

## Host Specificity of the Anemoneshrimp *Periclimenes pedersoni* and *P. yucatanicus* in the Florida Keys

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### Abstract

Host specificity by *Periclimenes pedersoni* and *P. yucatanicus* to three species of sea anemone was investigated. Field associations, initial preferences (within 72 hr of collection) in the laboratory, and changes in preference after "conditioning" with an alternate host were compared. *Periclimenes pedersoni* associated with *Bartholomea annulata* in the field preferred this same anemone in choice trials. These shrimp changed preference after 2 to 8 weeks of conditioning with a different host species. *Periclimenes yucatanicus* associated with *Stichodactyla helianthus* in the field preferred this anemone in choice trials. Those *P. yucatanicus* collected from either *Condylactis gigantea* or *B. annulata* did not exhibit an initial preference for these respective hosts. *Periclimenes yucatanicus* initially found on and preferring *S. helianthus* did not change their preference after conditioning; those found on other hosts chose *S. helianthus* after conditioning.

Keywords: anemones, anemoneshrimp, conditioning, host preferences, *Periclimenes*, plasticity, symbiosis

### 1. Introduction

Symbiotic associations involving sea anemone (Actiniaria) hosts are common throughout tropical marine waters. Symbionts may be highly specific to one anemone host or may be generalists, associating with several hosts.

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The partnership between anemonefishes (Pomacentridae) of the Indo-West Pacific and anemones is a well known symbiosis (Mariscal, 1970; Fautin, 1986). Specificity by these fish for anemones varies, with closely related fishes often exhibiting similar host preferences (Verwey, 1930; Mariscal, 1970; Fautin, 1986). Another well known system involves anemones and shrimp. One genus of shrimp (*Periclimenes*) contains species that vary in their preferences for particular species of anemones (Mahnken, 1972; Herrnkind et al., 1976; Stanton, 1977; Mihalik, 1989; Nizinski, 1989). In the Florida Keys, *Periclimenes yucatanicus* (Ives) is most often found on the anemone *Stichodactyla helianthus* (Ellis), even when other known hosts (*Condylactis gigantea* Weinland, *Bartholomea annulata* Le Sueur) are present (Limbaugh et al., 1961). *P. pedersoni* Chace is most frequently found with *B. annulata*, although *C. gigantea*, a known host for this species (Limbaugh et al., 1961), is present (Mihalik, 1989). In choice tests conducted in the laboratory, *P. pedersoni* preferred to associate with the anemone it inhabited in the field (Mihalik, 1989). These findings imply that host preferences by shrimp may be strongly influenced by previous experience with anemone hosts.

In this study, we compare the host preferences of *P. yucatanicus* and *P. pedersoni* for anemone hosts in the Florida Keys, then determine through forced contact with alternative hosts ("conditioning") if these preferences can be modified. We asked two questions. Do the two shrimp species show an initial preference for the host species upon which they were found in the field? Can these preferences be modified by experience with an alternative host?

## 2. Materials and Methods

### *Collection and maintenance of specimens*

We collected shrimp and anemones by snorkeling and scuba diving from August 1990 to June 1991 at three locations in the Florida Keys (24°N 81°W). Shrimp were captured with a small dip net, then transferred to bait buckets labeled to indicate the host anemone and collection site. An anemone was collected by detaching its pedal disc from the substrate with fingers or a dull knife. Additional anemones were obtained from the Keys Marine Laboratory, Long Key, Florida. All animals were kept in aerated sea water for 6–10 hr while in transit between the collecting site and laboratory aquaria at Florida Atlantic University. In the laboratory, all animals were maintained in 75 l aquaria using artificial seawater (30 ppt), and exposed to a 12L-12D photoperiod at 25–28° C. Shrimp and anemones were housed in separate aquaria (by species and collection site) and fed live *Artemia* weekly. Animals were not fed within 24 hr of, or during, choice trials.

*Identification of Periclimenes spp.*

We identified shrimp using the key in Chace (1972). However, we were unsure of the identity of *P. pedersoni*, as individuals had banded rather than solid white antennae. Their identity was verified by M. Nizinski of the National Museum of Natural History, Washington, DC.

*Collecting sites*

Long Key: specimens were collected at depths of 1–2 m along the shoreline on the bay side of the island, just north of the Keys Marine Laboratory. The substrate was sandy and interspersed with many rocks and small corals (*Porites* spp.). Anemone species present were *Stichodactyla helianthus* and *Bartholomea annulata*.

Conch Key: specimens were collected from the Atlantic Ocean side of the island, within 60 m of the shoreline at depths of 1–3 m. The substrate was a sandy bottom interspersed with rocks. There were numerous large sponges (*Speciospongia* sp.; *Ircinia* spp.) and gorgonians (*Pterogorgia* spp.). Anemones present were *S. helianthus* and *Condylactis gigantea*.

West Summerland Key: specimens were collected from an abandoned rock quarry on the bay side of the island, at depths of 2–10 m. The quarry was connected to the bay by a channel. Specimens were collected from the southern wall of the quarry (no shrimp were found on any other wall) that sloped outward to a depth of 2 m, then dropped vertically to the bottom (8–10 m deep). The wall face consisted of coral rocks with crevices and ledges. The only anemone species present was *B. annulata*.

*Host preference trials**Initial preference tests*

Trials were carried out within 72 hr of collection to determine whether shrimp preferred the species of anemone upon which they were initially found. Each shrimp was offered two anemones of approximately equal size when fully expanded: one of the host species and one of another species found at the collection site. Shrimp collected from West Summerland Key (where only *B. annulata* was present) were given a choice between the host species and another anemone likely to be encountered as an alternate host for each shrimp species (Mihalik, 1989). The two anemones were placed at opposite ends of a 38 l (50×26×27 cm) aquarium and allowed to attach for 1 hr. In half these tests, the anemone species occupied in the field was in the right half of the tank. A single shrimp was introduced into the tank halfway between the two

anemones. Position of the shrimp was recorded after 24 hr. A choice was established if, at that time, the shrimp was touching the anemone or beneath its tentacles.

#### *Conditioning and later preference tests*

After completion of the initial host preference test, each shrimp was placed in a 26 l aquarium (30×15×18 cm) with an anemone of the species not chosen in the initial preference test. The shrimp and anemone were observed daily to determine if contact was established and maintained. Preference tests were then repeated for each shrimp at 2 week intervals for up to 8 weeks, using the following protocols.

Shrimp were removed from their "conditioning" tank and placed in another tank for 24 hr where they were again given a choice between the same species of anemones presented in the initial preference tests. Shrimp choosing the "conditioned" anemone host were not used in further trials. Shrimp that again chose their "initially-preferred" host species were returned to the "conditioning" tank for another 2 week interval.

Controls were established because re-exposure to the "initially-preferred" host for 24 hr at each interval test may affect the length of time needed for "conditioning". Shrimp were placed in an empty tank at two-week intervals, then given a final choice trial at the end of 4 or 8 weeks. Data for all preference trials were analyzed using binomial tests (Zar, 1974).

### 3. Results

#### *Associations in the field*

*Periclimenes yucatanicus* was found at all three collection sites (Table 1). At Long Key, this shrimp was found exclusively on *S. helianthus*, despite the

Table 1. Numbers of shrimp collected on anemone species at each site. S, *Stichodactyla helianthus*; B, *Bartholomea annulata*; C, *Condylactis gigantea*. NO, anemones of that species not observed at the site.

	S	C	B
<i>Periclimenes yucatanicus</i>			
Long Key	19	NO	O*
Conch Key	37	14*	NO
W. Summerland Key	NO	NO	12
<i>Periclimenes pedersoni</i>			
W. Summerland Key	NO	NO	43

\* Most common anemone at that collecting site

abundance of *B. annulata*. Shrimp at Conch Key were also found most often with *S. helianthus*, although *C. gigantea* were more abundant. Both *P. yucatanicus* and *P. pedersoni* were found on *B. annulata* at West Summerland Key (Table 1).

#### Initial preference tests

*Periclimenes yucatanicus* collected from *S. helianthus* in the field (Long Key and Conch Key) showed a significant preference for this anemone over *B. annulata* and *C. gigantea* (Table 2). However, shrimp found on *C. gigantea* or *B. annulata* did not prefer these anemones in choice tests with anemones of other species. In fact, of 12 shrimp found on *B. annulata*, 7 chose *S. helianthus* despite the absence of this anemone at West Summerland Key. *Periclimenes pedersoni* found on *B. annulata* preferred this anemone over *C. gigantea* (Table 2).

#### Post-conditioning preferences

*P. yucatanicus* found on *S. helianthus* continued to prefer this species when the conditioning host was *B. annulata*. When the conditioning host was *C. gigantea*, the preference for *S. helianthus* was weakened ( $p=0.06$ , Table 3), but still evident. Those *P. yucatanicus* collected from *C. gigantea* showed no initial preference for this species (Table 2), but after conditioning preferred their

Table 2. Results of preference tests made within 72 hr of collection. Each shrimp was given a choice between an anemone of the species it was found on in the field and an anemone of another species found in the Florida keys. P = probability for binomial test.

N	Field host	Lab hosts	Selected host	P
<i>Periclimenes yucatanicus</i>				
19	S	S	19	< 0.01
		B	0	
37	S	S	29	< 0.001
		C	8	
14	C	C	10	n.s.
		S	4	
12	B	B	5	n.s.
		S	7	
<i>Periclimenes pedersoni</i>				
43	B	B	30	< 0.01
		C	13	

Table 3. Results of post-conditioning preference tests, carried out at 2 week intervals over 8 weeks. In each test, shrimp were given a choice between two anemones: one was the same species as its host in the field; the other was the same species as its "conditioning" host.

N	Field host	Alt. host	Host Preference:		P
			changed	not changed	
<i>Periclimenes yucatanicus</i>					
18	S	B	4	14	< 0.05
20	S	C	6	14	n.s.*
10	C	S	9	1	< 0.01
6	B	S	4	2	<sup>1</sup>
<i>Periclimenes pedersoni</i>					
21	B	C	15	6	< 0.05

\* P = 0.06

<sup>1</sup> Sample size is too small for analysis of trends.

"conditioning" host (*S. helianthus*). Finally, *P. yucatanicus* collected from *B. annulata* showed no preference for *S. helianthus*. However, only six shrimp survived testing in this group.

When *P. pedersoni* showed an initial preference for its field host (*B. annulata*; Table 2), its preference changed after conditioning (Table 3). In Table 4, we compare post-conditioning host preferences of shrimp which made specific initial choices. In most cases *P. yucatanicus*, which initially preferred either *C. gigantea* or *B. annulata*, changed its preference to the conditioning host (*S. helianthus*). *Periclimenes pedersoni* changed preference to the conditioning host regardless of the host species it had initially preferred (Table 4).

#### Conditioning time

A total of 23 *P. yucatanicus* and 15 *P. pedersoni* showed a change in host preference after conditioning (Table 3). Eight *P. yucatanicus* changed host preferences at 2 weeks, eight at 4 weeks, and seven at 6–8 weeks, for *P. pedersoni*, the comparable data were: two at 2 weeks; 10 at 4 weeks; and three at 6–8 weeks. Most shrimp (70% for *P. yucatanicus*, 80% for *P. pedersoni*) that changed host preference did so within four weeks.

## 4. Discussion

### Field distribution and host preferences

*Periclimenes yucatanicus* has been observed living on *C. gigantea*, *B. annulata*, and *S. helianthus* (Limbaugh et al., 1961; Mahnken, 1972; Mihalik, 1989),

Table 4. Results of post-conditioning preference tests, comparing specific initial host preferences with subsequent preferences after "conditioning" (final choice)

N	Field host	Initial choice	Final choice	P
<i>Periclimenes yucatanicus</i>				
18	S	S=18 B=0	S=14, B=4	< 0.05
20	S	S=16 C=4	S=13, C=3 S=3, C=1	< 0.05 *
10	C	C=8 S=2	S=8, C=0 S=1, C=1	< 0.01 *
6	B	B=3 S=3	S=3 S=2, B=1	* *
<i>Periclimenes pedersoni</i>				
21	B	B=15 C=6	B=5, C=10 B=5, C=1	n.s. n.s.

\* Sample size is too small for analysis of trends.

as well as *Lebrunia danae* (Herrnkind et al., 1976). We found them on three species (Table 1). These results might imply that *P. yucatanicus* should exhibit little preference for particular host anemones. However, shrimp collected from either *C. gigantea* or *B. annulata* did not prefer these hosts when given a chance to occupy *S. helianthus* in choice experiments (Table 2). Furthermore, only 8 of 48 shrimp found on *S. helianthus* selected an alternative host before conditioning (Table 2), and only 10 of 38 individuals found on that anemone could be conditioned to switch their preference (Table 3).

These results suggest that preferences for *S. helianthus* by *P. yucatanicus* may involve processes other than recent association with a host. If only recent associations determined their preference, then all shrimp, including those found on *C. gigantea* and *B. annulata*, should have chosen the field host in initial preference tests, and all shrimp should have conditioned, regardless of their original field host. That was not the case (Tables 3 and 4).

*Periclimenes pedersoni* was most frequently found on *B. annulata* (Limbaugh et al., 1961; Mahnken, 1972; Williams, 1984; this study). It has also been reported to occupy *C. gigantea* (Limbaugh et al., 1961; Mahnken, 1972; Mihalik, 1989), *Aiptasia pallida* (Limbaugh et al., 1961), and *Lebrunia danae* (Herrnkind et al., 1976). Thus *P. pedersoni*, like *P. yucatanicus*, can occupy several host anemones. We found it exhibited a significant initial preference for the host it occupied in the field (*B. annulata*; Tables 1 and 2), but could be induced to change that preference through conditioning to another (*C. gigantea*) anemone host (Table 3). Mihalik (1989), also working in the Florida

Keys, found *P. pedersoni* on both *B. annulata* and *C. gigantea*. In choice tests, shrimp from *C. gigantea* preferentially selected this host over *B. annulata*; those from *B. annulata*, however, did not exhibit a preference for either host species (Mihalik, 1989).

Several generalizations are implied by these findings. First, generalist symbionts may be found on several hosts because a preferred species is locally absent or in short supply (*P. yucatanicus*), or because they exhibit no apparent preference for a particular species (*P. pedersoni*). Second, an initial preference for a particular host is insufficient evidence to conclude that a symbiont is host-specific. For example, *P. pedersoni* showed a strong preference for *B. annulata* (Table 2), but this preference could be reversed through conditioning (Table 3). Conditioning experiments, carried out with several potential hosts, are necessary to establish whether preferences are transitory functions of experience, or whether (as in *P. yucatanicus*) they persist regardless of contact with alternative hosts.

Unfortunately, few species of marine symbionts have been subjected to such systematic testing. One notable exception is the polychaete *Arctonoe pulchra*, which inhabits the sea cucumber *Stichopus parvimensis*. In this instance, conditioning could induce the polychaete to occupy an alternate (sea star) host (Dimock and Davenport, 1971).

Given these complexities, it seems premature to assign degrees of host specificity on the basis of field distributions. The practice, however, is common. For example, several authors (Sargeant and Wagenbach, 1975; Levine and Blanchard, 1980; Nizinski, 1989) have concluded that *P. anthophilus* shows a high degree of host specificity because it is found on one (*C. gigantea*) species of anemone, even when others are present. However, alternative explanations for this distribution remain unexplored, and no preference tests have been conducted.

#### *Preference patterns in relation to function*

The preference of *P. yucatanicus* for one anemone host, and the apparent absence of such preferences in *P. pedersoni*, suggest a fundamental difference between the two species in the nature of their association with anemone hosts. Here, we review the evidence suggesting that there are important correlations between host preference patterns and the function of the symbiotic relationship.

There is good evidence that *P. pedersoni* is a cleaner shrimp (Limbaugh et al., 1961; Chace, 1972; Roessler and Post, 1972). Cleaner species are well known for their conspicuous coloration and behavior (shrimp: Limbaugh et

al., 1961; Roessler and Post, 1972; fishes: Feder, 1966; Wickler, 1968), which advertise their presence and make them conspicuous to potential "customers."

*Periclimenes pedersoni* is conspicuously colored, possessing elongate, white antennae that are visible (at least to a diver) at several meters. They couple this coloration with behavioral attributes (approaching fishes, including predatory species, with apparently little "fear") characteristic of other cleaner organisms on the reef. Mahnken (1972) suggested that *P. pedersoni* often selects *B. annulata* as a host because the anemone's dark color serves as a contrast that makes the shrimp more conspicuous and easier for fish to locate. Mahnken also noted that *P. pedersoni* sought out anemones where fish traffic was greatest. These findings suggest that for *P. pedersoni*, anemones may be selected primarily on the basis of color and/or location, attributes independent of their characteristics as sources of protection. If true, these shrimp might be opportunistic with regard to species of anemone host they occupy; any species presenting a good color contrast or found in an area of high fish abundance might be suitable.

While *P. yucatanicus* has also been reported as a cleaner (Jonasson, 1987), the evidence is equivocal. We frequently saw cleaning behavior by *P. pedersoni* (waving antennae, swaying, and picking at our hands), but never (in more than 60 hr of observations) by *P. yucatanicus*. Others have also noted the absence of cleaning by *P. yucatanicus*, as well as its reluctance to leave the shelter of its host anemone to approach fishes; these characteristics have led to the conclusion that it may be a cleaner mimic (Limbaugh et al., 1961; Mahnken, 1972; Criales and Corredor, 1977).

A comparable situation may exist in Bermuda. There *P. anthophilus* has been reported as a cleaning shrimp (Sargeant and Wagenbach, 1975). However, in an intensive study of their ecology and behavior, Nizinski (1989) observed no cleaning by this species. Nizinski reported that *P. anthophilus* exclusively occupied morphs of *C. gigantea* that provided the best color camouflage for the shrimp.

We found that *P. yucatanicus* was difficult to collect, primarily because it was nearly invisible against the background of the preferred host, *S. helianthus*. The saddles and spots characteristic of *P. yucatanicus* appear similar to the short, knobby tentacles of this anemone. In contrast, we found *P. yucatanicus* easy to detect on both *C. gigantea* and *B. annulata*. If predators can also see the shrimp on these hosts, and follow up detection with attacks, shrimp found on alternative hosts may be subject to greater mortality than those found on *S. helianthus*. Unfortunately, no data document survival probabilities of the shrimp on different species of hosts.

These observations, then, lead to the hypothesis that *P. pedersoni* and *P. yucatanicus* occupy distinctly different niches, and that these differences shape the behavioral variation they show of host preference. Future studies should focus on the ecological significance of their associations, in terms of costs and benefits to both the shrimp and their anemone hosts. Such studies are few (Cushman and Beattie, 1991), but are essential to establishing relationships between functional significance and behavior in symbiotic relationships.

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