

# Is the Collapse of Mud Shrimp (*Upogebia pugettensis*) Populations Along the Pacific Coast of North America Caused by Outbreaks of a Previously Unknown Bopyrid Isopod Parasite (*Orthione griffenis*)?

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**Abstract** A dramatic increase in prevalence of the recently discovered bopyrid isopod parasite, *Orthione griffenis*, likely introduced in the 1980s from Asia to the Pacific coast of North America, coincided with the 2002 collapse of a population of its burrowing mud shrimp host, *Upogebia pugettensis*, in Willapa Bay, Washington that had been stable since monitoring began in 1988. An examination of whether *O. griffenis* infections were sufficient to cause this decline and other recently noted *U. pugettensis* population collapses in Pacific Coast estuaries was conducted. *O. griffenis* prevalence was the highest in large reproductive-sized female shrimp and caused an

estimated average 68% loss of *U. pugettensis* reproduction in Yaquina Bay, Oregon over a 5-year period. *O. griffenis* prevalence fluctuated from year to year, but trends were similar in all estuaries sampled. Uninfected shrimp transplanted back into locations from which they had disappeared acquired the parasite, suggesting that *O. griffenis* is extremely effective at finding its host even in estuaries with very low host density. Since both *U. pugettensis* and *O. griffenis* have pelagic larval stages, their population dynamics are also influenced by coastal nearshore oceanography and estuarine recruitment success. Coastwide lack of estuarine recruitment appears to coincide with declines in density of a co-occurring thalassinid shrimp, *Neotrypaea californiensis*, but cannot alone explain *U. pugettensis* population collapses. Although patterns observed to date could be explained by the presence of either a native or introduced parasitic castrator, assumptions of a resilient co-evolved host–parasite relationship do not apply for introduced species, so continued efforts to follow the spatial extent and consequences of the *O. griffenis*–*U. pugettensis* host–parasite relationship are warranted.

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## Introduction

*Upogebia pugettensis* is a common species of thalassinid shrimp that inhabits intertidal mudflats in estuaries along the Pacific Northwest coast of North America. This species builds permanent y-shaped burrows (up to 1 m deep) in the sediment and filters large quantities of estuarine phyto-

plankton (Swinbanks and Luternauer 1987; Dumbauld et al. 1996; Griffen et al. 2004). *U. pugettensis* and a co-occurring thalassinid shrimp (*Neotrypaea californiensis*) are considered to be ecosystem engineers, substantially influencing the estuarine benthic community and carbon and nitrogen cycling in areas they inhabit (Bird 1982; Posey 1986; Dumbauld et al. 2001; Ferraro and Cole 2004; Griffen et al. 2004; D'Andrea and DeWitt 2009). Beds of both species once covered thousands of hectares (Hornig et al. 1989; Dewitt et al. 2004; Griffen et al. 2004) and thus included thousands of tons of shrimp biomass. Since 1998, however, most *U. pugettensis* populations examined between California and British Columbia have declined, and this shrimp appears to be at least locally extinct in Bodega Bay, Tomales Bay, Bolinas Lagoon, San Francisco Bay, and Elkhorn Slough, California where it was previously abundant (J.W. Chapman, B.R. Dumbauld, G. Itani, and J. C. Markham, unpublished manuscript).

A population of *U. pugettensis* in Willapa Bay, Washington that has been monitored since 1988 (Dumbauld et al. 1996; Dumbauld et al. 2004) declined precipitously at the same time that prevalence of a recently described parasite, the bopyrid isopod, *Orthonoe griffenis* Markham 2004, increased. Bopyrid isopods are parasitic castrators that effectively block reproductive capability of their crustacean hosts (Tucker 1930; Anderson 1977; O'Brien and Van Wyk 1985; Munoz and George-Nascimento 1999; Astete-Espinoza and Caceres-Martinez 2000; Calado et al. 2005). Thalassinid shrimp around the world are parasitized by bopyrid isopods (Markham 1986, 2001), but prevalence in natural populations is usually low (<5%). A native bopyrid, *Phylloporus abdominalis* Stimpson 1857, parasitizes *U. pugettensis* (Markham 1977), but it has only rarely been observed in recent surveys. Likely introduced to North America from Asia before the late 1980s (though AMK and MET maintain that there is insufficient evidence to state this and confirmation of the source awaits further genetic analysis), *O. griffenis* is now widespread and infects *U. pugettensis* at high prevalence along the Pacific Coast of North America (Smith et al. 2008; Griffen 2009; Williams and An 2009; J.W. Chapman, B.R. Dumbauld, G. Itani, and J.C. Markham, unpublished manuscript). Relatively high prevalence of other bopyrid species has sometimes been observed, e.g., *Progebiophilus bruscai* on *Upogebia dawsoni* (Leija-Tristan and Salazar-Vallejo 1991), *Parapenaeon consolidatum* on *Metapenaeopsis dalei* (Choi et al. 2004), *Entophilus omnitectus* on *Callinassa aquabaensis* (Markham and Dworschak 2005), and *Argeia pugettensis* on *Lissocragon stylirostris* (Marrin Jarrin and Shanks 2008); however, the origin of these parasites has not been questioned and population dynamics of parasite and host have not been monitored over time (but see Perez 1923 for a generalist cryptoniscid isopod *Hemioniscus balani*, a parasitic castrator of multiple species of barnacle hosts).

Parasites, including bopyrid isopods, are ubiquitous and their significant role in natural communities is becoming increasingly clear (Windsor 1998; Hudson et al. 2006; Dobson et al. 2008; Kuris et al. 2008). Laboratory and field studies have indicated that they can reduce host population densities and growth rates and alter community structure under specific conditions (Stiven 1964; Keymer 1981; Scott and Anderson 1984; Scott 1987; Crofton 1971; Anderson and May 1978; Hudson et al. 1998; Dobson and Hudson 1992). Mathematical models of parasite–host population dynamics assume that parasites are density-dependent sources of mortality or reproductive impairment and identify conditions where macroparasites and pathogens have the potential to regulate populations (Anderson and May 1979). While introduced parasites and diseases have been associated with species declines and extinctions (Warner 1969; Wilcove et al. 1998; Edgerton et al. 2004), most of the evidence for exotic species being the sole cause of extinctions is circumstantial (Gurevitch and Padilla 2004) and most research on parasite–host relations has been conducted in terrestrial environments.

Here, we evaluated data collected over a 20-year period on the bopyrid isopod parasite *O. griffenis* and its host *U. pugettensis* in one estuary and four additional years of data in three other estuaries along the Pacific Coast of North America. We used these data to address five questions that explore the host–parasite relationship for this isopod, but particularly to discern whether the association we observed between the appearance of *O. griffenis* and the population declines and local extinctions of *U. pugettensis* populations in these estuaries were causal:

1. Is *O. griffenis* merely a parasitic castrator or can this parasite also cause host mortality? Conversely, did some other factor cause *U. pugettensis* to die or disappear from locations where it was once abundant?
2. Does *O. griffenis* cause important loss of host fecundity at the population level?
3. Both *U. pugettensis* and *O. griffenis* have pelagic larval stages that disperse in the coastal ocean and contribute to larger West Coast metapopulations. Do different estuarine populations respond individually or is there evidence of synchronicity in host and/or parasite recruitment and population dynamics?
4. Parasite transmission is usually density dependent, allowing hosts to escape their parasites at low abundance. Is this the case for *O. griffenis*?
5. *O. griffenis* was likely introduced to the US West Coast from Asia and thus did not co-evolve with *U. pugettensis*. Could this affect host–parasite population dynamics and host persistence?

Addressing these questions at the temporal and spatial scales necessary to test and ultimately resolve parasite host

population dynamics in an open marine system is difficult. We were able to examine the maximum overall effects of *O. griffenis* on *U. pugettensis* population dynamics by comparing variations in *U. pugettensis* density and *O. griffenis* prevalence over an extended period in three estuaries and by comparing *U. pugettensis* reproduction and recruitment with later population changes in these estuaries. Finally, we estimated *U. pugettensis* reproductive losses to *O. griffenis* castration at the population level in order to gauge its potential magnitude.

## Methods

### Density and Prevalence

*U. pugettensis* were collected from a mudflat near the Cedar River channel in Willapa Bay, Washington from 1988 through 2002, after which they disappeared, and from a second location near Goose Point from 2003–2009 (see online resource 1 Table S1 and Fig. S1 for locations). Sampling occurred in late summer/early fall (August–November) from 1988 to 2003 and then in June from 2003 to 2009. Sampling began in 2004 at two locations in Tillamook Bay and Yaquina Bay, Oregon (online resource 1 Table S1 and Fig. S1). Quarterly samples of *U. pugettensis* were collected from Idaho Flats in Yaquina Bay from June 2006 to June 2007. Ten samples were taken at each location with a large corer (40 cm diameter × 60 cm depth). Contents were removed by shovel and sieved for shrimp (3-mm mesh, see Dumbauld et al. 1996 for methodology). Retained shrimp were measured (carapace length (CL) to the nearest 0.5 mm) and sex determined by the presence of anterior pleopods in females and absence in males. The presence of *O. griffenis* was easily noted by the characteristic bulging carapace over the branchial cavity. Detailed inspections of the branchial chamber for smaller newly settled isopods were made using a dissecting microscope for a subset of the samples taken from Yaquina Bay.

### Mortality

An experiment designed to test whether *O. griffenis* might reduce *U. pugettensis* survival was conducted in the laboratory. Thirty-two infected and uninfected shrimp were placed in individual plastic centrifuge tubes (50 ml, 2.5 cm diameter) with holes drilled in the top and bottom to allow for water circulation to mimic the burrow environment. The tubes were gravity-fed filtered seawater from elevated header tanks to maintain constant head pressure and flow. Shrimp were measured at the start of the experiment and ranged in size from 15 to 28 mm CL with roughly equal sex ratios of both infected and uninfected shrimp. To evaluate

potential interactions of diet and parasitism, shrimp were randomly separated into two treatments: fed (algae added to their respective header tank periodically) or unfed (no algae added). Shrimp molting and mortality were noted daily, and all surviving shrimp were returned to their tubes after recording size of exuvia and of newly molted and dead shrimp.

### Reproduction

Since *U. pugettensis* extrude eggs in the fall (October–November) which hatch in the spring (February–April; Dumbauld et al. 1996), the annual samples taken in June–July missed the reproductive period. We therefore used historical data from Willapa Bay to estimate fecundity in uninfected *U. pugettensis* (Dumbauld et al. 1996). After 2005, the embryonic stage of eggs on the pleopods was recorded in quarterly data from Yaquina Bay when eggs were present. Eggs were removed from nine ovigerous uninfected female *U. pugettensis* sampled in Jan 2009 in Yaquina Bay to compare with historical fecundity. A subsample was counted from each brood, and both the subsample and the remaining portion were weighed (dry and wet weight) to estimate fecundity. We estimated the overall effect of *O. griffenis* prevalence at the population level by integrating castration effects over all female *U. pugettensis* size classes between 2005 and 2009 (20–32 mm CL by 1-mm increments). We conservatively assumed that *O. griffenis* castration affects only female shrimp reproduction and therefore estimated the maximum annual *U. pugettensis* reproductive potential without castration ( $F$ ) as the sum of average individual fecundities,  $f_i$ , in size classes  $i$  times the number of females,  $n_i$ , per size class  $i$ :

$$F = \sum_{i=1}^{13} f_i n_i \quad (1)$$

We estimated cumulative reproduction with *O. griffenis* castration over all female reproductive size classes ( $F_c$ ) using the relation:

$$F_c = \sum_{i=1}^{13} f_i n_i c_i \quad (2)$$

where  $c_i$  is the proportion of uncastrated females in size class  $i$ , based on size-adjusted isopod prevalence (logistic regression model, see “Statistical Analysis” section).

### Recruitment

*U. pugettensis* postlarvae recruit from the ocean to estuaries along the West Coast of the USA from April to July (Dumbauld et al. 1996). Juvenile *U. pugettensis* were

sampled along with older shrimp using the large corer described above from 1988 through 2003 in Willapa Bay; the 0+ age class was distinguished by size because they rapidly grew to 5–13 mm CL by late summer. Beginning in 2004 when large corer sampling shifted to June, separate samples using a 26.5-cm-diameter corer to 10 cm depth were required to sample the newly recruited shrimp (2–5 mm CL) in all three estuaries. Ten of these small cores were taken at each location, contents sieved through 1-mm mesh, and retained shrimp measured under a dissecting microscope (CL to the nearest 0.2 mm).

### Survival

A transplant experiment was conducted to determine whether (1) *U. pugettensis* survived at locations where they were formerly present but had disappeared, (2) recruitment could be a mechanism limiting their recovery, and (3) such isolated shrimp become infected by *O. griffenis*. Newly recruited shrimp (5–12 mm CL) were collected from Yaquina Bay in September 2007, held and transported in seawater, and transplanted to both the Cedar River location in Willapa Bay from which they had disappeared and the Goose Pt. location where some remained. A second set of these shrimp was transplanted back to the high-density site in Yaquina Bay where they were collected and a second location where they were reported to have been previously abundant but had since disappeared. At all four locations, four shrimp were placed in each of four buckets (19 liters) which had the bottoms removed allowing existing shrimp and burrows to remain in contact with transplanted shrimp. In both estuaries at the locations where adults were present, we added a second treatment consisting of four buckets containing sieved sediment that had been allowed to settle for 24 h. The bottoms of these buckets were intact, preventing contact with and movement below the sediment. Only bottomless buckets were used at the locations where no shrimp were present. Mesh covers were placed over the tops of buckets for the first 24 h until transplanted shrimp had burrowed. All buckets were resampled in 2008, 1 year after placement, and all shrimp found were measured, sexed, and examined for the presence of *O. griffenis*.

### Statistical Analysis

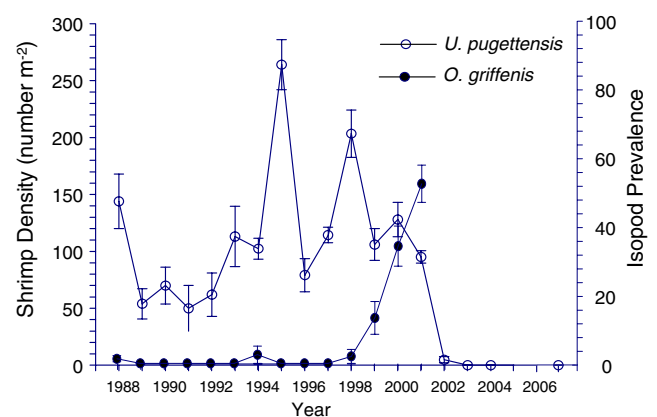
Isopod prevalence was analyzed using a logistic regression model (GLM function, binomial family, and logit link) in the statistical program R (R Development Core Team 2008) with shrimp host size (CL) as a continuous variable and host sex, location, and time entered as categorical factors. Final models were selected using Akaike Information Criteria (AIC; Burnham and Anderson 2002). Annual shrimp recruitment (mean density of recruits at a given

location) was analyzed using standard least squares regression with larger juvenile and adult shrimp density as a continuous variable and year and estuary as categorical factors. Recruit density was ln-transformed to normalize data. Mortality experiment results were analyzed using a survival model in R with a censoring indicator to code for time of death and a parametric Weibull model in which hazard increases with time. Isopod presence, host sex and size, and whether the host molted were entered as factors. Ovigery was initially analyzed using a logistic regression model with shrimp host size as a continuous variable, but once the minimum size at maturity was reached, size was not a significant factor so simple contingency tables adequately described the effects of location and time. Results from the transplant experiment were analyzed with two-way ANOVA for *U. pugettensis* density and *O. griffenis* prevalence with location and treatment (bucket type) as fixed factors.

## Results

### Shrimp Density and Bopyrid Isopod Prevalence

*U. pugettensis* density at the initial sampling location near Cedar River in Willapa Bay was variable, but averaged 118 shrimp m<sup>-2</sup> until 2002 when the population suddenly collapsed and no *U. pugettensis* were found at this location thereafter (Fig. 1). The abrupt decline in *U. pugettensis* abundance at this location was preceded by a dramatic increase in prevalence of *O. griffenis* after 1998, reaching over 50% prevalence in 2001 (Fig. 1). *O. griffenis* only infected larger mud shrimp (>15 mm CL), and prevalence appeared to be higher in female shrimp (Fig. 2). However, when data from the Cedar River location were analyzed



**Fig. 1** Density of *U. pugettensis* and prevalence of the introduced parasitic bopyrid isopod *O. griffenis* at Cedar River in Willapa Bay, Washington from 1988 to 2007. Note the dramatic increase in isopod prevalence and subsequent *U. pugettensis* population crash

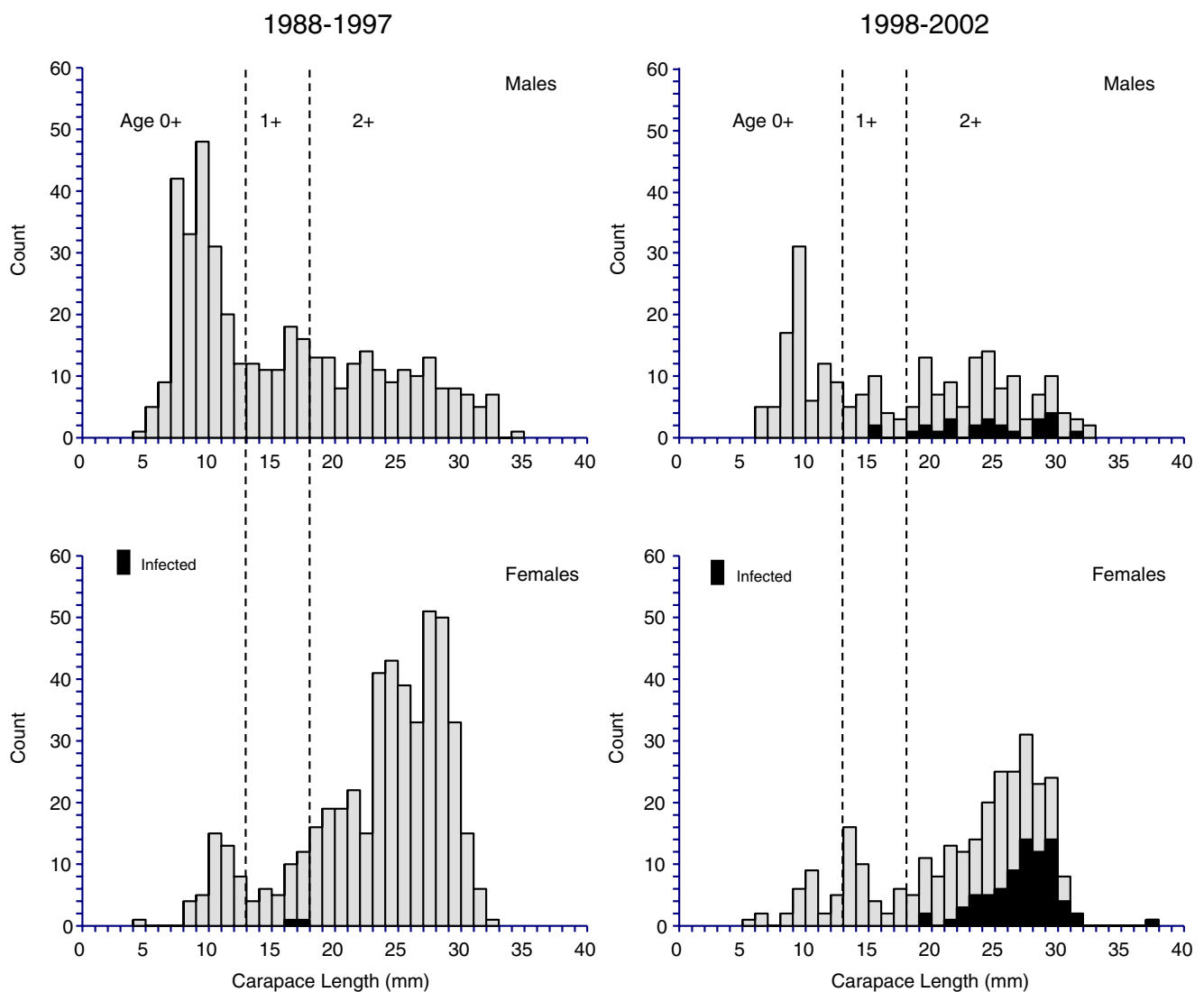
with logistic regression, gender did not explain prevalence after controlling for shrimp size and year (online resource 1 Table S2).

Density of *U. pugettensis* at sampling locations in Oregon estuaries (Tillamook Bay and Yaquina Bay) was the highest at Idaho Flats in Yaquina Bay ( $150 \text{ shrimp m}^{-2}$ ) in 2005, increased at all locations in 2007, and declined thereafter, while density at the Willapa Bay location remained low and continued to decline (Goose Pt.; Fig. 3). *O. griffenis* prevalence varied from year to year but declined at most locations in 2007 and 2008 (Fig. 4). Patterns were similar at all locations; location was not a significant factor in the logistic regression model while host size and sex were (higher prevalence in females and

increasing prevalence with size, Fig. 5, online resource 1 Table S3).

Quarterly data collected for *O. griffenis* in Yaquina Bay suggested that isopod prevalence increases in summer months ( $x = 64\%$  and  $73\%$  in 2005 and 2006, respectively) and declines in the winter ( $x = 48\%$  and  $49\%$  in 2005 and 2006, respectively). This effect was significant when carapace size was accounted for in the logistic model; however, there was interaction caused by the influence of smaller shrimp, and host size was not significant when a separate analysis was conducted for shrimp  $>24 \text{ mm CL}$ .

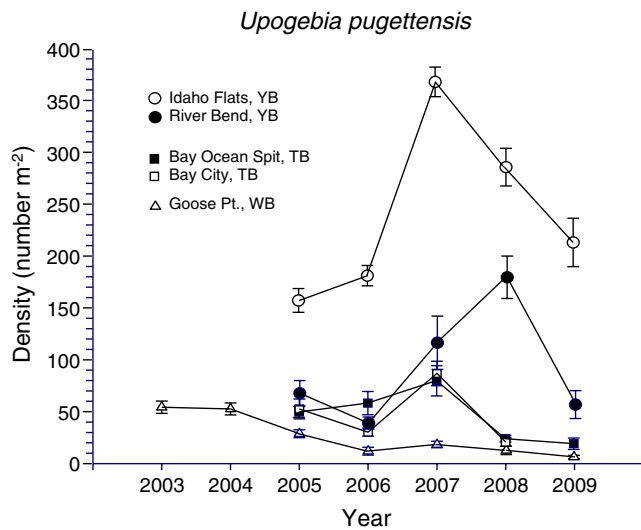
Several size classes of mud shrimp were routinely captured. In samples taken during the fall at the Cedar River location (1988 to 2002), only the first three smaller



**Fig. 2** Size (CL in millimeters) of male (*top*) and female (*bottom*) *U. pugettensis* collected at Cedar River, Willapa Bay before (1988–1997, *left*) and after *O. griffenis* became abundant (1998–2002, *right*). The higher overall prevalence of isopod parasites on female hosts can be

explained by their presence on  $>18 \text{ mm CL}$  shrimp which are presumably 2+ animals (presumed age classes divided by *dashed lines*) and a skewed sex ratio with more large females present regardless of whether the parasite is present





**Fig. 3** *U. pugettensis* density at one location in Willapa Bay (WB), Washington, and two locations each in Yaquina Bay (YB) and Tillamook Bay (TB), Oregon from 2005 to 2009

size classes were visually distinguishable and likely represented 0+, 1+, and 2+ age classes (Dumbauld et al. 1996; Fig. 2). In samples taken during early summer at other locations, newly recruited shrimp were rarely encountered and not accurately sampled using the large corer; consequently, these same size ranges likely represented 1+, 2+, and 3+ age classes. If these age class estimates are correct, then *O. griffenis* infects 1-year-old shrimp only in the latter part of their second summer and isopod prevalence is expected to increase during a shrimp cohort's second year. Therefore, the large cohort of *U. pugettensis* which recruited in 2006 may have contributed to the decrease in average prevalence we observed in 2007 and perhaps 2008 before these relatively young shrimp also became infected.

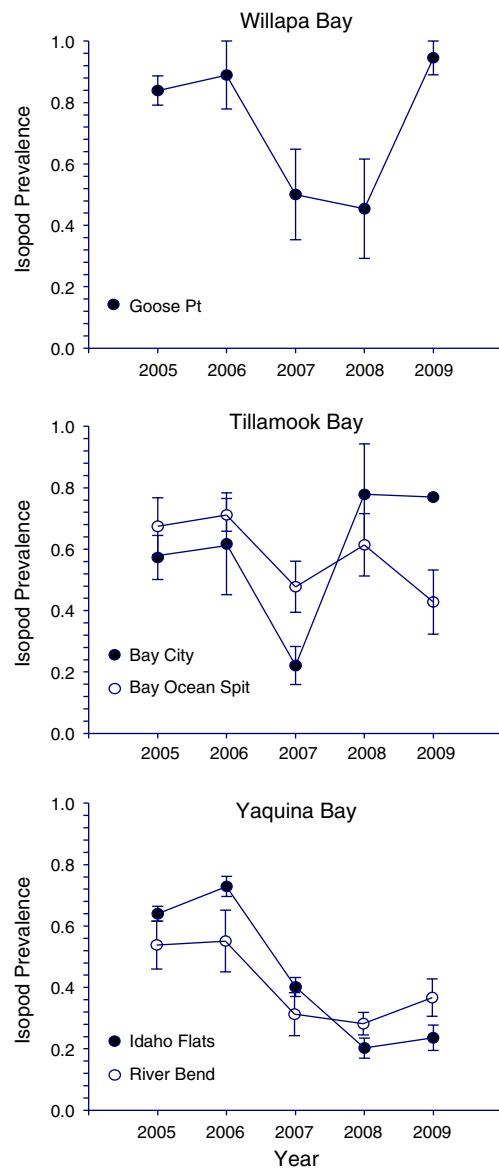
**Mortality**

Some of the shrimp held in centrifuge tubes in the laboratory survived for the 108-day duration of our mortality experiment, but average survival was 62 days. There was no significant effect of isopod infection, shrimp size, or sex on survival, nor an effect of feeding (starved or fed; online resource 1 Table S4). Almost half of the shrimp molted during the course of the experiment (29 of 64) and molting and survival were positively correlated. The average length of shrimp survival was the greatest for shrimp that molted and were uninfected (86 days) but also higher (65 days) for infected shrimp that molted than for either infected or uninfected shrimp that did not molt (51 and 41 days, respectively; Fig. 6). While there were significant higher order interactions between molting and some of the other factors, AIC values suggest that molting

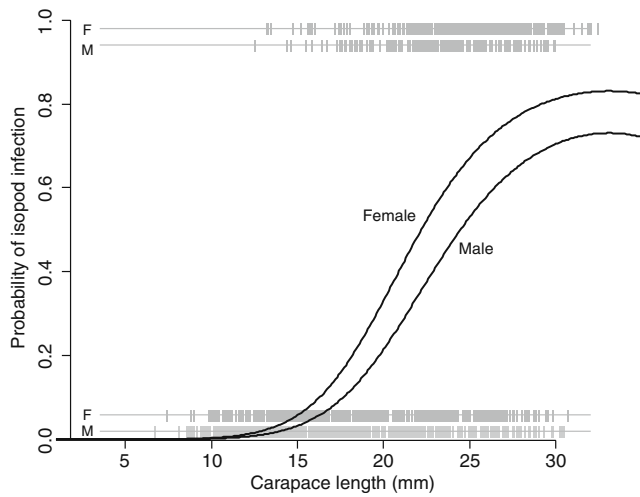
was the most significant factor. When molting was removed from the model, none of the other factors, including infection, were significant (online resource 1 Table S4). Shrimp did not appear to increase in size and average molt increment was not significantly different (*t* test, *p*=0.825) between infected and uninfected shrimp (0.42 and 0.49 mm, respectively).

**Reproduction**

Only *U. pugettensis* larger than 20 mm CL extruded eggs, and not all of these females were ovigerous when sampled during fall or early spring. No infected female shrimp

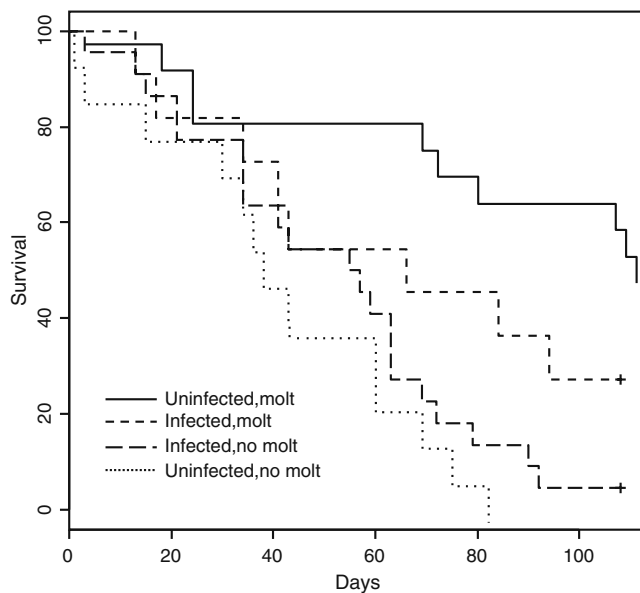


**Fig. 4** Prevalence of *O. griffenis* in >15 mm CL *U. pugettensis* from Willapa Bay, Washington and Tillamook and Yaquina Bay, Oregon from 2005 to 2009. Note significant interannual differences but similar trends among estuaries



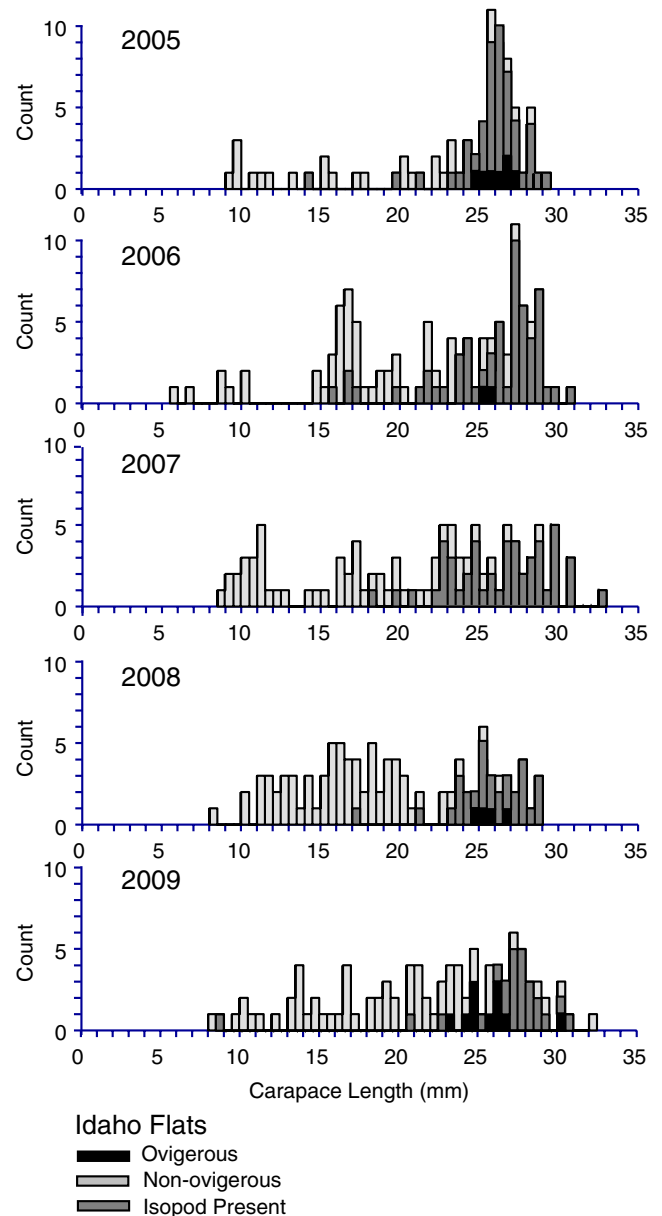
**Fig. 5** Proportion of *U. pugettensis* population infested by *O. griffenis* by size (CL in millimeters) and sex as predicted by logistic regression model (like that shown in online resource 1 Table S3, but averaged across years;  $\text{Logit} = 0.8846 \text{ CL} - 0.01337 \text{ CL}^2 - 13.0460$  for females and  $\text{Logit} = 0.8846 - 0.01337 \text{ CL}^2 - 13.6388$  for males). Frequency of infected shrimp was coded as 1 and shown as bars for each sex along the top and uninfected shrimp as zeros along the bottom. Note higher isopod prevalence in large female shrimp

sampled after 1998 at the Cedar River site in Willapa Bay were ovigerous. Ovigery in this Willapa Bay host population was significantly reduced from 35% of females in 1997 to only 1% in 2001 ( $X_{0.05, 1}^2=9.14, p=0.002$ ) just before the population crashed in 2002. The proportion of ovigerous shrimp sampled in Yaquina Bay fluctuated from 0% to 27% from the few samples collected during the fall and

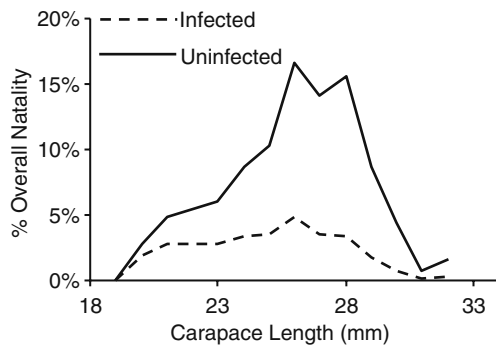


**Fig. 6** Stepwise survivorship curve for infected and uninfected shrimp that either molted during the course of a laboratory experiment or did not molt. Molting was the most significant factor in a survivorship model

winter months of 2005 to 2009, but these interannual differences were not significant ( $X_{0.05, 1}^2=4.02, p=0.4$ ; Fig. 7). We found no difference in the relationship between size (CL) and fecundity ( $E$ ) for uninfected *U. pugettensis* from Yaquina Bay sampled in January 2009 compared with that estimated by Dumbauld et al. (1996) before they were infected ( $E=0.008 \text{ CL}^{4.12}$ ), though the data were highly variable and fit a linear relationship as well. At the population level, size-corrected reproduction of uninfected (uncastrated) female *U. pugettensis* in Yaquina Bay between 2005 and 2009,  $F_c$ , was estimated to be 32% ( $c=$



**Fig. 7** Length frequency of female *U. pugettensis* present at Idaho Flats in Yaquina Bay, Oregon during the winter and spring from 2005 to 2008 including infected and uninfected ovigerous shrimp

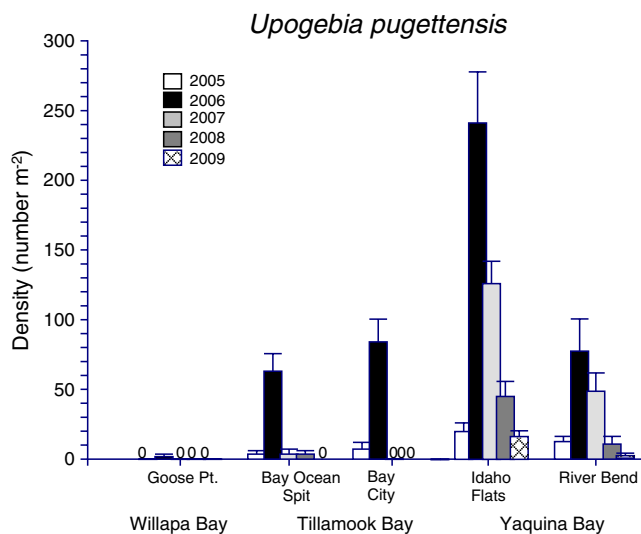


**Fig. 8** Cumulative uninfected natality,  $b$  (under solid line), and uninfected natality with *O. griffenis*,  $b_c$  (area under dashed line), and lost natality ( $b_1 = b - b_c$ ) by carapace length frequency ( $N$ , 20–32 mm CL) for *U. pugettensis* females in Yaquina Bay, 2005–2009

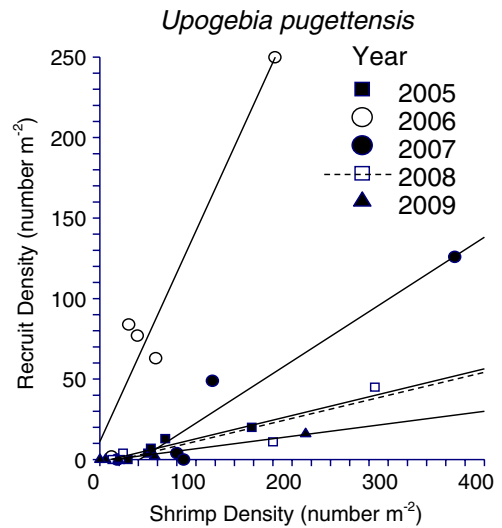
0.32) of the expected reproduction without *O. griffenis*, indicating a reproductive loss ( $F - F_c$ ) of 68% (Fig. 8).

**Recruitment**

Annual *U. pugettensis* recruitment covaried in all estuaries with highest recruitment in 2006 and 2007 (Fig. 9). Recruitment was the highest to Yaquina Bay, and new recruits were only observed in Willapa Bay during 2006, the year of highest recruitment in all estuaries. A significant linear relationship between juvenile recruits and adult density was observed each year (Fig. 10; Table 1), possibly resulting from preferential settlement with adults; however, the highest density of adults also occurred in Yaquina Bay so this pattern may just reflect overall recruitment by estuary.



**Fig. 9** *U. pugettensis* recruitment (density of <10 mm CL shrimp in the top 10 cm of substrate) to Willapa Bay, Washington and Tillamook and Yaquina Bay, Oregon from 2005 to 2009



**Fig. 10** Relationship between density of newly recruited *U. pugettensis* sampled in the top 10 cm of sediment and density of older shrimp sampled in the top 60 cm in Willapa Bay, Washington and Tillamook Bay and Yaquina Bay, Oregon each year

**Survival**

Newly recruited *U. pugettensis* transplanted in buckets survived for 1 year and grew from 5 to 10 mm CL when transplanted to 15–25 mm CL at all locations including those where they had previously disappeared. At locations where *U. pugettensis* populations remained, buckets with bottoms prevented larger shrimp from entering as expected; however, smaller shrimp recruited or moved into these buckets from the surrounding colony in Yaquina

**Table 1** Density of *U. pugettensis* recruits (postlarval shrimp sampled in the top 10 cm) as a function of larger adult and juvenile shrimp density (sampled in top 60 cm), estuary, and year (2005–2009) based on least squares regression model

	Estimate	df	Sum of squares	F ratio	p
Intercept	0.034	1	109.121	na	na
Tillamook	1.153	2	7.903	6.688	0.018
Yaquina	2.086				0.002
Density	0.008	1	4.925	8.336	0.011
2006	2.098	4	26.393	11.169	<0.001
2007	-0.277				0.596
2008	-0.542				0.288
2009	-0.945				0.087
Error		16	9.45		

Overall model fit: null deviance=75.80 on 23 df; residual deviance=9.45 on 16 df; model AIC=63.75. Models with density × year and density × estuary interaction terms not supported (AIC values 71.10 and 63.82, respectively). Model with estuary × year interaction term supported (AIC=56.62), but interaction terms not significant



Bay, given that an average of 6.8 shrimp per bucket was retrieved and only four shrimp were originally transplanted. The only significant difference was attributable to location with highest density found within the existing *U. pugettensis* colony in Yaquina Bay (two-factor ANOVA, location  $F_{1, 13}=33.94$ ,  $p<0.001$ ; treatment  $F_{1, 13}=1.29$ ,  $p=0.28$ , location  $\times$  treatment  $F_{1, 13}=3.86$ ,  $p=0.07$ ). Transplanted shrimp also became infected with *O. griffenis*. Moreover, three of four shrimp retrieved (75% prevalence) from the Cedar River location in Willapa Bay were infected though nearby hosts and therefore parasite source populations could not be found in a bay-wide survey (Dumbauld, unpublished data). No significant differences in isopod prevalence were found by treatment or location (two-factor ANOVA, location  $F_{1, 13}=0.13$ ,  $p=0.72$ ; treatment  $F_{1, 13}=2.13$ ,  $p=0.17$ , location  $\times$  treatment  $F_{1, 13}=0.13$ ,  $p=0.72$ ).

## Discussion

Prevalence of the bopyrid isopod parasite *O. griffenis* in *U. pugettensis* was high in all populations sampled from 2005 to 2009, infecting 17–94% of these shrimp. Historical prevalence of this isopod was low and increased exponentially beginning in 1997 at the Cedar River location in Willapa Bay. This remarkably rapid increase is correlated with the sharp decline and ultimate population collapse of its host, *U. pugettensis*, at this site and corroborated by direct accounts of the disappearance of this shrimp at many other locations along the Pacific Northwest coast of North America (J.W. Chapman, B.R. Dumbauld, G. Itani, and J. C. Markham, unpublished manuscript). We attempted to answer several questions in order to elucidate the underlying mechanism for these dynamics and further link these events.

Is *O. griffenis* Simply a Parasitic Castrator or Can It also Cause Host Mortality?

Bopyrid isopods cause blood loss and effectively castrate their decapod crustacean hosts (Kuris 1974; Walker 1977; O'Brien and Van Wyk 1985), but are not expected to cause mortality. Since *U. pugettensis* is likely a novel host for *O. griffenis* and some bopyrids are not full castrators, we wanted to verify this relationship for this host/parasite system. Smith et al. (2008) determined from field collections that *O. griffenis* caused significant weight loss in *U. pugettensis* but found the relationship to be variable and could not control for other possible factors like molting and feeding history. We found no evidence that infection, shrimp size, or sex affects survival of shrimp over a 108-day period in the laboratory. Furthermore, both infected and uninfected hosts molted during the experiment and al-

though we saw a positive correlation between molting and shrimp survival, there were complex interactions between molting and other factors and no direct influence of infection on survival. This suggests that isopod presence itself is not a direct source of the shrimp's disappearance from locations where they were historically abundant. Results of our reciprocal field transplant experiment also provided evidence that *U. pugettensis* could survive at locations such as the Cedar River site in Willapa Bay from which they had disappeared and that there was no significant difference between survival at these sites and locations where they are still present.

Changes in secondary sexual characteristics, particularly feminization of male hosts, are reported for other species of thalassinidean shrimps infected with bopyrids (Tucker 1930; Munoz and George-Nascimento 1999). This could indirectly influence mortality by changing the host's susceptibility to predation, if, for example, males are more likely to leave their burrows and/or fight to mate with females (Bass and Weis 1999). While Griffen (2009) hypothesizes that this could be an important factor in the *O. griffenis*–*U. pugettensis* relationship, we found little evidence of male feminization (ovipores were consistently present on females with modified first pleopods and absent on males without these pleopods; as noted previously by Smith et al. 2008). We did not examine ovary and testis size or development; however, both male and female chela morphometry has been shown to be slightly but significantly affected in infected *U. pugettensis* (Woods et al. 2006). Tucker (1930) found feminization of male *Upogebia pusilla* (previously *Upogebia littoralis*) infected by *Gyge branchialis* but noted that secondary formation of female pleopods occurred primarily in those shrimp with large parasites, indicating that they were infected at smaller sizes before the onset of sexual maturity. Perhaps male feminization does not occur for *U. pugettensis* because infection by *O. griffenis* only occurs at larger host size. Tucker also found that infected males outnumbered females while females outnumbered males in uninfected shrimp. We saw no such trend for *U. pugettensis* with large female shrimp outnumbering males regardless of infection, presumably due to other sources of sex-specific direct or indirect mortality like the agonistic mating behavior mentioned above.

Does *O. griffenis* Impact *U. pugettensis* Fecundity?

We found significant effects of *O. griffenis* on female shrimp ovigery and fecundity. With the exception of two female shrimp infected with small isopods, no infected ovigerous females were observed in any of our collections; these two females bore reduced clutches of 15 eggs and 1,120 eggs versus an expected fecundity of 7,443 and 6,314

eggs, respectively (based on size–fecundity relationship in Dumbauld et al. 1996). Fecundity of uninfected shrimp collected from the extant Yaquina Bay population was similar to that observed historically in both Willapa Bay and Yaquina Bay populations (Bird 1982; Dumbauld et al. 1996). The high levels of parasite prevalence we observed between 2005 and 2009 led to significant reproductive loss (68%) at the population level in Yaquina Bay

A lack of information on postlarval recruitment relative to previous years' fecundity complicates estimates of the reproductive costs of *O. griffenis* to *U. pugettensis* production at the population level. We therefore explored the potential effects of *O. griffenis* on population growth rate ( $dN/dt$ ) as a function of population size  $N$  over time  $t$  between uninfested and infested populations of *U. pugettensis* using a logistic model (see online resource 2). Infection and therefore castration decreased population growth. For West Coast groundfish stocks, a precautionary management threshold of 40% unfished biomass is used as a rebuilding target for overfished stocks that could still be potentially very slow to recover (Hutchings 2000; NMFS 1999). We estimate that *U. pugettensis* populations previously could have reached 40% of unfished biomass in less than 2 years, but may require 7 years to do so under current conditions with egg production losses due to *O. griffenis*. Logistic growth estimates presume interactions similar to a fishery on reproductive females, yet the effects of *O. griffenis* on the dynamics of *U. pugettensis* populations are more complex. Lost reproduction increases the relative importance of all other factors affecting *U. pugettensis* population dynamics including larval production and survival, and the resilience of these populations is likely compromised by *O. griffenis*. Since this isopod does not affect *U. pugettensis* mortality (Fig. 6; online resource 1 Table S4), castrated *U. pugettensis* females and males remain in the population to compete with the remaining reproductive members and produce new *O. griffenis* propagules independent of reproduction by the uncastrated *U. pugettensis* population.

#### Is Shrimp Recruitment Affected by Lost Fecundity?

Annual *U. pugettensis* recruitment and *O. griffenis* prevalence were temporally synchronous among estuaries suggesting that both host and parasite are part of larger West Coast metapopulations which are greatly influenced by dynamics of the coastal ocean where their larval stages develop. We suspect that local *U. pugettensis* recruitment occurs in most years due to their relatively short 3-week pelagic larval period (Hart 1937; D'Andrea and Dumbauld, unpublished data). One hypothesis is that, in some years (those characterized by delayed spring transition and/or more wind relaxations), shrimp larvae transit the entire

coast and larger populations to the south populate those to the north (due to the predominantly northward currents during this period), while in others (early transition and fewer relaxations), larvae are transported south or offshore and do not recruit anywhere in abundance. If true, then *U. pugettensis* populations in isolated estuaries or estuaries with few source populations to the south (e.g., Willapa Bay) would only receive nonlocal recruits in a few years (e.g., 2006; Fig. 9) and might decline rapidly once their populations became significantly infested and reproduction compromised by *O. griffenis*. While this physical oceanographic pattern enabled Shanks and Roegner (2007) to predict recruitment patterns for Dungeness crab (*Cancer magister*) along the Pacific Northwest coast of the USA, their larvae reside in the coastal ocean for several months and can transit broad areas of the continental shelf and settle in nearshore ocean areas as well. *U. pugettensis* larvae reside in the plankton for a much shorter period, must return to estuaries, and much less is known about the physical oceanographic processes in nearshore areas (<18.5 km from the shore) where their larvae are most abundant (D'Andrea and Dumbauld, unpublished data).

We were surprised by the rapid collapse of the mud shrimp population in Willapa Bay and intrigued by the correlation with rising prevalence of *O. griffenis* (Fig. 1), yet this may be merely a coincidence. Our results indicate that *U. pugettensis* recruitment also depends on density of adults, but estuary and adult shrimp densities are autocorrelated and differences between locations within estuaries are not sufficiently examined within a given year to clearly define the spatial scale at which recruitment and apparent aggregation occurs. Further, the concentrated recruitment of juvenile *U. pugettensis* into high-density areas of mature individuals could maintain patch density at the expense of patch area. Where recruitment is less than mortality, declining *U. pugettensis* abundances would result in declining patch areas in addition to declining density within patches. Movement of mature *U. pugettensis* is limited to extensions of their original burrows since these large shrimp are unable to reburrow after removal from their burrows (Chapman, unpublished data), but prereproductive *U. pugettensis* readily reburrow and anecdotal evidence indicates that such secondary dispersal of 1-year-old *U. pugettensis* has occurred (Feldman 2001). This adds further complexity to stationary measurements, and discrete *U. pugettensis* patches that diminish in size around stationary sampling locations, will appear as population collapses like those observed in Willapa Bay. Such declines will appear to occur much more slowly, if at all, however, when patches overlap with the stationary monitoring location. Observations suggest that this situation occurred at our long-term monitoring locations, but we are presently quantifying the

pattern by accurately mapping the spatial distribution and abundance of *U. pugettensis* over time in the remaining Yaquina Bay population.

The recruitment dynamics of a co-occurring shrimp, *N. californiensis*, which is parasitized by another bopyrid isopod, *Ione cornuta* Bates 1862, provide an instructive comparison. We sampled *N. californiensis* using the same large corer at nearby locations in each estuary (see online resource 1 Table S1 and Fig. S1 for locations). *I. cornuta*, which infects all sizes of shrimp, was only detected four times (<1% prevalence) during 1988 to 2009 at our long-term monitoring location near the Palix River in Willapa Bay (online resource 1 Fig. S2), and its prevalence was below 4% at all sites monitored in Oregon and Washington estuaries (online resource 1 Table S5). Very few *I. cornuta* were collected ( $n=30$ ), and we found no relationship between prevalence and location or host size or sex (logistic regression all  $p$  values >0.10). Therefore, *I. cornuta* is clearly not affecting *N. californiensis* reproduction at the population level. Nonetheless, density of shrimp at the long-term monitoring location also declined from a maximum of 472 shrimp $m^{-2}$  in 1995 to 52 shrimp $m^{-2}$  in 2008 (online resource 1 Fig. S2) and declined at some, but not all, locations in Oregon estuaries from 2005 to 2008 (online resource 1 Fig. S3). While ocean conditions clearly affect larval survival and recruitment of both burrowing shrimp species, reduced natality due to *O. griffenis* infection would be expected to substantially augment declines in *U. pugettensis* recruitment. Furthermore, while *N. californiensis* density has declined, we are unaware of any population extinctions or collapses like those observed for *U. pugettensis* (J.W. Chapman, B.R. Dumbauld, G. Itani, and J. C. Markham, unpublished manuscript).

Finally, while little is known about *O. griffenis* recruitment, their larvae (microniscans) rely on a secondary planktonic host (a copepod) that is found in the nearshore ocean and not in the estuary (Dumbauld and Chapman, personal observation). Personal observations of higher abundance of the cryptoniscid stage which returns to the estuary suggest that *O. griffenis* recruitment occurs throughout the summer. Further stochasticity and a time lag therefore complicate host–parasite population dynamics.

Is Transmission of *O. griffenis* Density Dependent, Allowing *U. pugettensis* to Escape Its Effects at Low Host Abundance?

Host population size, parasite population size, and parasite transmission are critical parameters in epidemiological models (Anderson and May 1979; May and Anderson 1979; Fenton et al. 2002; Lafferty and Gerber 2002; Deredec and Courchamp 2003). One essential feature of these models is a density-dependent threshold in host

population size below which parasite transmission cannot persist (first recognized by Kermack and McKendrick 1927). While both host and parasite populations can be affected by other phenomena including Allee effects at low population sizes, parasites are only expected to cause local host population extinctions under restricted circumstances (Kuris and Lafferty 1992; O'Keefe and Antonovics 2002; Deredec and Courchamp 2003; de Castro and Bolker 2005). Host extinction is most likely to occur when the parasite infects more than one host species (low specificity) with differential pathology in those hosts. Spillover to other less common hosts which act as reservoirs can also cause local or even global extinctions. This has been notably demonstrated for saturniid moths depleted by gypsy moth tachinid parasitoids and perhaps for the coconut moth and other zygaenid moths (Boettner et al. 2000; Kuris 2003). Extinctions might also occur if transmission is not density dependent (e.g., behaviorally controlled, as in sexually transmitted diseases) or when local spatial structure in density occurs for the host or parasite. Theoretical explorations of these effects have seldom been tested, particularly in marine systems (but see Blower and Roughgarden 1989; Lafferty 1993).

Results of our transplant experiment of uninfected shrimps to Willapa Bay where the population of *U. pugettensis* had collapsed to near zero and their subsequent infection within a year by *O. griffenis* at an equivalent prevalence to that in Yaquina Bay, where these shrimp were still relatively abundant and parasite prevalence also high, suggest that *O. griffenis* transmission was not locally density dependent. Similarly, while we saw interannual differences in *O. griffenis* prevalence, we found no significant differences in size-corrected prevalence between estuaries where shrimp density was markedly different. This was also true for populations sampled during 2008 from Morro Bay, California to Grays Harbor, Washington (J.W. Chapman, B.R. Dumbauld, G. Itani, and J. C. Markham, unpublished manuscript), suggesting that the density-dependent transmission threshold for *O. griffenis* is either extremely low or is influenced by factors that differ from those influencing its host. Two ways that this might occur are: (1) *O. griffenis*'s secondary planktonic host could be widespread and common in all years and (2) surviving infected *U. pugettensis* could act as temporary reservoir hosts, potentially allowing *O. griffenis* persistence below *U. pugettensis* Allee densities at least 1 year after shrimp recruitment declines or ends. Since reduced juvenile *U. pugettensis* abundances do not affect *O. griffenis* reproduction and each *U. pugettensis* female is not likely to produce more than three or four annual broods (Dumbauld et al. 1996), only three or four consecutive years of reproductive failure could be sufficient for local *U. pugettensis* extinction.

## Could the Lack of Co-evolution Between *U. pugettensis* and *O. griffenis* Influence Host Parasite Population Dynamics and Host Persistence?

Previous empirical (Perez 1923; Blower and Roughgarden 1989; Torchin et al. 2001) and theoretical (Blower and Roughgarden 1987; Kuris and Lafferty 1992) evidence suggests that both native and introduced marine parasitic castrators can control host population demographics. The parasitic barnacle, *Sacculina carcini*, appears to limit size and biomass of green crabs, *Carcinus maenas*, across several native populations in Europe, but where this crab is introduced it is not infected with parasitic castrators and is more abundant than in its native range (Torchin et al. 2001). Similarly, anecdotal information suggests that shipments to Chesapeake Bay containing live xanthid crabs (*Rhithropanopeus harrisi*) infected with the sacculinid barnacle, *Loxothylacus panopaei* (Van Engel et al. 1965), led to successful barnacle infection of this host along with another abundant xanthid, *Eurypanopeus depressus*. Both species of crabs soon became less common (Andrews 1980) while a third, formerly rare xanthid, *Dyspanopeus sayi* (= *Neopanope texana sayi*), was not susceptible to the barnacle and became the dominant mud crab in Chesapeake Bay (Andrews 1980). With the exception of work by Blower and Roughgarden (1987, 1989), who were able to predict biogeographic patterns of intra- and interspecific prevalence among three northeastern Pacific barnacle species and their cryptoniscid isopod parasite *H. balani*, our study is the first long-term quantitative description of the dynamics of an introduced marine parasitic castrator and its host.

Specialist predators and parasites coexist because they have not driven their prey to extinction over evolutionary time. Some introduced species may rapidly evolve or alter the evolution of other species in recipient communities (Vermeij 1996; Huey et al. 2005), but most introductions are not successful and result in rapid extinction due in part to Allee effects (e.g., Carlton and Geller 1993; Williams 1996; Taylor and Hastings 2005). The success of introduced species that do become established is often attributed to their escape from natural (co-evolved) enemies (Keane and Crawley 2002; Shea and Chesson 2002; Mitchell and Power 2003; Torchin et al. 2003). Similarly, the success of introduced predators and parasites can also be due to their escape from co-evolved relationships with their hosts and prey. Species invasions can provide insight into these co-evolved ecological relationships (Sax et al. 2007). In particular, invasions are consistent with “neoclassical biological control theory” which suggests that introductions can have maximum impacts on naïve prey when a reservoir of alternative hosts or prey is established and maintained (Hokkanen and Pimentel 1989; Kuris 2003). The pattern of local *U. pugettensis* population collapses we have observed

can be explained for either a native or introduced parasitic castrator, but if *O. griffenis* was introduced and *U. pugettensis* was a naïve host as we suspect, then assumptions of a co-evolved host–parasite relationship would not apply and broader impacts of *O. griffenis* on *U. pugettensis* populations should continue to be examined.

### Summary

The bopyrid parasite *O. griffenis* did not cause direct mortality of its host *U. pugettensis*, but significantly reduced fecundity at the estuarine population scale in all estuaries sampled. *U. pugettensis* recruitment and therefore population dynamics must also be affected. Because both host and parasite have pelagic larval stages, we have yet to resolve the complex dynamics of this relationship at the larger marine metapopulation scale. Infectious diseases and parasites are increasingly viewed as important forces controlling community dynamics. While available evidence suggests that they are rarely the sole cause of species extinctions (de Castro and Bolker 2005; Smith et al. 2006), marine parasitic castrators like *O. griffenis* can reduce host fitness to zero without increasing mortality and the castrated hosts compete with uninfected hosts while increasing their potential for new infestations on broader scales (Kuris and Lafferty 1992; Lafferty and Kuris 2002; McCallum et al. 2004; Kuris et al. 2008). Parasites can contribute to local host extinctions when they force host population instability (Boots and Sasaki 2003), when transmission is not density dependent, or when there is an abundant host reservoir (Boettner et al. 2000). Some of these factors appear to be at work in the nonco-evolved *U. pugettensis*–*O. griffenis* relationship. Due to the important role of these shrimp in West Coast estuaries (MacGinitie 1935; Dewitt et al. 2004; Dumbauld et al. 2004; Griffen et al. 2004; D'Andrea and DeWitt 2009), further investigation to understand recent declines and conserve remaining *U. pugettensis* populations is warranted.

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