on the tentacles of their anemone hosts (Bruce and Svoboda, 1983; Fautin *et al.,* 1995; Omori *et al.,* 1994), suggesting that the relationship is more complex than previously thought.

Several studies have focused on the interactions between *Periclimenes* shrimps and their anemone hosts in the tropical western Pacific (Guo *et al.,* 1996; Khan *et al.,* 2003, 2004; Omori *et al.,* 1994) and tropical western Atlantic (Gwaltney and Brooks, 1994; Herrnkind *et al.,* 1976; Levine and Blanchard, 1980; Mahnken, 1972; Mercado and Capriles, 1982; Nizinski, 1989; Spotte *et al.,* 1991; Stanton, 1977). These studies often revealed species-specific differences in the distributional ecology and behavioral interactions of shrimps, demonstrating that much remains to be learned regarding the ecology of shrimp-anemone symbioses.

The anemone shrimp *Periclemenes rathbunae* Schmitt, 1924 is a denizen of warm, shallow coastal waters of the tropical western Atlantic, where it has been reported to associate with at least seven species of sea anemones (see review by Spotte *et al.,* 1991) including *Bartholomea annulata* (Leseur, 1817), *Bunodosoma granulifera* (Leseur, 1817), *Condylactis gigantea* (Weinland, 1860), *Eunicea tourneforti* Milne Edwards and Haime, 1857, *Homostichanthus duerdeni* Carlgren, 1900, *Lebrunia danae* (Duchassaing and Michelotti, 1860), and *Stichodactyla helianthus* (Ellis, 1768). Nevertheless, few quantitative data are available on its association with these anemone hosts (Herrnkind *et al.,* 1976; Levine and Blanchard, 1980; Mercado and Capriles, 1982). In this paper we analyze several factors potentially affecting the distributional ecology of *P. rathbunae* associating with the sea anemone *S. helianthus* in the southeastern Caribbean Sea at Tobago, West Indies, and compare our results with other studies of *Periclimenes* shrimps associating with anemones.

Study Area and Methods

On 21 and 22 August 1997, we searched for *Periclimenes* shrimps and other decapod crustaceans associating with *Stichodactyla helianthus* on wooden pilings of a boat dock and on adjacent wooden, metal, and concrete objects within 3 m of the pilings at Pigeon Point, southwest Tobago. The dock was in calm, shallow water within a lagoon protected by Buccoo Reef, a fringing coral reef perhaps better described as a fringing-barrier reef (Milliman, 1973). The substrate was sandy and the dock was adjacent to a sandy beach. The marine environment of the Buccoo Reef complex is described in further detail by Laydoo (1985, 1998, 1991).

The shrimps were identified as *Periclimenes rathbunae* based on the descriptions and photographs of Spotte *et al.* (1991). Juveniles appeared identical in shape to the well marked adults but were more transparent, with intermediate sized individuals forming a continuum of size classes and colour patterns with minor individual variability typical of *P. rathbunae* (Spotte *et al.* 1991). No other species of *Periclimenes* was detected.

For each individual of *Stichodactyla helianthus* we measured its: (1) diameter (nearest cm) at the widest part of the oral disc; (2) depth (nearest cm) beneath the surface, measured from 1130-1500 h and 1510-1700 h on consecutive days when tidal height varied by ± 30 cm; and (3) its distance (nearest cm) from its nearest neighbor. We also counted the number of *S. helianthus* individuals in direct contact with each other within a cluster and, after gently prodding each anemone with a blunt stick both above and below the tentacles, the number of *Periclimenes rathbunae* and other decapod crustaceans associated with the anemone. The size class of each *P. rathbunae,* based on total length, was estimated by visual inspection for the intervals of (1) < 0.5 cm, (2) 0.5-1.0 cm, and (3) 1.0-1.5 cm.

Because the data did not meet the assumptions of normality and equal variances, non-parametric Spearman rank correlation coefficients (r_s statistic; Zar, 1999) were computed between paired variables to test the hypotheses that: (1) density of shrimps (number of individuals per anemone) was correlated with anemone size, depth of anemone, distance to nearest anemone, number of anemones in a cluster, and number of other decapod crustacean individuals and species per anemone; and (2) mean size class of shrimps associating with an anemone was correlated with the density of shrimps, anemone size, depth of anemone, distance to nearest neighboring anemone, and number of anemones in a cluster. The data were analyzed using Statistix 7.0 software (Anonymous, 2000). Means are followed by ± 1 standard deviation.

Results

The population of *Stichodactyla helianthus* included 83 individuals averaging 11.1 ± 3.7 cm in width (range = 4-21 cm). The average depth beneath the surface was 74.9 ± 48.9 cm (range = 10-170 cm). The average distance to the nearest neighbor was 9.9 ± 24.5 cm (range = 0-120 cm). Cluster size averaged 1.7 ± 1.1 (range = 1-7), with 61.2% of the anemones not touching another.

Periclimenes rathbunae occupied 83.1% of the anemones, with mean densities of 2.8 ± 2.6 shrimps per anemone within the entire anemone population and 3.4 ± 2.5 shrimps per occupied anemone. The shrimps occupied anemones singly or in groups of variable size, with up to 11 shrimps inhabiting a single anemone (Fig. 1). The shrimps occupied the tentacles of the anemone but occasionally retreated to the stalk beneath when pursued. The density of shrimps was significantly correlated with anemone size (r_s = 0.26, P = 0.02,

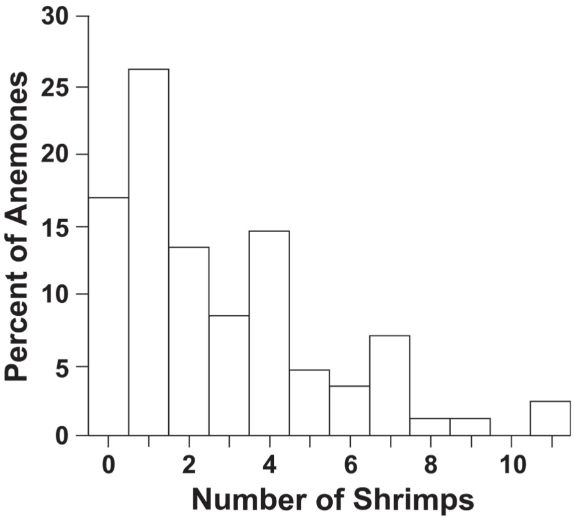

Figure 1. Frequency distribution of shrimp group size per anemone.

n = 83; Fig. 2) but not with the depth of anemones (r_s = 0.21, P = 0.06, n = 83), distance to the nearest neighboring anemone (r_s = 0.02, P = 0.86, n = 83), or the number of anemones in a cluster (r_s = -0.01, P = 0.92, n = 83).

The mean size class of shrimps per occupied anemone was significantly negatively correlated with the density of shrimps (r_s = -0.39, P = 0.001, n = 67; Fig. 3) but was not significantly correlated with anemone size (r_s = 0.18, P = 0.15, n = 67), the depth of anemones (r_s = 0.06, P = 0.66, n = 67), the distance to the nearest neighboring anemone (r_s = 0.05, P = 0.69, n = 67), or the number of anemones in a cluster (r_s = -0.12, P = 0.33, n = 67).

At least eight other species of decapod crustaceans were also found associating with the anemones. Other decapod crustaceans occupied 77.1% of the anemones, with a mean number of 1.8 ± 1.7 individuals (range = 0-7) and 1.1 ± 0.8 species per anemone (range = 1-3) in the anemone population, and a mean number of 2.4 ± 1.6 individuals (range = 0-7) and 1.5 ± 0.6 species (range = 1-3) per occupied anemone. The density of *Periclimenes rathbunae* was not significantly correlated with the number of other decapod crustacean individuals (r_s = 0.05, P = 0.67, n = 83) or species (r_s = 0.02, P = 0.89, n = 83).

Discussion

The percentage of anemone hosts occupied by *Periclimenes rathbunae* in our study (83%) and the mean number of shrimps per anemone host occupied (3.4) are relatively high but within the range of variation among six species of *Periclimenes* shrimps for which data have been reported thus far (Table I). The high values for occupancy and density may be due to the absence of other congeneric species, which were present in all other studies except that of *P. anthophilus* associating with *Condylactis gigantea* in Bermuda (Nizinski, 1989), which had the highest values (Table I). Alternatively, the high values may be due to the relatively high density of anemones in a small area, or the sandy substrate. In the Virgin Islands, the degree of association between shrimps and *Bartholomea annulata* varied greatly among different marine habitats, being highest on the "sand strip" for *P. pedersoni* and on

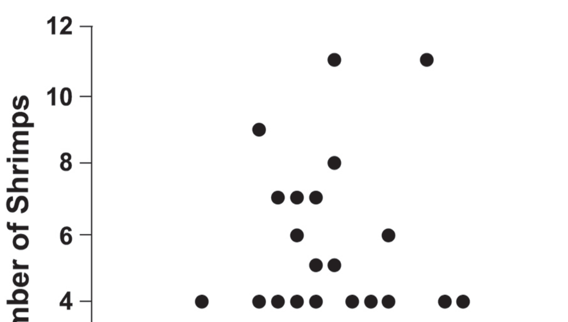

Figure 2. Relationship between the number of shrimps per anemone and anemone size.

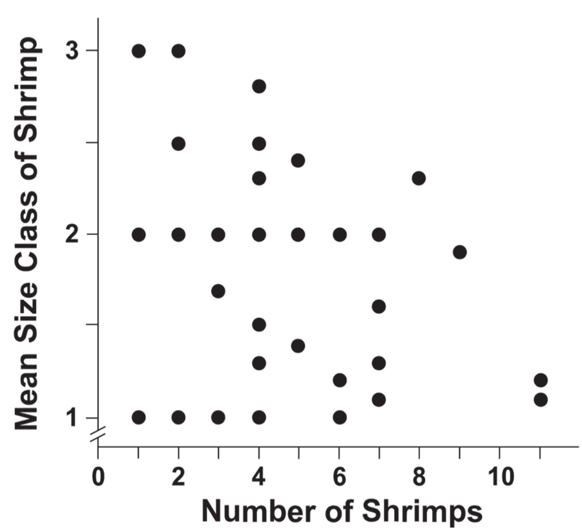

Figure 3. Relationship between mean size class of shrimps (class 1 < 0.5 cm, class 2 = 0.5-1.0 cm, and class 3 = 1.0-1.5 cm) per anemone and number of shrimps per anemone.

Table I. Percentage of anemones occupied by *Periclimenes* shrimps and mean number of shrimps per occupied anemone.

Species	Anemone	Location	% anemones occupied	$\overline{X}$ shrimps per anemone	Source
P. anthophilus	*Condylactis gigantea*	Bermuda	95	3.7	Nizinski (1989)
P. brevicarpalis	*Stichodactyla haddoni*	Australia	25	2.0	Khan *et al.* (2004)
P. holthuisi	*Stichodactyla haddoni*	Australia	70	3.2	Khan *et al.* (2003, 2004)
P. pedersoni	*Bartholomea annulata*	Virgin Islands	38-83	1.1-3.3	Mahnken (1972)
P. rathbunae	*Homostichanthus duerdeni*	Puerto Rico	57	–	Mercado and Capriles (1982)
	Stichodactyla helianthus	Puerto Rico	72	–	Mercado and Capriles (1982)
		Tobago	83	3.4	This study
P. yucatanicus	*Bartholomea annulata*	Virgin Islands	0-50	0.0-0.72	Mahnken (1972)
Periclimenes spp.	*Bartholomea annulata*	Grand Bahama	68	1.7	Herrnkind *et al.* (1976)
	Lebrunia danae	Grand Bahama	32	1.6	Herrnkind *et al.* (1976)

the "algal flat" for *P. yucatanicus* (Mahnken, 1972; Table I). However, we have no comparable data on the degree of association between *P. rathbunae* and *Stichodactyla helianthus* in other habitats in Tobago where *S. helianthus* is less common.

In Puerto Rico, *Periclimenes rathbunae* associated with 72.1% of *Stichodactyla helianthus* with up to ten individuals in a single anemone, values only slightly lower than ours, and associated with 57.3% of *Homostichanthus duerdeni* with up to five in a single anemone (Mercado and Capriles, 1982; Table I). The substrate of the study site included grass beds, sand, mud, and rocks. In Jamaica, only one or two *P. rathbunae* associated with *S. helianthus* at depths ranging from 0.3-3.0 m (Levine and Blanchard 1980). In Grand Bahama, three species of *Periclemenes* combined (due to uncertainty of identification), including the less common *"P.* c.f. *rathbunae,"* associated with 32% of *Lebrunia danae* and 68% of *Bartholomea annulata* (Herrnkind *et al.,* 1976; Table I). No other quantitative data are available on the association of *P. rathbunae* with anemones.

The presence of anemones not colonized by *Periclimenes* in all studies including ours (Table I) indicates that the shrimp population is not limited by the availability of potential anemone hosts. Because the number of shrimps per anemone in our study was not significantly correlated with the distance to the nearest neighboring anemone or the number of anemones in a cluster, colonization of anemones appears to be random or related to some unknown factor rather than degree of isolation.

Our data demonstrated a significant correlation between the density of shrimps and anemone size. However, no such significant correlation was found between *Periclimenes anthophilus* associating with *Condylactis gigantea* (Nizinski, 1989) in Bermuda, or between *P. holthuisi* associating with *Stichodactyla haddoni* in Australia (Khan *et al.,* 2003). In Madeira and the Canary Islands, the number of crustacean symbionts associated with the anemone *Telmatactis cricoides* (Cuchassaing, 1850) was positively correlated with anemone size (Wirtz, 1997), but the 19 species of symbionts did not include any species of *Periclimenes.*

Although male-female pairs of crustaceans have been reported in several crustacean-invertebrate associations (e.g., Castro, 1971; Knowlton, 1980; Patton, 1994; Seibt and Wickler, 1979) and pairs of simultaneous hermaphrodites have been reported in one shrimp-anemone association (Wirtz, 1997), no such social structure has been reported in *Periclimenes*-anemone associations. The significantly negative correlation between the density of shrimps and mean size class of shrimp per occupied anemone (Fig. 3) suggests that adult shrimps may limit the colonization of the anemones by smaller juvenile shrimps. Mahnken (1972) reported that larger *P. pedersoni* chased smaller individuals from *Bartholomea annulata* hosts. However, newly recruited individuals of *P. anthophilus* were not prevented by those already present from occupying space on *Condylactis gigantea* (Nizinski, 1989).

The high frequency of cohabitation between *Periclimenes rathbunae* and other decapod crustaceans, coupled with the lack of significantly negative correlation between the number of *P. rathbunae* and the number of individuals or species of other decapod crustaceans, suggests that the density of *P. rathbunae* was unaffected by interspecific competition. Cohabitation of congeneric *P. rathbunae* and *P. yucatanicus* (Ives, 1891) has been reported on *Bartholomea annulata* (Mahnken, 1972) and *Lebrunia danae* (Stanton, 1977); thus, it is not surprising that *P. rathbunae* cohabits anemones with more distantly related species of decapod crustaceans that are less likely to compete with it.

In conclusion, our study suggests that colonization of *Stichodactyla helianthus* by *Periclimenes rathbunae* occurs randomly, with the number of shrimps per anemone most strongly affected by anemone size and intraspecific interactions in which adults may preclude juveniles from colonizing an anemone.

Acknowledgments

Our field work in Tobago was funded indirectly by a grant (for studying birds) from the Lincoln Park Zoo. We thank Karen Thomas for patiently processing interlibrary loan requests.

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Received: March 2008
Accepted: July 2008