

Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance

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ABSTRACT: The burrowing shrimp *Upogebia pugettensis* is an abundant intertidal invertebrate of Pacific Northwest, USA bays and estuaries where it lives commensally with the bivalve *Cryptomya californica*. Suspension-feeding activities by the shrimp and by its commensal clam, as well as particle settlement within the burrow, represent 3 different components that could remove phytoplankton from water drawn into shrimp burrows. These 3 components together comprise what we call the '*U. pugettensis* shrimp-burrow complex'. In laboratory experiments, we measured particle removal by each of these components. Our results indicated that *U. pugettensis* itself is responsible for filtering the majority of phytoplankton removed by the *U. pugettensis* shrimp-burrow complex at phytoplankton concentrations of 0.12 mg C l⁻¹, with filtration by *C. californica* becoming increasingly important at phytoplankton concentrations of 0.48 mg C l⁻¹. Particle settlement in the burrow and adhesion to the burrow wall may also be responsible for removal of substantial proportions of phytoplankton. Using results from both laboratory and field experiments, we developed a population filtration model to examine the potential impacts of *U. pugettensis* shrimp-burrow complexes on phytoplankton in the Yaquina estuary, Newport, Oregon, USA. We showed that *U. pugettensis* shrimp-burrow complexes in this estuary may be capable of daily filtering the entire body of overlying water. We also examined the potential for food competition between *U. pugettensis* and other suspension feeders that are found in shrimp habitats, represented in this study by the Pacific oyster *Crassostrea gigas*. Comparison of retention efficiencies of shrimp and oysters indicated that they are both capable of utilizing phytoplankton-sized particles with similar efficiencies and, therefore, may compete for food when phytoplankton abundance is growth-limiting.

KEY WORDS: Suspension feeding · Burrowing shrimp · *Upogebia pugettensis* · *Cryptomya californica* · Yaquina

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INTRODUCTION

Filtration by dense populations of suspension-feeding organisms in semi-enclosed systems, such as bays and estuaries, can potentially reduce phytoplankton abundance in overlying waters. This can have important ecological consequences, such as directly regulating phytoplankton biomass (Cloern 1982, Carlson et al. 1984, Newell 1988, Riemann et al. 1988,

Peterson & Black 1991, Dame 1996, Padilla et al. 1996) and indirectly regulating secondary production of suspension feeders through removal of large proportions of seston (Peterson & Black 1988, Gili & Coma 1998). Officer et al. (1982) proposed criteria for identifying regions where benthic communities may potentially control phytoplankton abundance. These included partially enclosed shallow areas (<10 m in depth) with dense, widespread suspension-feeding benthic com-

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munities and extended periods of water retention. Such areas may be found in many Pacific Northwest estuaries, where populations of the suspension-feeding burrowing shrimp *Upogebia pugettensis* reach densities $> 300 \text{ m}^{-2}$ ($> 1 \text{ kg m}^{-2}$; Bird 1982, Dumbauld et al. 1996, T. H. DeWitt unpubl. data). Despite its prominence in West Coast bays and estuaries, little is known of the feeding physiology of *U. pugettensis* and its potential impact on phytoplankton abundance, as well as details of competition with other suspension-feeders.

Upogebia pugettensis primarily inhabits intertidal mud and sand flats in estuaries and bays of the west coast of North America, where they construct U- or Y-shaped burrows to depths of 1 m (Stevens 1929, Thompson 1972, Griffis & Suchanek 1991). Mucus secreted from the hindgut gland is used to cement sediment particles and other debris together to form the burrow wall (Thompson 1972). By beating their pleopods, *U. pugettensis* create a current through the burrow, from which food particles are filtered using setae spaced ca. $6 \mu\text{m}$ apart on their front appendages (Powell 1974).

The bivalve *Cryptomya californica* often commensally inhabits *Upogebia pugettensis* burrows (MacGinitie 1934, 1935). Several *C. californica* may inhabit a single burrow (an average of 8 per burrow in our study area). Situated in the wall of the shrimp's burrow, they extend their short siphons into the burrow cavity (Yonge 1951) and extract food from the water current that is generated through the burrow.

Removal of suspended food from water passing through the burrow can functionally be attributed to 3 components of the '*Upogebia pugettensis* shrimp-burrow complex': filtration by *U. pugettensis*, filtration by *Cryptomya californica*, and losses in the burrow due to physical factors such as settlement and adhesion to burrow walls. We examined each of these components separately in laboratory experiments in order to determine their relative importance in removal of phytoplankton.

We also measured particle retention efficiencies in laboratory experiments in order to determine whether *Upogebia pugettensis* utilize the same size range of particles as has been reported for bivalve species, many of which show maximum retention efficiencies for particles between 4 and $12 \mu\text{m}$ (Møhlenberg & Riisgård 1978, Winter 1978, Palmer & Williams 1980, Riisgård 1988, Barillé et al. 1993, Ropert & Gouletquer 2000). We measured feeding rates and particle retention efficiencies of Pacific oysters *Crassostrea gigas* as a representative bivalve species for comparison with those of *U. pugettensis*. This bivalve species was chosen because it is commercially important and is grown in many estuaries where *U. pugettensis* occur.

Lastly we explored the range of potential effects that *Upogebia pugettensis* populations may have on phytoplankton concentrations in Pacific Northwest estuaries, represented here by the lower portion of the Yaquina estuary, Newport, Oregon, USA. The data necessary to fully elucidate the effects of *U. pugettensis* shrimp-burrow complexes on estuarine phytoplankton abundance are not available. Such data include residence times, flow rates, and flow patterns within and over shrimp burrows, the degree of mixing of filtered and unfiltered water at both local and estuarine spatial scales, oceanic input of seston with tidal fluxes, and the degree of resuspension of benthic microflora. While it may be some time before these data are available, we have developed a simple population filtration model to derive a first approximation of the proportion of phytoplankton that could be removed daily from water overlying shrimp-dominated tide flats in the lower Yaquina estuary. This model is based on particle filtration data for *U. pugettensis* shrimp-burrow complexes from our laboratory and field experiments, *U. pugettensis* and *Cryptomya californica* population densities, and estimated estuarine water volumes.

MATERIALS AND METHODS

General laboratory procedures. We used a simple flow-through experimental apparatus to determine feeding rates and efficiencies of shrimp, *Cryptomya californica*, and the oyster *Crassostrea gigas* under laboratory conditions (Fig. 1). Flow-through systems are commonly used in feeding rate experiments with suspension-feeding bivalves (Bayne et al. 1987, Dame 1996, Newell & Langdon 1996), and have the advantage over static systems in that it is possible to maintain relatively constant particle concentrations over long periods of time. Furthermore, a flow-through system can consist of many flow-through chambers, allowing simultaneous measurements of numerous experimental variables. Flume systems are appropriate when experimentally determining the effects of flow on filtration rates of benthic suspension feeders (Wildish & Kristmanson 1997), but this was not the main objective of this study.

In determination of filtration rates, it is important to prevent localized depletion of suspended particles in the immediate vicinity of the filter-feeding organism because this could lead to re-filtration of un-mixed parcels of filtered water, reducing apparent filtration rates (Hildreth & Crisp 1976, Winter 1979). We used gentle aeration to achieve homogeneous particle concentrations in experimental chambers (Newell & Langdon 1996), verified by measuring cell concentrations in water samples taken from different locations within the chambers. Lastly, it is unlikely that parcels of parti-

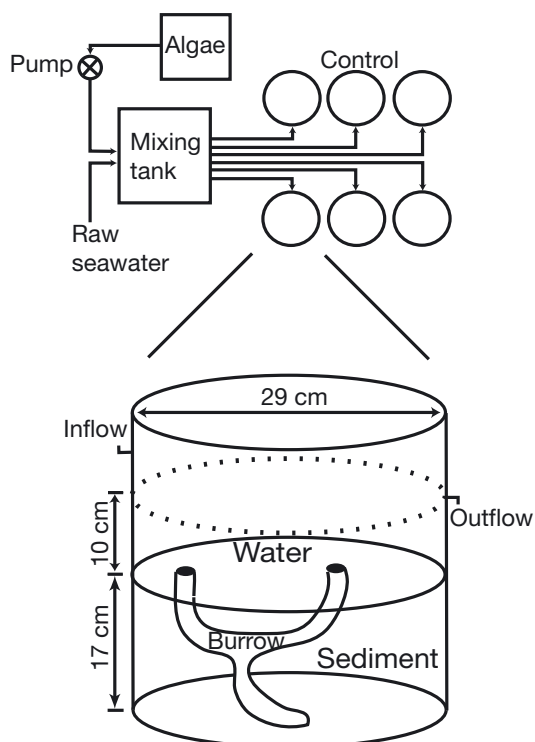


Fig. 1. Experimental apparatus for laboratory flow-through experiments. Six replicates of the design shown here were used in filtration experiments. For bivalve experiments, the diameter of each experimental chamber was 10 cm, and chambers contained no sediment. The single control chamber served as a control for each of the 5 experimental chambers within a block. Aeration tubes were placed 2 cm above the surface of the sediment (or above the bottom of the chamber for bivalves) in the center of each chamber

cle-depleted filtered water would be immediately re-filtered by *Upogebia pugettensis* under well mixed conditions because the burrow's inhalant opening is typically separated by more than 10 cm from the exhalant opening.

Flow-through chambers consisted of 19 l plastic buckets containing 10 l of sediment and 4 l of overlying water (Fig. 1). An individual shrimp was placed in each chamber and allowed to burrow for at least 2 wk before experimentation began. Shrimp that did not burrow within 48 h were replaced. Chambers used for bivalve experiments consisted of 1 l plastic containers with no sediment. Bivalves were placed in experimental chambers at least 12 h before experiments were initiated. Experiments were conducted at ambient water temperature, which ranged from 11.6 to 13.6°C (experimental period June to October 2000), with the exception of the burrow wall experiment, which was conducted at a temperature of 15°C. The temperature during any given experiment was maintained within a 0.2°C range. Salinity ranged from 32.5 to 35.5‰

among experiments; however, no change in salinity was detected during an experiment.

Sediment was collected from an area of high *Upogebia pugettensis* density (300 to 350 ind. m⁻²) in the lower Yaquina estuary, sieved to <4 mm in order to remove large macrofauna, placed in experimental chambers, and allowed to settle for at least 24 h under a constant flow of seawater before introduction of shrimp. We collected *U. pugettensis* (0.44 to 3.49 g ash-free dry tissue weight [AFDW], mean 1.69 g) using a manual shrimp-bait pump (a piston-like suction device used to extract shrimp from their burrows). *Cryptomya californica* (0.008 to 0.069 g AFDW, mean 0.36 g) were collected by hand from a *U. pugettensis* bed in the lower Yaquina estuary. *Crassostrea gigas* was obtained from an oyster nursery at the Hatfield Marine Science Center, Newport, Oregon. All animals were fed continuously from the time that they were collected until the end of each experiment (approximately 90 d) on the same algal species used in feeding experiments, at cell concentrations of 5000 to 8000 cells ml⁻¹. Animals were fed on experimental concentrations of algae for at least 1 h before the beginning of an experiment.

For algae, we used a mixture of *Isochrysis galbana* (Tahitian strain) and *Rhodomonas salina* in all feeding rate experiments. These species were selected on the basis of availability, size, and motility; motile species were used to minimize the amount of algal cell settling in experimental chambers. *I. galbana* has a mean diameter of 3 to 4 μm, and a mean length of 5.5 μm. *R. salina* is larger, with a mean diameter of 7 μm and a mean length of 9 μm. These 2 algal species, together with particles present in the sand-filtered seawater supply, resulted in suspended particles ranging in size from 1.99 to 10.21 μm. Particle size and concentration in all laboratory and field feeding experiments were determined using a Coulter Multisizer II (model #0217). Total volumetric cell concentrations (μm³ l⁻¹) were converted to mg C l⁻¹ using the conversion factor described by Strathmann (1967):

$$\log_{10}\text{carbon}(\text{pg}) = -0.314 + 0.712 \times \log_{10}\text{cell volume}(\mu\text{m}^3) \quad (1)$$

We adjusted the water and algal supply rate to each chamber until equilibrium was established at the desired concentration (Bayne et al. 1987). Rates of water inflow to each chamber were determined by measuring the volume of water leaving the outflow over a period of 1 min and ranged from 1.14 to 17.4 l h⁻¹. Seawater samples (20 ml) were collected from the outflow of each experimental or control chamber for determination of particle concentrations. Total volumes of particles in each of 8 equal size ranges between 1.99 and 10.21 μm were estimated for each water sample. We calculated filtration rates as follows:

$$F = D \times (V^* - V) \quad (2)$$

where F is filtration rate in μm^3 (total volume of 2 to 10 μm particles removed) hr^{-1} , D is the rate of water supplied to the chamber in ml h^{-1} , V^* is the volumetric concentration ($\mu\text{m}^3 \text{ml}^{-1}$) of particles in the outflow of the control chamber (identical to experimental chambers, but without shrimp or bivalves), and V is the volumetric concentration ($\mu\text{m}^3 \text{ml}^{-1}$) of particles in the outflow of the experimental chamber. Filtration rates were converted from $\mu\text{m}^3 \text{h}^{-1}$ to mg C h^{-1} using conversion factors given in Eq. (1).

Determination of allometric relationships between tissue weights and filtration rates. We determined allometric relationships between AFDW and filtration rates for *Upogebia pugettensis*, *Cryptomya californica* and *Crassostrea gigas* exposed to 3 different algal concentrations in order to obtain data for the development of the population filtration model for Yaquina estuary. Animals used to determine allometric relationships weighed 0.44 to 3.29 g (*U. pugettensis*), 0.009 to 0.07 g (*C. californica*), and 0.08 to 0.53 g AFDW (*C. gigas*). AFDWs were determined after depurating animals in sand-filtered seawater without sediment for 48 h, drying them in an oven at 60°C to constant total dry weight, ashing them at 450°C for 24 h to obtain ash weights (Walne & Millican 1978), and subtracting ash weight from total dry weights to obtain AFDW.

We determined feeding rates at 3 different algal concentrations: 5000 to 8000 cells ml^{-1} (low) 15 000 to 20 000 cells ml^{-1} (medium), and 30 000 to 35 000 cells ml^{-1} (high), which were equivalent to 0.12, 0.23, and 0.48 mg C l^{-1} , respectively. Algal carbon concentrations in Yaquina Bay during the summer months range from 0.15 to 0.5 mg C l^{-1} (Karentz & McIntire 1977). A total of 30 experimental chambers and 6 control chambers (sediment only) were set up, distributed among 6 replicate blocks of 5 experimental and 1 control chamber (Fig. 1). Because some *Upogebia pugettensis* did not feed, filtration measurements were made with only 13, 11, and 17 shrimp at high, medium, and low algal concentration treatments, respectively. Filtration rates were determined for individual large *Crassostrea gigas* (shell length ≥ 2 cm). Filtration rates for small *C. gigas* (shell length < 2 cm) and *Cryptomya californica* were determined for groups of 6 to 20 individuals of approximately the same size placed in a single chamber and results were averaged to give individual feeding rates. Grouping of small *C. gigas* and *C. californica* was necessary in order to obtain detectable reductions in cell concentrations under experimental conditions. Measurements were obtained for 18, 18, and 9 large individuals or groups of small *C. gigas* and 16, 14, and 11 groups of *C. californica* at high, medium, and low algae concentrations, respectively.

Determination of relative retention efficiencies. We compared relative retention efficiencies for different sized particles to examine potential food competition, based on particle size selection, among *Upogebia pugettensis*, *Cryptomya californica*, and *Crassostrea gigas*. Retention efficiencies for particles of different sizes were expressed relative to the average retention of the particle size range ($\pm 5\%$) retained with the highest efficiency (Riisgård 1988, Ropert & Gouletquer 2000). Suspended particles in a 2 to 10 μm size range were divided into 8 size classes (1.99–2.99, 3.24–3.98, 4.23–4.98, 5.23–5.97, 6.22–6.97, 7.22–7.97, 8.22–8.96, and 9.21–10.21 μm diameter, hereafter referred to by the median values for each size class, i.e. 2.5, 3.5, 4.5 μm , etc.). Retention efficiencies were arcsine square-root transformed for statistical comparisons (Sokal & Rohlf 1995). Transformed retention efficiencies for each particle size class were compared among species using 1-way ANOVA ($\alpha = 0.05$), followed by Tukey's multiple comparison of means test ($\alpha = 0.05$). Assumptions for normality and homogeneity of variances were verified by viewing normal probability plots of residuals and applying Bartlett's test (at the 5% level of significance), respectively.

Determination of burrow wall effects on filtration rates. Settlement and adhesion of particles to the burrow wall could contribute to particle loss from water drawn through burrows, and thus increase apparent filtration rates of *Upogebia pugettensis*. We hypothesized that loss of suspended particles due to burrow wall effects would increase as burrow length increased. We could not directly measure particle removal by the burrow in the absence of shrimp because we were unable to remove shrimp from their burrows without affecting the physical integrity of the burrow wall. However, we were able to cause *U. pugettensis* to vary the length (and thus surface area) of their burrows by varying the volume and depth of sediment in which shrimp were allowed to burrow. We were able to derive a relationship between particle loss and total burrow-wall surface area that allowed us to separate loss due to burrow effects versus those due to shrimp filtration. Similar-sized *U. pugettensis* (20 to 22 mm carapace length [CL], mean: 21.6 ± 1.3 mm) were allowed to construct burrows within 'small' (0.5 l sediment, 6.5 cm sediment depth), 'medium' (5 l, 14.5 cm), and 'large' (10 l, 17 cm) sediment volumes. For each sediment volume, 5 chambers with shrimp and sediment were set up together with 5 control chambers containing sediment alone.

Although similar sized shrimp were used in this experiment, we further minimized the effect of shrimp size on filtration rates by standardizing filtration rates for an animal of 1 g AFDW following the procedure used by Bayne et al. (1987) and Bayne & Newell (1983):

$$F' = F \times (W_s/W_e)^b \quad (3)$$

where F' is the filtration rate of the standard animal (1 g AFDW), F is the uncorrected filtration rate of the experimental animal, W_s is the AFDW of the standard animal (1 g), W_e is the measured AFDW of the experimental animal, and b is the allometric coefficient, determined in experiments described above (see 'Allometric relationships between tissue weights and filtration rates'). *Upogebia pugettensis* AFDW was calculated using the empirically derived relationship between AFDW and CL (AFDW = $0.14 \times \text{CL} - 1.78$, $R^2 = 0.89$, Griffen unpubl. data). This estimate of AFDW was used because it was not possible to remove shrimp from their burrows at the end of the experiment without affecting the integrity of the burrows. Undamaged burrows were required for determination of burrow surface areas after filtration measurements were complete.

Burrow surface areas were determined from length and diameter measurements of burrow casts made with Plaster of Paris. We measured the length and mean diameter (average of diameter measurements made at 1 cm intervals) of the U-portion of each burrow cast (i.e. the section of burrow actively irrigated). We found *Upogebia pugettensis* burrows to be generally cylindrical, with approximately circular cross sections, having consistent diameters along the length of the burrows, and therefore used the geometric equations for cylinders to estimate the volume and surface area of the burrows. A Model II regression analysis was used to determine the relationship between filtration rates and burrow wall surface areas (Sachs 1982, Sokal & Rohlf 1995) because both of these variables were measured with error.

Determination of filtration rates in the field. We measured filtration rates of *Upogebia pugettensis* shrimp-burrow complexes in their natural environment using static chambers agitated by aeration (Penn Plax air pump, Model No. B10) to maintain an even distribution of suspended particles. We chose to use static chambers rather than open flumes because we wanted to examine the effect of algal concentration on filtration rates. Manipulation of algal densities using open flumes was considered impractical for this application.

Localized depletion of suspended particles in the vicinity of inhalent burrow openings, due to the presence of non-mixed filtered exhalent water from neighboring shrimp, could have reduced apparent filtration rates, especially at high shrimp densities. However, experimental results indicated that although there was a slight decrease in weight-specific filtration rates with increasing shrimp density (see 'Results' section), it was not statistically significant, indicating that the chambers were well mixed. As an added precaution against

the effects of non-homogeneous mixing, spatially separated subsamples of water were collected from each of 4 quadrants within a chamber and composited for determination of particle concentrations and filtration rates.

Field filtration rate measurements were conducted on a Yaquina estuary tide flat, approximately 100 m south-east of the Hatfield Marine Science Center, Newport, Oregon, USA, at approximately 0.3 m above MLLW. Three chambers were deployed at each of 3 sites, each site separated by approximately 50 m. Each chamber was positioned to contain a small area (0.13 m^2) of either high (197 ± 39 shrimp m^{-2}), medium (143 ± 21 shrimp m^{-2}), or low (48 ± 29 shrimp m^{-2}) population densities of *Upogebia pugettensis*, based on the number of burrow openings and the determined relationship between burrow opening and shrimp densities (see Table 2). For each shrimp density, we determined filtration rates starting at the same initial concentrations of *Isochrysis galbana* and *Rhodomonas salina* used in laboratory experiments, i.e. 5000 to 8000 cells ml^{-1} (low), 15 000 to 20 000 cells ml^{-1} (medium), and 30 000 to 35 000 cells ml^{-1} (high). A control treatment was included at each site, consisting of a 40 cm diameter closed-bottom chamber containing 5 cm of sediment sieved to <4 mm to remove macrofauna.

At each site, we pushed open-ended cylinders (40 cm in diameter and 1 m long) into the sediment to a depth of approximately 75 cm, isolating *Upogebia pugettensis* shrimp-burrow complexes inside the cylinder from the surrounding sediment. The 25 cm length of cylinder protruding above the sediment surface formed a chamber that held seawater at low tide. We deployed cylinders 2 wk prior to experimentation to allow shrimp inside the cylinders time to repair burrows that may have been damaged with cylinder placement (a period of 2 wk was considered sufficient, based on observations of burrow excavation by shrimp in the laboratory). We adjusted the volume of water (by siphoning) above the sediment surface inside each cylinder to 10 to 18 l, depending on *U. pugettensis* density. Larger water volumes were used with higher shrimp densities to reduce rates of phytoplankton depletion and allow adequate time for sampling.

Initial decreases in phytoplankton concentrations at the beginning of each feeding experiment could have been due to both filtration of overlying water and to dilution by water expelled from *Upogebia pugettensis* burrows with the initiation of feeding activities, resulting in overestimated filtration rates. Consequently, we initially added 25 to 30% more phytoplankton to each chamber than was needed to achieve desired initial concentrations. Filtration rates were determined when cell concentrations reached 8000, 20000, or 35000 cells ml^{-1} , respectively. Samples were taken every 15 min

over a period of ca. 3 h and ceased when cell concentrations declined to 5000, 15 000, or 30 000 cells ml⁻¹, respectively. Temperature (14.0 ± 1.4°C), salinity (32 ± 1‰), and water depth (14.3 ± 1.0, 11.1 ± 0.9, 8.0 ± 0.6 cm for high, medium, and low density shrimp, respectively) were measured inside the chambers for each trial.

Water present in the U-portion of shrimp burrows would be exchanged with overlying water in the cylinder, and must therefore be included in the total water volume used for filtration rate calculations. The total volume of water in burrows within each experimental chamber was estimated as the sum of the volumes of burrows for all shrimps collected from the chamber. The volume of a single burrow was estimated as a function of a shrimp's carapace length (CL) using the following empirical relationships: burrow diameter = *Upogebia pugettensis* CL/1.1 (Thompson 1972); burrow U-portion length = 3.68 × burrow diameter (measurements of 18 resin casts of *U. pugettensis* burrows; R² = 0.43 [B. D. Griffen unpubl. data]); and the equation for volume of a cylinder. Based on these calculations, we estimated that on average 74 % (± 6 % SD) of the water volume inside experimental cylinders was overlying the sediment and 26 % (± 6 % SD) was inside burrows. Therefore, the volume of water used in calculating filtration rates was increased by 26 % to include burrow water volume.

We calculated filtration rates (*F*) for *Upogebia pugettensis* shrimp-burrow complexes as follows:

$$F = V_c \times \frac{C_0 - C_1}{T} \quad (4)$$

where *V_c* is the volume of water inside the chamber (l; combined volume above the sediment surface and in burrows), *C₀* and *C₁* are the initial and final phytoplankton concentrations (mg C l⁻¹), respectively; and *T* is the duration (h) of the experiment (Dame 1996).

We repeated filtration rate measurements several times on separate days at each site, and obtained 1 to 3 filtration rate measurements at each food concentration for each shrimp density treatment. No more than 1 trial per day was conducted with any given chamber. We randomized the order in which food concentrations were tested in each cylinder. Results from multiple trials with the same experimental cylinder/shrimp density were averaged for each tested phytoplankton concentration, resulting in a single filtration rate for each cylinder/shrimp density for that algal concentration at each site. At the

end of the experiment, we excavated the contents of each chamber and determined the numbers and sizes of *U. pugettensis* and *Cryptomya californica*.

Population filtration model. The model was developed using field measurements of filtration rates for *Upogebia pugettensis* shrimp-burrow complexes and laboratory estimates of allometric relationships between AFDW and filtration rates. We also included population data for *U. pugettensis* and *Cryptomya californica* and hydrographic data collected for the Yaquina estuary (DeWitt and US Environmental Protection Agency [EPA], Western Ecology Division, Newport, Oregon, unpubl. data). Assumptions of the population filtration model were as follows: (1) Eq. (1) was valid for phytoplankton used in our experiments and in the estuary; (2) the particulate carbon concentration in the lower Yaquina estuary was homogeneous and the water mass was well mixed; (3) filtration rates were determined by phytoplankton concentration and not concentrations of detrital carbon or total suspended material; (4) animals fed for 50 % of the average period of submergence (consistent with laboratory observations). As discussed previously, many aspects of flow within the estuary and within the shrimp burrows are not known. These factors may have significant impacts on the availability and distribution of phytoplankton, as well as on shrimp feeding behavior and efficiency (LaBarbera 1981). Allometric relationships and parameters used in model calculations are given in Tables 1 & 2.

Five AFDW classes of *Upogebia pugettensis* and *Cryptomya californica* were used in the model because filtration rates for each species were size dependent (Table 1). Data on the abundances of *U. pugettensis* and *C. californica* and AFDW frequency distribution of *U. pugettensis* in the Yaquina estuary were already available (T. H. DeWitt and US EPA, unpubl. data; Table 2). The AFDW frequency distribution of *C. cali-*

Table 1. *Upogebia pugettensis*, *Cryptomya californica*, and *Crassostrea gigas* filtration rates. Equations developed from results of laboratory experiments describing allometric relationships between filtration rate (*F*, mg C h⁻¹) and ash free dry weight (AFDW, g) (see Eq. 2 in text). Equations were used to derive relative filtration rates for different size classes of animals

Phytoplankton concentration (mg C l ⁻¹)	<i>Upogebia pugettensis</i>	<i>Cryptomya californica</i>	<i>Crassostrea gigas</i>
0.12	$F = 0.62 \times W^{0.58}$ (R ² = 0.59) (p = 0.001)	$F = 0.24 \times W^{0.84}$ (R ² = 0.47) (p = 0.005)	$F = 0.47 \times W^{0.43}$ (R ² = 0.47) (p = 0.0036)
0.23	$F = 1.03 \times W^{0.89}$ (R ² = 0.84) (p = 0.0002)	$F = 0.24 \times W^{0.54}$ (R ² = 0.72) (p < 0.00001)	$F = 1.42 \times W^{0.62}$ (R ² = 0.55) (p = 0.0002)
0.48	$F = 0.83 \times W^{1.84}$ (R ² = 0.69) (p = 0.0008)	$F = 0.56 \times W^{0.58}$ (R ² = 0.59) (p = 0.0037)	$F = 3.42 \times W^{0.77}$ (R ² = 0.96) (p < 0.00001)

Table 2. Population filtration model parameters

Model parameters	Value(s)	Source
Algal carbon concentration (particulate organic carbon: POC)	0.12, 0.23, and 0.48 mg l ⁻¹	Calculated using equation by Strathman (1967)
Water volume	3.88 × 10 ⁹ l	Calculated from area (3 437 300 m ²) and average depth (1.13 m) of modeled area
Feeding period	11.25 h d ⁻¹	Estimated average daily submergence period of 22.5 h (based on hourly water elevation data from the NOAA tide gauge for South Beach, Oregon from June 1 to September 30, 2001), and assumed feeding for 50% of time submerged
<i>Upogebia pugettensis</i> habitat	2 099 900 m ²	Estimated using spatial interpolation functions in ESRI ArcView from ground-based surveys of <i>U. pugettensis</i> burrow distributions (T. H. DeWitt unpubl.)
Average <i>U. pugettensis</i> density throughout modeled area	189.8 m ⁻²	Calculated from burrow count survey data and relationship: No. <i>U. pugettensis</i> m ⁻² = (0.58 × no. holes m ⁻²) - 1.16 (T. H. DeWitt unpubl.)
No. of <i>Cryptomya californica</i> per <i>U. pugettensis</i> burrow	8	Represents average for estuary; range = 3 to 30 (T. H. DeWitt unpubl.)
<i>U. pugettensis</i> AFDW frequency distribution	<0.03 g = 0.09 0.03–0.14 g = 0.21 0.15–0.42 g = 0.3 0.43–0.95 g = 0.3 0.96–1.81 g = 0.1	Obtained from size frequency distribution in lower Yaquina, based on carapace length (CL), and using the empirically derived relationship: AFDW (g) = 0.00005 × (CL) ^{3.17} (T. H. DeWitt & B. D. Griffen unpubl.)
<i>C. californica</i> AFDW frequency distribution	<0.001 g = 0.05 0.001–0.002 g = 0.35 0.003–0.007 g = 0.33 0.008–0.028 g = 0.18 0.029–0.128 g = 0.09	Obtained from size frequency distribution in lower Yaquina, based on shell length (SL), and using the empirically derived relationship: AFDW (g) = (0.29e ^{0.25 × SL})/1000 (T. H. DeWitt & B. D. Griffen unpubl.)

californica in the lower Yaquina was determined from (1) the relationship between shell lengths (SL) and AFDW for approximately 300 individuals collected from the estuary: AFDW = 0.29e^{0.25 × SL}, R² = 0.71; (2) measurement of SL frequency distribution for >3000 *C. californica* collected from several locations throughout the lower Yaquina estuary; and (3) applying the equation relating AFDW and SL to the SL size-frequency distribution to determine the AFDW frequency distribution (Table 2).

We calculated the proportion of the total filtration rate (P_{ix}) measured in each field experimental chamber (x) that was attributable to each AFDW class (i) of *Upogebia pugettensis* and *Cryptomya californica* using relative filtration rates derived from allometric equations obtained from laboratory experiments (F_i , Table 1), and abundances of each AFDW size class of shrimp and *C. californica* in experimental chambers (n_i):

$$P_{ix} = \frac{F_i \times n_i}{\sum_{i=1}^j F_i \times n_i} \quad (5)$$

where j is the number of size classes. We then determined the average per capita filtration rate of individ-

uals of each size class (F_i^*) in the field using the proportion filtered by each size class in each chamber (P_{ix}), the experimentally measured filtration in each chamber (C_x), the number of individuals of each size class within each chamber (n_{ix}), the number of chambers (k), and the duration of field trials (t) as follows:

$$F_i^* = \frac{1}{k} \times \left(\sum_{x=1}^k \frac{P_{ix} \times C_x}{n_{ix} \times t} \right) \quad (6)$$

The amount of phytoplankton filtered (mg C d⁻¹) in the lower Yaquina estuary by all individuals combined was estimated by multiplying F_i^* by the number of animals in that class in the lower Yaquina (N_i , Table 2), and by our estimate of the average time spent feeding each day (h , Table 2), and dividing this value by the mass of phytoplankton carbon available as determined by the volume of water in the lower Yaquina (V_Y , Table 2) and the phytoplankton concentration (Q) as follows:

$$F = \frac{\sum_{i=1}^j F_i^* \times N_i \times h}{V_Y \times Q} \quad (7)$$

Chl *a* concentrations in the lower Yaquina estuary range from <1 to approximately 10 mg l⁻¹, with sum-

mer values ranging from 3 to 10 mg l⁻¹ (Karentz & McIntire 1977). Converting these chl *a* concentrations to mg algal carbon using a C:chl *a* ratio of 50 (Raymont 1980, and references therein) resulted in a range of carbon concentrations from 0.15 to 0.5 mg C l⁻¹. We only applied the model to algal concentrations tested in our laboratory and field experiments (0.12, 0.23, and 0.48 mg C l⁻¹) because we had no data on filter feeding by *Upogebia pugettensis* or *Cryptomya californica* at other concentrations.

RESULTS

Feeding experiment

Relative retention efficiencies for each species generally increased with increasing particle size (Fig. 2). *Upogebia pugettensis* and *Crassostrea gigas* had significantly higher retention efficiencies than *Cryptomya californica* for 7.5 and 8.5 μm size classes (Tukey's test, $p < 0.05$). Retention efficiencies were similar among species for all other size classes of particles; however, *C. californica* may have filtered smaller particles (2.5 and 3.5 μm) more efficiently than oysters or shrimp plus burrow, although the differences were not statistically significant ($p > 0.05$).

Allometric equations for filtration rates (mg C h⁻¹) as a function of individual AFDW for *Upogebia pugettensis*, *Cryptomya californica*, and *Crassostrea gigas* at the 3 algal concentrations tested are given in Table 1. *C. californica* and *Crassostrea gigas* filtration rates

increased linearly with increasing phytoplankton concentrations for a given sized individual, indicating that these bivalve species did not adjust the volume of water filtered per unit time to maintain a constant algal removal rate. Filtration rates for *C. californica* and for the smallest size class of *C. gigas* may have been underestimated because filtration rates of groups of animals in the same chamber were determined, and algal concentrations may not have been homogeneous immediately surrounding individual bivalves in the group. *U. pugettensis* filtration rates increased to a lesser degree or decreased with increasing phytoplankton concentrations (Table 1), indicating that shrimp decreased the volume of water filtered per unit time as phytoplankton concentration increased.

Burrow wall experiment

There was a linear positive relationship between filtration rates of a standardized (1 g AFDW) shrimp plus burrow and burrow-wall surface area for the range of burrow sizes (length 27 to 93 cm, surface area 146 to 568 cm²) tested in this experiment (Model II regression, $p = 0.05$; analysis of the same data with Model I regression gave identical results; Fig. 3). Differences in particle removal rates observed with shrimp in burrows of various lengths did not appear to be due to differences in shrimp behavior because there were no noticeable differences in burrowing activities, frequency of feeding, or general burrow morphologies among treatments.

For simplicity, we assumed in our analysis that depletion of particles was a linear function of burrow surface area. This may not be the case because the chance of particles coming into contact with the burrow wall may be affected by burrow morphology, such as branching and turning frequency (Reist 1993, Zang

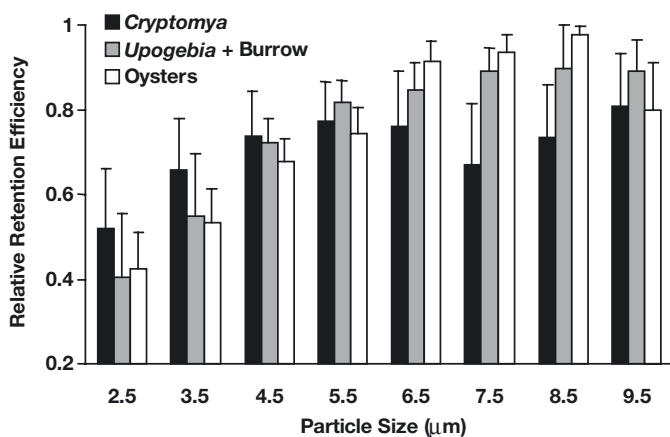


Fig. 2. *Upogebia pugettensis* plus burrow, *Cryptomya californica*, and *Crassostrea gigas*. Relative retention efficiencies (mean \pm 1 SD) for animals fed on a range of particle sizes of algae and natural seston. Efficiencies are expressed relative to the maximum retention efficiency observed for each species calculated separately. N = 16, 16, and 17, for *Upogebia*, *Cryptomya*, and *Crassostrea*, respectively

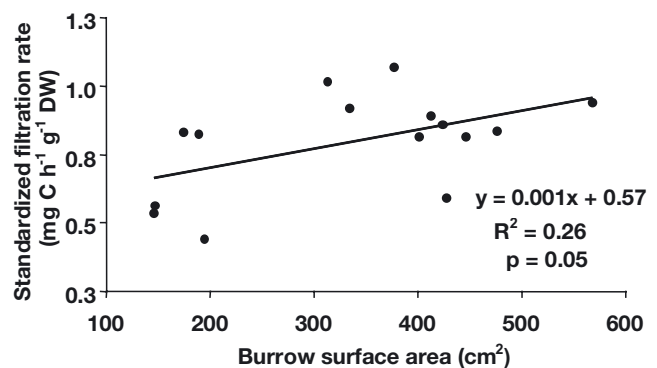


Fig. 3. *Upogebia pugettensis*. Filtration rate (mg C h⁻¹) as a function of burrow-wall surface area, standardized to a shrimp of 1 g ash free dry weight. N = 15

& Kleinstreuer 2000). These factors, in addition to behavioral differences among individual *Upogebia pugettensis*, are likely responsible for a major portion of the variability in particle removal rates, as indicated by the low R^2 (0.26) for the regression; however, the significant ($p = 0.05$) slope of the regression indicates that significant amounts of suspended material may be removed by the burrow itself.

The y -intercept of the regression of filtration rate against burrow-wall surface area (0.57 mg C h^{-1} , Fig. 3) can be considered as the filtration rate of a standard shrimp (1 g AFDW) in the absence of a burrow. As the average length of casts from 18 *Upogebia pugettensis* burrows in the field was approximately 100 cm, the surface area of an average burrow would be 577 cm^2 (described above: burrow wall surface area = $5.77 \times \text{burrow length}$; $R^2 = 0.91$). Therefore, based on the regression equation that described the relationship between filtration rate and burrow surface area (Fig. 3), we obtain an algal removal rate for a standardized *U. pugettensis* (1 g AFDW), occupying a burrow with a surface area of 577 cm^2 , of approximately 0.97 mg C h^{-1} , i.e. a rate that is approximately 1.7 times greater than that for a shrimp (1 g AFDW) without a burrow.

Field measurements of filtration rates

Filtration rates (mg C h^{-1}) of *Upogebia pugettensis* shrimp-burrow complexes in the field generally increased with increasing shrimp density (Fig. 4) and biomass (filtration rate = $0.38 \times \text{shrimp biomass} + 2.21$, $p = 0.004$, $R^2 = 0.73$), except that no increase in filtration rates was observed when shrimp densities increased from 143 to 197 m^{-2} at the highest phytoplankton concentrations (0.48 mg C l^{-1}). Filtration rates also increased with increasing phytoplankton concentrations (filtration rate = $7.51 \times \text{phytoplankton concentration} - 5.3$, $p = 0.0005$, $R^2 = 0.45$; Fig. 4). There was a slight negative relationship between *U. pugettensis* density and weight-specific filtration rate (filtration rate [$\text{mg C h}^{-1} \text{ g}^{-1}$ AFDW] = $-0.004 \times \text{shrimp biomass} + 0.63$, $p = 0.13$, $R^2 = 0.30$); however, this relationship was not statistically significant.

The effects of temperature and site (i.e. substrate or other site-specific factors) on field filtration rates were examined using data from chambers tested with the high phytoplankton concentration. Filtration rates were not affected by the range of temperatures occurring among chambers (12.6 to 17.7°C ; linear regression, $R^2 = 0.002$; $p = 0.89$) or among-site conditions (ANOVA; $df = 2, 6$; $p = 0.82$). Furthermore, there was no difference in shrimp size (CL) among the shrimp-density treatments (ANOVA, $df = 2, 143$, $p = 0.41$).

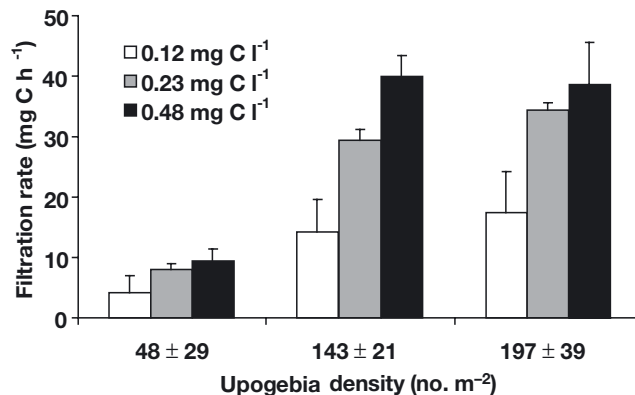


Fig. 4. *Upogebia pugettensis* and *Cryptomya californica*. Filtration rates (mean \pm 1 SD) for shrimp-burrow complexes as measured in field experimental chambers at $14.0 \pm 1.4^\circ\text{C}$ and 32‰ salinity. $N = 3$ for each shrimp density (mean \pm 1 SD) and phytoplankton concentration ($0.12, 0.23, 0.48 \text{ mg C l}^{-1}$) combination. Numbers of individuals inside chambers that were used to calculate densities per m^2 : high (24.7 ± 4.7 shrimp and 367 ± 49 *Cryptomya* chamber⁻¹), medium (16.3 ± 5.7 shrimp and 294 ± 198 *Cryptomya* chamber⁻¹), or low (7.7 ± 6.4 shrimp and 156 ± 161 *Cryptomya* chamber⁻¹)

Based on relative filtration rates, the number of *Cryptomya californica* per shrimp burrow in the lower Yaquina estuary, and the relationship that we observed between burrow surface area and particle removal (Fig. 3), we estimate that phytoplankton drawn into the burrows was removed by the 3 components of the shrimp-burrow complex in the following proportions (at low, medium, and high phytoplankton concentrations): *Upogebia pugettensis*: 57, 53, and 40%, the burrows: 31, 28, and 21%, and *C. californica*: 12, 19, and 39%, respectively. These estimates are based on the assumption that shrimp and commensal clams experience the same food concentration in filtered water, which may vary depending on whether individual *C. californica* are located upstream or downstream of the shrimp within the burrow.

Population filtration model

Results of our population filtration model, based on laboratory and field measurements, indicated that *Upogebia pugettensis* shrimp-burrow complexes in the lower Yaquina may be capable of filtering the entire volume of water overlying their burrows every day, ignoring tidal exchange (Table 3 and Fig. 5). The model estimated a 70% increase in the proportion of phytoplankton carbon filtered by *U. pugettensis* shrimp-burrow complexes as phytoplankton concentration increases from low (0.12 mg C l^{-1}) to medium (0.23 mg C l^{-1}) values, due to concentration-dependent

Table 3. *Upogebia pugettensis*, and *Cryptomya californica*. Daily population filtration rates (mg C d^{-1}) for *Upogebia* plus burrows, and *Cryptomya* in the lower Yaquina estuary, Oregon, as predicted by the population filtration model for each phytoplankton concentration (0.12, 0.23 and 0.48 mg C l^{-1}). Animal sizes correspond to ash free dry weight (AFDW) classes used in model calculations. Total population size refers to the number of individuals of each size class used in model calculations

	AFDW (g ind.^{-1})	Total population size	Population filtration rates (mg C d^{-1})		
			0.12 (mg C l^{-1})	0.23 (mg C l^{-1})	0.48 (mg C l^{-1})
<i>Upogebia</i> + burrow	<0.03	3.59×10^7	1.0×10^7	8.4×10^6	4.1×10^5
	0.03–0.14	8.37×10^7	4.3×10^7	7.9×10^7	1.1×10^7
	0.15–0.42	1.20×10^8	9.0×10^7	2.8×10^8	1.5×10^8
	0.43–0.95	1.20×10^8	2.0×10^8	5.4×10^8	7.1×10^8
	0.96–1.81	3.99×10^7	6.9×10^7	3.1×10^8	6.7×10^8
<i>Cryptomya</i>	<0.001	1.59×10^8	2.3×10^5	4.0×10^6	1.1×10^7
	0.001–0.002	1.12×10^9	4.1×10^6	4.3×10^7	1.3×10^8
	0.003–0.007	1.05×10^9	1.2×10^7	8.5×10^7	2.8×10^8
	0.008–0.028	5.74×10^8	8.5×10^6	7.9×10^7	3.1×10^8
	0.029–0.128	2.87×10^8	3.2×10^7	8.1×10^7	2.8×10^8

increases in filtration rates for both shrimp and *Cryptomya californica* (Fig. 5). However, the model estimated that the proportion of phytoplankton removed decreases from medium to high concentrations (0.48 mg C l^{-1}) because the increase in available phytoplankton from medium to high concentrations was proportionally greater than the increase in filtration rates of the *U. pugettensis* shrimp-burrow complexes. A sensitivity analysis indicated that model estimates of phytoplankton removal will depend both on the duration of feeding activity (our model assumes that *U. pugettensis* and *C. californica* actively feed 50% of

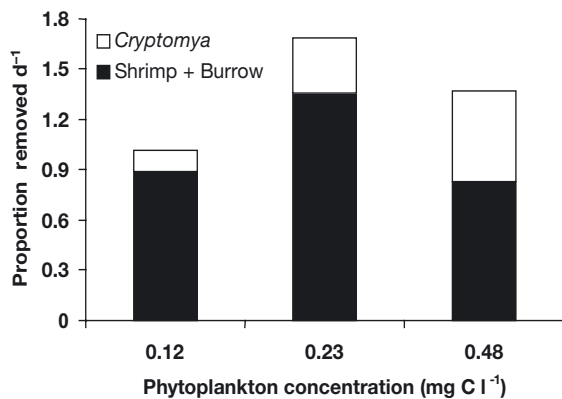


Fig. 5. *Upogebia pugettensis* and *Cryptomya californica*. Proportion of available phytoplankton potentially filtered by shrimp-burrow complexes (shown for shrimp plus burrow and *Cryptomya* separately) from overlying water in the lower Yaquina estuary only, without considering tidal exchange. Values representing the proportion potentially filtered by shrimp-burrow complexes in the lower Yaquina from the total tidally exchanged volume of water are given in Table 2

the time when shrimp burrow openings are submerged, based on laboratory observations) and tidal flux of water. Additionally, our model does not account for possible changes in feeding behavior and food availability as a function of current velocity above the shrimp burrow openings. We discuss the potential impacts of these factors on the model results below.

DISCUSSION

Based on field and laboratory measurements, our population filtration model indicated that *Upogebia pugettensis* shrimp-burrow complexes in the lower Yaquina

estuary may be capable of filtering the entire static volume of water overlying their burrows more than once per day (100% carbon removal = 4.66×10^5 to $1.86 \times 10^6 \text{ g C d}^{-1}$; Fig. 5). This finding is similar to that of Dworschak (1981) who estimated that Mediterranean populations of *U. pusilla* were capable of filtering 1.4 times the entire volume of water overlying their burrows in 24 h. Similar system-wide filtration rates have been estimated for suspension feeding bivalves in other estuarine and freshwater systems, such as for mussels in the Oosterschelde estuary (Netherlands, Smaal et al. 1990), for clams in the Providence River (Rice et al. 2000), and for zebra mussels in the Hudson River (Roditi et al. 1996).

Several factors may affect the accuracy of our model of phytoplankton reduction by *Upogebia pugettensis* shrimp-burrow complexes. First, we assumed that *U. pugettensis* feed for 50% of the time that they are submerged. This value was based on observations of *U. pugettensis* held in laboratory aquaria. However, *U. pusilla*, a related species, only actively pumps for 28% of the time, on average (with a range of 18 to 42%; Dworschak 1981). Decreasing the amount of time that *U. pugettensis* spend feeding in our model to 28% reduces the predicted amount of carbon removed by 44%. *U. pugettensis* may also spend less time suspension feeding at low food concentrations due to lower nutritional benefits compared to deposit feeding (Powell 1974). We observed *U. pugettensis* occasionally deposit feeding while in laboratory aquaria, although we have not investigated the importance of this feeding mode relative to suspension feeding. Reduced filtration rates at low phytoplankton concentrations observed in field experiments may therefore have been a result of some shrimp switching to deposit feed-

ing, or stopping feeding activities altogether. Salinity, temperature and the qualitative composition of food may also affect feeding behavior of *U. pugettensis* or *Cryptomya californica*, although differences in temperature and substrate among field sites did not affect filtration rates for *U. pugettensis* shrimp-burrow complexes in this study.

Hydrodynamic factors not examined here may also significantly affect particle removal by *Upogebia pugettensis* shrimp-burrow complexes. Renewal of depleted phytoplankton over shrimp beds (an assumption of the model) depends on circulation patterns within the estuary. If sufficient flow does not occur over shrimp beds, then at high densities, shrimp may deplete the overlying water and significant refiltration of previously filtered water may occur. Flow over shrimp beds may also create passive flow through burrows via the Bernoulli effect (Allanson et al. 1992), which may affect feeding rates. Additionally, flow patterns within the burrow may alter feeding rates of *U. pugettensis* and *C. californica* potentially due to both refiltration of previously filtered water and the effects of flow rate on particle removal by feeding appendages (LaBarbera 1981).

Secondly, a major portion of suspended particulate organic carbon in the Yaquina estuary is composed of detritus and resuspended benthic diatoms (Amspoker & McIntire 1978, Callaway et al. 1988). Water pumped through *Upogebia pugettensis* burrows most likely contains significant concentrations of detrital and resuspended particulate organic carbon, in addition to phytoplankton cells (Shaffer & Sullivan 1987). The gut contents of related species, *U. deltaura* and *U. stellata*, consisted of phytoplankton, sediment, and detritus in the same proportions as found in the water column (Pinn et al. 1998), indicating a lack of pre-ingestion sorting of filtered material. If the same is true of *U. pugettensis*, as is suggested by the findings of Powell (1974), it is possible that *U. pugettensis* filtration rates are a function of total suspended particulate organic matter concentration, rather than of phytoplankton concentration alone. Reduced filtration of phytoplankton in response to the use of suspended detritus by *U. pugettensis* or *Cryptomya californica* would cause the model to over-predict the proportion of phytoplankton removed by *U. pugettensis* shrimp-burrow complexes. Additionally, high levels of resuspended epibenthic food particles (e.g. pennate diatoms) have led researchers to conclude that depletion of water column phytoplankton may not occur in some areas (Judge et al. 1993). Further work is needed before conclusions can be reached regarding the relative importance of water column- and epibenthic-derived particulate matter as food sources for *U. pugettensis* shrimp-burrow complexes in Oregon estuaries.

Our model also does not fully account for tidal exchange of water in the lower Yaquina estuary. Approximately 70% of the 4.53×10^{10} l of water contained in the Yaquina estuary at high tide is exchanged with ocean water over a complete tidal cycle (i.e. approximately every 12 h) (Karentz & McIntire 1977). This entire exchanged volume of water must pass through the modeled area as it is situated near the mouth of the estuary. Therefore, the volume of water passing over *Upogebia pugettensis* populations may be almost 10-fold greater than the static volume of water overlying shrimp populations in the lower Yaquina (3.88×10^9 l), and equal to 70% of the entire volume of the Yaquina estuary (3.17×10^{10} l). Oceanic water brought into the estuary with the flood tide will replenish phytoplankton in the estuary. Consequently, based on our filtration measurements, *U. pugettensis* shrimp-burrow complexes in the lower Yaquina may potentially remove only 6, 10, and 8% of available phytoplankton from the tidally exchanged volume at low, medium, and high phytoplankton concentrations, respectively. However, *U. pugettensis* shrimp-burrow complexes in other parts of the estuary will also filter phytoplankton, increasing overall phytoplankton removal by *U. pugettensis* shrimp-burrow complexes within the estuary. Additional information is needed on the hydrodynamics of the Yaquina Bay estuary to estimate the volume of water and concentrations of ocean-derived phytoplankton that flow over intertidal mudflats in order to more accurately estimate the mass of phytoplankton removed from the water column by *U. pugettensis* populations.

Based on laboratory measurements and our population filtration model, *Upogebia pugettensis* will remove the majority of suspended material drawn into their burrows. The portion potentially removed by *Cryptomya californica* increases with increasing phytoplankton concentrations because filtration rates of *C. californica* increase to a greater extent with increasing phytoplankton concentrations than do filtration rates of *U. pugettensis* (Tables 1 & 3). At low phytoplankton concentrations, *C. californica* may only filter 12% of the total phytoplankton removed by *U. pugettensis* shrimp-burrow complexes, whereas as at high phytoplankton concentrations this amount may increase to 39%, approximately the same proportion as that removed by shrimp.

In addition, we determined that the *Upogebia pugettensis* burrow itself may remove a substantial proportion of phytoplankton drawn into the burrow. For example, we estimated that a burrow 100 cm long could remove phytoplankton at a rate that was equal to 70% that of a standard-sized shrimp (1 g AFDW). We suspect that phytoplankton removal by burrows was due to adhesion of cells to the walls rather than settle-

ment within the burrows, because the feeding experiments were conducted using motile algae that were unlikely to passively settle out of suspension. Settlement in the burrow may be more pronounced for non-motile algae, resuspended benthic microalgae, diatoms with spines, or detrital material, which could more readily drop out of suspension and adhere to the mucus-lined burrow wall. Our laboratory estimates of removal rates due to the burrow itself may, therefore, underestimate removal rates in the field where a high proportion of the seston may be composed of non-motile diatoms and detritus.

Particle removal by the burrow also may depend on the size of the resident shrimp. Small shrimp will excavate burrows with greater surface area to volume ratios than large shrimp because burrow diameter is proportional to *Upogebia pugettensis* carapace length (Thompson 1972, Dworschak 1987a,b); therefore, a greater proportion of the phytoplankton that passes through the burrows of small shrimp will likely come in contact with and adhere to the burrow wall than in burrows of large shrimp. We hypothesize that burrow walls will be more important in particle removal for populations of small individuals than for those dominated by large shrimp. Other effects of burrow morphology on particle removal, such as surface roughness or turning intensity, were not examined in this study (Reist 1993, Zang & Kleinstreuer 2000). These factors, together with flow patterns within the burrows, may affect particle losses to the burrow wall.

Once algae adhere to the burrow wall, they may serve as a food source for *Upogebia pugettensis*. *U. stellata* (Nickell & Atkinson 1995) and *U. pusilla* (Dworschak 1987b) have the ability to feed on material that has settled in the burrow. The presence of plant detritus and fine sediments in the digestive tracts of *U. pugettensis*, *U. affinis*, *U. africana*, and *U. deltaura* may also indicate an ability to feed on material from within the burrow (Griffis & Suchanek 1991). Laboratory observations of deposit feeding by *U. pugettensis* lead us to believe it too feeds on particulate material from the burrow wall.

We found limited evidence for resource partitioning between *Upogebia pugettensis* and the commensal *Cryptomya californica*, based on retention efficiencies for different sizes of food particles. Instances of resource partitioning based on particle size selection have been found in other benthic suspension-feeding communities (e.g. Stuart & Klumpp 1984). Shrimp retained 7.5 and 8.5 μm size classes more efficiently than *C. californica*, and there was an indication (although not statistically significant) that *C. californica* retained 2.5 and 3.5 μm particles more efficiently than shrimp. However, overall, both species showed a similar pattern of retention efficiencies for particles in the size range of 2 to 10 μm .

Similarity of retention efficiencies between Pacific oysters *Crassostrea gigas* and *Upogebia pugettensis* for particles 2 to 10 μm in diameter indicates that, if food is limiting (for which we have no data), the 2 species may compete for food where they co-occur. *C. gigas* filtration rates in this study were similar to those previously reported by others (Bougrier et al. 1995). We compared filtration rates of an average *U. pugettensis* shrimp-burrow complex with that for a 0.75 g AFDW *C. gigas* (4.06 cm shell length; Langdon & Robinson 1996), based on the combined AFDW of an average sized shrimp and *C. californica* inhabiting burrows in the Yaquina estuary. We estimated that it would require densities of 545, 433, and 300 *C. gigas* m^{-2} at low, medium and high algal concentrations, respectively, to remove the same amounts of phytoplankton as those predicted to be removed by densities of *U. pugettensis* shrimp-burrow complexes currently found in the lower Yaquina estuary. These *C. gigas* densities are high by commercial standards — intensively cultured Pacific oysters are planted at densities up to 200 to 300 m^{-2} . Because *C. gigas* and other bivalves are often cultured in proximity to *U. pugettensis*, competition between these species could be economically and ecologically significant (Feldman et al. 2000). However, measurements of *C. gigas* growth in plots with or without *U. pugettensis* did not indicate an effect of *U. pugettensis* on oyster growth rates (Dumbauld 1994). Additional studies are required to examine competition between *U. pugettensis* and other suspension-feeders, to better understand possible trophic inter-relationships, particularly under conditions in which food resources can be demonstrated to be growth limiting.

In summary, *Upogebia pugettensis*, as a component of an average *U. pugettensis* shrimp-burrow complex, removes the greatest proportion of phytoplankton. However, the walls of *U. pugettensis* burrows themselves may remove substantial proportions of phytoplankton, particularly where *U. pugettensis* populations are dominated by small individuals or in areas where burrows are long (>100 cm). *Cryptomya californica* remove a smaller proportion of phytoplankton than either shrimp or burrows at low phytoplankton concentrations, but this proportion may increase to rival that of *U. pugettensis* at high phytoplankton concentrations. Similarities in relative particle retention efficiencies of *U. pugettensis*, *C. californica*, and *Crassostrea gigas* indicate potential food competition between *U. pugettensis* shrimp-burrow complexes and other suspension-feeders under conditions where planktonic food is limiting. Our population filtration model indicated that *U. pugettensis* shrimp-burrow complexes are potentially capable of removing large proportions of available phytoplankton from water

overlying tide flats of the lower Yaquina estuary. Additional information on hydrodynamic flux of ocean-derived phytoplankton and resuspension of epibenthic particulate matter within Yaquina estuary, and the effect of detrital matter and current velocity on filtration by *U. pugettensis* shrimp-burrow complexes, are needed to improve the accuracy of our population filtration model.

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