POPULATION STRUCTURE AND ENERGETICS OF THE BOPYRID ISOPOD PARASITE *ORTHIONE GRIFFENIS* IN MUD SHRIMP *UPOGEBIA PUGETTENSIS*

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ABSTRACT

The population structure and energetic burden of bopyrid isopod parasite *Orthione griffenis* on the eastern Pacific mud shrimp *Upogebia pugettensis* are estimated from size and weight relationships between parasite and host. *U. pugettensis* weight loss increases with *O. griffenis* weight but the high variance in the relation indicates that direct weight comparisons are insufficient to reveal most of the host-parasite energetic interactions. Environment, reproductive development, age, molt stage and the feeding histories of the hosts and parasites, not apparent from weight ratio comparisons, are likely to be important factors in their interaction. The high prevalence of *O. griffenis* among *U. pugettensis* and positive correlation between host weight loss and parasite weight nevertheless, indicate large impacts of these parasites on mud shrimp populations are occurring with corresponding effects on estuarine dynamics in Pacific Northwest estuaries.

KEY WORDS: parasite, ecology, Crustacea, *Orthione*, *Upogebia*, *Neaeromya*, Thallassinidea, Northeast Pacific, estuaries

INTRODUCTION

The bopyrid isopod *Orthione griffenis* Markham, 2004 is a branchial parasite of the eastern Pacific mud shrimp *Upogebia pugettensis* (Dana, 1852) described from abundant populations in Yaquina Bay, Oregon (Markham, 2004). Bopyrid isopods parasitize and usually castrate their decapod hosts (Bourdon, 1968; Kuris, 1974; O'Brien and Van Wyk, 1985). Only the adult stages of *Orthione* are described, but initial sampling suggests that their life history is similar to other bopyrid isopods with three pelagic stages and a sequential hermaphroditic reproductive stage. The settling cryptoniscan stage metamorphoses into the reproductive stage on the final shrimp host. Reproductive female bopyrid isopods extrude eggs into an external marsupium where they are fertilized by a male. The eggs are brooded by the female until they develop into free swimming epicarids which are then released. Epicarids are flushed from the estuary and settle at sea onto a large crustacean zooplankter on which they metamorphose into a parasitic microniscus. Microniscans metamorphose into cryptoniscans, which return from the open ocean to infest the final shrimp host. Two infestations are thus required for reproduction. The first cryptoniscan to settle becomes a female and the second settling cryptoniscan becomes a male (O'Brien and Van Wyk, 1985).

Upogebia pugettensis is an almost exclusively intertidal species (Dumbauld et al., 1996; Posey, 1986) that burrows in intertidal mudflats and filter feeds on seston from the overlying waters. *Upogebia pugettensis* is the predominate organism in 40% of the total intertidal area of Yaquina Bay (DeWitt et al., 2004). Ignoring tidal exchange and vertical water movement, *Upogebia* filter the entire water column overlying their burrows in Yaquina Bay every day (Griffen et al., 2004). Large *Upogebia* populations in many northeast Pacific intertidal estuarine mudflats can therefore dominate benthic communities, sediment dynamics, and suspended particulate fluxes (Griffen et al., 2004; Posey et al., 1991; Swinbanks and Luternauer, 1987).

Marine parasitic castrators are particularly likely to affect their host populations because they can reduce host fitness to zero without increasing host mortality. Castrated hosts may thus compete with uninfested hosts while increasing their potential for new infestations on a broader scale (Lafferty and Kuris, 2002; McCallum et al., 2004). However, detailed information on population structure and natural history and ecology needed to determine whether these interactions occur are all but unknown for all bopyrid isopods (Shultz, 1969; John Markham, personal communication). *Orthione* is the largest bopyrid found in the eastern Pacific. We initiated this study to determine it's energetic burden and impact through comparisons of host and parasite sizes and weights.

MATERIALS AND METHODS

Yaquina Bay (124°02′30″W, 44°37′33″N) is a 1582 hectare estuary of which 548 hectares are intertidal (Oregon Division of State Lands, 1973). *Upogebia* were collected from ten 40 cm diameter by 60 cm depth core samples on 6 and 8 July 2005. Samples were spaced at 25 m intervals across an area 300 m SE of the Hatfield Marine Science Center (Fig. 1). The core sediments were washed on a 3 mm mesh sieve and retained *Upogebia* were placed into individual labeled bags.

Carapace length, sex, and reproductive condition were noted for all *Upogebia* collected. Carapace length (CL) of *Upogebia* was measured from the anterior tip of the rostrum to the posterior edge of the carapace

Fig. 1. Sampling site (circles) southeast of the Hatfield Marine Science Center in Yaquina Bay estuary, Oregon (modified from the Oregon Coastal Atlas: Orthophotos 1994). http://www.coastalatlas.net.

(Dumbauld et al., 1996) to ± 0.5 mm using digital calipers. Sex of *Upogebia* was determined from the presence of pleopods on the first pleomere and ovipores on females. Specimens lacking both the first pleopods and ovipores were considered males. Feminization of *Upogebia* males was assessed by examining a subset of these animals for the presence of ovipores in the absence of anterior pleopods.

The lateral position of *Orthione* and occurrence of the commensal clam *Neaeromya rugifera* (Carpenter, 1864) were noted for all *Upogebia* collected. Large *Orthione* are obvious externally while smaller isopods are apparent only by magnified examination of the gills and branchial chambers of each shrimp. All inspections were under 6 to 12 power magnification using a stereomicroscope. *Neaeromya* attach by byssal threads to the ventral pleon of *Upogebia* and are readily apparent.

Detailed observations and weights of *Upogebia* and associated organisms were made from three randomly chosen core samples that contained 69 shrimp. Wet weight was assessed within 24 h of collection while the shrimp and their parasites remained alive. *Upogebia* and *Orthione* were individually weighed wet in pre-weighed aluminum weighing boats, dried at 71°C for 48 h, and then immediately reweighed. All weights were measured to ± 0.001 gm. *Orthione* lengths and widths were measured to ± 0.5 mm using digital calipers. The sex of the *Orthione* was determined from size, overall shape (females are larger and more oval), and the presence of orange colored ovaries or egg broods. Brooding female *Orthione* were weighed wet with and without eggs. Egg numbers were estimated from volumetrically split samples. Eggs of each female were placed in 100-300 mL volumes of seawater in a 400-mL Erlenmeyer flask and vigorously suspended. Eggs in each of three 1 mL sub-samples of the agitated suspensions were pipetted into Petri dishes and counted (20X

magnification). Total egg counts were estimated from these sub-sample counts and multiplied by the total volume of suspension.

All bopyrid isopods, including *Orthione*, are obligate blood parasites (Anderson, 1977; O'Brien and Van Wyk, 1985) that feed on hemolymph of either the host or a female bopyrid feeding on the host. *Upogebia* weight loss proportional to *Orthione* feeding and energetic requirements was therefore expected. We assessed energetic effects of *Orthione*, in part, from length adjusted differences between parasitized and un-parasitized *Upogebia*. These comparisons assume that: 1) *Upogebia* molt in response to overall mass, and do so at approximately the same rate in parasitized and unparasitized hosts; 2) that hosts do not molt to smaller sizes in response to weight loss; 3) that hosts survive as well as otherwise similar unparasitized *Upogebia* and that host weight loss is directly related to parasite weight. Length adjusted body weights of infested and uninfested *Upogebia* (W_i and W_u) were used as an index of *Orthione* effects on *Upogebia* growth and energetics. Our null hypothesis is that the weight of *Upogebia* does not change in infested *Upogebia* ($W_i = W_u$). The size adjusted weight difference between uninfected and infected *Upogebia*:

$$L_O = W_u - W_i \qquad (1)$$

is thus an estimate of energetic cost of *Orthione* to *Upogebia*. We use length adjusted weight of uninfested shrimp, W_u, to predict uninfested weights of infested shrimp, P, from a power function and by substitution:

$$W_u = a*CL^b = P \qquad (2)$$

where a and b are estimated from regression of weight on carapace length (CL) among uninfested shrimp. We used regression and a *t* test to compare
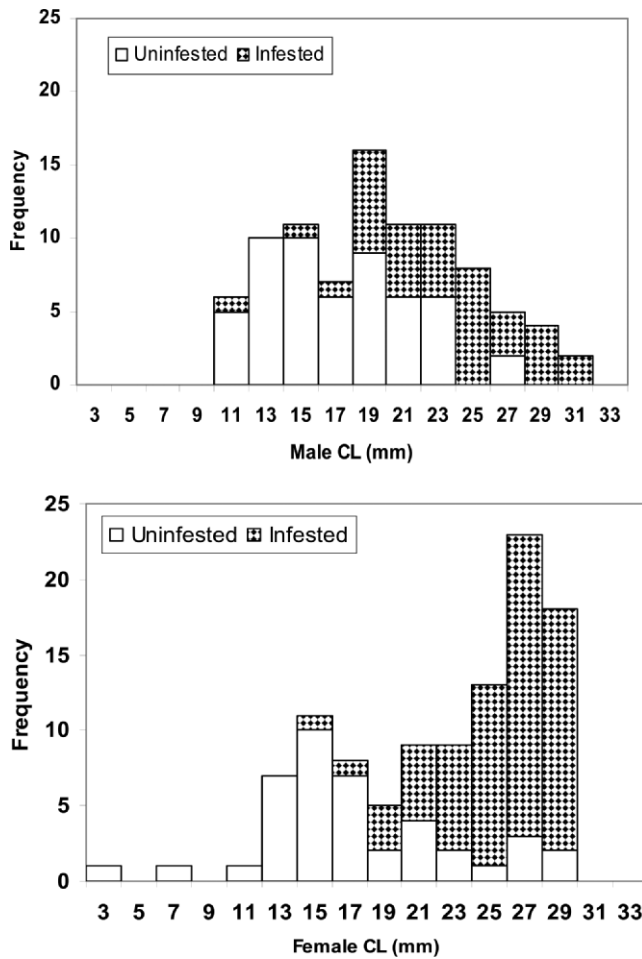
Fig. 2. Carapace length (CL) frequencies of infested and uninfested (diamonds and open) males and females of *Upogebia* from all samples at 2 mm midpoint intervals.

the slopes of the resulting equations. This and other statistical analyses followed standard methods as described in Zar (1998).

RESULTS

The average density of *Upogebia* at the sampling site in Yaquina Bay was 264 shrimp m^{-2}. Of 197 animals collected, 103 were females and 88 were males. Six individuals could not be sexed and the carapaces of two females, one male and one unsexed *Upogebia* were too damaged to measure. The proportion of females ranged from 42-69% and averaged 52%. Among reproductive sized *Upogebia* ($\geq$ 17 mm CL; Dumbauld et al., 1996), 57% of males and 80% of females were infested (Fishers exact test, $P = 0.017$, $d.f. = 1$, Fig. 2). No infestations were noted in shrimp less than 11 mm carapace length and right and left infestations were equal in male and female shrimp (Fishers exact test, $P = 0.675$, $d.f. = 1$). Nearly 100% of the largest shrimp were infested (Fig. 2). We found no evidence of feminized male shrimp based on the presence of ovipores.

Orthione brood weights ranged between 32-52% of body weight and averaged 40% $\pm$ 7.7% of total female mass. The broods ranged between 20,000 and 60,000 eggs and varied with female weight (*Orthione* brood wt $= 1.2454*$Body
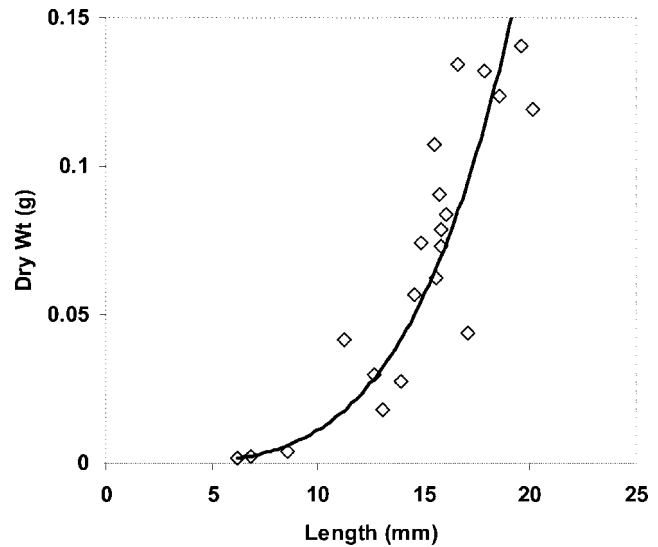

Fig. 3. Observed and estimated dry weight (diamonds and solid line, respectively) with body length of *Orthione* (Dry wt $= 1E$-06 $* BL^{4.019}$; $r^2 = 0.915$; $d.f. = 19$; $P < 0.01$).

$Wt^{1.5104}$; $r^2 = 0.594$; $d.f. = 10$, $P < 0.01$). Dry weight and length of *Orthione* are correlated (Fig. 3). Brooding *Orthione* were found only in *Upogebia* with carapace lengths greater than 18 mm (Fig. 4), but size and fecundity of *Orthione* are poorly correlated with host size. Weights of additional male *Orthione* associated with brooding female *Orthione* were less than 10% of the weight of the larger females.

Upogebia dry and wet weight were highly correlated with carapace length (Dry wt $= 0.0003*CL^{2.7185}$, $r^2 = 0.991$, $d.f. = 41$ (Fig. 5); wet wt $= 0.0004*CL^{3.1414}$, $r^2 = 0.990$;
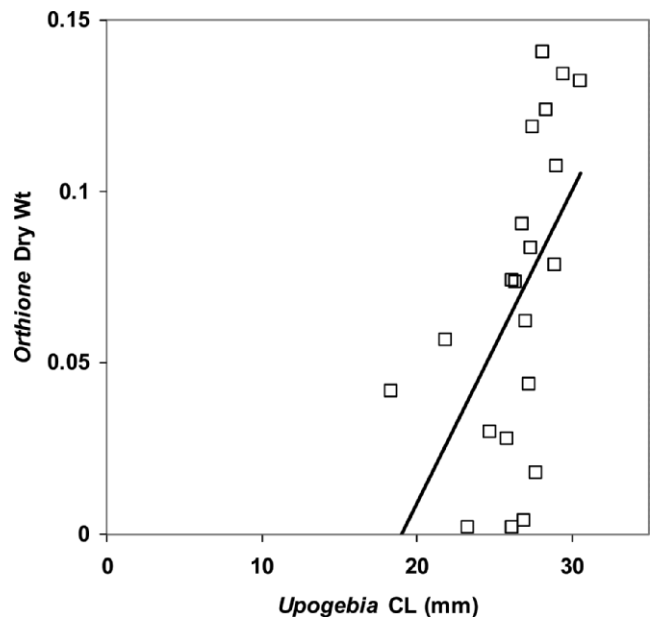

Fig. 4. Observed and predicted dry weight of *Orthione* (squares and solid line, respectively) with carapace length (CL) of *Upogebia* (*Orthione* dry wt $= 0.0091CL - 0.1722$; $r^2 = 0.297$; $d.f. = 19$; *ns*).
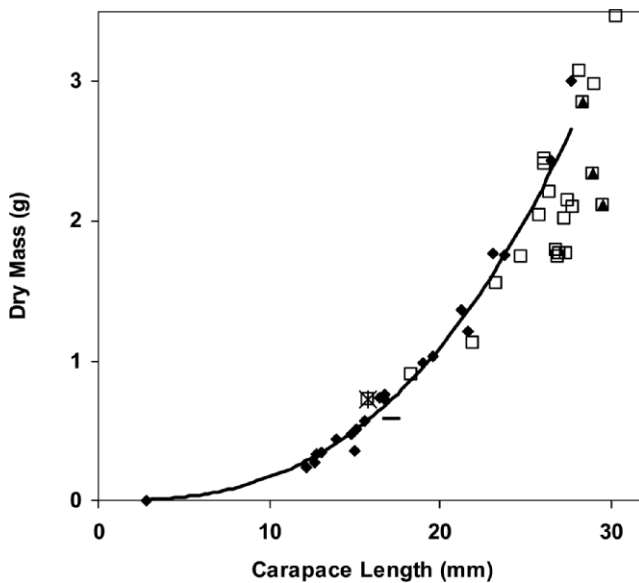
Fig. 5. Observed and predicted variation in dry weight with carapace length among uninfested *Upogebia* (solid diamonds and solid line) and observed variation in dry weight among infested *Upogebia* (open squares). (Uninfested *Upogebia* dry wt $= 0.000318*CL^{2.719}$ $R^2 = 0.991$), (Infested vs uninfested wt $t = 2.14$; $P < 0.02$; $d.f. = 20$). Also shown are shrimp that had a clam present (solid triangles), shrimp that had more than two isopods present (asterisks) and one shrimp that was ovigerous (dash).
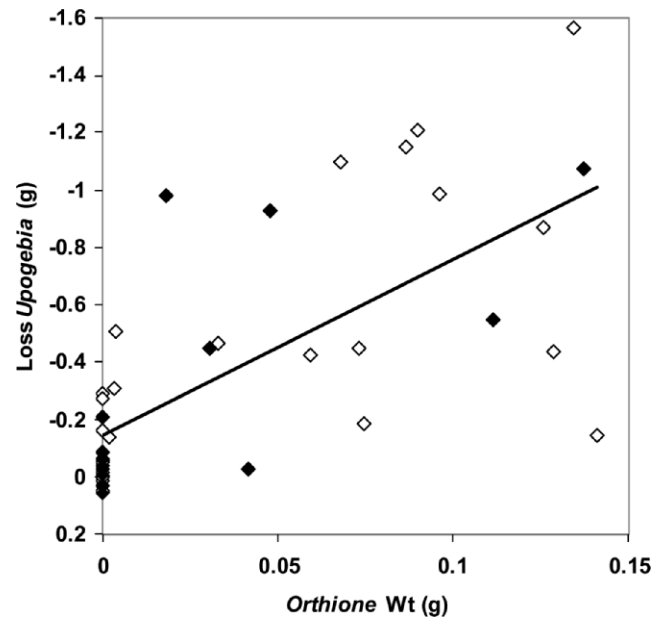

Fig. 6. Observed g dry weight loss of males and females of *Upogebia* (black and open diamonds, respectively) with g dry wt *Orthione* and predicted wt loss (solid line; $L_N = -0.145-6.141*Orthione$; $r^2 = 0.484$; $d.f. = 40$; $P + 0.01$) based on male and female *Upogebia* combined.

$d.f. = 25$) and the variances of wet and dry weights with length were not significantly different. Size adjusted weights of infested *Upogebia* were significantly less than expected weights of uninfested shrimp ($t = 2.14$, $P < 0.02$; $d.f. = 20$; Fig. 5).

Three shrimp infested by *Orthione* also had the clam *Neaeromya rugifera* present on their abdomens (Fig. 5). The weight loss in these shrimp was no greater than other similar sized infested shrimp lacking the clam and thus, *Neaeromya* had no measurable affect on shrimp weight.

The average infested host weight loss (0.22 g) was 7.8% of host body weight and 2.9 times the weight of the average *Orthione*. We therefore reject our null hypothesis ($W_i = W_o$). The poor correlation between *Upogebia* weight loss and *Orthione* weight (Fig. 6) however, indicates that a more complex relation than constant hemolymph extraction per gram of parasite occurs.

DISCUSSION

Prevalence of *Orthione griffenis* on *Upogebia pugettensis* in Yaquina Bay is higher than observed for many other bopyrids (Beck, 1980; O'Brien and Van Wyk, 1985), but comparable prevalences have been reported for *Parapenaeon* on *Metapenaeus dalei* in Korea (Choi et al., 2004), for *Ionella agassizi* on *Neotrypaea uncinata* in Chile (Munoz and George-Nascimento, 1999) and for *Progebiophilus bruscai* on *Upogebia dawsoni*, in Baja California, Sur, Mexico (Leija-Tristan and Salazar-Vallejo, 1991). Increased prevalence with host size has also been observed previously (but for the opposite pattern see VanWyck, 1982; Roccatagliata and Lovrich, 1999). *Orthione* were not present on small 0+ shrimp < 11 mm CL, and in reduced

frequencies among immature 1+ year-old shrimp (< 17 mm CL Fig. 2). This increasing prevalence with size is in contrast to observations by Tucker (1930) for *Gyge branchialis* who noted settlement "entirely or almost entirely" among the young *Upogebia littoralis* (now *U. pusilla*) and for *Probopyrus bithynis* in *Macrobrachium ohione* (Truesdale and Mermilliod, 1977). Early settling cryptoniscans were unlikely to have been overlooked since experimentally implanted cryptoniscans were readily apparent by our observation methods. Settlement into small *U. pugettensis* may not occur if cryptoniscan recruitment is reduced among small *Upogebia* (settling in April-July), if small *Upogebia* are insufficient food sources or die when infested, or if small shrimp are better at defending themselves from *Orthione*. The nearly 20% more frequent occurrences of *Orthione* among large female shrimp (Fig. 2) could result from greater parasite or host survival.

The large brood size of *Orthione* (20,000-60,000 eggs) relative to other bopyrids (28,000 *Anupodione carolensis*, a parasite of galatheid crabs) (Wenner and Windsor, 1979) is not surprising due to its large size. However, *O. griffenis* broods also comprised a large portion of the isopod's body weight (40%) versus 16.8% in *Probopyrus pandicola* (Anderson, 1977).

We found no evidence of feminized male *Upogebia* based on the presence of ovipores. However, we did not examine the allometry of male and female chelipeds, which is also a good indicator of feminization (Choi et al., 2004; Munoz and George-Nascimento, 1999; Beck, 1980; Tucker, 1930).

The clam *Neaeromya* is a filter feeder and attaches posterior to the feeding appendages of *Upogebia*, and thus is likely to feed after the host. We found that weights of shrimp infested with both isopod and clams were not significantly different from average weights of shrimp with *Orthione* only

(Fig. 5). Energetic demands of *Neaeromya* therefore, seem to be of minor importance even though they could interfere with host mating, brood care, or pleopod motion.

The energetics of marine bopyrid isopods are poorly known due to the low prevalence of these parasites, their complex life history, and the difficulties experienced in culturing them in the laboratory. Walker (1977) traced radioactive amino acids in the brackish water grass shrimp, *Palaemontes pugio*, and estimated that this host loses up to 25% of its hemolymph volume daily to the bopyrid *Probopyrus pandalicola*. Anderson (1977), compared oxygen flux rates in *P. pugio* infested by *P. pandalicola* and estimated that 10% of daily energy intake by *P. pugio* was lost to the parasite. O'Brien and van Wyk (1985) reanalyzed the data of Walker (1977) and Anderson (1977), and concluded that bopyrids ingest 4.3-4.4% of the daily energy intake of their hosts and this energy loss is equivalent to the energy devoted to reproduction in non-parasitized shrimp. We did not estimate rates of energy uptake. However, the average dry weight loss in *Upogebia* due to *Orthione* (7.8%), is much less than the the 30-40% of body weight represented by an average egg brood (Dumbauld et al., 1996).

Relative weight comparisons require similar size dimensions, molt frequencies, molt size increments, and longevity among un-infested and infested hosts and that molting occurs only in response to increasing body mass. Few of the larger shrimp (> 15 mm CL) were in early molt stages (most were in Stage D). This suggests that these large individuals molted infrequently and thus molt rates were similar among all larger shrimp. Without measures of molt increments, we could not test for induced molt disruptions. Mortality was similar in infested and un-infested *Upogebia* maintained several weeks in laboratory cultures (Katelyn Cassidy, personal communication), indicating that it is also similar in infested and un-infested shrimp. These possibilities all warrant further study under controlled conditions except for increases in molt frequency, these factors would result in low estimates of weight loss and seem unlikely to have affected our results.

Baudoin (1975) proposed that castration benefits the parasite by increasing the amount of energy available from the host. Anderson (1975) found greater weight specific metabolic rates in *Probopyrus* microniscans on female copepod hosts than on male hosts. The high metabolic rates of rapidly growing microniscans could indicate access to high quality food sources in correspondence with Boudoin's (1975) proposal. Moreover, Anderson (1975) concluded that the non-linear decline in weight adjusted oxygen consumption in *Probopyrus pandalicola* with size is due also to their greater lipid requirements. Similarly, the much higher infestation rate we found in female *Upogebia* may suggest that they are likely to produce more lipids than males and thus be better food sources for *Orthione* growth, reproduction and survival.

Weight loss in infested *Upogebia* was nearly three times the *Orthione* weight, but less than half of the loss varied directly with *Orthione* weight (Fig. 6). Weight loss did not conform to a constant weight-specific metabolic rate as a decreasing function of size that is most common among animals (Peters, 1983) and did not vary with host sex. Parasitized *Upogebia*

gained up to 13% and lost as much as 32% of predicted unparasitized weight (Fig. 5). Other bopyrid isopods have more constant host weight losses per gram of parasite (Anderson, 1975; Astete-Espinoza and Caceres, 2000).

Variation associated with small weight changes in *Upogebia* (Fig. 5) and low weights of *Orthione* (Fig. 3) are likely sources of error in per gram weight loss estimates. However, the uniform variation over the ranges of *Orthione* and *Upogebia* sizes (Fig. 6) indicates these sources of error are minor. Factors controlling *Upogebia* weight loss are likely to include more than parasite weight. Feeding rate could vary with parasite and host development, hormonal disruption (O'Brien and van Wyk, 1985) and differences in metabolic demands among *Orthione* sexes and reproductive development or life history stages. *Orthione* feeding may increase until egg deposition occurs and then stop during brooding periods when host survival is paramount. Sexual differences in *Upogebia* weight loss to *Orthione* (Fig. 6) could be obscured by variable parasite feeding rates with host physiology. This study occurred in July which is outside of the November to May brooding period (Dumbauld et al., 1996) and may even pre-date ovary production in *Upogebia* when, presumably, maximum feeding occurs.

Host responses are also likely to vary with size, age, life history stage, sex, reproductive condition, molt stage, feeding history, and trauma from parasite derived starvation, diseases, hormonal disruption, or wounds. Environmental variables likely to affect host condition include food availability, temperature, salinity, competition, burrow maintenance and defense costs.

The broad geographical occurrence, 50-100% prevalence and the 7.8% average dry weight loss among reproductive sized *U. pugettensis* infested by *O. griffenis* we found, indicates that overall *Upogebia* population reproduction could be greatly reduced. The prevalence of *Orthione* among reproductive sized females however, is incomplete evidence that castration is prevalent. Only two egg-bearing female *Upogebia* were available for this study. One unparasitized egg-bearing female, from an area near the study site, was close to the expected weight for its length but 19.3% below expected weight without eggs ("Egg", Fig. 5). Dumbauld et al. (1996) estimated that average *Upogebia* invest 30 to 40% of body mass to reproduction. The average 7.8% weight loss for infested *Upogebia* could thus be less than 25% of the mass needed for reproduction, but is more than the 4.5% biomass loss sufficient to prevent reproduction in *Palaemonetes pugio* (O'Brien and van Wyk, 1985). A second infested ovigerous shrimp, collected in January (BRD), carried only 15 early stage eggs, in contrast to 1800 to 11,000 typical of egg bearing non-infested *Upogebia* (Dumbauld et al., 1996). This latter female is the only parasitized shrimp with extruded eggs we have observed in multiple collections. Since egg bearing *Upogebia* were extremely rare in Yaquina Bay and *Orthione* infestations appeared to be equally prevalent during the 2004-2005 reproductive season (JWC, BRD personal observations), widespread castration and consequent severe effects on the larger *Upogebia* population seem likely.

Extensive population declines due to reduced *Upogebia* reproduction could benefit oyster production in some eastern

Pacific estuaries where dense shrimp populations turn over sediments and bury oyster spat (Feldman et al., 2000). However, mud shrimp are lesser pests for oyster culture than ghost shrimp (*Neotrypaea californiensis*) and most mud shrimp populations occur in intertidal estuary areas where benthic oyster culture does not occur. Large scale changes in sediment, phytoplankton and benthic community dynamics of many eastern Pacific estuaries due to the loss of these shrimp (MacGinitie, 1930; Swinbanks and Luternauer, 1987; Feldman et al., 2000; Dumbauld et al., 1996, 2001; Griffen et al., 2004) may be occurring if *Orthione griffenis* are similarly prevalent among all populations of *Upogebia* outside of Yaquina Bay.

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