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ECOLOGY OF A POPULATION OF *LISSOCRANGON STYLIROSTRIS* (CARIDEA: CRANGONIDAE), WITH NOTES ON THE OCCURRENCE AND BIOLOGY OF ITS PARASITE, *ARGEIA PUGETTENSIS* (ISOPODA: BOPYRIDAE)

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ABSTRACT

The smooth bay shrimp, *Lissocrangon stylirostris*, was sampled using a beach seine and a hyperbenthic sledge in the summer of 2006 at a dissipative sandy beach in southern Oregon. We investigated possible variations in the population structure due to environmental variables, preferred prey, sexual system employed, impacts due to parasitism by the bopyrid isopod *Argeia pugettensis*, and possible predators. The population was 63% female, and females were generally larger than males. The density of *L. stylirostris* varied significantly with the time of day. A cohort of small shrimp was observed from July to September while large adult shrimps were rare during the same months. The net effect was that shrimp densities were stable over the summer. The shrimps fed mostly at night on the mysid *Archaeomysis grebnitzkii*. The differences in female to male ratio, the larger size of females relative to males, and the relatively little overlap in size frequency distribution between males and females could be because this species exhibits a type of protandry. Both male and female shrimps supported an equal, high prevalence of, level of infestation by *A. pugettensis* (62%). The parasitized shrimps were larger in size than normal shrimps but had lower weight per length ratio. Very few brooding shrimps were parasitized (0.2%), and a higher percentage of parasitized shrimps had empty stomachs and significantly lower stomach contents. We hypothesize that the parasite is affecting the shrimp by producing variation in its normal size and weight, sterilizing females, and reducing its ability to capture food. Finally, individuals of English sole and Pacific staghorn sculpin individuals preyed on the shrimps.

KEY WORDS: *Argeia pugettensis*, *Lissocrangon stylirostris*, parasitism, sandy beach, sexual system

INTRODUCTION

The smooth bay shrimp, *Lissocrangon stylirostris* Holmes, 1900, ranges from Chirikof Island, Alaska, to San Luis Obispo, California (Jensen, 1995). It is common in the surf-zone of high-energy sandy beaches as well as subtidally on sand or rock down to 80 m (Jensen, 1995). While the adult shrimps are thought to be limited to cool, high salinity waters (Hieb, 1999), studies suggest this and other crangonid species use the estuary as a nursery (Krygier, 1974; Hoeman, 1982). The reproductive population has been suggested to be concentrated in the nearshore coastal habitats (Hieb, 1999) and is mostly composed of females that are often larger in size than males (Hoeman, 1982). However, reproductive *Crangon crangon* (Linnaeus, 1758) have been known to migrate from nearshore to offshore habitats during the autumn to release their larvae, and all individuals migrate back to the coast in the spring to feed (Boddeke, 1976). In *L. stylirostris*, population size has been observed to vary with seasons, tides and time of day (Hoeman, 1982; Marin Jarrin, 2007).

The sexual system exhibited by *L. stylirostris* is unknown. Crangonid shrimp exhibit several sexual systems. Many crangonid species are considered gonochoristic, but there are also many species that exhibit protandry. According to Bauer (2004), protandry can be recognized by relatively little overlap in size-frequency distributions between male and female phases. Juvenile females are usually absent in strictly protandric species. Simple protandry, protandry with primary females, protandry with early maturing and primary females, protandry with primary males, and protandric simultaneous hermaphroditism are types of protandry known to occur among the crangonids (Bauer, 2004). These types vary depending on the several types of females or males, the timing of sex change, or the number of sexes per individual that each species presents.

Epicaridean bopyrid isopods have evolved as branchial parasites of crustaceans and are known to affect aspects of their host's reproduction, growth, metabolism, environmental tolerances, and the partitioning of the host's energy budget (Anderson, 1977; Beck, 1980; Nelson et al., 1986; Jay, 1989; Smith et al., 2008). At least 20 species, including *L. stylirostris*, are hosts to *Argeia pugettensis* Markham, 1977. This isopod ranges circum-boreally in the Pacific, from Korea to San Francisco Bay, California (Markham, 1977). Numerous workers have documented the effects of *A. pugettensis* on the growth and reproduction of crangonid shrimp (Nelson et al., 1986; Jay, 1989). Several studies have reported parasitism by *A. pugettensis* on *L. stylirostris* (Markham, 1977; Hoeman, 1982), but no study has analyzed the effect of the parasite on the shrimp. However, studies on other epicaridean parasites have suggested that potential negative effects include castration of female hosts,

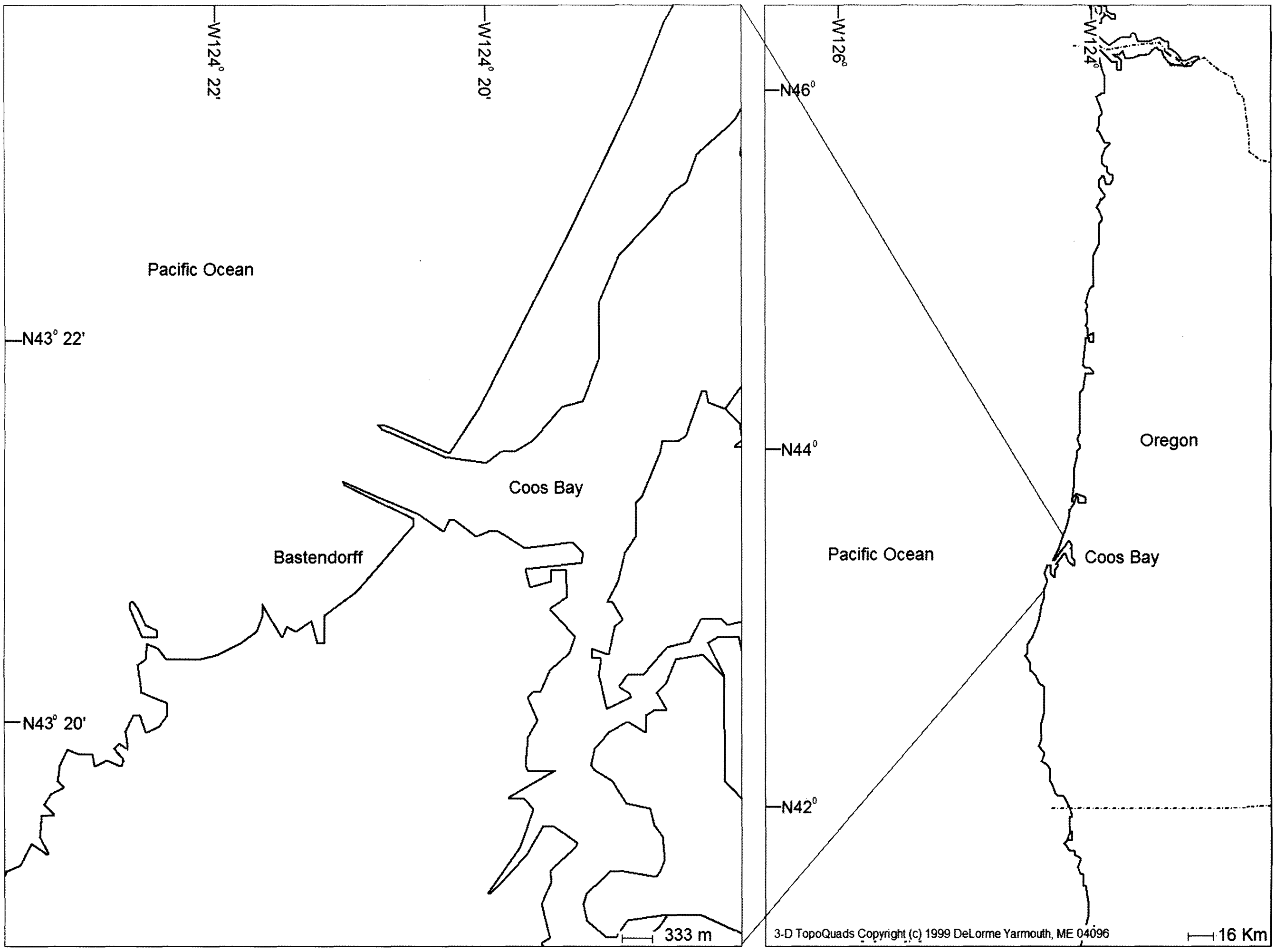

Fig. 1. Study area with location of Bastendorff, a dissipative sandy beach sampled in southern Oregon during the summer of 2006.

variation in host growth, and feminization of male hosts (O'Brien and Van Wyk, 1985).

The present study of *L. stylirostris* attempted to: 1) describe the population present at a dissipative sandy beach in southern Oregon and the environmental variables that influence it, 2) identify the preferred prey, 3) analyze variation of the sexual composition of the population to gain insight into the sexual system employed by the species, 4) observe differences between parasitized and non-parasitized individuals, and 5) investigate possible fish predators.

MATERIALS AND METHODS

Study Area

This study was conducted at Bastendorff Beach (43°35′N, 124°35′W), which is located immediately south of the mouth of Coos Bay in southern Oregon, U.S.A (Fig. 1). Bastendorff is a 3 km long semi-exposed dissipative sandy beach bordered by a rocky shore on the south and a rock jetty at the mouth of the Coos estuary to the north. Dissipative beaches are flat beaches in which the wave energy is dissipated in the surf-zone rather than reflected from the beach face (McLachlan, 1980; Masselink and Short, 1993). Additional details of the study site are given in Marin Jarrin (2007).

Sampling

Samples were taken on 14 dates throughout the summer of 2006. Collections were made during high, mid and low tides, spring and neap tides, and the day and night. Samples were collected using a beach seine and a hyperbenthic sledge (Hamerlynck and Mees, 1991). The beach seine was 1.5 m high and 15 m wide with a 5 mm mesh. Three people carried the net at shoulder height into the surf-zone to an approximate depth of 1 m, where the shallow surf-zone borders with the swash zone (McLachlan and Brown, 2006). The net was then opened parallel to shore and towed towards the shoreline. This procedure was followed one to three times, with fewer tows made when the surf was rough. The distance from the shoreline to where the beach seine was first opened and the maximum depth of the water column were measured. The hyperbenthic sledge sampled the swimming fauna present in the whole water column at ~ 50 cm of depth and was only used on the first six sampling dates. The sledge has a 50 × 70 cm mouth connected to a 4 m long cone-shaped net with 1 mm mesh. The sledge was hand towed parallel to the shoreline at approximately ~ 50 cm water depth for 400 m during high, mid and low tides, spring and neap tides, and during the day and night. Because of how much time it takes to obtain a sample with the sledge, we considered it was impossible to take replicates, a conclusion also reached in previous works (Watkin, 1941). Therefore the tows were made sufficiently long for them to account for possible variances in the fauna because of the different areas that can form in the surf-zone of dissipative sandy beaches due to water circulation and to the patchy distribution that species may present (Mees and Jones, 1997; Lock et al., 1999). All samples were preserved in 10% buffered formalin.

In the laboratory, organisms were identified to species when possible. Individuals of *L. stylirostris* were separated from the rest of the fauna (see Marin Jarrin, 2007), and all individuals caught in the beach seine were measured, sexed, and checked for the bopyrid isopod *A. pugettensis*. The sex of each shrimp was determined by examining the endopod of the first and second pleopods, as described by Butler (1980). The possibility of different types of females was noted but was not quantified, as described by

Boddeke et al. (1991). A bulge in the shrimp's carapace over the right, the left, or both branchial chambers indicated parasitized shrimp.

The length measurements were taken from the tip of the rostrum to the tip of the telson. Individuals were grouped into categories of parasitized male (PM), parasitized female (PF), non-parasitized male (NPM), non-parasitized female (NPF), brooding non-parasitized (B), and brooding parasitized (BP). Density data are presented as individuals per 100 m^2, and these were calculated using the total area sampled, which was calculated by multiplying the length of the tow and the length of the beach seine. We estimated the volume of water sampled by determining the slope, or the hypotenuse of a triangle, by using the depth and the length of the tow, and then multiplying by the length of the seine.

We were not able to use a three-way ANOVA to analyze variances due to tides, lunar cycles, and time of day because we did not sample during all three tides at night. Instead, densities were compared separately among samples taken during the four months (June, July, August, September), three tides (high, mid and low tide), two lunar cycles (spring and neap tide), and two times of day (day and night) using one-way ANOVAs. Pair-wise comparisons were conducted using Tukey's test. We tested for effects of lunar tide and time of day on low tide densities using a partially nested mixed model two-way ANOVA. The ANOVA design was unbalanced; thus the type III sum of squares was computed for determining significance (Underwood, 1981). Pair-wise comparisons were conducted using Tukey's test. All of the assumptions for the analysis of variance were met after the data were $\log_{10}(x+1)$ transformed. Homogeneity of variance was tested with an F max test. The data were plotted as size frequency histograms to observe possible effects of sex and parasitism on size. These size class data were statistically compared using a Kolmogorov-Smirnov test (K-S test) (Sokal and Rohlf, 1995).

To determine where and on what the shrimps were feeding, individuals sampled with the beach seine and hyperbenthic sledge were analyzed. We used both methods because when employed, the bottom of the seine is dragged on the sediment while the bottom of the mouth of the sledge is not. Therefore, the seine would probably sample individuals that were in the sediment and the water column, while as the sledge would probably only sample individuals that were in the water column. From the 7/VI/06, 30/VII/06, 13/VIII/06, 8/IX/06 beach seine samples, 10 parasitized and 10 non-parasitized individuals (80 individuals in total) were selected randomly. Seventy-one randomly selected shrimps caught with the hyperbenthic sledge in six dates, 21 non-parasitized and 60 parasitized, were selected. All individuals were wet weighed, stomach contents analyzed, and observed for parasitism. Additionally, the parasites were all counted and sexed based on Kozloff (1987). The stomach content index (SCI) was calculated as an indicator of stomach fullness in all of the samples using the following equation:

$$\mathrm{SCI} = \frac{\mathrm{SW}}{\mathrm{BW}} \times 100,$$

where SW is the wet weight (g) of the stomach contents and BW is the wet weight (g) of the body of the shrimp (Takahashi et al., 1999). The percentage of empty stomachs was recorded, but these were not used in further analysis. The SCI of parasitized and non-parasitized individuals, and individuals caught during the night and day were compared using two one-way ANOVAs (day vs night and parasitized vs non-parasitized). Because of the different time at which the night samples were taken, the data from the three night time dates were compared between each other using a one-way ANOVA and a post-hoc comparison of means test (Tukey's test).

The number of individuals, frequency of occurrence (%F), numerical percentage (%N) and wet weight of each food item in grams was recorded. The frequency of occurrence (%F) of a diet component was the percentage of the shrimps in a sample, which contain the component in their digestive tracts (Hynes, 1950). Finally, the selectivity in natural feeding behavior was calculated using the Shorigin index (Berg, 1979), which is as follows:

$$\mathrm{Sel.} = \frac{\%\mathrm{N_i} \text{ in the ingested food}}{\%\mathrm{N_i} \text{ in the potentially available food}},$$

where Sel is the feeding selectivity and $\%N_i$ is the numerical percentage of an item. The data for $\%N_i$ in the potentially available food were obtained from the samples taken with the hyperbenthic sledge. The data from these samples are detailed in Marin Jarrin (2007). This index was chosen because it is considered an accurate way to compare ingested food items with the potentially available food at the sampling site.

To observe possible effects of the parasite on the host, 20 parasitized and 20 non-parasitized individuals were taken randomly from four low tide beach seine samples, one sample from each month sampled (7/VI/06, 30/VII/06, 13/VIII/06, 8/IX/06) to include possible seasonal, lunar or time of day effects. Individuals were grouped by size and divided into parasitized and non-parasitized shrimps. All individuals were dried in a hood for 24 hours. The side in which the parasite was attached on parasitized individuals, and the dry weight and length of the individuals were recorded. The weight of the parasite was subtracted from the weight of the shrimp to obtain the shrimp's real weight.

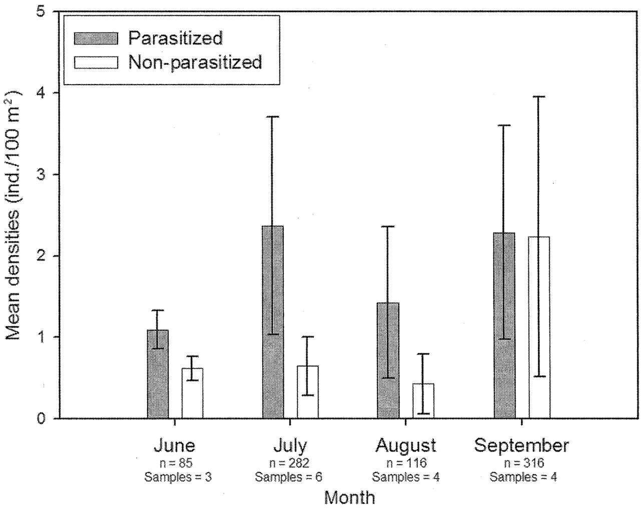

Fig. 2. Mean monthly day time densities (ind/100 $m^2 \pm$ S.E.) of parasitized and non-parasitized *L. stylirostris* observed during the four months sampled in the summer of 2006. There was no significant difference between the monthly densities of parasitized and non-parasitized shrimp ($P > 0.05$).

Finally the fish caught in the beach seine, which according to a stomach content analysis had preyed on *L. stylirostris*, were recorded along with the presence or absence of *A. pugettensis* on these shrimp prey.

RESULTS

The volume of water sampled with one beach seine tow varied from 451 to 461 m^3. The area sampled with one beach seine tow varied from 694 to 708 m^2, of which a mean of 701 m^2 was used to determine density. In the beach seine, a total of 2,134 individuals were caught at Bastendorff during the 14 dates sampled, with a mean of 15 ± 24 individuals per 100 m^2 (±S.D.). The majority of these individuals were females (63.1%) and most of the individuals (61.7%) were parasitized by the bopyrid isopod, *Argeia pugettensis*. Of the 63.1% of females, 39.3% were PM, 4.82% were NPF, 18.7% were B, and 0.2% were BP. Two types of females, primary and secondary, were observed. Of the 36.9 % of males, 22.2% were PM and 14.7% were NPM. On the 6 dates sampled with the hyperbenthic sledge a total of 453 individuals were caught, with an average density of 25 ± 68 individuals per 100 m^2.

Temporal Variation

Higher mean densities of both methods were observed during September (Fig. 2), on low tides, and spring tides. Significantly higher mean densities were observed at night and only for five groups (PM, PF, NPM, B, BP) ($n = 3$, $F \geq 13.26$, $P \leq 0.001$). As observed in Fig. 3, non-statistically significant higher densities were usually observed during night spring tides (two-way ANOVA, $P \geq 0.05$).

Size frequency distributions of *L. stylirostris* varied over time. In June, *L. stylirostris* ranged between 3 and 5.4 cm in length (Fig. 4a). In July, a cohort of small individuals with lengths between 1.5 and 3 cm (Fig. 4b) appeared. The abundance of this cohort increased through August and September (Fig. 4c and d), while the percentage of larger individuals (3 to 5.4 cm) began to decrease in July, and continued to decrease through August and September.

The stomachs of the individuals caught with the beach seine contained primarily detritus and sand with low percentages of gammarid amphipods, and the mysid, *Archaeomysis grebnitzkii* Czerniavsky, 1882. We observed three prey items in the stomachs of the individuals caught with the hyperbenthic sledge. The most frequent food item was *A. grebnitzkii*. The frequency of occurrence (90 ± 22) and the numerical percentage (87 ± 30) of *A. grebnitzkii* were significantly higher than any other food item (n = 7, $F \geq 21.33$, $P \leq 0.0001$). The other prey items identified were the amphipods *Proboscinotus loquax* Barnard, 1967 and *Lycaeopsis themistoides* Claus, 1879. Finally, the feeding selectivity of the shrimp towards the mysid *A. grebnitzkii* was low in the five dates analyzed. A one-way ANOVA (n = 3, $F = 21.27$, $P = 0.02$) showed that significantly lower feeding selectivity values were observed in the shrimps caught at night (1.1 ± 0.1) than in the day (1.9 ± 0.3).

Sex and/or Parasitic Variation

Female shrimps varied in size from 2 to 7 cm with the majority between 4-4.9 cm (80%) (Fig. 5a). Males varied from 1.5-4.9 cm with the majority being between 2.5-2.9 (35%) and 4-4.5 cm (20%). There was a significant difference in the size frequency distributions of female and male shrimps (K-S test, n = 797, D = 0.38, $P < 0.01$), with little overlap between male and female size distributions. Parasitized shrimps varied in size from 1.5-6.2 cm, with the majority between 4-4.9 cm (71%) (Fig. 5b). Non-parasitized shrimps varied in size from 1.5- 6.9 cm, with the majority between 2.5-3.4 cm (38%) and between 4.5-5.4 cm (43%). The size frequency distribution of these two groups differed significantly (n = 826, D = 0.22, $P < 0.01$). The majority of B shrimps ranged from 4.5-5.4 cm (81%), while BP females mostly ranged from 3.5 and 4.9 cm (80%). The size frequency distributions of these two groups of brooding females were not statistically compared due to the small sample size of the brooding parasitized females (n = 5). The PF ranged from 4 to 4.9 cm (88%), where as the NPF ranged between 2.5-4.9 cm (83%) (Fig. 5c). The size frequency distribution of these two female groups differed significantly (n = 104, D = 0.35, $P < 0.01$). The majority of PM ranged from 2-4.4 cm (69%) whereas NPM were smaller; 81% were between 2.5-3.4 cm (Fig. 5d). The size frequency

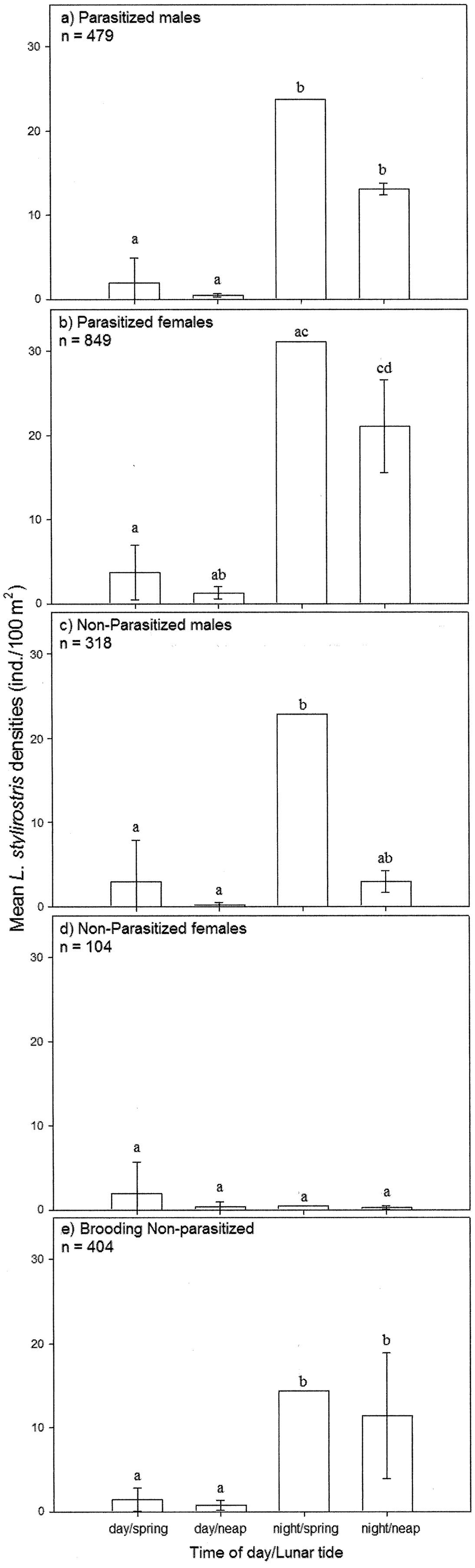

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Fig. 3. Mean densities (ind./100 m^2 ± S.D.) of parasitized males, non-parasitized males, parasitized females, non-parasitized females and non-parasitized brooding females *L. stylirostris* observed during day and night and spring and neap tides. Samples were taken at low tide in the surf-zone of a dissipative sandy beach in southern Oregon during summer 2006. n = number of shrimps in lunar tide/time of day combination. Different letters represent statistically significant differences ($P \leq 0.05$).

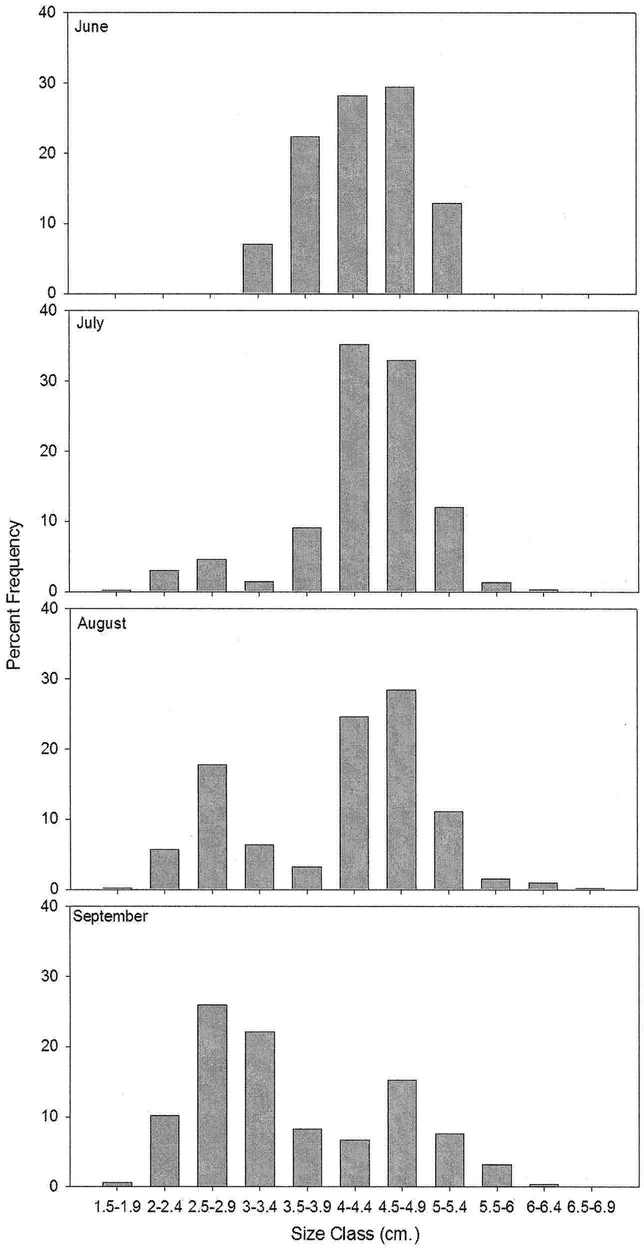

Fig. 4. Size percent frequency distribution of *L. stylirostris* collected in the summer 2006 from the surf-zone of a dissipative sandy beach in southern Oregon.

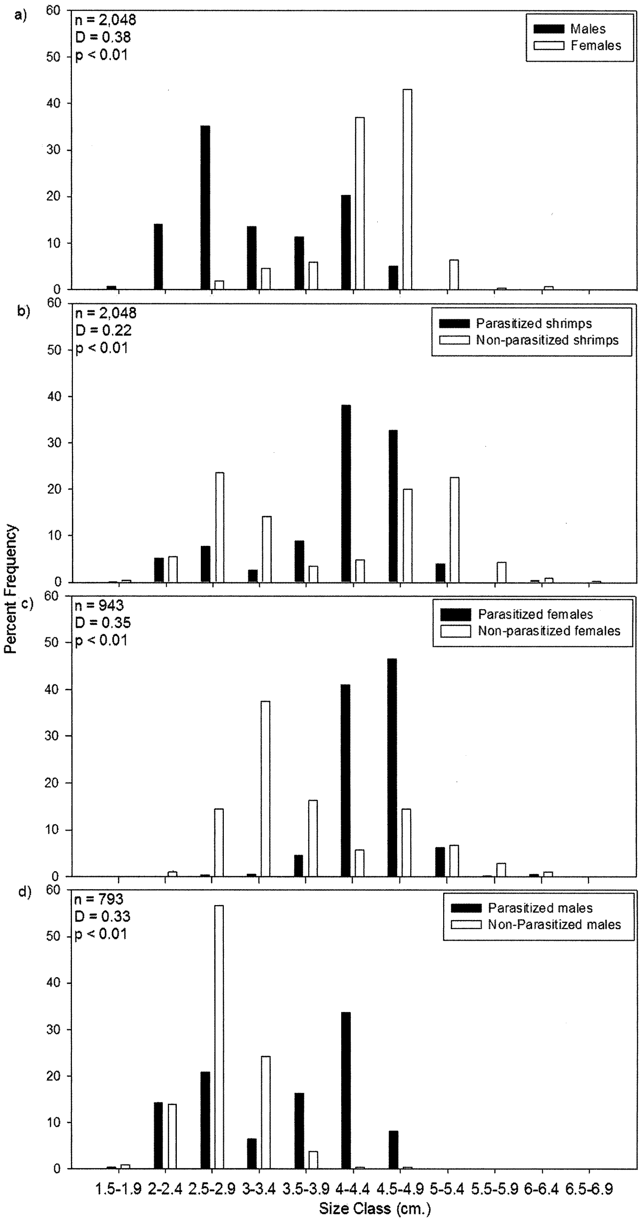

Fig. 5. Size frequency distribution of *L. stylirostris* for (a) males and females, (b) parasitized and non-parasitized shrimps, (c) parasitized females and non-parasitized females (NPF), and (d) parasitized males and non-parasitized males. Samples were collected in the surf-zone of a dissipative sandy beach in southern Oregon. All comparisons differed significantly (K-S test, $P \leq 0.01$).

distributions of PM and NPM shrimps were significantly different (n = 318, D = 0.33, $P < 0.01$).

Adult female isopods were larger than males. A male isopod was always present with a female isopod, whether the female was gravid or not. Males attached to the posterior of gravid females and in the brood pouch of non-gravid females. Parasites occupied the right side of the host (58%) slightly more than the left side (42%). Few shrimps were parasitized by female isopods on each side (<1%). Non-gravid female isopods were usually present in shrimps smaller than 3.2 cm. Juvenile isopods were present only during the last two dates (13/VIII/06 and 8/IX/06) when gravid and non-gravid female isopods were present.

Differences Between Parasitized and Non-Parasitized Individuals

Non-parasitized shrimps had statistically different dry weight than parasitized shrimps, 0.66 ± 0.44 g and 0.38 ± 0.16 g, respectively (n = 160, $F = 28.8$, $P = 0.001$). Separating non-parasitized and parasitized shrimps by size class, we observed several differences. In small shrimps (2.1 to 3 cm) the weight of the non-parasitized and parasitized individuals did not differ significantly. This changed for shrimps between 3.1 and 4 cm, where the parasitized individuals weighed significantly more (58%) than the

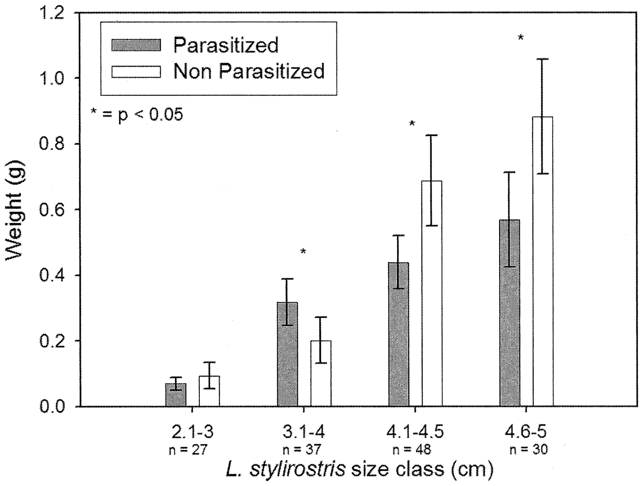

Fig. 6. Dry weight comparison by size class between parasitized and non-parasitized *L. stylirostris* (±SD). Samples taken throughout the summer of 2006 at a dissipative sandy beach of southern Oregon. * Significant difference ($P \leq 0.005$).

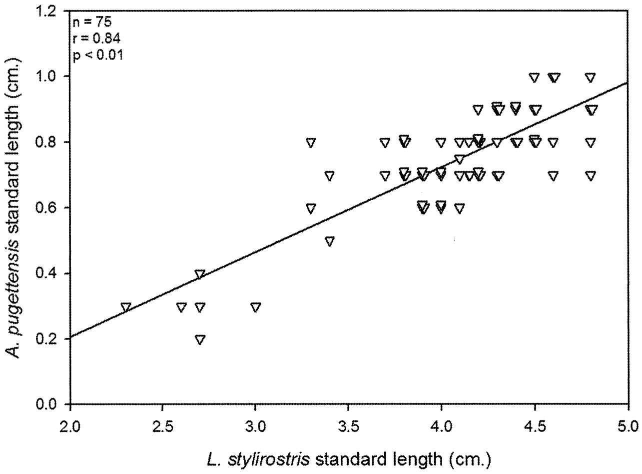

Fig. 7. Linear correlation between lengths of *L. stylirostris* and its parasite, *A. pugettensis*. Samples taken in summer 2006 at a dissipative sandy beach of southern Oregon.

non-parasitized individuals (n = 37, $F = 17.02$, $P = 0.002$). Interestingly, this pattern changes again in individuals between 4.1-5 cm, with non-parasitized individuals weighing significantly more (36%) than the parasitized individuals (n = 68, $F = 8.18$, $P = 0.005$) (Fig. 6). Based on length measurements of host and parasite, we observed a positive correlation between the length of the isopod parasite and the length of the host shrimp (n = 75, $r = 0.84$, $P < 0.01$) (Fig. 7), regardless of the host gender.

In the beach seine samples, the stomach analysis revealed 18 of the 40 non-parasitized individuals (45%) and 12 of the 40 parasitized individuals (30%) had empty stomachs. No significant differences in SCI values were observed between non-parasitized (0.74 ± 1.32) and parasitized individuals (0.69 ± 0.76). When comparing values for the four combinations of lunar tides and time of day at low tide, highest SCI values where observed during spring night time (0.93 ± 1.41), followed by spring day time (0.88 ± 1.25), neap night time (0.74 ± 0.83) and neap day time (0.31 ± 0.5). However, there were no significant differences due to these factors.

In the sledge samples, sixteen of 71 individuals had empty stomachs (23%), including the only individual caught on 7/VI/06. Parasitized individuals had a higher percentage of empty stomachs (12 of 42, 29%) compared to non-parasitized individuals (4 of 29, 14%). Individuals caught in the day also had a higher percentage of empty stomachs (8 of 23, 35%) than individuals caught during the night (8 of 48, 17%). No significant difference in SCI values was observed when comparing parasitized (1.4 ± 1.6) and non-parasitized individuals (2 ± 1.5), and individuals caught during the day (1.5 ± 1.9) and night (1.8 ± 1.4). However, significantly higher SCI values were observed in individuals caught at night on 2/VIII/06 (2.8 ± 1.3) than during the day (n = 27, $F = 14.25$, $P = 0.0007$). The SCI of the individuals caught during the three night samples differed significantly from each other (n = 48, $F = 7.76$, $P = 0.001$). A post-hoc mean comparison showed that the SCI of 2/VIII/06 was the only significantly different sample ($P \leq 0.01$). When comparing the individuals caught during 2/VIII/06, significantly higher values were observed in non-parasitized individuals than in parasitized individuals, with values of 3.6 ± 1.3 and 2.1 ± 0.7, respectively (n = 15, $F = 8.21$, $P = 0.01$).

Only two species of fish in the seine samples had preyed on *L. stylirostris*, English sole/*Pleuronectes vetulus* (2 individuals) and Pacific staghorn sculpin/*Leptocottus armatus* Girard, 1854 (4 individuals). In total, the six fish preyed on nine individuals of *L. stylirostris*; of which five were parasitized by *A. pugettensis* and three were not. Whether or not the ninth *L. stylirostris* was parasitized was impossible to determine due to an advanced deterioration of the shrimps' body. The shrimp composed 63 ± 53% and 75 ± 32% of prey items for the two English sole and four Pacific staghorn sculpins , respectively.

DISCUSSION

The presence of *L. stylirostris* in high abundances at Bastendorff Beach during the summer of 2006 was not surprising considering this species has been reported as an inhabitant of high-energy semi-exposed sandy beaches (Kuris and Carlton, 1977; Rudy Jr. and Rudy, 1983). The density of the population of *L. stylirostris* present at Bastendorff beach was maintained stable throughout the summer. The similar densities observed during the four summer months seem to be due to a recruitment event that was observed throughout the months of July, August, and September, and to the disappearance of the larger shrimps during the same months, probably due to mortality. However, the larger shrimps could have also migrated to another habitat as has been suggested with this and other crangonid species (Boddeke, 1976; Hieb, 1999). Hieb (1999) and Jay (1989) reported that in California abundances of *L. stylirostris* and *Crangon franciscorum*, Stimpson, 1856, respectively, peaked between July to September, with highest densities during August and lowest between April and June. We found highest densities during September and lowest during June. Hieb (1999) also observed recruitment events during the summer, however, in California these events began in June instead of July. These observations suggest that the life cycle of the shrimp in Oregon follows a similar pattern to that observed in California, where the life span of crangonid shrimp is believed to be one to two years, depending on the sex (Hieb 1999).

When comparing population densities during the day and night, significantly higher values were found at night. This could be due to a vertical migration of the shrimps from the sediment into the shallow water column during the night. Higher densities at night have been reported in previous studies (Hoeman, 1982) (0.2-1.0 ind/100 m^2 during the day and 6-11 ind/100 m^2 during the night). The vertical migration of the shrimp may occur in order to feed, primarily on *A. grebnitzkii*, the preferred food item, which presents higher densities during low tide at night (Marin Jarrin, 2007). This feeding behavior is also suggested by the higher SCI values and lower percentage of empty stomachs observed at night in both beach seine and hyperbenthic sledge samples. The significantly higher SCI values found in the 2/VIII/06 sample were probably due to the time at which this sample was taken (0020). This would suggest the shrimps are in fact feeding at night, and that by midnight the shrimps have eaten significantly more than by 2200, which is when the other two night samples were taken. Feeding during the night would also reduce the risk of predation by visual predators such as sea birds and fish. Finally, the higher density values observed at low, night, spring tides suggests the three factors are influencing the population but that the time of day is the strongest influence, a finding supported by previous studies (Hindell et al., 2000; Beyst et al., 2002).

Sex Variation

The higher percentages of female *L.stylirostris* that were significantly larger size than males and the relatively little overlap in size frequency between males and females have been reported previously (Hoeman, 1982; Hieb, 1999). Female shrimp may grow faster and become larger than male shrimp (Meixner, 1969; Oh et al., 1999). However, we also observed a small percentage of males >4.5 cm (5%) and females <3.5 cm (4%). There are three possible hypotheses for these observations: 1) The males are not present in the same environment with females during the whole or part of the year due to different patterns of migration or zonation (Hoeman 1982), 2) Individuals of this species are gonochoristic, but females are larger than males, and 3) This species exhibits a type of protandry. While the first hypothesis would explain the difference in sex percentages and the two first hypotheses would explain the higher percentage of females, they do not explain the presence of large males and small females, and the relatively little overlap in size frequency distribution between males and females observed in this study. The higher percentages of females, the larger size of females, the presence of large males and small females, and the little overlap in size distribution could be explained if the shrimp exhibited a type of protandry, as mentioned in the third hypothesis. However, the method we employed in this study is not appropriate to determine which type.

Parasite Prevalence

Previous studies have described parasitazation of *Lissocrangon stylirostris* by the bopyrid isopod *A. pugettensis* (Markham, 1977; Hoeman, 1982), but the percentage of individuals parasitized in this study (63%) was higher than reported in previous works. Hoeman (1982) reported that 8% of the 1,611 *L. stylirostris* caught over a year carried the parasite. The prevalence increased to 44% of 66 individuals during the summer season. Nelson et al. (1986) and Jay (1989) also reported lower percentages of infestation of *A. pugettensis* in *Crangon franciscorum*, a closely related species. These studies were conducted in Grays Harbor and San Francisco Bay in Washington and California, respectively, which may account for their observed lower infestation rate. The fact that the host inhabited an estuary could have made it more difficult for the parasite to infest the host, for the parasite to survive the host's migration between estuary and open-ocean due to changes in the physical characteristics of the water, or for the appropriate intermediate host, which is usually a copepod, to be available. Migration of crangonid shrimp between an estuary and the open coast has been suggested to occur during the reproductive and recruitment periods (Hoeman, 1982; Jay, 1989). The difficulty of infesting hosts due to change in water characteristics has been suggested in previous studies (Walker and Lester, 2002; Boone et al., 2004). Another explanation for the higher percentages of infestation we found could be the higher densities of the host observed in our study (0.2-16 ind/100 m^2 during the day and 18-86 ind/100 m^2 during the night) compared to those reported by Hoeman (1982) (0.2-1.0 ind/100 m^2 during the day and 6-11 ind/100 m^2 during the night). A host's density can be a limiting factor in the spread of parasites (Nelson et al., 1986; Høeg et al., 2005). In the present study, difficulty for isopods to infest shrimps due to difference in habitats or to host densities could explain the higher percentage of infestation, since our study showed higher shrimp densities but was conducted on the open coast while previous studies showed lower shrimp densities but were conducted in estuaries. Finally, based on the presence of juvenile isopods only in the August and September samples and the cohort of small shrimps observed from July to September, we suggest that the isopod and the shrimp's recruitment to the sandy beach are coordinated or that the isopod is infecting the shrimp before they recruit to the surf-zone. However no conclusions could be made since this study only looked at four months of the year in the surf-zone of a sandy beach. To reach further conclusions a study of the shrimp's and isopod's life cycles inside estuaries, offshore and on sandy beaches should be carried out simultaneously.

Differences Between Parasitized and Non-Parasitized Individuals

Three differences were observed between parasitized and non-parasitized shrimps: 1) non-parasitized individuals had higher weights per length ratio but smaller sizes than parasitized individuals, 2) small percentage of brooding parasitized females, and 3) higher percentages of empty stomachs and lower SCI values in parasitized individuals. Parasitized individuals presented a larger size but a lower weight per length ratio than their non-parasitized counterparts. This could have been due to the parasite, or to the appearance of the cohort of small mostly non-parasitized shrimps observed from July to September and the disappearance of larger individuals some of which were probably parasitized. When divided into size classes different results were observed. When the individuals were between 2.1 and 3 cm in length, the weight of parasitized and non-parasitized shrimps did not differ significantly. In individuals between 3.1-4 cm, parasitized shrimps had higher weights than non-parasitized individuals. This greater weight in parasitized shrimps may have occurred because the parasites forced the shrimps to increase their weight by increasing the shrimps' feeding (Lester, 2005). The higher weights in non-parasitized shrimps between 4.1-5 cm in length may be due to the fact that 4.1-5 cm is the host size at which female parasites are either reproductive or brooding, and potentially draining more energy from the host (O'Brien and Van Wyk, 1985; Nelson et al., 1986).

If we compare length and sex of the host shrimp, excluding brooding female hosts, parasitized males and females were significantly larger and more abundant than their non-parasitized counterparts. Studies have reported that bopyrids might cause a slight decrease in host growth rate (Somers and Kirkwood, 1991; Lester, 2005), a slight increase in overall male shrimp length (Somers and Kirkwood, 1991; Lester, 2005), or an increase in overall female shrimp length (Nelson et al., 1986). In our study, the parasite could have forced the shrimps to increase its size, which would have allowed the parasite to increase its size since parasite and host length was positively correlated. This positive correlation has also been reported in previous studies (Jay, 1989). However, the largest individuals (6.5-6.9 cm) were all NPF. This suggests that even though parasitized shrimps grow faster, they might not attain the maximum possible size, a suggestion also made by previous authors (O'Brien and Van Wyk, 1985). This last suggestion should be taken cautiously due to the low number of very large females ($n = 2$).

Only a small percentage of female shrimps were both brooding and parasitized, 0.2% of female shrimps and 1.2% of brooding females. This could have been because the bopyrid parasite commonly sterilizes the host female or reduces its metabolic activity such that it cannot brood. The inability to produce broods in females has been previously observed by several studies (Nelson et al., 1986; O'Brien and Van Wyk, 1985; Jay, 1989; Lester, 2005). The inability of females to brood could reduce the size of the population present at Bastendorff and it could eventually become ecologically extinct.

The higher percentages of empty stomachs and lower SCI values (significantly lower only on 2/VIII/06) in parasitized individuals were observed in both the beach seine and the hyperbenthic sledge samples. This effect may be due to the parasite reducing the shrimps's feeding capabilities. Several authors have previously suggested that bopyrid isopods might reduce their host's ability to capture food by reducing their metabolic activity (Bergey et al., 2002; Høeg et al., 2005; Smith et al., in press). This reduction in host metabolic activity and/or feeding capabilities could explain the higher percentage of empty stomachs and lower SCI values, especially since the host's preferred prey are mysids which are considered good swimmers with a strong predatory attack response (Ritz et al., 1997).

Throughout the summer, *L. stylirostris* was present in the surf-zone of a dissipative sandy beach in southern Oregon. The population remained stable throughout the summer of 2006, possibly due to a recruitment event and the disappearance of large individuals. The population presented a higher percentage of females (63%) that were usually larger than males. Their densities varied significantly with the time of day (day and night), and less intensely with tidal level and lunar tide. Individuals fed mostly at night and mostly in the water column on the mysid, *Archaeomysis grebnitzkii*. The population had a high prevalence of the bopyrid isopod, *Argeia pugettensis* (62%). Parasitized shrimps were usually larger than non-parasitized shrimps, but the largest shrimps were NPF. We observed the following differences between non-parasitized and parasitized individuals: 1) lower weight per length ratio in parasitized shrimps, 2) very few brooding parasitized female shrimps, and 3) higher percentage of empty stomachs and a lower amount of food in stomachs of parasitized shrimps. These differences led us to hypothesize that this parasite affects the shrimps by increasing the host's size and varying the host's weight at different size classes, sterilizing female hosts, and reducing their capability to feed.

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