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Prevalence, Size and Fecundity of the Parasitic Isopod Argeia pugettensis on its Host Shrimp Crangon francisorum

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ABSTRACT.—Monthly samples of shrimp, *Crangon* spp., were collected from Hookton Channel in South Humboldt Bay, California, from April 1983 through April 1984. A total of 5790 *Crangon franciscorum* and 9741 *C. nigricauda* and *C. nigromaculata* (in combination) were collected. *Crangon nigromaculata* was collected only occasionally. Of the total shrimp collected, 169 *C. franciscorum* and one *C. nigromaculata* were infested with the bopyrid isopod *Argeia pugettensis*. Infestation of *A. pugettensis* on *C. nigricauda* in other localities has been recorded; however, no *C. nigricauda* were found infested in this study. Parasite prevalence on *C. franciscorum* ranged from 0% to 34%. Prevalence fluctuations apparently resulted from shrimp migration. Frequency of infestation did not differ significantly between the right and the left branchial chambers of the host shrimp and no shrimp had multiple infestations. Female shrimp were infested more frequently (85%) than males (15%) even though females were often less abundant. Infested female shrimp were significantly smaller than noninfested females. Ovigerous isopods occurred whenever isopods were collected (April through January). Female isopods apparently become reproductively mature between 3.0 and 4.0 mm long. Isopod brood sizes ranged from 1600 to 38,300 eggs and increased with female length. Male isopod length increased with female isopod length, which increased with host shrimp length. Host shrimp were probably infested early in their life.

INTRODUCTION

Most adult isopods of the epicaridean family Bopyridae occur either on the abdomen or within the branchial chamber of decapod crustaceans. The female branchial bopyrid attaches to the underside of its host's branchiostegite, inducing a bulge in the host's carapace (Beck, 1980a; Danforth, 1963). The mature female bopyrid incubates a large number of small eggs in her marsupium. After hatching, the first stage larva, the epicaridium, swims away from the marsupium and attaches to the intermediate host, a calanoid copepod. On the copepod, the bopyrid larva develops from the epicaridium through two subsequent larval stages, the microniscus followed by the cryptoniscus. The cryptoniscus detaches from the copepod, is free-swimming, and subsequently attaches to the definitive host (Beck, 1980a; Dale and Anderson, 1982). Upon attachment to the host, the cryptoniscus develops into a female. A second cryptoniscus attaches to the bopyrid female and develops into a male. The adult male is much smaller than the female and is usually found attached to her abdomen (Reinhard, 1949; Beck, 1980b).

The branchial bopyrid *Argeia pugettensis* has been found on at least 21 species of caridean shrimp and ranges from Korea, circumboreally in the Pacific, to San Diego Bay, California (Markham, 1977). Markham (1977) has assigned *A. pauperata,* found only from San Francisco Bay, California, to *A. pugettensis,* a synonymy assumed correct and accepted here.

Apart from limited life history information provided by Gifford (1934) on *Argeia pugettensis* infesting *Crangon franciscorum* in San Francisco Bay, and laboratory observations by Danforth (1963) on the life cycle of *A. pugettensis* on *C. nigromaculata,* information on

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the biology of *A. pugettensis* is lacking. The objectives of the present study are to investigate the prevalence of *A. pugettensis* on three species of potential *Crangon* hosts in Hookton Channel within South Humboldt Bay, California, estimate the bopyrid's fecundity, and determine size relationships between the female bopyrid and its brood, attached male and host shrimp.

MATERIALS AND METHODS

From April 1983 through April 1984, monthly samples of shrimp, *Crangon* spp., were collected from Hookton Channel in South Humboldt Bay, California. Shrimp were collected with a small otter trawl with a cod-end mesh size of 1.25 cm and a cod-end liner mesh size of 0.65 cm. Samples were collected with varying fishing effort and contained from 451 to 2603 shrimp. Specimens from each sample were fixed for about 3 days in 10% formalin solution buffered with sodium borate, and subsequently transferred to 70% ethyl alcohol for preservation.

Infested shrimp were recognized by a bulge in the shrimp's carapace over either the right or the left branchial chamber and were sorted from each sample. The branchial chamber occupied by the parasite was noted (*i.e.,* right or left) and each infested shrimp was placed in a separate vial containing 70% ethyl alcohol.

About 10% of the shrimp that were recognized as being infested had lost their parasite prior to the time that the samples were sorted; therefore, some isopod length data were not obtained.

Three species of *Crangon* were collected, *C. franciscorum, C. nigricauda* and *C. nigromaculata. Crangon nigromaculata* was collected only occasionally. Of the former two species, only *C. franciscorum* was infested with *Argeia pugettensis.* Therefore, *C. nigricauda* and *C. nigromaculata* together were sorted from each sample and counted only.

After the infested shrimp were sorted from each sample, a subsample of 100 *Crangon franciscorum* was drawn from the remainder of each sample. If the remainder of each sample contained fewer than 100 *C. franciscorum,* than all remaining *C. franciscorum* in the sample constituted the subsample. These subsampled shrimp and all of the infested shrimp were sorted according to sex and measured. The sex of noninfested shrimp was determined by examining the endopod of the first and second pleopods as described by Butler (1980). Bopyrids may feminize their male host shrimp, and thus cause a change in the male's external secondary sex characteristics (Beck, 1980c). Since it is not known what effects *Argeia pugettensis* has on the secondary sex characteristics of male *C. franciscorum,* the sex of infested shrimp was determined by examining for the presence or absence of the female gonopore on the medial side of the coxa of the third pleopod. Shrimp were measured to the nearest millimeter, from the tip of the rostrum to the tip of the telson.

The positions of the male and female isopod within the branchial chamber of their host were noted, and the isopods were removed. The eggs from gravid females were emptied into a dish, separated with forceps, and collected on a 24-μm mesh sieve. The eggs were transferred to a 100-ml graduated cylinder (volume calibrated with a 100-ml volumetric flask) and the cylinder was filled to volume with sea water. The cylinder was agitated to homogeneously suspend the eggs in the sea water, and six 2-ml samples were immediately drawn from the suspension, except in a few cases when very large broods were encountered and six 1-ml samples were drawn. Each sample was placed in a petri dish and the eggs were counted using a dissecting microscope set at 60×. A mean and 95% confidence interval was calculated from the counts obtained from the six samples and the total number of eggs in the brood was estimated by direct proportion from the sample mean. The 95% confidence intervals of the estimates ranged from ±2% to ±41% of the mean. This variability was independent

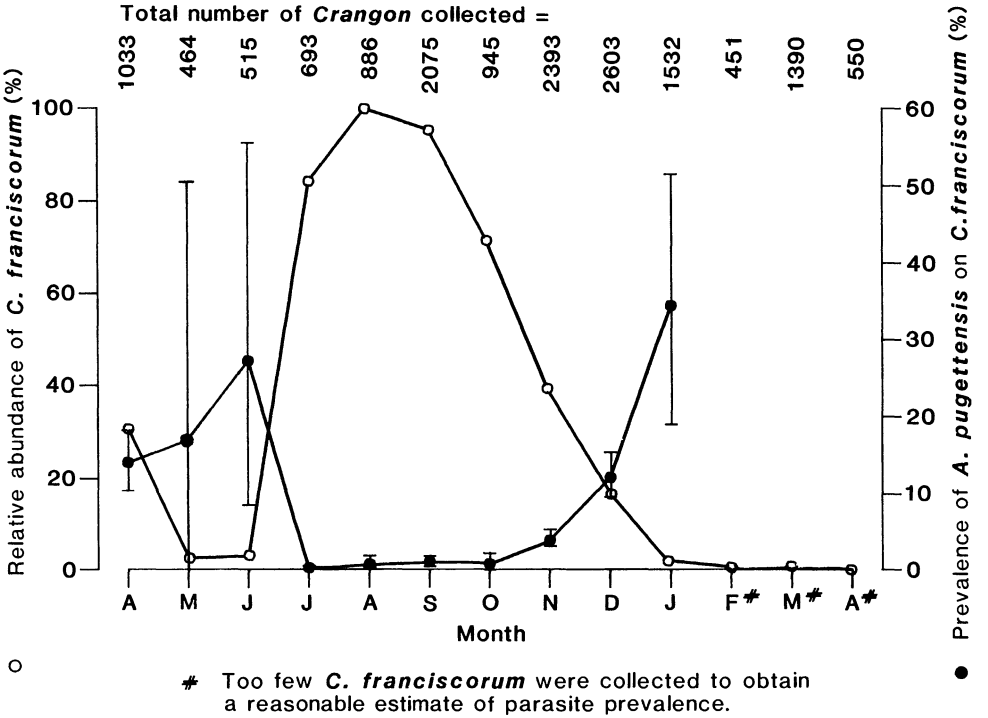

FIG. 1.—Relative abundance of *Crangon franciscorum*, and estimates with 95% confidence limits of the prevalence of *Argeia pugettensis* on *C. franciscorum* in Hookton Channel from April 1983 through April 1984

of the mean and was largely due to varying difficulty in separating the eggs in a given brood in order to obtain a homogeneous suspension from which the random samples were drawn.

Using a dissecting microscope equipped with an ocular micrometer, I measured the length of each male and female isopod to the nearest 0.1 mm, from the middle of the anterior margin of the cephalon to the posterior margin of the pleotelson.

RESULTS

During the study 5790 *Crangon franciscorum* and 9741 *C. nigricauda* and *C. nigromaculata* (in combination) were collected. *Crangon nigromaculata* was collected only occasionally. Of the total shrimp collected, 169 *C. franciscorum* and one *C. nigromaculata* were infested with *Argeia pugettensis*.

Female *Crangon franciscorum* were infested more frequently (85%) than males (15%) (n = 169). Frequency of infestation did not differ significantly between the right and left branchial chambers ($\chi^2 = 1.33$, P = 0.25, n = 169). No shrimp with more than one female isopod were found.

Relative abundance of *Crangon franciscorum* and estimates of parasite prevalence for each month were calculated (Fig. 1). Ninety-five percent confidence limits for the estimates of parasite prevalence were calculated using the equation given in Rohlf and Sokal (1981). The 95% confidence limits for the estimates for May and June 1983 and January 1984 were quite broad, because few *C. franciscorum* were collected during these months. Too few

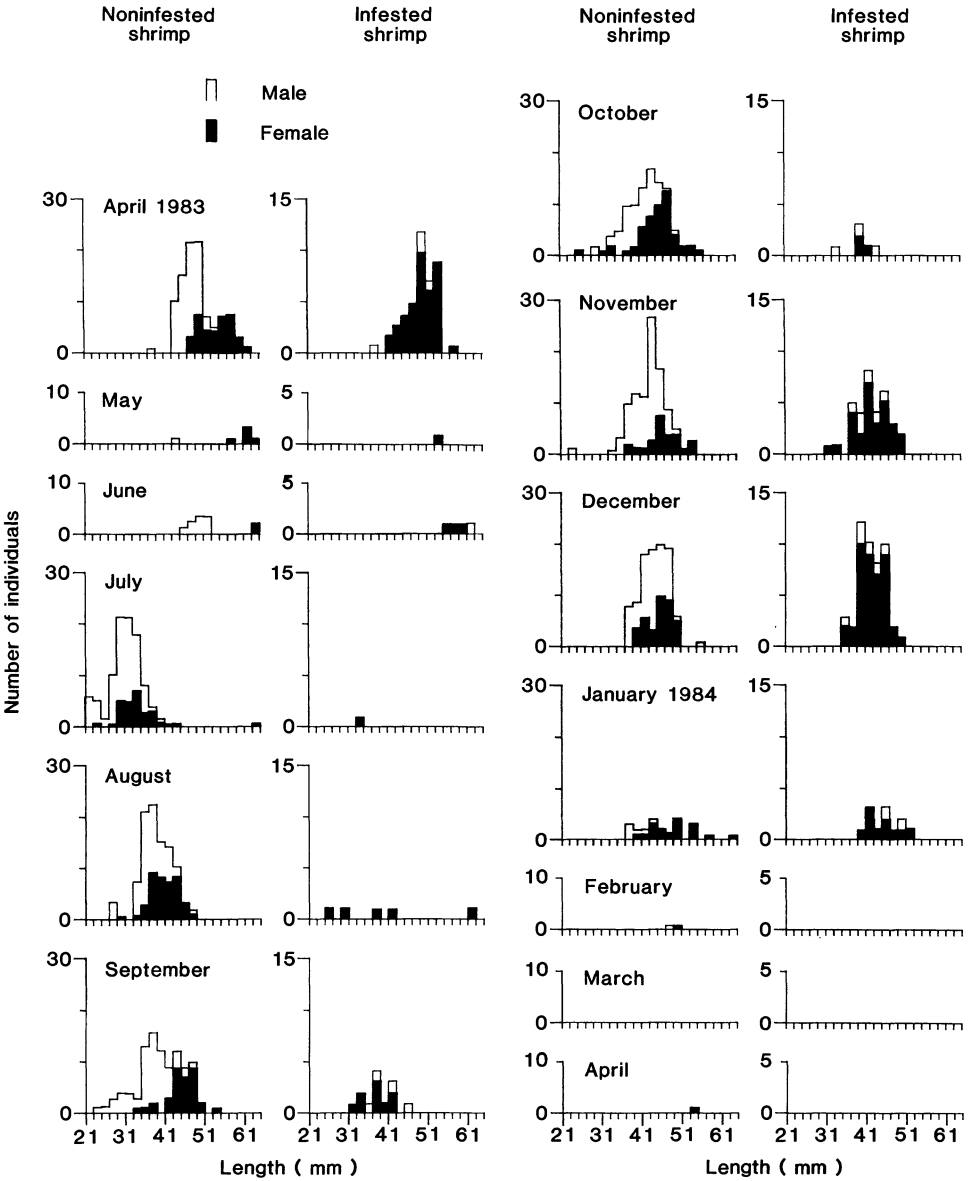

FIG. 2.—Length frequency histograms of noninfested and infested *Crangon franciscorum* collected from Hookton Channel from April 1983 through April 1984

C. franciscorum were collected from February through April 1984 to obtain reasonable estimates of parasite prevalence during these months.

Monthly length frequency histograms of the subsampled noninfested and of all infested *Crangon franciscorum* were constructed (Fig. 2). Noninfested shrimp ranged from 21–64 mm long. A cohort of large noninfested shrimp was clearly evident in April 1983, but was

TABLE 1.—A. Estimates of the percentage of noninfested and infested female *C. franciscorum* in Hookton Channel during a given month. B. Estimates of the mean length with 95% confidence intervals of noninfested and infested female *C. franciscorum* in Hookton Channel during a given month

A.	Noninfested		Infested	
Month	% ♀	n	% ♀	n
April	36	100	91	44
July	29	100	—	—
Aug.	41	100	—	—
Sept.	35	100	69	13
Oct.	52	100	—	—
Nov.	27	100	82	34
Dec.	39	100	88	48
Jan.	74	23	83	12

B.	Noninfested		Infested	
Month	♀ $\bar{x}$ length (mm)	n	♀ $\bar{x}$ length (mm)	n
April	54 (±1.1)	36	49 (±1.3)	40
July	34 (±2.6)	29	—	—
Aug.	40 (±1.1)	41	—	—
Sept.	44 (±1.3)	35	37 (±2.9)	9
Oct.	45 (±1.5)	52	—	—
Nov.	46 (±1.7)	27	42 (±1.7)	28
Dec.	45 (±1.1)	39	42 (±1.0)	42
Jan.	49 (±3.1)	17	45 (±2.7)	10

Note: For a given month, noninfested and infested female mean lengths differ significantly at $P < 0.005$, except January when mean lengths differ at $P < 0.1$

not well-represented during the following 2 months. A cohort of small noninfested shrimp appeared in July, and shrimp length increased through September. After September, increase in shrimp length was not apparent, because shrimp larger than ca. 50 mm were not commonly collected during these months. Infested shrimp ranged from 26–61 mm long. Although infested shrimp were not well-represented during months with low infestation levels (July through October 1983), it is clear that their appearances and disappearances from Hookton Channel and their general growth pattern were similar to those of noninfested shrimp. No infested shrimp were collected from February through April 1984, corresponding to the low number of *C. franciscorum* collected during these months.

Estimates of the percentage and mean length of noninfested and infested female *Crangon franciscorum* in Hookton Channel during a given month were calculated, except for some months when none or very few *C. franciscorum* were collected (Table 1). Female shrimp were infested more frequently than males, even though females were often less abundant (Table 1A). Additionally, infested female shrimp were significantly smaller than noninfested females (Table 1B).

The adult female isopod was attached in the typical branchial bopyrid position, with her head directed posterodorsal to the host and her dorsum against the host's gills. The adult male was usually attached diagonally to the ventral surface of the female's pleon, immediately posterior to the fifth pair of oostegites, with his head directed posteroventral to the host shrimp.

The length of female isopods ranged from 2.7–9.3 mm, had a mean of 5.6 mm and

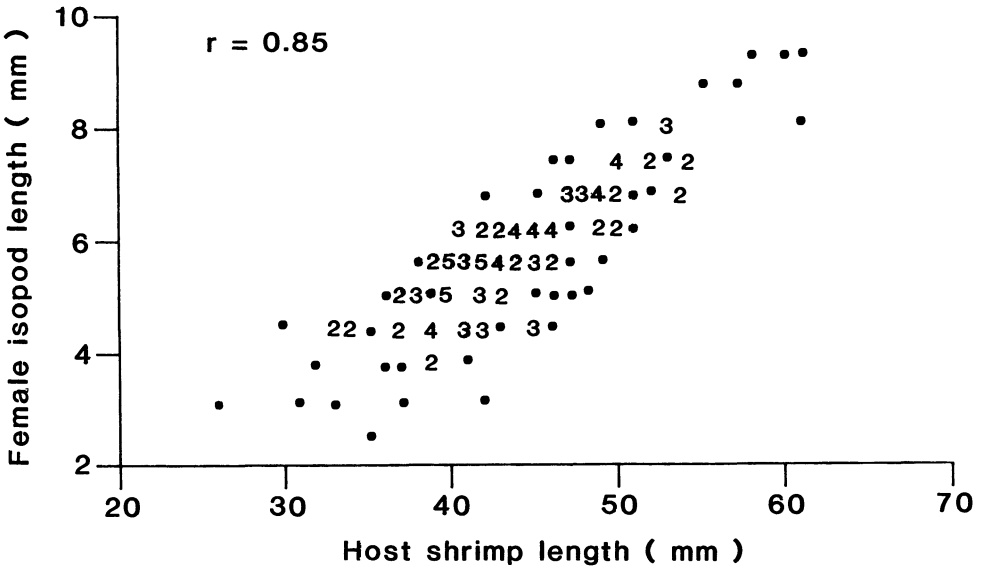

FIG. 3.—Correlation between female isopod length and host shrimp length. A given numeral represents multiple observations at that coordinate

increased with host shrimp length (r = 0.85, n = 150, Fig. 3). Ovigerous isopods occurred whenever isopods were collected (April 1983 through January 1984) and ranged from 3.9–9.1 mm long and had a mean length of 6.0 mm. Failure to collect isopods after January 1984 was probably associated with the low number of *Crangon franciscorum* collected during these months. Four female isopods from 2.7–3.1 mm long were apparently immature, since they possessed reduced oostegites and apparently immature ovaries. Mature ovaries were distinguished by their opaque yellow to orange color as viewed through the isopod's exoskeleton.

The brood size of 80 isopods was estimated. Brood sizes ranged from 1600 eggs from a female 4.2 mm long, to 38,300 eggs from a female 9.0 mm long and increased with female isopod length (r = 0.81, n = 80, Fig. 4).

The length of male isopods ranged from 1.5–3.2 mm, had a mean of 2.1 mm and increased with female isopod length (r = 0.82, n = 142, Fig. 5).

Regression equations were calculated for female isopod length (Lf) on host shrimp length (Ls), brood size (B) on female isopod length, and for male isopod length (Lm) on female isopod length. These equations are, respectively: $Lf = -1.49 + 0.17Ls$ ($r^2 = 0.91$, n = 22), $\sqrt{B} = -62.9 + 26.4Lf$ ($r^2 = 0.78$, n = 22), $Lm = 0.92 + 0.23Lf$ ($r^2 = 0.86$, n = 33). The variance in brood sizes of females in a given size class increased with female length; therefore, brood size was transformed by the square root to calculate the given regression equation.

DISCUSSION

In San Francisco Bay, California, and Yaquina Bay, Oregon, *Crangon franciscorum* larvae apparently settle at a length of 7 mm and become benthic on mud, in shallow, low saline water, and with growth, move steadily into deeper, higher saline water (Israel, 1936; Krygier and Horton, 1975). Therefore, it is plausible that *C. franciscorum* larvae in South Humboldt Bay settle on the lower intertidal mudflats surrounding the main channels and with growth,

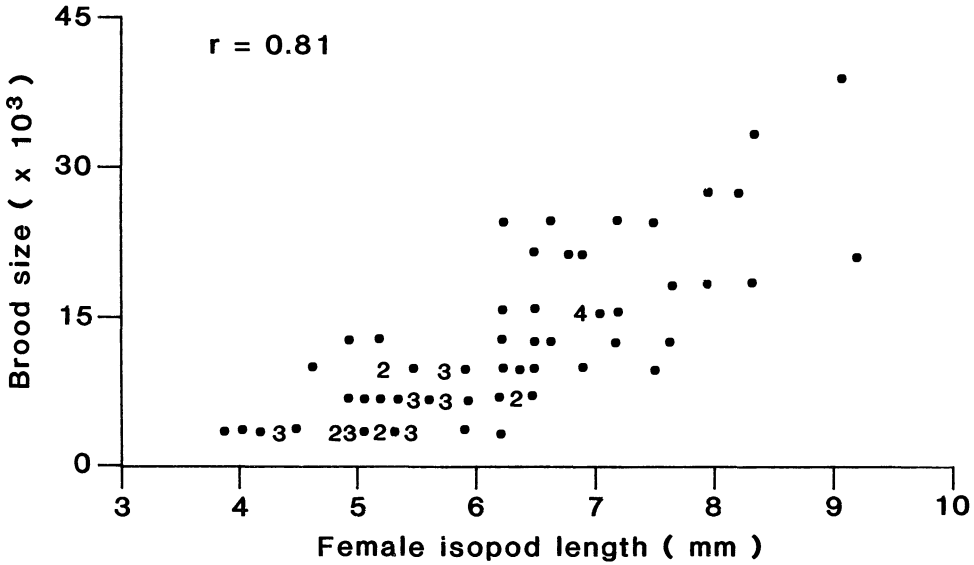

FIG. 4.—Correlation between isopod brood size and female isopod length. A given numeral represents multiple observations at that coordinate

move into the cooler, higher saline water in the channels. Movement of shrimp into Hookton Channel is indicated by the sudden appearance of a cohort of small noninfested shrimp with a normal size distribution during July (Fig. 2).

The positive linear relationship between the length of female isopods and their host shrimp, beginning at a host shrimp length of 26 mm, indicates that the parasites attached to their host early in the host's life. This agrees with Danforth's (1963) laboratory observations on *Argeia pugettensis* infesting *Crangon nigromaculata* and supports Beck's (1980a) generalization that the definitive hosts are most frequently infested early in their life.

However, the recruitment of small shrimp into Hookton Channel in July (Fig. 2) was accompanied by a low prevalence of infestation (Fig. 1), and infestation levels remained low through October, even though *Crangon franciscorum* was relatively abundant. After October, parasite prevalence steadily increased to a high of 34% in January 1984, while the relative abundance of *C. franciscorum* decreased. This increase was apparently not due to new infestations, since no small isopods were collected during this time and, as stated previously, evidence indicates that the host shrimp were infested early in their life. Furthermore, a comparison of length frequency histograms of noninfested and infested shrimp (Fig. 2) indicates that fluctuations in parasite prevalence throughout the year were not the result of the recruitment of a separate shrimp population.

The increase in parasite prevalence in Hookton Channel after October may have resulted from emigration of noninfested shrimp. This emigration may have been associated with reproductive maturation as described by Krygier and Horton (1975) and was indicated by the low occurrence of gravid female shrimp during the study period and by the disappearance of female shrimp from Hookton Channel upon reaching a size of reproductive maturity of ca. 50 mm beginning in September (Fig. 2). Additionally, noninfested female mean length increased from 34 mm in July to 44 mm in September, but remained between 44 and 46 mm from September through December (Table 1B). Infested shrimp may have been delayed

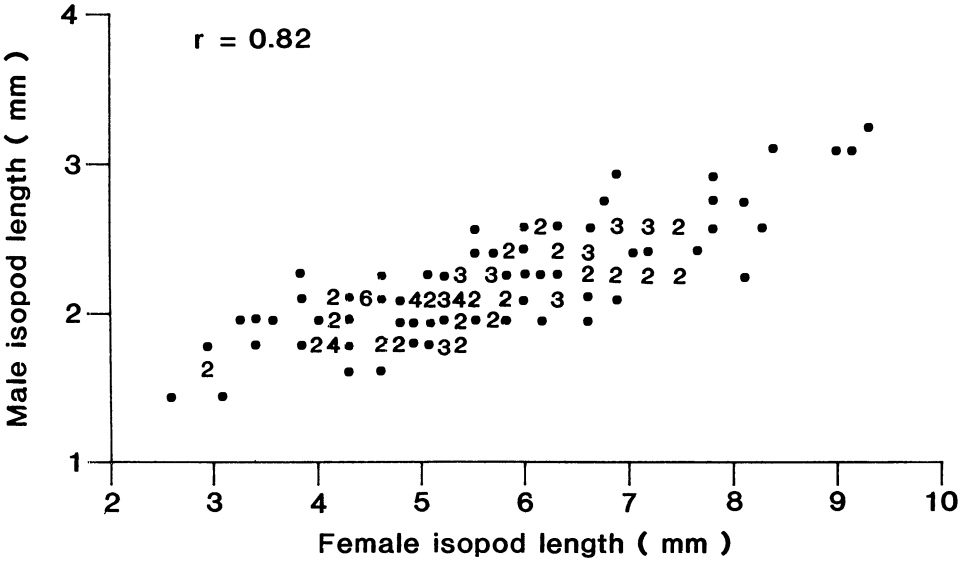

FIG. 5.—Correlation between male isopod length and female isopod length. A given numeral represents multiple observations at that coordinate

in attaining sexual maturity due to decreased growth rates and, therefore, may not have undergone the same spawning migration as noninfested shrimp, thus causing the observed increase in parasite prevalence.

Slower growth among infested shrimp is indicated by the smaller size of infested female shrimp when compared to noninfested females (Table 1B). Anderson (1977) found that the bopyrid *Probopyrus pandalicola* inhibited tissue growth in its host shrimp, *Palaemonetes paludosus,* and, in a different study (Anderson, 1975), caused a decrease in the metabolic rate in its host shrimp *Palaemonetes pugio.* Van Wyk (1982) observed slower growth rates resulting from decreased molt increments in the host crab *Pachycheles rudis* infested with the bopyrid *Aporobopyrus muguensis* and found that host female sexual maturity was apparently delayed. These observations, together with an observation by Krygier and Horton (1975) that no *Crangon franciscorum* females infested with *Argeia pugettensis* in Yaquina Bay, Oregon, were gravid during the normal spawning period, suggest that *A. pugettensis* causes its host, *C. franciscorum,* to grow more slowly than noninfested shrimp and may alter the shrimp's normal spawning behavior.

The higher prevalence of infestation among *Crangon franciscorum* females (Table 1A) parallel Gifford's (1934) observations on shrimp collected from San Francisco Bay. Beck (1979) studied the population interactions between the bopyrid *Probopyrus pandalicola* and its host shrimp *Palaemonetes paludosus* and observed that female shrimp were infested more frequently than males. He indicated that isopod brood size increases with host shrimp length and that noninfested female shrimp are larger, live longer and, at larger size classes, are more abundant than males. Therefore, Beck suggested that it would be advantageous for *Probopyrus pandalicola* to infest female shrimp so that more and larger broods could be produced. Beck (1979) pointed out that although there are other bopyrids that infest members of the sex of the host that grows largest, this type of selection is not universal among all bopyrids. In the present study, isopod brood size was correlated indirectly with host shrimp

length (Figs. 3, 4). Therefore, in accordance with Beck's argument, since female *C. franciscorum* apparently live longer and grow larger than males (Krygier and Horton, 1975), *Argeia pugettensis* females may realize maximum fecundity during their lifetime by infesting female shrimp.

Parasite prevalence reached peak levels of 27% during June 1983 and 34% during January 1984, in contrast to Gifford's (1934) observations of peak levels occurring in San Francisco Bay of 24% and 10% during September and December, respectively. Among other bopyrids, infestation levels vary between species and within species in different localities (Beck, 1979). Because fluctuation in parasite prevalence is the result of complex interactions between various environmental factors and the abundance and behavior of the various stages in the life cycle of both the parasite and host, these variations in prevalence might be expected.

Argeia pugettensis occupied the left and the right branchial chambers of *Crangon franciscorum* with equal frequencies, similar to Gifford's (1934) observations on shrimp collected from San Francisco Bay. Beck (1980b) stated that most branchial bopyrids are similarly nonselective and that all but one species of the several selective bopyrids belong to Pseudioninae and occur on anomurans.

In the present study, no *Crangon franciscorum* with more than one female isopod were found. Gifford (1934) reported that some shrimp collected from San Francisco Bay possessed bilateral double infestations (a female isopod in each branchial chamber), but he gave no additional information on the occurrences. Beck (1979) observed *Palaemonetes paludosus* with both bilateral and unilateral double infestations with *Probopyrus pandalicola,* but in lower than expected frequencies. He suggested that the first established female may inhibit attachment of subsequent females, resulting in low frequencies of double infestations. Beck states that unilateral double infestations are rare, but many different bopyrid hosts have been found with bilateral double infestations. In the present study, perhaps bilateral double infestations occurred on some shrimp in Hookton Channel, but were not encountered because they occurred in very low numbers.

The size of immature female isopods (2.7–3.1 mm long) and the size of the smallest ovigerous isopod (3.9 mm long) collected suggest that female isopods on *Crangon franciscorum* become mature at a length between 3.0 and 4.0 mm. Accordingly, from the regression equation of female isopod length on host shrimp length, female isopods in Hookton Channel would have become sexually mature when their host shrimp were ca. 27–33 mm long.

Isopod brood sizes increased with female isopod length (Fig. 4) and ranged from 1600 to 38,300 eggs. Beck (1980a) indicated that among other bopyrids, brood sizes increase with female isopod length and range up to 41,000 eggs. In addition, Beck suggested that brood size variability among isopods of the same length may result from variability in the size of the bulge in the host's carapace induced by the isopod. This correlation of brood size with bulge size may have existed among isopod–host pairs observed in the present study, and account for the observed variability in brood size among female isopods of the same length.

Crangon nigricauda is recorded as a host for *Argeia pugettensis* (Markham, 1977); however, a large number of *Crangon nigricauda* were collected from Hookton Channel during most of the study period and none was infested. Gifford (1934) observed this same phenomenon in San Francisco Bay. This type of phenomenon has been observed in other bopyrids (Warren, 1974; Owens and Glazebrook, 1985). Warren (1974) observed that only the host shrimp *Pandalus montagui* was infested with the bopyrid *Hemiarthrus abdominalis,* even though the recorded host *P. borealis* was more common. Owens and Glazebrook (1985) suggested that cryptonisci of the bopyrid *Epipenaeon ingens* selectively search for the host prawn *Penaeus semisulcatus* and only infests other prawns if *P. semisulcatus* is not found within a reasonable period of time.

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