

# Host selection of the symbiotic copepod *Clausidium dissimile* in two sympatric populations of ghost shrimp

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**ABSTRACT:** Ghost shrimp, *Lepidophthalmus louisianensis* (Schmitt 1935) and *Sergio trilobata* (Biffar 1970) are 2 common burrowing decapod crustaceans in Tampa Bay, Florida, which affect the benthic community through bioturbation. The burrow also plays a crucial role in determining benthic community structure, since it may house several symbionts, one of which is the copepod *Clausidium dissimile* Wilson, 1921. This study was conducted to investigate factors that affect the density of *C. dissimile* on ghost shrimp specimens both in the field and in the laboratory. Collections of *L. louisianensis* and *S. trilobata* were made over a 15 mo period to determine the prevalence of *C. dissimile* in the field. Analysis of monthly field data showed that host shrimp ( $p = 0.0001$ ), and sampling month ( $p = 0.0310$ ) were significantly correlated with the host-size adjusted density of the symbiont *C. dissimile*, with more copepods preferring specimens of *S. trilobata* over *L. louisianensis*. Although host sex did not have a significant effect on host-size adjusted copepod density, percentage prevalence of copepods was significantly higher for females than males in *S. trilobata* ( $p < 0.0001$ ). Laboratory experiments supported observations from the field in that *C. dissimile* significantly preferred *S. trilobata* over *L. louisianensis* ( $p < 0.001$ ). However, unlike the field data, copepods did not appear to prefer female over male hosts when size was held constant. Higher colonization of females than males in the field may instead be attributed to differences in size and behavior between the sexes.

**KEY WORDS:** *Clausidium dissimile* · Ghost shrimp · Host selection · Copepod · *Sergio trilobata* · *Lepidophthalmus louisianensis*

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## INTRODUCTION

Ghost shrimp are burrowing decapod crustaceans that predominantly inhabit shallow intertidal and occasionally subtidal areas with soft sediment in tropical and temperate regions (Berkenbusch & Rowden 1999). They are also typically found in regions of high organic content, which triggers settlement in at least 1 species (Strasser & Felder 1999). They are an important component of the ecosystem, affecting nutrient cycling, sediment turnover rates and benthic community structure, as well as aquaculture through bioturbation (Felder & Griffis 1994, Nates & Felder 1998, Berkenbusch & Rowden 2000). Like many species of

ghost shrimp, those in the genus *Lepidophthalmus* impact penaeid aquaculture by decreasing shrimp production in the ponds (Nates & Felder 1998). *Lepidophthalmus louisianensis* (Schmitt, 1935) is also thought to influence the structure and species composition of natural intertidal habitats due to bioturbating activities (Jackson 1996). Sediment suspended during construction and maintenance of their burrows (Lafferty & Kuris 1996) may impact filter-feeding organisms, such as oysters, by reducing their ability to feed effectively (Stevens 1929). Temperature and salinity affect intertidal decapod populations (Berkenbusch & Rowden 2000). Low temperatures cause ghost shrimp to be relatively inactive, leading to a decrease in sediment

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turnover rates (Berkenbusch & Rowden 1999) and in the effect these organisms have on their environment.

The burrows of ghost shrimp may house several species. These symbionts are generally thought to be either parasitic or commensal and include a variety of organisms, such as copepods, pea crabs, Leptalpheid shrimp, clams, gobiid fish and polychaete worms (Jackson 1996). The symbiotic copepod of interest in this study is *Clausidium dissimile* Wilson, 1921, which lives mainly in the gill chamber and on the body surface of many species of ghost shrimp (Wilson 1935, Gooding 1963). *Clausidium* spp. have a wide distribution and occur on both coasts of the USA, the Gulf of Mexico, Canada, India, Senegal and Peru. *C. dissimile* has also been found on *Callichirus major* in North Carolina (Pohl 1946), *Callianassa stimpsoni* in Massachusetts (Humes 1949), and *Sergio trilobata* (Biffar 1970) and *Lepidophthalmus louisianensis* in Pensacola Bay, Florida (Hayes 1976).

Although it has often been suggested that members of the genus *Clausidium* spp. are parasitic on their host organisms (Wilson 1935, Pillali 1959), this has yet to be shown quantitatively (Hayes 1976). There is very little information regarding the behavior of these copepods or how they interact with their host and with the environment they inhabit. Marin & Nascimento (1993) analyzed the body size and habitat of *Callichirus garthi* as factors affecting the distribution, abundance and fecundity of *Clausidium* spp. The results of that study suggested that the density of *Clausidium* spp. per host was dependent upon host habitat type and recruitment. The diet of *C. dissimile* has been studied through gut content analysis, and found to contain diatom frustules from *Actinoptychus*, *Codinodiscus*, *Thalassiosira* and an unidentified genus, as well as an unidentifiable mass (Hayes 1976). It has not been determined whether these copepods consume part of their host, or whether diatoms are consumed without harm to the host (Hayes 1976). Adult copepods attach to the host with 2 sucking disks located on the endopod of leg 1 and commonly skim along the surface of the host without losing contact (Hayes 1976). They are occasionally observed swimming free of the host; however, this behavior is rare and lasts only 1 to 2 s (Hayes 1976).

Two species of ghost shrimp, *Sergio trilobata* and *Lepidophthalmus louisianensis*, have been observed in the Tampa Bay area. *L. louisianensis* is distributed over the western Atlantic coast and the Gulf of Mexico (Manning & Felder 1991, Felder & Rodrigues 1993, Nates et al. 1997). The highest densities of *Lepidophthalmus* spp. have typically been found in regions of high organic content in the sediments (Nates & Felder 1998, Nates & Felder 1999). *S. trilobata* was described from Tampa Bay but has also been reported in Miami and Lemon Bay, Florida (Biffar 1971, Manning &

Lemaitre 1993). *Sergio* spp. also thrive in regions of high organic content and are thought to have a thicker burrow than other species of ghost shrimp in south Florida (Biffar 1971).

The density of symbiotic copepods appears to vary between the similar-sized host species *Sergio trilobata* and *Lepidophthalmus louisianensis*. This study investigated factors that may affect the host selection process of *Clausidium dissimile*. The first objective was to determine the factors that affect the density of *C. dissimile* on individual ghost shrimp hosts. The tested factors were the species of ghost shrimp (*L. louisianensis* or *S. trilobata*), month of collection, sex of the host organism, size of the host organism, reproductive activity of the host organism and ovary width of the host organism. The second objective of this study was to determine whether (1) specimens of *C. dissimile* would preferentially choose a host (based on species, sex and size of the host) in laboratory experiments and (2) observed preferences correspond to frequencies observed in natural populations.

## MATERIALS AND METHODS

**Preference of *Clausidium dissimile* in the field.** Collections of *Lepidophthalmus louisianensis* and *Sergio trilobata* were made on an intertidal sand flat located on the SW end of the Gandy Bridge in Tampa, Florida from June 2000 to November 2001. Specimens were extracted from randomly chosen burrow holes using yabby pumps and 1 mm mesh sieves (Felder 1978). Monthly samples consisted of ca. 30 animals: 15 of each species. Each shrimp was placed in an individual clean whirl-pack plastic bag (177 ml) to prevent loss or movement of copepods.

In the laboratory, each shrimp was removed from its bag and carefully examined to remove and count female specimens of *Clausidium dissimile* living with the animal. Copepods were removed from their hosts into a clean petri dish by carefully spraying the ghost shrimp with freshwater. Sex, total length (TL, measured from the tip of the rostrum to the posterior end of the telson) and carapace length (CL, measured from the tip of the rostrum to the posterior end of the carapace) were recorded for each ghost shrimp. The ovary width of females was recorded dorsally on the second abdominal segment at the widest point visible. All measurements were made to the nearest mm. The eggs of ovigerous ghost shrimp were counted, when possible. After all measurements were recorded, individual specimens were preserved in 70% ethanol.

**Analysis of field data.** Fisher's Exact Test was used to determine whether the prevalence of *Clausidium dissimile* (proportion of hosts with at least 1 copepod)

varied between host species *Sergio trilobata* and *Lepidophthalmus louisianensis*, between adults and juveniles, and between the sexes of each host species for all monthly samples combined. The number of copepods per host (copepod density) was divided by the TL of the ghost shrimp to normalize for size of the host (host-size adjusted copepod density). A Mann-Whitney *U*-test was used to compare the copepod density, and host-size adjusted copepod density of each host species, males versus females, and adults versus juveniles of each host species for all samples combined. A repeated measures ANOVA (Model II sum of squares) was used to determine whether host-size adjusted copepod density varied significantly between host species, sexes and month of collection. A Mann-Whitney *U*-test was used to test whether the presence of eggs had a significant effect on the density of copepods per female host. A simple linear regression was used to determine whether ovary width of females and size of the host organism (males and females) had significant effects on the density of copepods.

**Behavioral preference experiments in the laboratory.** To determine whether findings from field collections reflected preferences of *Clausidium dissimile*, a series of 7 experiments (Table 1) were conducted in the laboratory. Collections of *Lepidophthalmus louisianensis* and *Sergio trilobata* for use in preference experiments were made from the same location in Tampa,

Florida in July and August 2001. Ghost shrimp were placed in perforated plastic vials with each species in a separate bucket for transportation to the laboratory to assure that the host species of copepods could be ascertained. Prior to use, all ghost shrimp were carefully dipped in deionized water until all specimens of *C. dissimile* were removed and hosts were then maintained in filtered sea water (30‰ salinity) with no *C. dissimile* present. Copepods were placed in filtered seawater in separate containers according to what species of ghost shrimp they had inhabited. Therefore copepods could be identified as originating from *S. trilobata* or *L. louisianensis*. Sea water used in preference experiments was collected from Fort Desoto State Park, Florida, filtered through steel wool and diluted with deionized water to 30‰ salinity.

For each of the 7 experiments, a testing chamber (Fig. 1) was placed in each of 5 aquariums (9.5 l) filled with filtered sea water. The testing chamber was constructed using a small circular plastic container with 4 equidistant holes drilled into the bottom. To house the ghost shrimp, 4 clear vinyl (PVC) tubes (1.59 cm in diameter, 15.24 cm in length) were secured in place with non-toxic silicone. The end of each tube was covered with 3 overlapping layers of screening (1 mm × 1 mm) and secured with a rubber band to ensure that all the animals remained in the testing chamber while allowing water exchange.

Table 1. *Clausidium dissimile*. Summary of host preference experiments. Factors tested were host species (*Sergio trilobata* or *Lepidophthalmus louisianensis*), host sex, host size and species of ghost shrimp originally inhabited by the copepods. Trials used 20 copepods (40 for Expt 7) and up to 4 shrimp

Expt	Factor tested	Host species	Sex of host	Size of host in mm (mean TL ± SD)	Source of copepods	No. of trials
1	Host species	<i>L. louisianensis</i> and <i>S. trilobata</i>	Female	Hosts within 5 mm TL of each other	<i>S. trilobata</i>	10
2	Host species	<i>L. louisianensis</i> and <i>S. trilobata</i>	Female	Hosts within 5 mm TL of each other	<i>L. louisianensis</i>	5
3	Host size	<i>S. trilobata</i>	Male	Small 44.8 ± 0.5 Large 67.8 ± 3.1	<i>S. trilobata</i>	5
4	Host size	<i>S. trilobata</i>	Female	Small 51.6 ± 2.9 Large 75.8 ± 4.1	<i>S. trilobata</i>	5
5	Host sex	<i>S. trilobata</i>	Male/ female	Small Males 48.6 ± 4.5 Females 48.6 ± 5.4	<i>S. trilobata</i>	5
6	Host sex	<i>S. trilobata</i>	Male/ female	Large Males 67.8 ± 4.6 Females 70.0 ± 1.7	<i>S. trilobata</i>	5
7	Host sex and size	<i>S. trilobata</i>	Male/ female	Small Males 50.0 ± 2.0 Females 51.0 ± 2.9 Large Males 70.6 ± 1.7 Females 72.4 ± 2.7	<i>S. trilobata</i>	5

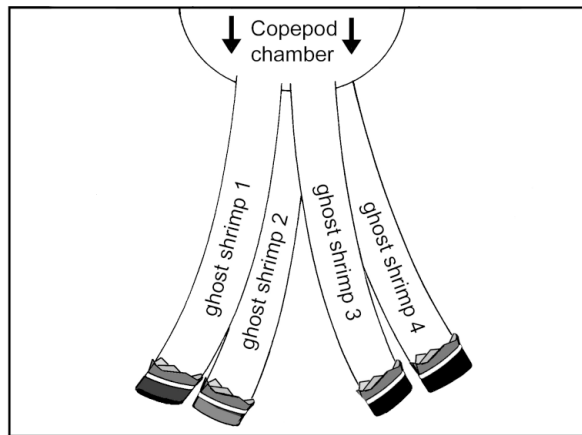


Fig. 1. Experimental chamber used in laboratory preference experiments. Arrows indicate where copepods were introduced into the chamber at the beginning of the experiment. Ghost shrimp were located near the bottom of the tubes throughout each experiment

During each experimental trial (see Table 1), ghost shrimp were randomly assigned to the tubes (1 shrimp in each), generally maintaining a position near the bottom of the tubes. Two tubes were filled with cotton for trials in which only 2 host specimens were used, and 20 specimens of *Clausidium dissimile* were then placed in the center of the copepod chamber using a pipette. The copepods could then swim horizontally for a short distance in order to reach the tubes in which the host

organisms were located. Although ghost shrimp were not physically prevented from entering the copepod chamber and subsequently switching tubes, this activity was not observed. Similarly, ghost shrimp in the field are thought not to leave their burrows through the top opening. Copepods were taken originally from either *Sergio trilobata* or *Lepidophthalmus louisianensis*, depending on the experiment (Table 1). In Expt 7, however, 40 specimens of *Clausidium dissimile* were placed in the testing chamber because there were 4 shrimp used in each trial. In all experiments in which size was not the tested factor, the ghost shrimp used were within 5 mm TL of each other. In experiments in which size was the tested factor, ghost shrimp had a minimum size difference of 20 mm TL.

The number of copepods located on each ghost shrimp (or not attached to a host) was determined after an 8 h period. At this time, ghost shrimp were removed from the tubes by taking the testing chamber out of the aquarium, removing the screening and placing the shrimp from each tube in separate glass bowls. All organisms used in trials were preserved in 70% ethanol.

In Expts 1 to 6 the proportion of copepods selecting a particular host was analyzed using a replicated goodness-of-fit test, the *G*-test (Sokal & Rohlf 1981). This proportional data is presented as percentages in the text and figures. Expts 1 and 2 were conducted to determine whether *Clausidium dissimile* would exhibit a preference for either *Sergio trilobata* or *Lepidophthal-*

Table 2. *Clausidium dissimile*. Data from field collections. n = individuals from all sample months combined. Percent prevalence compared between total specimens of each host species, males versus females *Sergio trilobata* and adults versus juveniles of *S. trilobata* with Fisher's Exact test. Copepod density (mean  $\pm$  SE) and host-size adjusted copepod density (copepod density/TL of host, mean  $\pm$  SE) compared between total specimens of each host species, males versus females *S. trilobata*, and adults versus juveniles of *S. trilobata* with the Mann-Whitney *U*-test

Host species	n	Prevalence (% of hosts with $\geq 1$ copepod)	Copepod density (ind. per host; mean $\pm$ SE)	Host-size adjusted copepod density (mean $\pm$ SE)
<b><i>Lepidophthalmus louisianensis</i></b>				
Adult	233	67	5.4 $\pm$ 0.7	0.088 $\pm$ 0.011
Male	65	65	4.2 $\pm$ 0.9	0.069 $\pm$ 0.015
Female	168	68	5.9 $\pm$ 0.1	0.095 $\pm$ 0.015
Juvenile	10	50	2.1 $\pm$ 1.0	0.079 $\pm$ 0.042
Total	243	66	5.3 $\pm$ 0.7	0.087 $\pm$ 0.011
<b><i>Sergio trilobata</i></b>				
Adult	298	97	13.3 $\pm$ 0.8	0.203 $\pm$ 0.011
Male	93	92	10.0 $\pm$ 1.0	0.180 $\pm$ 0.017
Female	205	99 <sup>a</sup>	14.8 $\pm$ 1.1 <sup>a</sup>	0.210 $\pm$ 0.014
Juvenile	21	71 <sup>b</sup>	2.4 $\pm$ 0.5 <sup>b</sup>	0.075 $\pm$ 0.017 <sup>b</sup>
Total	319	95 <sup>c</sup>	12.6 $\pm$ 0.8 <sup>c</sup>	0.194 $\pm$ 0.001 <sup>c</sup>

<sup>a</sup>Significantly higher for female *S. trilobata* than for males. Prevalence: p = 0.012; copepod density: p = 0.0084  
<sup>b</sup>Significantly higher for adult *S. trilobata* than for juveniles. Prevalence and host-size adjusted copepod density: p = 0.0002; copepod density: p < 0.0001  
<sup>c</sup>Significantly higher than for *L. louisianensis*, p < 0.0001

*mus louisianensis*, and differed only in terms of the source host. Expts 3 to 7 were conducted to examine how size and sex of the host affected selection behavior. Expts 3 and 4 tested the preference of *C. dissimile* for large or small male (Expt 3) and female (Expt 4) hosts. Expts 5 and 6 were conducted to determine if copepods would exhibit a preference for either sex when size of the host was held constant, using either small (Expt 5) or large (Expt 6) host specimens. Expt 7 tested the preference of *C. dissimile* for the sex and size of the host, when both factors were combined; the data were analyzed using Fisher's Exact Test.

## RESULTS

### Monthly field collections

*Clausidium dissimile* colonizes *Sergio trilobata* at a higher frequency than *Lepidophthalmus louisianensis*. When data from all months were combined, the mean percentage prevalence (percentage of shrimp with at least one copepod attached), copepod density (number of copepods per host), and host-size adjusted copepod density (number of copepods/TL of host) were all significantly higher for *S. trilobata*, than for *L. louisianen-*

Table 3. Results of repeated measures ANOVA (Model II sum of squares) showing the effects of host species, host sex, sampling month, and interaction effects on the host-size adjusted copepod density (no. of copepods per host/TL of host). Significant independent variables are shown in **bold**

Source	df	SS	MS	F	p
<b>Host species</b>	1	0.994	0.994	53.1	0.0001
Host sex	1	0.005	0.005	0.253	0.6258
Host species × Host sex	1	0.003	0.003	0.140	0.7464
Subject (group)	10	0.187	0.019		
<b>Months</b>	16	1.001	0.063	1.833	0.0310
Months × Host species	16	0.642	0.040	1.175	0.2930
Months × Host sex	16	0.325	0.020	0.596	0.8840
Months × Host species × Host sex	16	0.712	0.045	1.304	0.2002
Months × Subject (Group)	160	5.461	0.034		

*sis* (Table 2). For *S. trilobata*, the percentage prevalence and copepod density were significantly higher for adults than for juveniles, and for females over males. When host size was eliminated as a factor by examining host-size adjusted copepod density, adults differed significantly from juveniles, but males and females did not differ significantly for *S. trilobata*. There were no significant differences in percentage prevalence, copepod density, or host-size adjusted copepod density between adults and juveniles and between males and females of *L. louisianensis*.

Host species and sampling month had significant effects on host-size adjusted copepod density (Table 3). Although female specimens of each host species generally had a higher host-size adjusted copepod density than males, host sex was not a significant factor. None of the interaction effects were significant. Juveniles were not present all year and thus only adult specimens were included in this analysis. For all but 2 collections (September 2000 and September 2001, Fig. 2), specimens of *Sergio trilobata* had a higher mean host-size adjusted copepod density than specimens of *Lepidophthalmus louisianensis*. Host-size adjusted density of *Clausidium dissimile* also varied seasonally (Fig. 2). Overall, host-size adjusted densities of *C. dissimile* were higher in the fall than they were in the spring and summer on both species of ghost shrimp with the exception of *S. trilobata* in the fall of 2001 where a decline in host-size adjusted copepod density was observed (Fig. 2).

Copepod density on *Sergio trilobata* was correlated with TL ( $F = 75.241$ ;  $df = 1, 423$ ;  $p < 0.0001$ ) and CL ( $F = 58.299$ ;  $df = 1, 423$ ;  $p < 0.0001$ ) of the host shrimp.

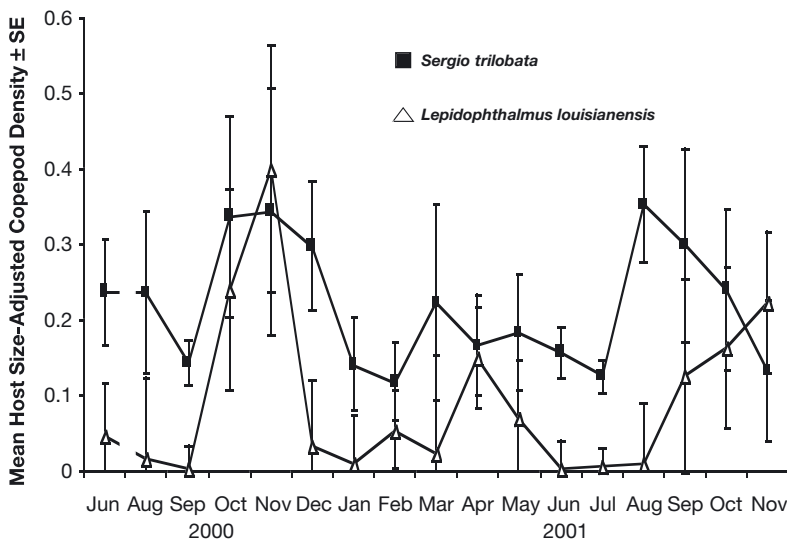


Fig. 2. *Clausidium dissimile*. Mean host-size adjusted copepod density ( $\pm$ SE) (no. of copepods per host/TL of host) found on specimens of *Sergio trilobata* and *Lepidophthalmus louisianensis* during each month of collection from June 2000 to November 2001 (excluding July 2000)

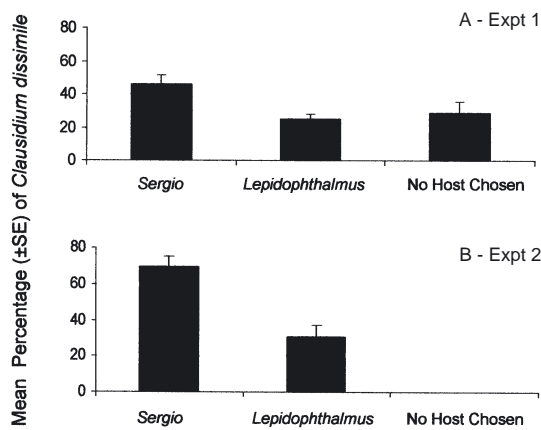


Fig. 3. *Clausidium dissimile*. Mean percentage ( $\pm$ SE) of copepods that chose *Sergio trilobata* and *Lepidophthalmus louisianensis* and those that did not choose a host using (A) copepods initially taken from *S. trilobata* or (B) copepods initially taken from *L. louisianensis*

However, the copepod density on *Lepidophthalmus louisianensis* was not dependent on TL ( $F = 3.312$ ;  $df = 1, 423$ ;  $p = 0.07$ ) or CL ( $F = 1.142$ ;  $df = 1, 423$ ;  $p = 0.2826$ ) of the host shrimp. The field data also showed that reproductive activity of females, measured as the presence of eggs, did not have a significant effect on the density of *Clausidium dissimile* (*S. trilobata*:  $p = 0.7457$ ; *L. louisianensis*:  $p = 0.3334$ ). Ovary size had a significant effect on copepod density on *L. louisianensis* ( $F = 5.999$ ;  $df = 1, 156$ ;  $p = 0.0154$ ;  $r^2 = 0.037$ ), as greater ovary widths correlated with lower copepod densities. However, for *S. trilobata*, ovary width did not have a significant effect ( $F = 2.44$ ;  $df = 1, 172$ ;  $p = 0.12$ ;

$r^2 = 0.014$ ).

### Laboratory preference experiments

Results of Expt 1 using copepods collected from *Sergio trilobata*, mirrored the field data in that *Clausidium dissimile* exhibited a significant preference for *S. trilobata* over *Lepidophthalmus louisianensis* ( $G = 19.176$ ;  $df = 7$ ;  $p < 0.001$ ) (Fig. 3A). The mean percentages ( $\pm$  SE) of *C. dissimile* that chose *S. trilobata* and *L. louisianensis* were  $46.0 \pm 5.7$ , and  $25.0 \pm 2.8$ , respectively. Expt 2 (using copepods taken from *L. louisianensis*) also revealed a preference of *C. dissimile* for *S. trilobata* over *L. louisianensis* ( $G = 22.041$ ;  $df = 7$ ;  $p < 0.0005$ ). The mean percentages of *C. dissimile* that chose *S. trilobata* and *L. louisianensis* were  $69.1 \pm 6.2$  and  $30.9 \pm 6.22$ , respectively (Fig. 3B).

In Expt 3, *C. dissimile* showed a significant preference for small males of *S. trilobata* over large males ( $G = 20.502$ ;  $df = 7$ ;  $p < 0.0005$ ). The mean percentage ( $\pm$ SE) of copepods that chose small male shrimp ( $58.0 \pm 3.4$ ) was significantly higher than the mean percentage that chose large male shrimp ( $21.0 \pm 3.7$ ) (Fig. 4A). This data differs from the results of Expt 4 (Fig. 4B) in which the mean percentage of *C. dissimile* that chose small females ( $25.0 \pm 2.2$ ) was significantly lower ( $G = 16.718$ ;  $df = 7$ ;  $p < 0.05$ ) than the mean percentage that chose large females ( $61.0 \pm 6.4$ ) (Fig. 4B). To isolate host sex as a potential factor, experiments were conducted with only small (Expt 5) or large (Expt 6) potential hosts; however, no significant preference for males or females was determined (Fig. 4 C, D). Expt 5 demonstrated that

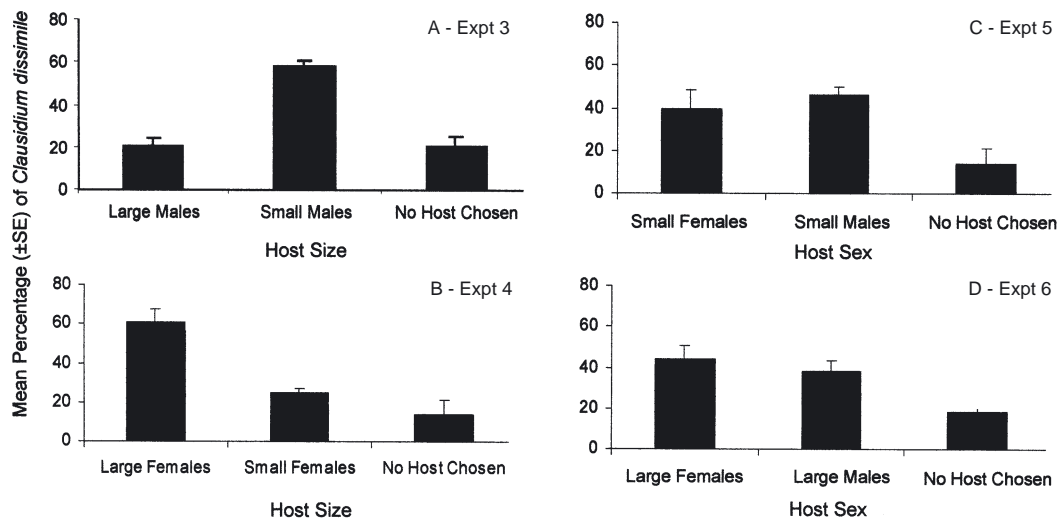


Fig. 4. *Clausidium dissimile*. Mean percentage ( $\pm$ SE) of copepods that chose each sex or size of host *Sergio trilobata* and those that did not choose a host (A) large and small male hosts, (B) large and small female hosts, (C) small male and female hosts, (D) large male and female hosts

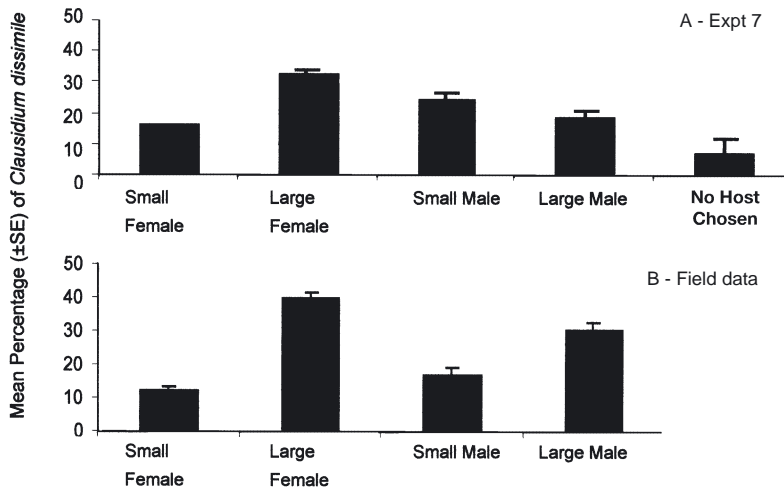


Fig. 5. *Clausidium dissimile*. Mean percentage ( $\pm$ SE) of copepods that chose each sex and size of host *Sergio trilobata*. (A) data taken from Expt 7. (B) data taken from specimens collected in the field that matched size-ranges used in Expt 7

*C. dissimile* had no preference for small males or females ( $G = 5.747$ ;  $df = 7$ ;  $p < 0.50$ ) (Fig. 4C). The mean percentage of copepods that chose small males ( $46.0 \pm 4.0$ ) was slightly larger than the mean percentage that chose small females ( $40.0 \pm 6.4$ ) (Fig. 4C). Similarly, Expt 6 indicated that *C. dissimile* had no preference for large males or females ( $G = 7.969$ ;  $df = 7$ ;  $p < 0.40$ ). The mean percentage of *C. dissimile* that chose large males ( $38.0 \pm 5.4$ ) was slightly lower than the mean percentage that chose large females ( $44.0 \pm 6.8$ ) (Fig. 4D). When sex and size of *S. trilobata* were tested simultaneously in Expt 7, the higher percentages of *C. dissimile* were found on large females ( $33.0 \pm 2.3$ ) and small males ( $24.5 \pm 2.7$ ), whereas small females ( $16.5 \pm 1.5$ ) and large males ( $18.5 \pm 5.0$ ) had fewer *C. dissimile* ( $G = 15.045$ ;  $df = 1$ ;  $p = 0.0001$ ) (Fig. 5A). A comparison with shrimp of a similar size collected in the field demonstrated an inconsistency with the experimental data. In the field, *C. dissimile* was found more frequently on large females ( $39.8 \pm 1.7\%$ ) and large males ( $30.5 \pm 2.4\%$ ), than on small females ( $12.6 \pm 0.8\%$ ) and small males ( $17.1 \pm 2.5\%$ ) (Fig. 5B).

## DISCUSSION

The host-size adjusted density of *Clausidium dissimile* was affected by the host species and the month sampled. The results of both monthly field collections and preference experiments showed that *C. dissimile* significantly preferred *Sergio trilobata* over *Lepidophthalmus louisianensis*, no matter which host *C. dissimile* had formerly inhabited. It could be that either *C.*

*dissimile* is attracted to *S. trilobata* or *L. louisianensis* repels the symbiont, possibly through removal by grooming behavior. Another possibility is that the feeding mechanism of *S. trilobata* and *L. louisianensis* may influence the abundance of copepods. Ghost shrimp feed in a variety of ways including filtration of plankton and deposit feeding, and generally consume microalgae and other diatoms (Felder & Griffis 1994). Most callinassid ghost shrimp feed by sifting sand for microscopic organisms using their mouth parts to remove food particles from setae of the maxillipeds (Pohl 1946). Gut content analysis of *L. louisianensis* has shown that the main dietary constituents are diatoms and other microalgae commonly found in the sediment (Felder & Griffis 1994), while both the feeding mechanisms and dietary intake of *S. trilobata* are

unknown. Nevertheless, recruitment of the planktonic host-seeking stage of copepods—Copepodid I in *C. dissimile* (Hayes 1976)—may depend on the host's feeding mechanism.

The apparent preference for host sex was not consistent between the field and experimental evidence for *Sergio trilobata*. In field collections the proportion of hosts with *Clausidium dissimile* (percentage prevalence) was significantly higher for females than males, except when corrected for host size (Table 2). No such relationship was observed in preference experiments with *S. trilobata*. There was no significant difference in the number of copepods selecting either sex when the size of each potential host was similar. This could signify that copepods base their selection of host primarily on the size of the organism. Since females are generally larger in size ( $68.2 \pm 2.2$  mm, mean  $\pm$  SE) in the field than males ( $54.6 \pm 5.4$  mm), higher copepod infestation on female specimens may be a result of size and not sex. The lack of a significant difference between the sexes in copepod density supports this hypothesis.

TL in *Sergio trilobata*, but not in *Lepidophthalmus louisianensis*, was correlated with the mean number of *Clausidium dissimile* present. This could be a sampling artifact because there were simply too few copepods found on *L. louisianensis* to determine a preference for the host size or sex. In *S. trilobata*, the total length of the organism was indicative of the number of symbionts present, which suggests that there is a host carrying capacity. Smaller individuals may be able to support fewer copepods than larger host specimens. Copepods may redistribute themselves to reduce competition for food resources, assuming they feed on sus-

pended plankton and other particles pumped into the burrow by the shrimp (Hayes 1976). The correlation between abundance of copepods and the size of *S. trilobata* confirms the results of another study in which the abundance of *Clausidium* sp. was directly related to the size of *Callinectes garthi* (= *Callinectes garthi*, Marin & Nascimento 1993). The authors suggested that the larger the animal the more time the copepods have had to associate with the host (Marin & Nascimento 1993). This explanation suggests that copepods remain with the host initially colonized. In our study, copepods moved between host shrimp kept in the same collecting bucket. This was especially apparent when host specimens were injured; copepods generally abandoned injured or dying ghost shrimp specimens.

Chemoreception serves for host recognition in many groups of symbiotic crustaceans (Jackson 1996). The size of *Sergio trilobata* could be related to its chemical cue; a larger animal may emit a stronger signal than a smaller animal. During laboratory experiments, *Clausidium dissimile* displayed a significant preference for small males and large females of *S. trilobata*. However, in field data, large males and females were preferred over smaller specimens. If the strength of the signal was a critical factor in promoting a preference for a host, perhaps activity level contributes to disseminating this chemical signal. While only healthy shrimp were used, larger specimens exhibited higher mortality rates than smaller specimens. Although no attempt was made to quantify activity level, larger specimens appeared to be less active than smaller specimens. Therefore, the higher activity of small males may have attracted more copepods to them. However, this does not explain why copepods selected larger females in the laboratory.

If a size-related chemical signal is used to explain copepod preference, it does not account for the significantly higher prevalence of copepods on females than males of *Sergio trilobata*. However, the differences in behavior between the sexes could be a factor. In our experience, females are generally collected from the field more often than males. Although natural populations of *S. trilobata* could be female biased, this deviation in the sex ratio could also be due to the behavior of the ghost shrimp. Females more continuously inhabit the upper reaches of the burrow (Nates & Felder 1999) and could therefore be collected more frequently than males, which may remain deeper in the burrow. The proximity of the shrimp in the burrow may have an effect on the strength of the chemical signal and therefore females living higher in the burrow may attract more copepods. In laboratory experiments, all shrimp were located near the surface of the burrow since the artificial burrow constructed was only approximately 15 cm in length.

The density of copepods on female ghost shrimp

did not differ significantly between ovigerous and non-ovigerous females for either *Sergio trilobata* or *Lepidophthalmus louisianensis*. Females with larger ovaries did not have higher copepod densities. In addition, peak periods of reproductive activity for *S. trilobata* do not coincide with seasonal trends in copepod abundance (Corsetti & Strasser in press) suggesting that the presence of eggs and or developed ovaries has no benefit to the copepods, such as a possible food source. Although copepods inhabit the abdomen and cephalothorax, the greatest density was typically observed in the gill chamber of host specimens.

In the case of a parasitic relationship, potential costs to the host organisms could be decreased mobility, respiration efficiency and feeding efficiency, which could all impact potential reproductive success. However, infested hosts did not appear to be less viable than those without a high copepod load. Even at the maximum infestation rates observed, ca. 90 to 100 copepods per host, the infested shrimp did not exhibit adverse effects. Additionally, reproductive potential of females, assessed as egg number or ovary size, was not negatively affected by increased densities of copepods in this study. Thus we have no evidence that the relationship between *Clausidium dissimile* and *Sergio trilobata* or *Lepidophthalmus louisianensis* is parasitic.

Although it is unclear why copepods would preferentially colonize *Sergio trilobata* over *Lepidophthalmus louisianensis*, the consistency between data from field collections and laboratory experiments suggests that such a preference exists. Host sex seems to be unimportant, while host species and size have an impact. Both the mechanism of this selection and the precise nature of the copepod-host relationship warrants further study.

*Acknowledgements.* We would like to thank all those that assisted in collection of organisms: Mark Driscoll, Amanda Kahn, Kelly Graham and students in the University of Tampa's Ecology class in 2000 and 2001. Funding for this study was provided to J. Corsetti by the University of Tampa Biology Research Fellowship and the University of Tampa Honors Research Fellowship, and to KM Strasser by a University of Tampa Delo grant and Dana grant. We would also like to thank W. Wayne Price, Kevin Beach, and 3 anonymous reviewers for their helpful comments on this manuscript.

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Editorial responsibility: Gareth Harding (Contributing Editor), Dartmouth, Nova Scotia, Canada

Submitted: December 19, 2001; Accepted: February 18, 2003  
Proofs received from author(s): May 28, 2003