AN ABSTRACT OF THE THESIS OF

Blaine D. Griffen for the degree of Master of Science in Marine Resource Management presented on February 26, 2002. Title: Feeding Rates of the Mud Shrimp *Upogebia pugettensis* and Implications for Estuarine Phytoplankton Abundance.

Abstract approved: _____
Christopher Langdon

The suspension-feeding mud shrimp, *Upogebia pugettensis,* is a common inhabitant of intertidal mudflats in estuaries throughout the Pacific Northwest, where it develops extensive burrows. Also inhabiting the shrimps' burrow is the commensal bivalve, *Cryptomya californica.* Filtration by dense populations of the shrimp and its commensals may have a negative impact on phytoplankton abundance within these estuaries. The presence of the shrimp introduces three possible sinks for phytoplankton: filtration by the shrimp, filtration by the commensal bivalve, and removal of phytoplankton by the burrow itself. Together, the shrimp, commensal bivalve, and burrow, comprise the shrimp-burrow complex. Laboratory feeding experiments were conducted to measure particle removal rates of the shrimp-burrow complex, and to determine the relative importance of each of the three components of the complex in particle removal. For comparison, the same experiments were conducted with the Pacific oyster, *Crassostrea gigas.* Retention efficiencies were determined for particles in the size range from 2 to 10 μm in an effort to determine whether shrimp utilize the same size range of particles as other suspension feeders. Using data from our filtration experiments, a simple

box model was developed to predict the proportion of the total volume of water in the lower Yaquina Bay, Oregon, that is filtered by shrimp-burrow complexes over a 24-hour period. Results indicate that the burrow wall may be an important factor in removal of phytoplankton (expressed as suspended POC), potentially accounting for 0.7 that removed by the shrimp alone. The model predicts that, for the phytoplankton concentrations tested, the shrimp-burrow complex may potentially remove 0.152-1.667 times the total amount of phytoplankton found in the lower Yaquina each day, depending on tidal-flow dynamics. We conclude that the shrimp-burrow complex is capable of removing large proportions of available phytoplankton, and may potentially deplete phytoplankton in some areas of the lower Yaquina Bay.

Master of Science thesis of Blaine D. Griffen presented on February 26, 2002.

APPROVED:

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Blaine D. Griffen, Author

Feeding Rates of the Mud Shrimp *Upogebia pugettensis* and Implications for Estuarine Phytoplankton Abundance

by
Blaine D. Griffen

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CONTRIBUTION OF AUTHORS

Dr. Chris Langdon assisted in development of the project, interpretation of results, and editing of manuscripts. Laboratory experiments were conducted in the laboratory of Dr. Theodore H. DeWitt, who also assisted in the development of the project, interpretation of results and editing of manuscripts.

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Feeding Rates of the Mud Shrimp *Upogebia pugettensis*
and Implications for Estuarine Phytoplankton Abundance

Introduction

The mud shrimp *Upogebia pugettensis* is one of the dominant benthic invertebrates in many Pacific Northwest estuaries where it is found in dense populations in intertidal and shallow subtidal areas. Despite its prominence in West Coast bays and estuaries, little is known about shrimp feeding rates and the impact that they may have on phytoplankton abundance and food availability for other suspension-feeders inhabiting these environments.

This study was conducted in the lower region of Yaquina Bay, Oregon, which is characterized by large intertidal mud flats that are densely inhabited by mud shrimp. Food competition with other suspension feeders may exist if filtration by mud shrimp populations significantly reduces phytoplankton abundance in this part of the Bay.

Firstly, we measured filtration rates of shrimp, a commensal bivalve *Cryptomya californica*, and the Pacific oyster *Crassostrea gigas* as a function of body size and phytoplankton concentration. Relative retention efficiencies were measured for particles in the two to ten μm size range in order to determine whether shrimp utilize particles in the same size range as the Pacific oyster, an important commercial species in Yaquina Bay.

Measured particle-removal rates for shrimp, *Cryptomya* and the burrow itself (the shrimp-burrow complex) were used to develop a mathematical model that

predicts the proportion of available phytoplankton in the lower Yaquina Bay, at concentrations similar to those used in our experiments, that may be removed by shrimp populations and associated shrimp-burrow complexes.

Chapter 1: Feeding Rates of the Mud Shrimp *Upogebia pugettensis*

INTRODUCTION

One of the dominant benthic species throughout Pacific Northwest (PNW) estuaries is the burrowing shrimp *Upogebia pugettensis*, hereafter referred to as shrimp. This suspension-feeding thalassinid reaches densities greater than 300 m^{-2} (>1 kg m^{-2}) in some PNW estuaries (DeWitt, US EPA, unpubl. data; Bird, 1982), such as Yaquina Bay (OR), Coos Bay (OR), and Willapa Bay (WA). Despite its prominence in West Coast bays and estuaries, sites important to other suspension feeders (including commercially important bivalves), little is known about shrimp feeding rates and the impact that they may have on phytoplankton abundance. Shrimp primarily inhabit intertidal mud and sand flats in estuaries and bays, where they construct burrows that may reach depths of one meter (Griffis and Suchanek 1991, Thompson 1972, Stevens 1929). Shrimp secrete mucus from their hind-gut glands that cements sediment particles and other debris together to form the burrow wall (Thompson 1972). By beating their pleopods, shrimp create a current through the burrow. Various types of setae are spaced about 6 μm apart over the front appendages of shrimp. These are used to form a setal basket with the chelipeds and the second pair of walking legs. As the pumped water is passed through the setal basket, suspended particles are removed by the setae. The third pair of walking legs is then used to sweep particles from the setal basket and pass them to the mouth (Powell 1974).

The commensal clam, *Cryptomya californica*, hereafter referred to as *Cryptomya*, often inhabits the burrow along with the shrimp (MacGinitie 1934,

1935). Several *Cryptomya* may inhabit a single shrimp burrow (approximately eight per burrow in lower Yaquina Bay, DeWitt unpubl data). 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 current that is generated through the burrow by the pumping activities of the shrimp.

Removal of suspended food as water is pumped through the burrow can functionally be attributed to three components – filtration by shrimp, filtration by *Cryptomya*, or losses in the burrow due to physical factors such as settlement and adhesion to burrow walls. The mucus used by the shrimp to construct their burrow walls (Thompson 1972) may potentially "capture" a portion of the suspended food material. These three components together comprise what we call the "shrimp-burrow complex." We examined each of these components separately in an effort to understand their relative importance in removal of phytoplankton.

In our experiments, we were unable to test the feeding rates of shrimp in the absence of the burrow (see Appendix 1). Also, due to dimensional constraints of laboratory experimental chambers, shrimp in the laboratory developed shallower burrows than those observed by other researchers in the field (Griffis and Suchanek 1991; Thompson 1972; Stevens 1929; current authors, unpubl. data). For these two reasons, references throughout this paper to particle removal (both rates and efficiencies) by shrimp in the laboratory are actually referring to particle removal by a shrimp plus a truncated burrow. Effects of this experimental system on results of this study and their application to the natural environment will be discussed.

To determine the effect of food concentration and animal size on shrimp and *Cryptomya* feeding rates, we conducted laboratory experiments at three different algae concentrations (5-8,000 cells/ml, 15-20,000 cells/ml, and 30-35,000 cells/ml) and with various sizes of animals from 0.6 to 2.3 g dry tissue weight for shrimp, and from 0.01 to 0.07 g dry tissue weight for *Cryptomya*.

Powell (1974) examined the gut contents of *Upogebia pugettensis*, and reported that they may consume particles up to 50 μm in diameter. However, because more than 95% of suspended particles in Yaquina Bay are < 10 μm in diameter (from water column samples analyzed with a Coulter Counter; Griffen, unpubl. data), this study is concerned only with particles in this lower size range. While the less abundant, larger particles could be an important part of the shrimps' diet, they were not examined in this study.

Prior research on suspension-feeding thalassinids indicates that they are non-selective feeders. For instance, Pinn et al. (1998) compared gut contents with materials in overlying water and found that *Upogebia deltaura* and *Upogebia stellata* were both non-selective suspension feeders, with respect to phytoplankton, detritus, and suspended sediment. Nguyen (1984) showed that *U. deltaura* mainly fed on particles from 2 to 10 μm in diameter. No difference in retention of particles in this size range has been reported for suspension-feeding burrowing shrimp. However, Pinn et al. (1998) indicated that because the setae on mouth-parts of *U. deltaura* are spaced at ca. 6 μm, particles with a diameter < 6 μm would easily pass through the setal basket and no relative difference in capture would be observed for

these particles. Because setae used by *U. pugettensis* to capture food particles are also spaced 6 μm apart (Powell 1974), the same relative non-selectivity for particles < 6 μm in diameter could be inferred. However, as seen with numerous bivalve species (Riisgård 1988), particles in this size range are retained, but with different efficiencies - larger particles being captured with a higher efficiency than smaller particles. As water passes through the shrimp's setal basket, suspended particles will either impact the setae and be captured, or will remain in suspension and will pass around the setae. Because particle encounter is directly proportional to particle size (see Shimeta & Jumars 1991), large particles are more likely to be captured than smaller particles. It therefore seems reasonable that a similar phenomenon of variable retention of particles < 6 μm may be found with mud shrimp.

We examined particle retention efficiencies in an effort to determine whether shrimp utilize the same size range of particles as has been reported for other suspension feeders. Many bivalve species have been found to show maximum retention efficiencies with particles between 4 and 12 μm (Ropert & Goulletquer 2000, Barillé et al. 1993, Riisgård 1988, Palmer & Williams 1980, Møhlenberg & Riisgård 1978, and Winter 1978). If shrimp were found to have a similar range of particle retention efficiencies as those reported for bivalves, it would suggest the possibility of food competition between shrimp and bivalves in areas where they co-occur.

We also measured feeding rates and particle retention efficiencies of the Pacific oysters, *Crassostrea gigas*, (hereafter referred to as oysters) fed on the same algal diets, as a representative bivalve with which to compare shrimp feeding dynamics.

MATERIALS AND METHODS

Definitions: Filtration rate is defined as the volume of particles or the mass of organic carbon removed from suspension per unit time; pumping rate is defined as the rate at which shrimp move water through the burrow; retention efficiency is defined as the efficiency of particle removal, relative to a maximum shown by the organism, for a particle of a specific size within a size range of 2 to 10 μm (*sensu* Riisgård 1988).

General Procedures

A preliminary experiment was conducted to examine the feasibility of conducting feeding experiments with shrimp in artificial burrows (see Appendix 1). The results of this experiment indicated various problems with using artificial burrows. Subsequent experiments were, therefore, conducted with shrimp-constructed burrows in sediment.

Sediment for all experiments was collected from Idaho flat, situated southeast of the Hatfield Marine Science Center (HMSC) on Yaquina Bay. Sediment was

collected randomly from within an area of high mud shrimp density (300-350 ind./m^2), no less than ten meters from the edge of the shrimp patch. Sediment was sieved to ≤ 4 mm in order to remove megafauna, placed in experimental chambers, and allowed to settle for at least 24 hours under constant flow of fresh seawater before introduction of shrimp.

Experimental animals were collected at various times as needed, from March to July 2000. Shrimp were collected from Idaho flat using a manual shrimp-bait pump. Carapace length of each shrimp was measured, and a single individual was placed in each experimental chamber and allowed at least two weeks to burrow before experimentation began. Shrimp that did not burrow within 48 hours were replaced. Shrimp were fed continuously, from the time that they were introduced into the lab until the end of each experiment (approximately 90 days), on 5-8,000 cells/ml of the same species and relative proportions of algae that were used in experiments.

Cryptomya were collected by hand from a shrimp bed just south of the parking lot of HMSC. Pacific oysters were obtained from HMSC. Bivalves were maintained in the laboratory in a flow-through tank with unfiltered seawater at the same temperature (± 2 °C) and salinity (± 1 ppt) as was used in experiments, and were fed continuously on 5-8,000 cells/ml of the same species of algae used in experiments for two weeks prior to experimentation. Oysters and *Cryptomya* were placed in experimental chambers at least 12 hours before experiments were initiated.

Two species of algae were used in all feeding rate experiments, *Isochrysis galbana* (Tahitian strain) and *Rhodomonas salina*. These species were selected based on availability, size, and motility. Motile species were chosen to minimize the amount of settling in experimental chambers and within shrimp burrows. *I. galbana* has a mean diameter of 3-4 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 two species, together with background particles present in the sand-filtered seawater supply (< 4 μm) gave a full range of particles from 1.99 μm in diameter (spherical equivalent; the smallest size detectable with a Coulter Counter Sample Stand IIA, model # S/STD IIA, using a 100 μm aperture tube) up to 10.21 μm in diameter. This upper limit was chosen to include the distribution of particles present in samples taken from a culture of *R. salina*.

A flow-through design was used for all feeding rate experiments. The configuration of the experimental setup is shown in Figure 1.1.

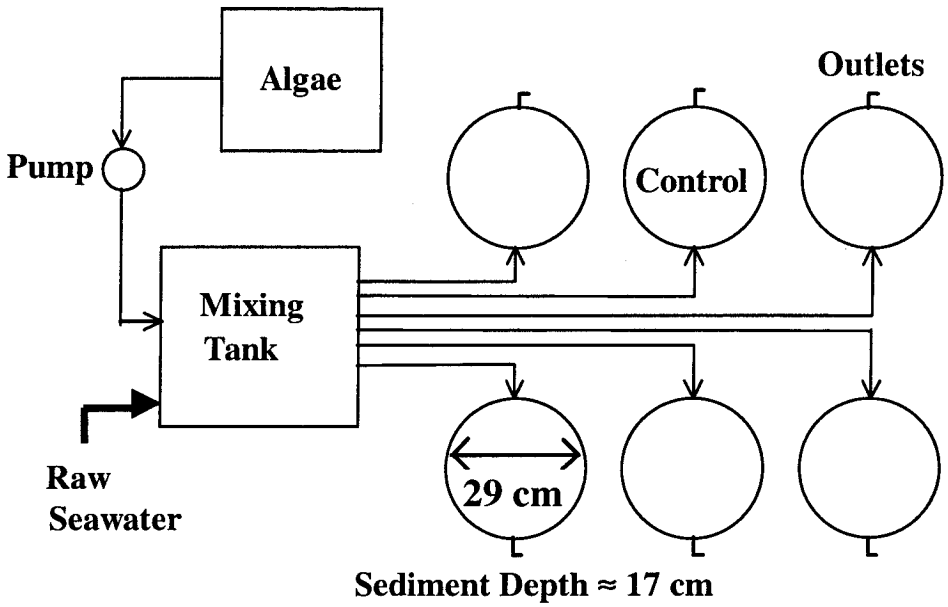

Figure 1.1 Experimental set-up for flow-through experiments. Each chamber (represented by the large circles) was 35 cm deep. Chambers used in bivalve experiments did not contain sediment.

Seawater samples were collected during experiments by holding a vile under the outflow spout of each experimental or control chamber. Sample volumes were approximately 20 ml. Samples in non-flow-through experiments were taken from the center of each experimental chamber, from approximately 3 - 4 cm below the water surface (see Burrow Wall Experiment for description of experimental system), using a graduated pipette. Samples were analyzed using a Coulter Sample Stand IIA (model # S/STD IIA) and Coulter Multisizer II (model # 0217). A 100 μm aperture tube was used for all analyses. With all algal concentrations tested, coincidence was below 8% at all times, and usually below 5%. Unless noted

otherwise, the total volume of particles (Newell & Langdon 1996) in each of eight equal size ranges between 1.99 and 10.21 μm were measured for each water sample. Water in each chamber was aerated continuously during each experiment to ensure even distribution of suspended material within the chamber.

Water temperature during the experimental period (June to October 2000) ranged from 11.6 to 13.6 °C, with the exception of the burrow wall experiment, for which the temperature was 15°C. The temperature during any given experiment was maintained within a 0.2 °C range. Salinity was measured using a Salt Refractometer (model # 300011), and ranged from 32.5 to 35.5 ppt over the course of the experiments; however, no change in salinity was detected during any particular experiment.

All animals were depurated in sand-filtered marine water, absent sediment, for 48 hours after experimentation and before obtaining dry weights to allow time for ingested food to be cleared from the gut. Dry tissue weights for large oysters (≥ 2 cm shell length) were obtained by dissecting out all soft parts and drying at 60 °C to constant weight. Shrimp, small oysters (< 2 cm shell length), and all *Cryptomya* were dried to constant whole weight (shell and carapace included), and were then ashed at 450 °C for 48 hours to obtain ash-free dry weights.

Burrow Wall Experiment

Because we were unable to remove the shrimp from the burrow, while maintaining the physical integrity of the burrow wall, we were unable to test particle removal by the burrow in the absence of shrimp. Loss of particles due to settlement and possible adhesion to the burrow wall would, in effect, increase the apparent filtration of the shrimp. We hypothesized that, as the length of burrow increases, loss of algae due to adherence of cells or settlement in the burrow would increase. We caused similar sized (20-22 mm carapace length, mean: 21.6 ± 1.3 mm) shrimp to vary the length of their burrow in an effort to derive a relationship between apparent shrimp feeding rate and burrow wall surface area. This provided an opportunity to test the hypothesis that shrimp with burrows of greater surface area will have a higher apparent filtration rate due to greater algal adhesion to the burrow wall.

Surface areas of the burrow wall were manipulated by varying the volume (0.5, 5, and 10 L) of sediment in which shrimp were allowed to burrow. Sediment depth in the small, medium, and large treatments were 6.5, 14.5, and 17 cm, respectively. Eight replicates of each treatment were tested, as well as the same number of controls (identical chambers and sediment volume, but without shrimp). Only 15 shrimp fed during the experiment (five from each treatment), therefore, three controls from each treatment were randomly removed from the experiment to maintain the same number of controls and experimental chambers.

During the experiments, water flow was shut off and overlying water volume was adjusted to 7, 10, and 7 liters for the small, medium, and large treatments, respectively. The microalga *Rhodomonas salina* was added to each chamber at initial concentration of approximately 35,000 cells/ml. Twenty-ml samples were taken at 30-minute intervals and particle concentrations were analyzed within 20 minutes of collection. Only particles in the size range of the algae (5.4 - 9.4 μm) were analyzed in an attempt to include mainly suspended algae (and not inert particles) in the particle concentration measurements. Each chamber was sampled for 10 hours, or until shrimp had depleted the algae in each chamber. The average percent removal of algae was 78% (± 9%) over the duration of the experiment.

Filtration rates for each shrimp were calculated using an adaptation of the equation given by Coughlan (1969):

$$F = V \times (\ln C_1 - \ln C_0) - A \qquad (1.1)$$

Where F is filtration rate in mg C/h; V is volume (liters) of water in the experimental chamber; C_1 and C_0 are the concentrations of carbon in mg/l (see Determination of Filtration Rates for conversion of volume of particles to mass of carbon) from phytoplankton in experimental chambers at time one and time zero, respectively; and A is the same calculation, $V \times (\ln C_1 - \ln C_0)$, for a control chamber to account for algal settling from time zero to time one. Filtration rates were standardized to an animal of 1-g dry organic weight using the method discussed in the section on flow-through experiments. Shrimp organic dry weights were calculated using the empirically derived relationship between organic dry

weight and carapace length ($y = 0.1376x - 1.7802$, $R^2 = 0.89$). This was necessary as it was not possible to extract shrimp from their burrows without compromising the structural integrity of the burrow.

Following filtration rate measurements, burrow casts were made with Plaster of Paris. Casts were left overnight to harden, and were then excavated. The length of each cast was measured. The average diameter of each burrow was estimated by averaging measurements made at 1-cm intervals along the entire length of the cast. The burrows were approximately cylindrical, and the mean diameter was used to calculate the surface area of the burrow. Simple linear regression analysis was used to determine the relationship between filtration rates and burrow wall surface area

.

Determination of Feeding Rates

Upon concluding the experiment on burrow wall effects, it was determined that filtration rates would be more accurately measured using a flow-through experimental design because of the changes in feeding rates with changes in food concentration and the difficulty of measuring these changes in a static body of water (Winter 1978, and references therein). That design was subsequently used for all feeding rate experiments for shrimp and bivalves. Six replicates of the block shown in Figure 1.1 were used for each treatment, giving a total of 30 experimental units and 6 controls (a bucket with sediment, but no shrimp), each control serving as a comparison for the five experimental units in the same block. Because some shrimp in the experiments did not feed, measurements were obtained for low,

medium, and high algal concentrations with N=17, 11, and 13 shrimp, respectively. Large oysters (shell length ≥ 2 cm) were tested individually. Small oysters (shell length < 2 cm) and all *Cryptomya* were tested in groups of 6 to 20 individuals of approximately the same size in a single chamber, and results were averaged based on per-individual feeding rates. At high, medium, and low algae concentrations, measurements were obtained for N=18, 18, and 9 groups of oysters (a group consisting of all the individuals in a single chamber), and N=16, 14, and 11 groups of *Cryptomya*, respectively.

Algae concentration in the head tank was maintained at 30-50% above the desired concentration in the experimental chambers. Animals were fed with experimental concentrations of algae for at least one hour before the beginning of the experiment to allow time to adjust feeding rates to those concentrations. Flow rate to each chamber was adjusted until equilibrium was established between the inflow from the head tank and filtration by the animal, which gave the desired concentration in experimental chambers. Flow rates through each experimental chamber were obtained by measuring the volume of water leaving the outflow during one minute, using a graduated cylinder. Feeding rates were tested at three different concentrations: 5-8,000 cells/ml, 15-20,000 cells/ml, and 30-35,000 cells/ml. Bivalves were tested with the same algal concentrations as shrimp in order to facilitate comparison of results.

Determination of Retention Efficiencies

Retention efficiencies (R_s) were measured to examine the potential for food competition, based on particle size selection, between shrimp and Pacific oysters. R_s was defined as the efficiency with which particles of different sizes were removed relative to a maximum value measured for a specific particle size range (Riisgård 1988). Particles (algae and particles in unfiltered seawater) from 2 to 10 μm were divided into 8 relatively equal size classes using a Coulter Multisizer (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, 9.21-10.210 μm diameter, hereafter referred to by the approximate median value for each size class, i.e. 2.5, 3.5, 4.5 μm, etc.). The proportions of particles of a given size range (R_s) that were removed were calculated as follows:

$$R_s = (V_s^* - V_s)/V_s^* \qquad (1.2)$$

Where V_s^* is the volume of particles of a given size range from the outflow of the control chamber ($\mu m^3/ml$), and V_s is volume of particles ($\mu m^3/ml$) of a given size range from the outflow of the experimental chamber (Ropert & Goulletquer 2000). The R_s for the particle size range with the greatest percent removal (as determined for each animal, or group of animals) was then averaged with the value of R_s for any other particle sizes with percent removal within 5% of its value. This averaged R_s was divided into the R_s values from each of the size ranges to give relative retention efficiencies for each size range of particles. Values representing proportions of removed particles in each size class were transformed using the arcsine square root transformation for comparison of proportions (Ramsey &

Schafer 1997). Transformed data were compared using ANOVA, followed by Tukey's test for multiple comparisons of means ($\alpha = 0.05$).

Dependence of Retention Efficiency on Surface Characteristics

It is possible that the observed retention efficiencies of shrimp fed on different species of algae were a true reflection of the animal's ability to retain differently sized particles, or an artifact of different surface characteristics of the algal species. To address this uncertainty, animals were experimentally fed neutrally buoyant, lipid beads that varied in size from < 2 to 15 μm. This allowed comparison of retention efficiencies of various sizes of particles that were all composed of the same material, and had the same surface properties.

Neutrally buoyant beads were composed of 45% ethylcellulose, 40% tripalmitin, 10% carotene, and 5% monopalmitate. Only removal of particles in the same size range as the algal species used in experiments were analyzed (1.99-10.21 μm). Distribution of the beads within this size range was fairly even, with 12.5% (± 3%) of the beads in each of eight size classes. The experiment was performed with shrimp, *Cryptomya*, and oysters; however, only shrimp and *Cryptomya* consumed the beads.

Five shrimp were chosen randomly from those already established in the lab for the flow-through feeding rate experiments. A control was included consisting of a chamber with the same volume of sediment (ten liters) and water, but no shrimp present. Flow was stopped and the water volume in each chamber was

adjusted to five liters. Algae (*Isochrysis galbana* and *Rhodomonas salina*) or lipid beads were added to each tank to bring the concentration of 2-10 μm particles to 15,000 particles per ml. Water samples were taken at 0, 15, 30 and 45 minutes. Retention efficiencies of particles in the different size classes were calculated as described above (see Determination of Retention Efficiencies). Each of the five chambers received first algae and then beads separately, with a two-hour delay between the two treatments during which time water flow was restored to the chambers. Each chamber was constantly aerated during the experiments. For the bead treatment, only four of the five shrimp consumed the beads. Paired t-tests ($\alpha = 0.05$) were used to compare retention efficiencies of beads vs. algae for each of the different size classes of particles.

The experiment was also conducted with *Cryptomya* and oysters using the same methods described above, with a water volume of 250 ml per chamber. Seven individuals of each species were tested. Controls were included, consisting of chambers with the same volume of water, but no *Cryptomya* or oysters added.

Determination of Filtration Rates

Filtration rate was calculated as follows:

$$F = D \times (V^* - V) \qquad (1.3)$$

Where F is filtration rate in μm^3 (particle volume)/hr, D is flow rate of water through the chamber in L/hr; other symbols are defined above. A single filtration rate was calculated for all particles size ranges combined, and was then converted

from $\mu m^3\ hr^{-1}$ to mg C hr^{-1} using the equation experimentally derived by Strathman (1967) for conversion of phytoplankton cell volume to mass of carbon:

$$\log_{10}Carbon(pg) = -0.314 + 0.712 \times \log_{10}Cell\ Volume(\mu m^3)$$

In order to obtain the filtration rate of the entire shrimp-burrow complex, we needed to know whether the sum of the filtration rates of the shrimp + burrow and the *Cryptomya*, which we measured separately, was equal to the filtration of the entire complex together. This was determined to be correct in a separate experiment (see Appendix 2).

Filtration rates were standardized to an average shrimp-burrow complex to facilitate comparison between the filtration rates of the shrimp-burrow complex and oysters. This was done following the procedure by Bayne et al (1987) and Bayne & Newell (1983):

$$F' = F_e' \times (W_s/W_e)^b \qquad (1.4)$$

where F' is the filtration rate of the standard animal, F_e' is the uncorrected filtration rate of the experimental animal, W_s is the dry organic weight of the standard animal (see below), W_e is the measured dry organic weight of the experimental animal, and b is the allometric coefficient obtained by plotting filtration rate vs. dry tissue weight of the animal. The value for W_s varied for each species. For shrimp and *Cryptomya*, the value used was the average ash-free dry weight (g) per individual from Yaquina Bay. These values (0.6 g for shrimp, and 0.019 g for *Cryptomya*) were obtained from data collected by the U.S. E.P.A. (DeWitt, unpubl. data). Standardized filtration rate values for *Cryptomya* were then multiplied by eight

because there were an average of eight *Cryptomya* per shrimp in Yaquina Bay (DeWitt, unpubl. data). The standardized filtration rates for all tested *Cryptomya* were then averaged, and this value was added to each standardized filtration rate for shrimp. This gave the standardized filtration rate of the average shrimp-burrow complex. Because the purpose of this standardization was to facilitate comparison between predicted filtration rates of the shrimp-burrow complex and oysters in Yaquina Bay, the value of W_s used for oysters was the sum of the average ash-free dry weights of the shrimp and *Cryptomya*, or 0.752 g. The values of *b* varied for each species and at each food concentration, and are given in Table 1.1 (see Results: Determination of Filtration Rates). The large range of *b* values reported in Table 1.1 for shrimp are a result of different filtration rates under different phytoplankton concentrations (Hawkins et al. 2001).

Within-species standardized filtration rates at different algal concentrations were compared using one-way ANOVA ($\alpha = 0.05$), followed by Tukey's test for multiple comparisons of means ($\alpha = 0.05$). Interspecific comparisons of retention efficiencies for each particle size class were made using the same statistical tests. Comparison of standardized filtration rates between the shrimp-burrow complex and oysters were made using a two-sample t-test, assuming equal variance ($\alpha = 0.05$). All statistical analyses were performed using S-plus Student Edition 4.5.

RESULTS

Burrow Wall Experiment

A significant relationship existed (simple linear regression, $p = 0.05$) between burrow wall surface area and standardized filtration rate for shrimp in the laboratory, for the range of burrow sizes (surface area: 146-568 cm^2; length 27-93 cm) obtained in this experiment (Figure 1.2).

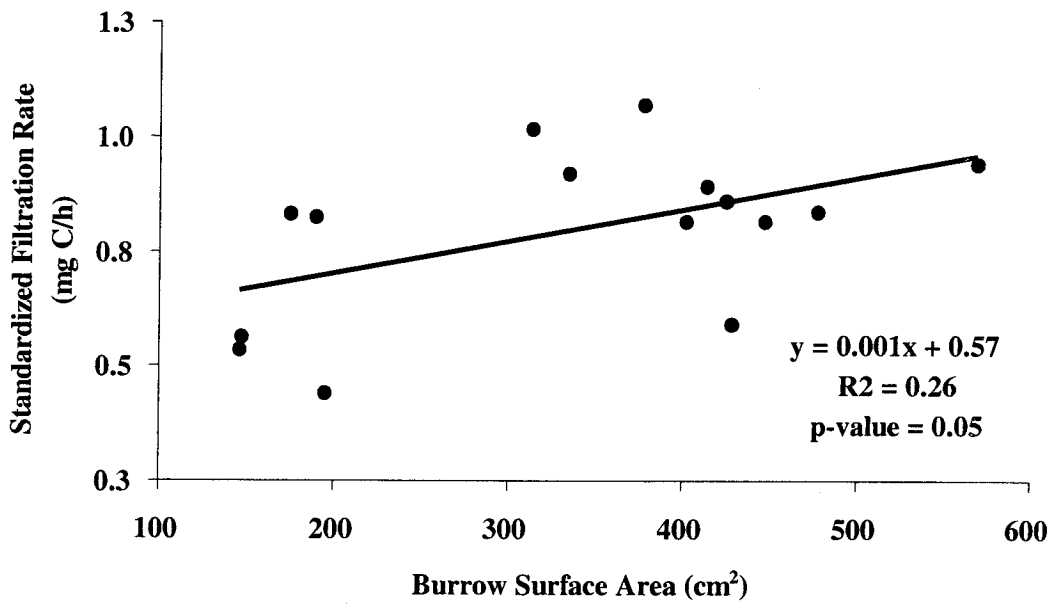

Figure 1.2 Standardized filtration rate of *Upogebia pugettensis* as a function of burrow wall surface area at 15°C and 32 ppt salinity.

Feeding Experiments

Both shrimp and oysters had significantly higher retention efficiencies than *Cryptomya* for the 7.5 and 8.5 μm size classes (Tukey's, $p < 0.05$; Figure 1.3). There were no significant differences in retention efficiencies among species for any other size class of particles. Although the differences were not statistically significant ($p > 0.05$), the results suggest that *Cryptomya* may have had higher retention efficiencies for 2.5 and 3.5 μm particles than oysters or the shrimp + burrow.

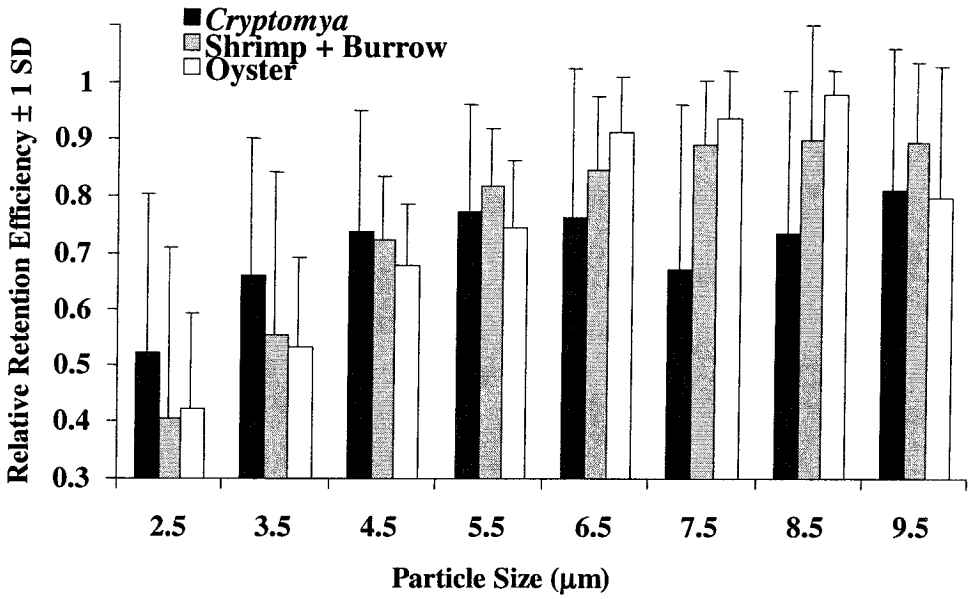

Figure 1.3 Relative retention efficiencies for various particles sizes (mean + 1 SD) for *Upogebia pugettensis*, *Cryptomya californica*, and *Crassostrea gigas* at 12-13°C and 34-35 ppt salinity. Relative retention efficiencies were calculated based on the maximum value for each species separately (i.e. the values are relative values within each species).

Dependence of Retention Efficiency on Surface Characteristics

Shrimp retained algae and beads equally in six of eight size classes, but retained algae with significantly greater efficiency in the 3.5 μm and 6.5 μm size classes ($p = 0.037$ and 0.004 respectively; paired, two-tailed t-test; Figure 1.4). *Cryptomya* showed no difference in particle retention efficiency for any particle size class (paired, two-tailed t-test, $p > 0.05$). Oysters did not feed when given lipid beads.

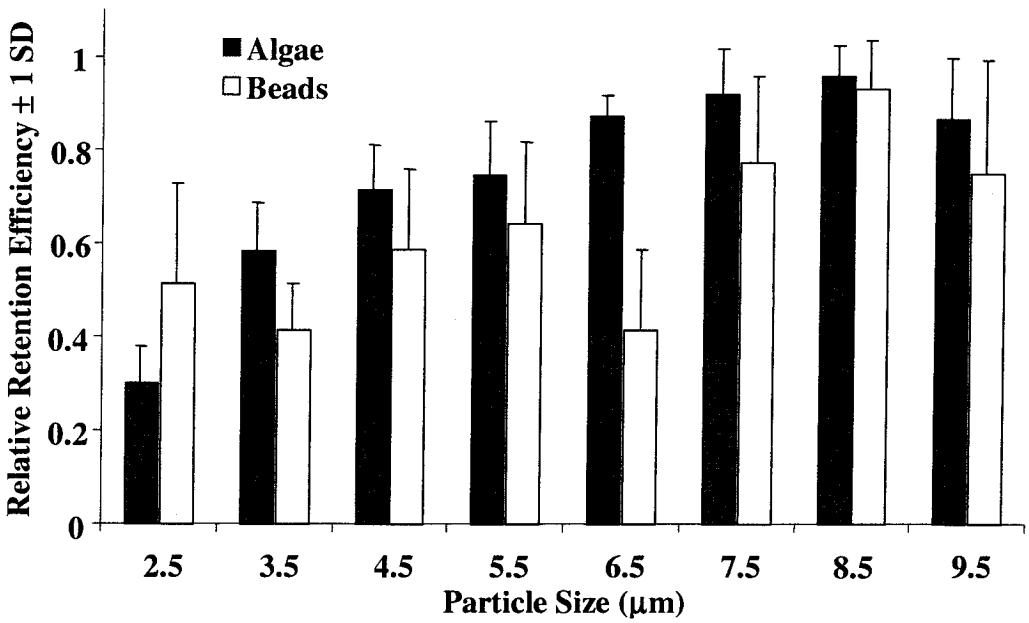

Figure1. 4 Relative retention efficiencies of *Upogebia pugettensis* feeding on algae (*Isochrysis galbana* and *Rhodomonas salina*) vs. lipid beads.

Equations for filtration rates as a function of animal size for shrimp, *Cryptomya*, and oysters at the three algal concentrations tested are given in Table 1.1.

Table 1.1 Equations describing relationships between filtration rate (FR, mass of phytoplankton, expressed as carbon, filtered per hour) and dry tissue weight (W). Values of *b* used in the equation [$F' = F_e' (W_s/W_e)^b$] for standardization of filtration rates for *Upogebia pugettensis, Cryptomya californica, and Crassostrea gigas* at low, medium, and high algal concentrations are exponents in equations (W^b).

Relationship	*U. pugettensis*	*C. californica*	*C. gigas*
FR (mg C/h) at 5-8,000 cells/ml	$FR = 0.62 \times W^{0.58}$ ($R^2 = 0.59$)	$FR = 0.24 \times W^{0.84}$ ($R^2 = 0.47$)	$FR = 0.47 \times W^{0.43}$ ($R^2 = 0.4660$)
FR (mg C/h) at 15-20,000 cells/ml	$FR = 1.03 \times W^{0.89}$ ($R^2 = 0.84$)	$FR = 0.24 \times W^{0.54}$ ($R^2 = 0.72$)	$FR = 1.42 \times W^{0.62}$ ($R^2 = 0.55$)
FR (mg C/h) at 30-35,000 cells/ml	$FR = 0.83 \times W^{1.84}$ ($R^2 = 0.69$)	$FR = 0.56 \times W^{0.58}$ ($R^2 = 0.59$)	$FR\ 3.42 \times W^{0.77}$ ($R^2 = 0.96$)

Standardized filtration rates associated with the shrimp-burrow complex and for oysters at different experimental algal concentrations are shown in Figure 1.5. Standardized filtration rates associated with the shrimp-burrow complex were significantly different from those of an oyster of equal dry tissue weight (0.752 g) at all phytoplankton concentrations (two-sample, two-tailed t-test, $p < 0.05$). Intraspecific *Cryptomya* and oyster standardized filtration rates were significantly different at all three food concentrations (Tukey's, $p < 0.05$). Shrimp + burrow standardized filtration rates were also significantly different at low vs. high and medium vs. high concentrations (Tukey's, $p < 0.05$).

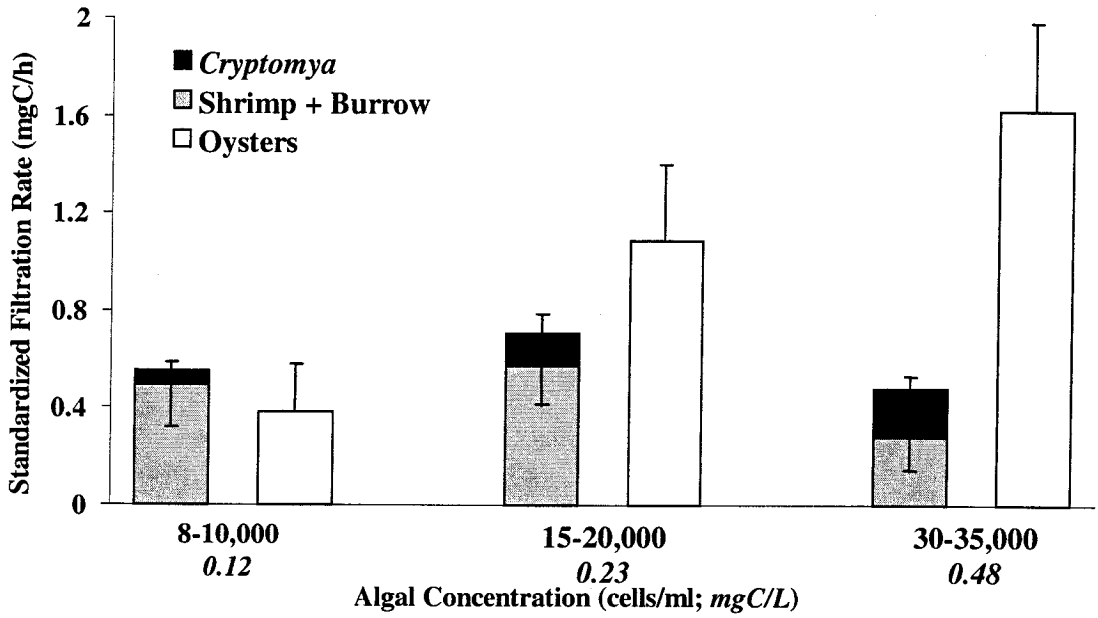

Figure 1.5 Filtration rates (mean ± 1 SD) associated with an average shrimp-burrow complex vs. that of *Crassostrea gigas* of similar dry organic weight at different food concentrations, at 12-13°C and 34-35 ppt salinity

DISCUSSION

Loss of Particles to the Burrow Wall

Results of the burrow wall experiment indicate that the burrow may remove a significant amount of suspended material. The point where an extrapolation of the line intercepts the y-axis in Figure 2 (0.57 mg C/h) can be considered as the filtration rate of a shrimp of 1 g dry weight, in the absence of any burrow. Casts from 18 shrimp burrows in the field, averaged approximately 100 cm long. Using

this burrow length estimate to extrapolate to burrow wall surface area (burrow wall surface area = 5.77 x burrow length; $R^2 = 0.91$, Griffen, unpubl. data), the surface area would be 577 cm^2. Therefore, using our relationship for filtration rate and burrow surface area, we obtain a filtration rate for the shrimp + burrow of approximately 0.97 mg C/h/g dry organic weight, or approximately 1.7 times greater than the filtration rate of a shrimp without any burrow. Shrimp in this experiment were given 17 cm of sediment in which to burrow, whereas in the field, shrimp have been observed to burrow to depths of approximately one meter (Stevens 1929, MacGinitie 1930 and 1934, Thompson 1972, Swinbanks and Luternauer 1987). If this relationship holds true for longer field burrows, the burrow may potentially remove more phytoplankton than is removed by shrimp filtration.

It should also be noted that our feeding experiments were conducted using motile algae that were less likely to settle in a burrow than non-motile cells. Particle removal in the burrow is more likely to be due to adhesion to the burrow walls rather than settlement. Settlement in the burrow may be more pronounced with unflagellated algae or algae with spines, such as diatoms, that could cause the cells to more easily stick to the mucus-lined burrow wall. Our estimate of removal rates due to the burrow may, therefore, be less than removal rates in natural systems with mixed motile and non-motile algal cells.

Because burrow diameter is proportional to shrimp carapace length (Thompson 1772, Dworschak 1987a,b), small shrimp have a larger ratio of burrow

wall surface area to burrow volume than do large shrimp. Therefore, in burrows of small shrimp, a larger proportion of the water (and phytoplankton) that passes through the burrow will likely come in contact with the burrow wall than in burrows of large shrimp. This means that the proportion of algae removed by smaller diameter burrows should be greater than the proportion removed by burrows with larger diameters, given the same volume of water flow through the burrows. Therefore, it could be hypothesized that the burrow wall should be more important in particle removal in populations dominated by small individuals than those dominated by large individuals. Other aspects of burrow morphology not examined in this study, such as turning intensity, may also significantly impact settlement of particles in the burrow, as has been shown for the analogous system of aerosol particulate deposition in human lungs (Zang & Kleinstreuer 2000),. Particle deposition will also be affected by factors that affect the properties of fluid flow near the burrow wall, such as burrow wall roughness (Reist 1993).

Algae adhered to the burrow wall may serve as a food source for shrimp. *U. stellata* (Nickell and Atkinson 1995) and *U. pusilla* (Dworschak 1987b) have the ability to feed on resuspended material that has settled in the burrow. Griffis and Suchanek (1991) hypothesized that the presence of plant debris and fine sediments in the digestive tracts of *U. pugettensis, U. affinis, U. africana,* and *U. deltura* may indicate an ability to feed on resuspended material from within the burrow in these species as well. Video observations of feeding by *U. pugettensis* in laboratory

aquaria lead us to believe that feeding on resuspended material from inside the burrow wall may also be an important mode of feeding for these shrimp.

Particle Retention

Particle retention efficiencies for *Crassostrea gigas* in this study were similar to those reported previously (Ropert & Goulletquer 2000, Barillé et al. 1993), with the exception of retention of particles in the 9.5 μm size class. We found maximum retention efficiency for 8.5 μm particles, and a decrease in retention for 9.5 μm particles (Figure 1.3). Ropert and Goulletquer (2000) reported an increase in retention of particles up to 12 μm, while Barillé et al. (1993) reported maximum retention for particles in the 6 to 10 μm size range. It is unclear whether the differences in size-specific retention efficiencies among these studies reflect real differences among the oysters, or are simply experimental artifacts. The latter is suggested by the high variability in retention efficiency of particles in the 9.5 μm size class in the present study (see Figure 1.3). The similarity in retention efficiencies for oysters and shrimp for particles 2-10 μm in diameter, indicate that the two species may compete for the same food resources.

Results of the feeding experiment with lipid beads verify that retention efficiencies obtained in experiments with algae were not a result of experimental artifacts and cell surface effects, but represented particle retention capabilities of shrimp and *Cryptomya* based on particle size alone. The reason for the discrepancy in retention efficiencies for algae and beads by shrimp for the 3.5 μm and 6.5 μm

size classes is not clear. These size ranges of 3.5 and 6.5 μm include smaller sized cells of populations of *Isochrysis galbana* and *Rhodomonas salina* respectively. However, retention efficiencies for the larger cells of each algal species (size ranges 4-5 μm and 7-10 μm) were not significantly different from retention efficiencies for similar sized beads. The differences in retention efficiencies for shrimp and *Cryptomya*, with shrimp retaining 5-10 μm particles more efficiently than *Cryptomya*, and *Cryptomya* retaining 2-4 μm particles more efficiently than shrimp (though not statistically significant), suggest that resource partitioning may occur between shrimp and its commensal. Similar instances of resource partitioning based on particle size selection have been found in other benthic suspension-feeding communities (e.g. Stuart & Klumpp 1984).

Filtration Rates

The similarity in filtration rates for shrimp fed low and medium algal concentrations, suggests that shrimp alter the volume of water filtered in response to particle concentration to maintain constant carbon removal rates (Figure 1.5). This phenomenon has been shown for several bivalve species (Winter 1969, 1970, 1973; Ali 1970; and Walne 1972). Winter (1973) suggested that it holds true for all bivalves, and possibly for other suspension feeders as well; however, our results do not support this. Oysters and *Cryptomya* examined in this study showed increasing rates of carbon removal with increasing particle concentrations, suggesting that the volume of water filtered remained relatively constant (see Figure 1.5). The

decrease in filtration rate by shrimp fed high algal concentrations may indicate an increase in handling time due to clogging of filtering mechanisms.

The particle size distribution used in our experiments differed from that found in Yaquina Bay. In laboratory experiments, we provided a relatively even distribution in the number of particles > 5 μm (*Rhodomonas salina*) and particles ≤ 5 μm (*Isochrysis galbana*), whereas in field samples, there was a far greater proportion of smaller particles (≤ 5 μm = 0.96 ± 0.009) than larger particles (> 5 μm = 0.04 ± 0.009). The implications of this for filtration rates by *Cryptomya*, oysters and shrimp may be different. We hypothesize that filtration rates of shrimp in the field should not be affected by the particle size distribution because shrimp alter the volume of water filtered to maintain a relatively constant filtration rate for particulate carbon. However, because the volume of water filtered by *Cryptomya* and oysters remains relatively constant with different algal concentrations, we hypothesize that their carbon removal rate should be reduced in an environment dominated by small particles with lower carbon concentrations (Yaquina Bay), as compared to an environment with relatively equal numbers of small and large particles and higher carbon concentrations (laboratory experiments).

Pumping rates for *U. pugettensis* were similar to those of other suspension feeders. Using Riisgård's (2001) equations for filtration as a function of body weight, the average pumping rate for a one-gram bivalve is 3.89 L/h (average across 13 species; range 2.04 – 7.64 L/h). In the present study, a one-gram shrimp pumped 2.74 L/h.

Filtration by dense populations of bivalves has been shown to have important ecological consequences, such as regulating primary production and indirectly regulating secondary production through the removal of large proportions of available particles (Gili & Coma 1998). If the filtration rates for shrimp-burrow complexes reported here are representative for shrimp populations in the field, suspension feeding by dense populations of *U. pugettensis* in Pacific Northwest estuaries may have significant impacts on the standing stock of phytoplankton and resuspended benthic micro-algae, and on estuarine trophodynamics (see Chapter 2).

If food is limiting (for which we have no data), it is possible that *U. pugettensis* and *C. gigas* could compete for food, as claimed by some commercial oyster growers (Feldman 2000). Preliminary experiments on oyster growth in the presence and absence of *U. pugettensis* showed no effect of the shrimp on oyster growth rates (Dumbauld 1994). Thus, data do not as yet support the hypothesis that *U. pugettensis* deprive oysters of food. In contrast, efflux of nutrients from shrimp populations, resulting from the decomposition of organic matter subducted by shrimp bioturbation, may promote growth of phytoplankton within the estuary.

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Chapter 2: Effects of the Mud Shrimp *Upogebia pugettensis* on Estuarine Phytoplankton Abundance

INTRODUCTION

Dense populations of suspension-feeding animals in semi-enclosed systems, such as bays and estuaries, can potentially reduce phytoplankton abundance in overlying waters. Such decreases in phytoplankton abundance have been examined in various systems. For example, Cloern (1982) noted that chlorophyll levels from May through December in South San Francisco Bay are considerably lower than would be predicted based on light and nutrient levels. He calculated that suspension-feeding bivalves are sufficiently abundant to process the volume of the South Bay at least once daily, and suggested that this was the primary mechanism controlling phytoplankton biomass during summer and fall. Similarly, Newell (1988), in examining the effects of declines in oyster populations on eutrophication in Chesapeake Bay, showed that oysters, at historical abundances, could filter the entire Bay in three to six days. Carlson et al. (1984) reported that suspension feeders, including *Mytilus edulis* and *Mya arenaria* removed up to 70% of chlorophyll from water overlying a mudflat. Riemann et al. (1988) measured phytoplankton biomass in marine enclosures with and without suspension-feeding mussels, and found that mussels reduced phytoplankton by as much as 59% compared with enclosures without mussels. Peterson and Black (1991) sampled water flowing over an intertidal sand flat occupied by numerous suspension-feeding bivalves and found that 25% of the chlorophyll was depleted within 3 h 25 min. Padilla et al. (1996) used a computer model to demonstrate that zebra mussels may remove up to 80% of the available chlorophyll in regions of Lake Michigan.

Officer et al. (1982) proposed some criteria for identifying regions where the benthic community may potentially control phytoplankton abundance. Regions fitting their criteria include partially enclosed, shallow areas (two to ten meters in depth) with dense, widespread suspension-feeding benthic communities. Such areas may be found in Pacific Northwest (PNW) estuaries, where the suspension-feeding burrowing shrimp, *Upogebia pugettensis* (also referred to here as mud shrimp, or shrimp), often occur at densities ≥ 125 m^{-2} (Bird 1982, Dumbauld et al. 1996, and DeWitt unpubl data). Laboratory experiments demonstrated that *U. pugettensis* can remove < 0.3 – 2.0 mg C/hr per individual (depending on shrimp size and phytoplankton concentration) (Griffen et al. 2002). The purpose of this paper is to test the hypothesis that *U. pugettensis* populations can substantially graze down phytoplankton concentrations in PNW estuaries.

We used particle filtration data for shrimp-burrow complexes from laboratory experiments (see Griffen et al. 2002), animal abundance data, and hydrographic data to construct a simple population filtration model to describe the amount of phytoplankton that could be removed daily from the water column by shrimp-burrow complexes. To verify the model, we conducted field experiments to measure *in situ* filtration rates of the shrimp-burrow complex across a range of population densities and phytoplankton concentrations. For comparison with the shrimp, we also determined the density of oysters (*Crassostrea gigas*) that would be needed to consume the same amount of phytoplankton in the lower Yaquina estuary as was projected to be removed by mud shrimp populations.

This study was conducted in the lower portion of Yaquina Bay, OR, which exhibits many of the criteria outlined by Officer et al. (1982) (see Figure 2.1). Shrimp are present on large areas of the two tide flats that dominate this portion of the bay, with densities averaging 189 m^{-2} (DeWitt, US EPA, unpubl. data). The daily average water depth over these tide flats is 2.7 m (DeWitt, US EPA, unpubl data). The presence of shrimp presents three possible mechanisms for removal of suspended food: filtration by the shrimp, filtration by a commensal bivalve, *Cryptomya californica*, and deposition of phytoplankton on the mucus-lined burrow wall. Combined, these three components represent the "shrimp-burrow complex" (Griffen et al. 2002).

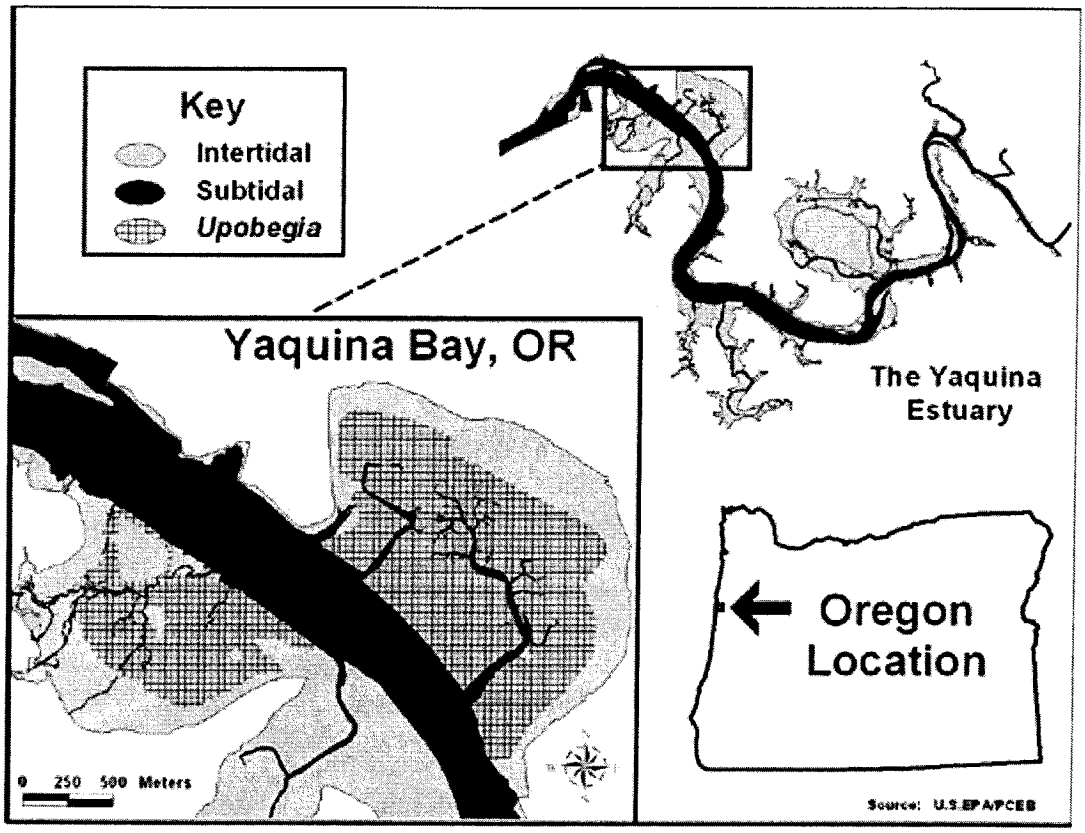

Figure 2.1 Distribution of *Upogebia pugettensis* in the lower Yaquina River estuary, located on the coast of central Oregon. (DeWitt, United States Environmental Protection Agency, unpubl. data).

Removal of phytoplankton by shrimp-burrow complexes could affect several components of the ecosystem. For instance, if mud shrimp consume the same size particles as do other suspension feeders, and if food is limiting, competition for food may occur between mud shrimp and those other species. Because Pacific oysters (*Crassostrea gigas*) and other bivalves are often cultured in proximity to mud shrimp habitats, competition between these species could be economically, as

well as ecologically, significant. In contrast, filtration of suspended material by shrimp-burrow complexes may benefit macrophytes, such as seagrass, by reducing turbidity. Additionally, mud shrimp may stimulate the production of phytoplankton and macrophytes by enhancing the flux of nutrients from sediments to the water column via irrigation of their burrows.

MATERIALS AND METHODS

In order to eliminate confusion in terminology, filtration rate is defined here as the mass of organic carbon removed from suspension per unit time; pumping rate is the rate at which shrimp move a volume of water through the burrow.

Population Filtration Model

We focused our analysis on two large tidal flats in the lower Yaquina estuary, named Idaho Flat and Sally's Bend (see Figure 2.1). The analysis does not include the channel between Idaho Flat and Sally's Bend because subtidal shrimp densities are unmeasured.

Proportional removal of phytoplankton by the shrimp-burrow complex is defined as:

$$\%R_{total} = \sum \%R_{shrimp\ +\ burrow} + \%R_{Cryptomya} \qquad (2.1)$$

where $\%R$ is the percent of total available algae that is removed. Only development of the model for the shrimp + burrow is shown. Removal of phytoplankton by *Cryptomya* is modeled in the same manner.

$$\%R_{shrimp\ +\ burrow} = \frac{\text{Mass of carbon removed}}{\text{Mass of available carbon}} = \frac{\sum\{M_i \times F_i\} \times T}{C \times V} \qquad (2.2)$$

Where M_i is the biomass (g) of shrimp of size class i (five size classes of shrimp and *Cryptomya* were modeled because filtration rates for *U. pugettensis* and *Cryptomya* are size dependent; Griffen et al. 2002); F_i is the filtration rate (mg C/h/g dry weight) of shrimp in size class i; T is time spent feeding (h; observations of shrimp in laboratory aquaria indicated that they actively fed approximately 50% of the time that they were submerged); C is phytoplankton concentration (mg C/l); and V is volume of water (L) overlying the tide flat. Feeding time (T) was estimated as 50% of the time that mid-elevation mud shrimp were submerged during a 24 h period with the greatest tidal-height change during the summer.

The size (dry organic weight, DW) frequency distribution of *Cryptomya* in the population filtration model was determined as follows. Approximately 300 individuals were measured (shell length) and weighed (DW). The relationship between shell length and DW was determined as $DW = 0.2911e^{0.2485 \times length}$, $R^2 = 0.71$. Shell lengths of >3,000 bivalves were then measured from samples taken at various locations within the lower Yaquina, and the relationship between shell length and DW was used to calculate the DW frequency distribution (Table 2.2). Data on the abundance of shrimp, their sizes, and *Cryptomya* abundance in Yaquina Bay were also available (DeWitt and Ferraro, EPA, unpubl. data).

While the current study describes feeding rates as a function of carbon concentration, no data on carbon concentration were available for Yaquina Bay. However, chlorophyll *a* data were available from the EPA (Eldridge, EPA, unpubl. data). The data were derived from samples taken at the dock of Oregon State University, situated on the seaward edge of Idaho Flat in March 1999, August 1999 and June 2000. Chlorophyll *a* concentrations were converted to mg algal carbon using a carbon:chlorophyll *a* ratio of 50 (Raymont 1980, and references therein). This resulted in a range of values from 0.0004 to 0.82 mg C/l. We only applied the model to algal concentrations tested in the laboratory (0.12, 0.23, and 0.48 mg C/l) because we have no data on filter feeding by shrimp, *Cryptomya*, or oysters at other concentrations.

Because filtration rate of shrimp in the lab is relatively constant at different food concentrations (Griffen et al. 2002), regression analysis was used to derive an equation for filtration rate (F) of shrimp as a function of shrimp size alone. Multiple regression analysis was used to derive an equation for filtration rate (F) for *Cryptomya*, as a function of animal size and carbon concentration. The resulting equations were:

$$F_{shrimp} = -0.2667W + 0.9896;\ R^2 = 0.84 \qquad (2.3)$$

$$F_{Cryptomya} = -0.5515 - 0.6229(\ln W) + 0.5848(\ln C);\ R^2 = 0.64 \qquad (2.4)$$

where W is dry weight (g), and C is concentration of suspended algal carbon (mg/l) available for food.

Assumptions of the population filtration model are given in Table 2.1 and parameters used as input for the population filtration model are given in Table 2.2.

Table 2.1 Population filtration model assumptions

#	Assumption
1	Strathman's (1967) calculation of the mass of organic carbon per volume of algal cells is valid for phytoplankton used in laboratory and field experiments $\log_{10}Carbon(pg) = -0.314 + 0.712 \times \log_{10}Cell\ Volume(\mu m^3)$
2	The carbon concentration in the region of the estuary described by the model is homogeneous and the water mass is well mixed
3	Filtration rate is based on phytoplankton concentration and not on concentrations of total suspended material or detrital carbon
4	Animals feed for 50% of the average period of submergence (consistent with laboratory observations)

Table 2.2 Population filtration model parameters. See text for model equations.

Symbol	Model parameter	Value(s)	Source
C	Algal carbon concentration (POC)	0.115, 0.231, and 0.478 mg/l	Calculated using equation by Strathman (1967)
V	Water volume	9.22×10^9 l	Calculated from tide flat area and average depth; does not include the channel
Used to calculate V	Tide flat area	3375593 m^2	DeWitt, US EPA (unpubl.)

Table 2.2 Continued

Symbol	Model parameter	Value(s)	Source
Used to calculate V	Average water depth over tide flats	2.73 m	DeWitt, US EPA (unpubl.)
Used to calculate biomass (M_i) of shrimp	Shrimp habitat	2056308 m^2	DeWitt, US EPA (unpubl.)
Used to calculate biomass (M_i) of shrimp	Shrimp density	189.8 m^{-2}	Calculated from burrow count survey data and relationship: #shrimp/m^2 = (0.5803 x #holes/m^2) - 1.1554 (DeWitt, US EPA, unpubl.)
Used to calculated biomass (M_i) of Cryptomya	# of Cryptomya to # of Shrimp per burrow	8	This value represents the ave. for the estuary, the range is 3 to 30 (DeWitt, US EPA, unpubl.)
T	Feeding time	10 h/day	Estimated average daily submergence time of 20 hrs, and assumed feeding 50% of time submerged
Used to calculate filtration rate per gram dry weight (F_i) of shrimp	Relative proportion of shrimp in each size class	< 0.03 g = 0.09 0.03 < 0.15 g = 0.21 0.15 < 0.43 g = 0.3 0.43 < 0.96 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: dry weight (g) = 0.00005 x $(CL)^{3.168}$ (DeWitt, US EPA & Griffen unpubl.)
Used to calculate filtration rate per gram dry weight (F_i) of Cryptomya	Relative proportion of Cryptomya in each size class	< 0.001 g = 0.05 0.001 < 0.002 g = 0.35 0.002 < 0.008 g = 0.33 0.008 < 0.029 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: dry weight (g) = $(0.2911e^{0.2485 \times SL})/1000$ (DeWitt, US EPA & Griffen, unpubl.)

Oyster-equivalents, or the density of oysters of standard DW (number/m^2) that would consume the same proportion of phytoplankton as consumed by shrimp-burrow complexes, was determined as follows. An oyster of standard DW is defined as having the same biomass as the average shrimp and *Cryptomya* within a shrimp-burrow complex (i.e., 0.752 g). The average shrimp burrow complex consists of one average-sized shrimp (0.6 g) and eight average-sized *Cryptomya* (8 $\times$ 0.019 g). A 0.752 g oyster has an equivalent shell length of approximately 4.06 cm (Langdon & Robison, 1996). Using oyster biomass-specific filtration rate data from laboratory experiments (see Griffen et al. 2002), the following filtration rate equation was obtained for oysters by multiple regression ($R^2 = 0.73$):

$$F_{oysters} = 3.8234 - 0.3926 \times \ln(W) + 1.5618 \times \ln(C) \qquad (2.5)$$

Where F_{oyster} is the filtration rate of an individual oyster, W is the dry organic weight (g) of an individual oyster, and C is the algal carbon concentration in mg C/l.

Oyster-equivalents was determined by dividing the amount of carbon filtered by a standard oyster over 24 hours into the total amount of carbon consumed by the shrimp-burrow complexes m^{-2} over 24 hours (assuming, as with shrimp, that feeding only occurs during half of the submerged time). This results in the population density of oysters of standard DW needed to filter the same amount of phytoplankton that is filtered by shrimp in the lower Yaquina Bay, at a given phytoplankton concentration.

Field Experiments

We conducted feeding experiments on shrimp in their natural environment. This was done in an effort to validate the model, which was developed using shrimp filtration rates measured in the laboratory. Experiments were conducted on Idaho flat (see Figure 1) approximately 100 m off the west shore of Yaquina Bay (Idaho flat). Patches (0.126 m^2) of the tide flat containing shrimp were isolated using stainless steel cylinders 40 cm in diameter and 1 m high. These cylinders were pushed into the sediment to a depth of approximately 75 cm, creating an *in situ* chamber that isolated the shrimp, burrow walls, and associated commensal bivalves inside the cylinder from the surrounding sediment and infauna. The ≈ 25-cm portion of the chamber protruding above the sediment surface held water at low tide that shrimp inside the chamber were able to filter during experiments. Replicate chambers were deployed simultaneously in areas with high (200 ± 37 ind./m^2), medium (132 ± 45 ind./m^2), and low (62 ± 52 ind./m^2) population densities of shrimp. These areas were chosen based on the number of burrow openings. After experimentation, the contents of each cylinder were excavated and the numbers and dry weights of shrimp and *Cryptomya* were determined. Enclosed in the chambers were 25 (± 5; S.D.), 16 (± 6; S.D.), and 8 (± 6; S.D.) shrimp in high, medium, and low-density chambers respectively.

All population-density treatments were conducted at each of three locations on Idaho flat, resulting in three replicates per treatment. The three sites were separated by approximately 50 m and were located in the center of a patch of *U. pugettensis*.

Sites 1, 2, and 3 were located at tidal heights of approximately 2, 2.5, and 3 m above MLLW, respectively. High, medium, and low population-density chambers were established within two meters of each other at each site. Chambers were deployed two weeks prior to experimentation to allow shrimp inside the chambers time to repair burrows that may have been damaged with the introduction of the chambers.

The height of water above the sediment surface inside each cylinder was adjusted (by siphoning) to a volume of 10 to 18 liters, depending on shrimp density inside the chamber (higher volumes were used in higher density treatments to decrease the rate that phytoplankton was depleted by filtration, allowing adequate time for sampling). Additional water was also present within the shrimps' burrows, the volume of which was estimated as follows. Eighteen resin casts of *U. pugettensis* burrows were obtained on Idaho flat. The diameter of each burrow cast was measured at 10-cm intervals over the length of the U-portion of the burrow cast, and averaged to obtain a mean burrow diameter. Only the U-portion was used, as water in this portion is exchanged with overlying water when the shrimp irrigates its burrow. We assumed that water in blind-end portions of burrows will not exchange as readily as in the U-portion. The length of the U-portion of each cast was measured. The relationship between burrow diameter and length of the U-portion was determined (U-portion length = 3.6782 × burrow diameter; $R^2 = 0.43$). As it was not possible to measure the actual diameters of burrows in our experimental chambers, the diameter of each burrow inside the experimental

chamber was determined based on shrimp carapace length (CL), using the relationship observed by Thompson (1972) that *U. pugettensis* burrow diameter = shrimp CL ÷ 1.1. Length of the U-portion of each burrow was then estimated using the relationship reported above, and volumes of the U-portions were calculated, assuming that the burrows were cylindrical. This volume was added to the volume of water overlying the sediment to give the total volume of water inside each chamber. Based on these calculations, an average of 74% (± 6% S.D.) of the total water volume inside the experimental chambers was overlying the sediment and 26% (± 6% S.D.) was inside the burrows.

Filtration rates for each chamber were measured at each of three phytoplankton concentrations that corresponded to the concentrations used in laboratory experiments (see Griffen et al. 2002): 5-8,000 cells/ml, 15-20,000 cells/ml, and 30-35,000 cells/ml. A control treatment was established at each site consisting of a closed-bottom chamber of 40 cm diameter containing 5 cm of sediment, collected at each site respectively, which had been sieved to 4 mm to remove large shrimp and bivalves. Sufficient phytoplankton (*Rhodomonas salina*) was added to each chamber to give the desired initial concentration. *R. salina* was chosen because of its availability, and because it was motile and likely to remain in suspension. Water inside each chamber was mixed during experiments by air bubbled from battery-operated Penn Plax air pumps (model no. B10). Fifteen-ml water samples were collected from each chamber at 15-minute intervals over three hours. Temperature, salinity, and water depth were measured at each sampling.

Samples were analyzed using a Coulter Sample Stand IIA (model no. S/STD IIA) equipped with a 100 μm aperture tube, and Coulter Multisizer II (model no. 0217). The volume of phytoplankton (μm^3) per sample was converted to mass of carbon (mg) using the following equation (Strathman 1967):

$$\log_{10}Carbon(pg) = -0.314 + 0.712 \times \log_{10}Cell\ Volume(\mu m^3)$$

The net filtration rate for all shrimp-burrow complexes within a chamber was calculated using an adaptation of the equation given by Coughlan (1969):

$$F = V/T \times [(\ln C_1 - \ln C_0) - A] \qquad (2.6)$$

where F is filtration rate in mg C/h; V is volume (l) of water in the burrows and experimental chamber; T is the elapsed time from time zero to time one; C_1 and C_0 are the concentrations of phytoplankton-carbon in mg/l from water samples collected at time one and time zero, respectively; and A is the change of concentration of phytoplankton-carbon measured in the control chamber, ($\ln C_1 - \ln C_0$), over the same time interval.

The length of time between C_0 and C_1 was determined as follows. When the concentration of algal cells inside a chamber reached 8,000, 20,000, or 35,000 cells/ml, this was defined as C_0 for the low, medium, or high carbon concentration respectively. C_1 was defined as being the time at which, due to algal removal from filtration, the concentration reached 5,000, 15,000, or 30,000 cells/ml for low, medium, and high carbon concentrations respectively.

Initial decreases in phytoplankton concentrations at the beginning of an experiment could have been due to filtration of overlying water by animals and to

dilution by water in shrimp burrows, exchanged when the shrimp began feeding. Thus filtration rates calculated at the initiation of an experiment would overestimate particle removal rate. Therefore, we initially added 25-30% more phytoplankton to each chamber than was needed to establish the desired concentration. Initial decreases in phytoplankton concentration were not used in calculations, but rather calculations were made after the removal of this initial 25-30% of phytoplankton. Thus we believe that our calculated filtration rates represented actual filtration rates and not a dilution artifact. Filtration rate measurements were repeated several times on separate days at each site, with one to three filtration rate measurements obtained for each chamber, at each food concentration. The order in which food concentrations were presented in each chamber was randomized.

After feeding trials were completed, sediment in each chamber was excavated by hand and sieved through a 4 mm screen. Shrimp and *Cryptomya* found in each chamber were measured and separated into size classes that corresponded to those used in our model. These data, the total volume of water in each chamber, and the concentration of carbon, were input into the population filtration model and the model was then run for each chamber. The model was run for each trial separately because volume of water and concentration of phytoplankton varied among trials. The expected results obtained from the population filtration model were compared to the actual filtration measured during experiments for each food concentration separately using a paired t-test.

RESULTS

Population Filtration Model

The population filtration model predicts that at low carbon concentrations (i.e., low phytoplankton abundance), the shrimp-burrow complexes remove a significant portion of the available suspended carbon in the lower Yaquina estuary (Figure 2.2).

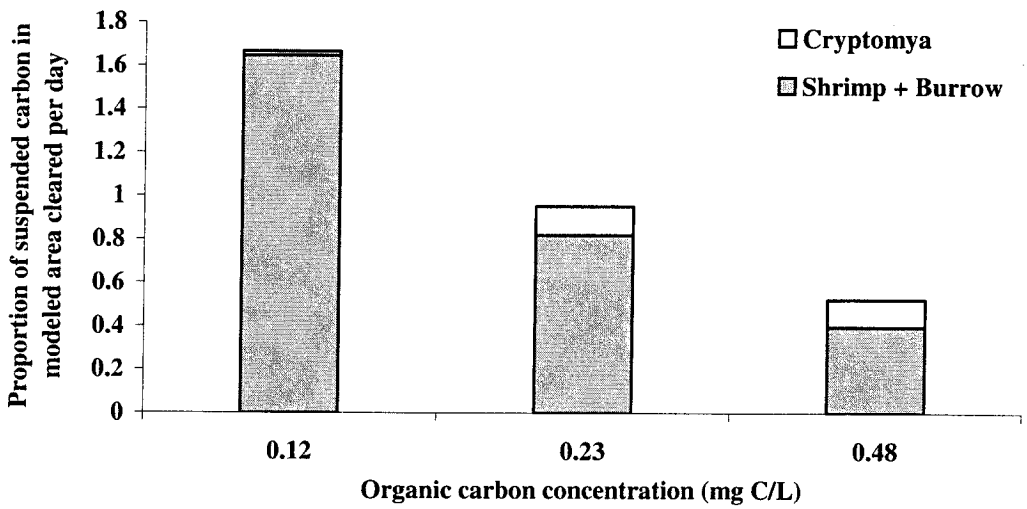

Figure 2.2 Population filtration model predictions of shrimp-burrow complex filtration in the lower Yaquina tide flats for the high, medium, and low concentrations of carbon (phytoplankton) used in laboratory feeding experiments.

The range of carbon concentrations observed in Yaquina Bay from March to August (0.0004 to 0.82 mg C/l) was greater than the range of carbon concentrations used in laboratory experiments (0.115 to 0.478 mg C/l).

Based on model predictions of removal rates, equivalent densities of oysters for shrimp-burrow complexes at high, medium and low algal concentrations are 203, 80, and 53 oysters per m^2, respectively. These oyster equivalents represent the number of oysters (with shell length ≈ 4 cm) that would be required over the entire area of the tide flats in the lower Yaquina to filter the same proportion of phytoplankton that shrimp-burrow complexes are predicted to filter at an average density of 189 m^{-2}.

Field Experiments

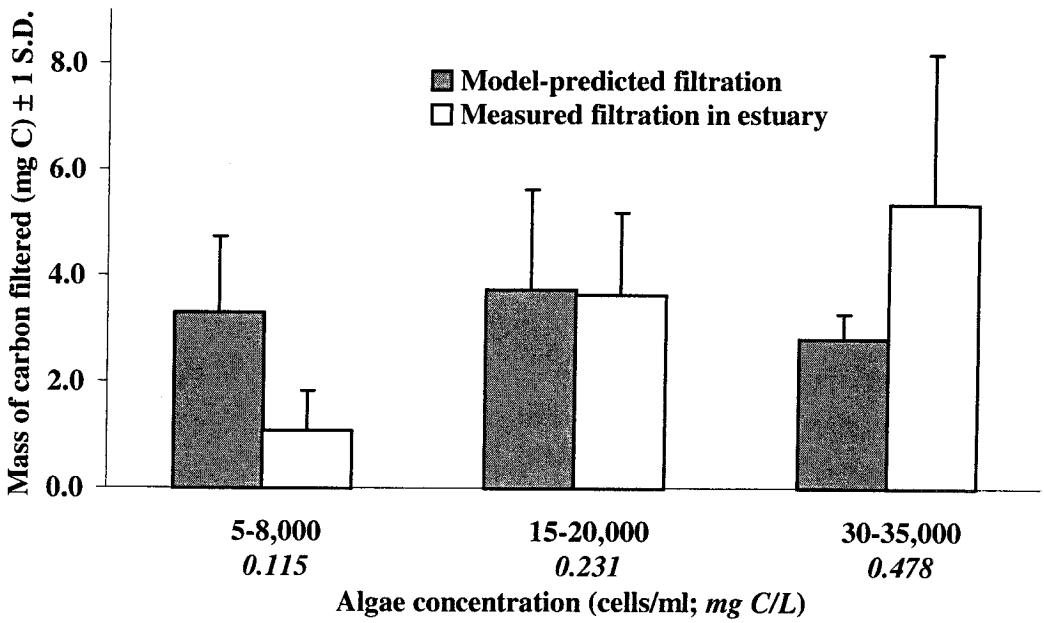

Figure 2.3. Results of field experiments compared to population filtration model predictions (mean ± one std dev.) at low, medium, and high food concentrations.

The population filtration model predictions of carbon filtered (Figure 2.3) are not significantly different from experimentally measured filtration at low or medium phytoplankton concentrations (paired t-test, two-sided p-value = 0.067 and 0.894, respectively). However the model prediction is significantly different from experimentally measured filtration at high phytoplankton concentrations (paired t-test, two-sided p-value = 0.022). Even though there was not a statistically significant difference between model and experimental results at the low phytoplankton concentration, inspection of Figure 2.3 reveals that the model may be somewhat inaccurate at low phytoplankton concentrations.

The population filtration model was developed using data from laboratory experiments in which shrimp altered pumping rates based on phytoplankton concentration. The differences in the measured amount of phytoplankton consumed and that predicted by the model at low and high phytoplankton concentrations indicate that shrimp in the estuary may not alter their pumping rate in order to maintain a constant filtration rate at varying food concentrations. To examine this, we calculated pumping rates using the equation given by Coughlan (1969):

$$P = V/MT \times [(\ln N_1 - \ln N_0) - A] \qquad (7)$$

Where P is pumping rate in l/h; V is the total volume (l) of water in the chamber; M is mass (g) of shrimp in the chamber; T is the amount of time (h) that algal concentrations in chambers were at the concentration of interest, and ranged from 15 minutes to one hour; N_1 and N_0 are the concentration of algal cells in the

chamber (no./l) at time one and zero respectively; and A is a term to correct for settling in the experimental chamber ($\ln N_0 - \ln N_1$; as measured in control chamber). The length of time between N_0 and N_1 was determined as stated above for the time between C_0 and C_1 (see Methods: Field Experiments).

Linear regression analysis of pumping rates indicates that pumping rate increases with increasing phytoplankton concentrations (p-value = 0.001, Figure 2.4). This pattern was the reverse of that observed in laboratory experiments, where shrimp decreased their pumping rate with increasing phytoplankton concentration (see Griffen et al. 2002). In the laboratory, filtration rate remained relatively constant at different phytoplankton concentrations, indicating that different volumes of water must have been processed. Alternatively, retention efficiencies may not be constant at all concentrations. The calculation of pumping rate given above assumes that particles removed with the greatest efficiency were removed with 100% efficiency. Increasing retention efficiencies with increasing phytoplankton concentrations would also give the pattern shown in Figure 2.4.

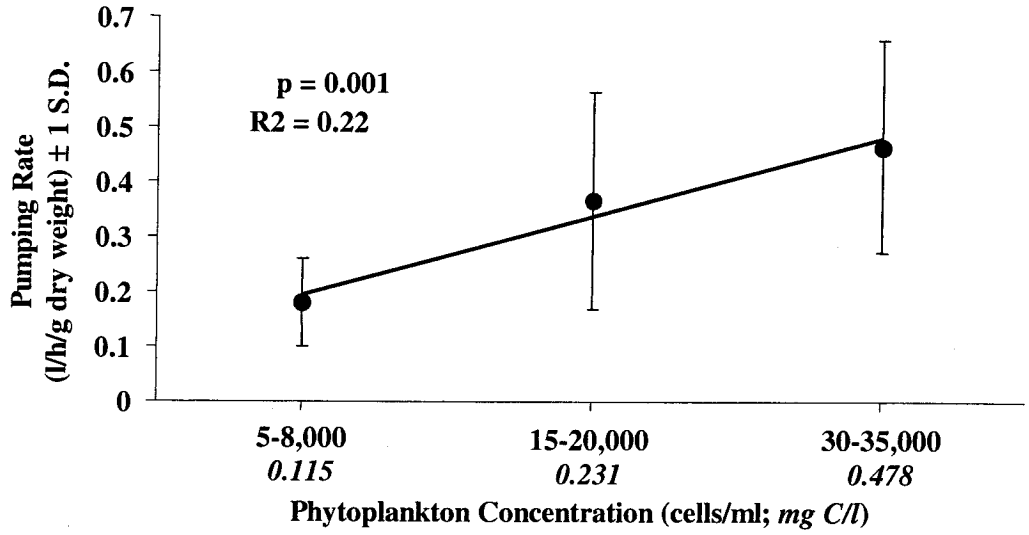

Figure 2.4 Pumping rate (l/h/g dry weight) ± 1 std. dev. of shrimp-burrow complexes at three food concentrations in field experiments.

Population Density Effects

There was a negative relationship between shrimp density and filtration rate (Figure 2.5), however, this relationship was not statistically significant (linear regression analysis, $p = 0.13$). Data from high phytoplankton concentrations were used in this analysis because there were more data points obtained at this concentration than at low and medium concentrations. The decrease in filtration at higher shrimp densities may be due to refiltration of previously filtered water. If so, the trend may be eliminated with perfect, immediate mixing of the overlying water. Water in field chambers was mixed via vigorous aeration with battery-operated air pumps. However, this mixing was not likely perfect. Alternatively,

shrimp at high densities may experience intraspecific food competition that could impose stress and decrease filtration rates.

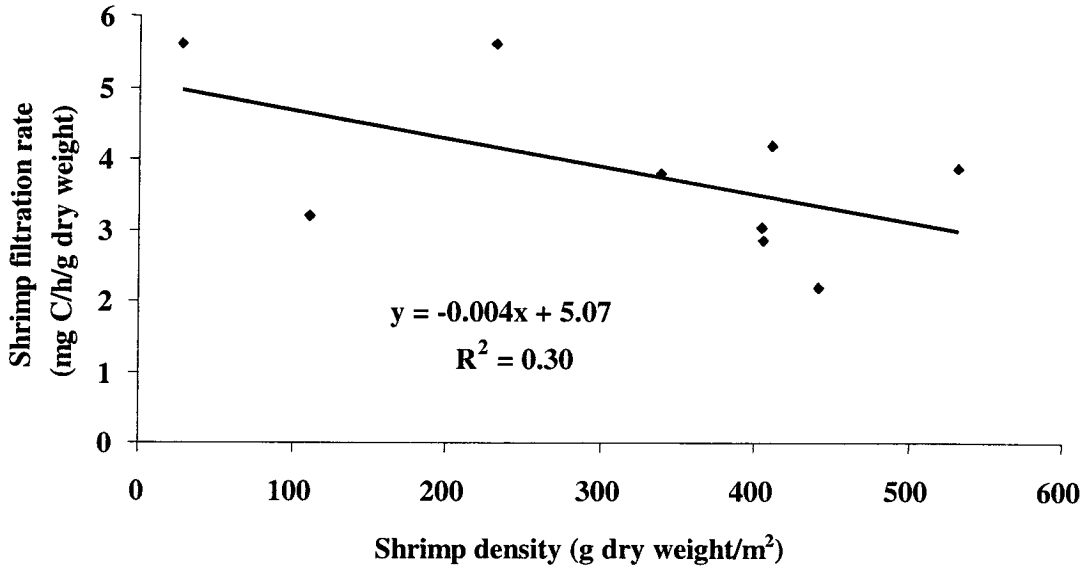

Figure 2.5 Filtration rate per gram dry weight at high food concentrations (30-35,000 cells/ml, 0.48 mg C/l) as a function of shrimp density in experimental field chambers.

Confounding Factors

Tidal elevation, differences in substrate, and ambient temperature could have affected filtration rates of shrimp among chambers. However, we found no significant difference among sites (elevations and substrate types) in filtration rate (ANOVA; $p = 0.82$), nor was there any effect of temperature on filtration rate (linear regression, $R^2 = 0.002$; $p = 0.89$). The lack of significant effect of site or temperature on our results indicates that the filtration rates observed in our field

experiments were predominantly functions of phytoplankton concentration and shrimp density.

DISCUSSION

Results of field experiments support our population filtration model findings that shrimp-burrow complexes are capable of consuming large portions of the available phytoplankton in the lower Yaquina Bay. Results from our field experiments indicate that the model accurately predicts removal of suspended food by the shrimp-burrow complex at medium phytoplankton concentrations. At high and low phytoplankton concentrations the model predicts phytoplankton removal by shrimp-burrow complexes within a factor of two and three, respectively. In the laboratory, shrimp filtration rates (mg C removed per hour) were similar at low phytoplankton concentration to those at higher concentrations (see Griffen et al. 2002), which was not the case in the field (see Figure 2.3). This may have been caused by shrimp in the laboratory being fed a continuous supply of phytoplankton at a concentration similar to the low concentration used in our laboratory and field experiments. Shrimp were kept in the laboratory under these conditions for over two weeks prior to experimentation. The higher rate of consumption in the laboratory at these low phytoplankton concentrations may represent a behavioral adaptation of shrimp due to the constant feeding at this low concentration before and between experiments. Another possible explanation is that shrimp in the field may spend a lower proportion of time suspension feeding at these low food

concentrations due to the lower benefit as compared to filtration at higher food concentrations. Our model assumes, based on laboratory observations, that shrimp feed for 50% of the time, regardless of the amount of food available.

While it was observed that shrimp in the laboratory ceased suspension feeding activities when suspended carbon concentrations decreased below approximately 0.035 mg C/l (see Figure A3-5), shrimp in the field ceased suspension feeding activities around 0.115 mg C/l (Griffen, pers. obs.)– the lowest food concentration used in our experiments. It has been hypothesized that while *U. pugettensis* is predominately a suspension feeder, it may switch at times to deposit feeding (Powell 1974). If this is the case, then shrimp may switch to deposit feeding when concentrations of suspended food decrease to the point where pumping is no longer energetically favorable. Because shrimp in the laboratory were only given 17 cm of sediment in which to burrow, shrimp in the field presumably have longer burrows than did shrimp in the laboratory. The energy required to pump water through the longer burrows in the field (due to increased resistance, see Vogel 1994) may increase the energetic requirements of shrimp in the field over that of shrimp in the laboratory. Suspension feeding at low phytoplankton concentrations may not provide sufficient food to meet these increased metabolic requirements in longer field burrows. Also, sediment in the field may provide a richer food source than did sediment in the lab. If so, this may explain the difference in minimum food concentration that elicits suspension feeding in the laboratory and the field. Lower net filtration rates may be due to lower individual filtration rates by all

animals, or to fewer animals filtering during the sampling interval. Our experiments provided no means of distinguishing between these alternatives. Lower filtration rates at low phytoplankton concentration may be a result of some, but not all, of the shrimp contained in a chamber switching to deposit feeding, or stopping feeding activities altogether.

The population filtration model, with further modifications, may be used to describe the shrimps' affect on phytoplankton concentrations in all of Yaquina Bay, and possibly other water bodies where *U. pugettensis* is found.

Some factors may effect our predictions of phytoplankton reduction by shrimp-burrow complexes. 1) We assumed that shrimp feed 50% of the time that they are submerged. This value is based on observations of shrimp while in laboratory aquaria, and seems reasonable. Dworschak (1981) estimated that *U. pusilla*, a related species, actively pumped an average of 28% of the time (with a range of 18 to 42%). Decreasing the assumed amount of time spent feeding in our model to 28%, decreases the amount of available carbon predicted to be removed by 44%. This sensitivity of our model to the proportion of time spent feeding indicates the importance for accurate estimates of this variable. 2) It is possible that suspended carbon concentrations encountered by shrimp in the field are higher than those observed in water column measurements. Amspoker and McIntire (1978) found an extensive community of benthic diatoms in Yaquina Bay sediments. Water pumped through the burrow by the shrimp is presumably drawn from the region next to the sediment-water interface, and may have elevated

organic carbon concentrations due to resuspension of benthic diatoms and other particulate organic matter (Shaffer & Sullivan 1987). If resuspended particulate organic matter is included in the filtered material, this may decrease the rate at which phytoplankton in the lower Yaquina are removed by shrimp. 3) Finally, another possibility is that a major portion of particulate organic carbon in the estuary is composed of detritus, in addition to phytoplankton, estimated by chlorophyll *a* concentrations. This detritus, as well as other suspended material, may be consumed by the shrimp, and would therefore potentially increase food concentrations (our model assumes that shrimp filtration is governed by phytoplankton concentration and not by the concentration of total suspended material, see Table 2.1). If shrimp are consuming significant quantities of detritus or other suspended material, this may cause our model to over-predict the proportion of phytoplankton removed by shrimp-burrow complexes.

Pinn et al. (1998) found that the gut contents of *U. deltaura* and *U. stellata* were composed of the same relative proportions of suspended matter (phytoplankton, sediment, detritus) as found in the water column, indicating a lack of pre-ingestive 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 filtration rate is, for this species, a function of total suspended particulates, rather than simply phytoplankton abundance, or even the concentration of organic carbon. The average concentration of total suspended matter in lower Yaquina Bay is 10 mg/l (Callaway et al. 1988), but will likely vary greatly with time and space in the

estuary. A valuable experiment would be to determine to what extent filtration rates of shrimp and *Cryptomya* are determined by algal concentration, and to what extent they are affected by total suspended particulate load.

The discrepancy of lab and field results indicate that there are aspects of *U. pugettensis* feeding dynamics, particularly at low food concentrations, that require further examination. Better knowledge of the proportion of time spent feeding, carbon concentration in water drawn into burrows (i.e. due to possible resuspension of benthic diatoms), and of the effect of suspended inorganics and detritus on shrimp filtration would improve the accuracy of our model. In addition, hydrographic factors that influence food availability, environmental factors (i.e. salinity, temperature, etc.) that affect shrimp feeding behavior, and qualitative composition of food may also affect shrimp filtration rates. However, our model provides a good first order estimate of the potential reduction of phytoplankton concentration by shrimp-burrow complexes in Yaquina Bay.

The results of our population filtration model and field experiments may be combined with tidal flow to derive upper and lower estimates of filtration by shrimp-burrow complexes. Approximately 70% of the 4.53×10^{10} liters of water contained in the Yaquina Bay at high tide are exchanged with ocean water over a complete tidal cycle (i.e. each 24 hrs) (Karentz & McIntire 1977). Oceanic water brought into the estuary with rising tide carries phytoplankton that would replenish the estuarine phytoplankton stock that was depleted by the shrimp. Because the

area we modeled is located near the mouth of the estuary, this entire volume of water (3.171×10^{10} l) must pass through the modeled area as it is exchanged.

Running through the center of the modeled area is a channel that divides the two large tidal flats (see Figure 2.1). Two scenarios, or a mixture of two scenarios, may exist. On an incoming tide, water may fill up the tide flats, with the remainder of the water passing through the central channel, while the standing water over the tide flats remains stationary. Or alternatively, incoming water may fan out evenly as it passes through the modeled area, with the entire exchanged water volume passing over the tide flats. If we assume that these two scenarios are the extreme possibilities, with the actual tidal volume moving over the modeled area in a manner that is likely intermediate, then these two extremes may be used to derive the upper and lower estimates of removal of phytoplankton by shrimp-burrow complexes in the lower Yaquina Bay. These estimates were derived as follows. We determined the ratio of carbon removed in field experiments to that predicted to be removed by the population filtration model at each phytoplankton concentration (values given in Figure 2.3). We multiplied these ratios by the model predictions given in Figure 2.2 for the proportion of phytoplankton removed from the lower Yaquina. This product resulted in model predictions based on shrimp feeding behaviors observed in the field, while still maintaining the allometric feeding relationships observed in the laboratory. The volume of water filtered in the two flow scenarios described above (only water over tide flats or all water exchanged

with tides) were then used to derive the upper and lower estimates of phytoplankton removal by shrimp-burrow complexes in the lower Yaquina (Figure 2.6)

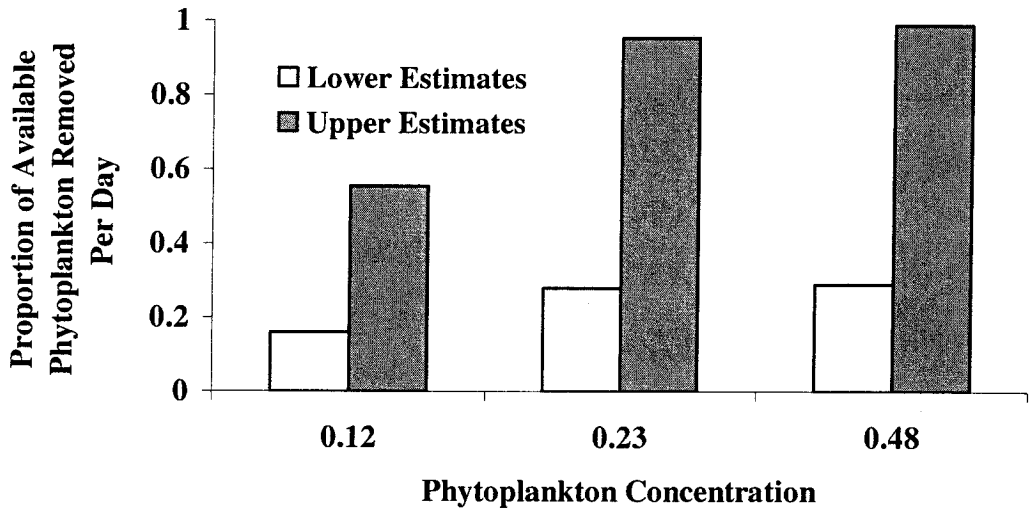

Figure 2.6 Upper and lower estimates of the proportion of phytoplankton removed by shrimp-burrow complexes from water in the lower Yaquina Bay at three phytoplankton concentrations.

For the scenario in which all water passes over the tide flats as the tide goes in and out, 70% of the water in Yaquina Bay passes through the modeled area. The values shown in Figure 2.6 therefore indicate the proportion removed from 70% of the water in the Bay as it passes through the lower Yaquina. The volume of water over the tide flat at any given time (see Table 2.2) represents only 29% of the water that is exchanged over a complete tidal cycle, or approximately 20% of the water in Yaquina Bay. In either scenario, shrimp-burrow complexes found further up the estuary may then further filter water that passes through the modeled area on flow

tides. Similarly, shrimp-burrow complexes may have previously filtered water passing the modeled area on ebb tides.

The highest values given in Figure 2.6 may be similar to values obtained for populations of related species of burrowing shrimp. For example, Dworschak (1981) estimated that populations of *Upogebia pusilla,* occurring in the Mediterranean, pump the entire volume of water overlying their burrows 1.4 times in 24 hours. Depending on particle retention efficiencies for this species, Dworschak's findings indicate that *U. pusilla* could remove similar proportions of phytoplankton as are predicted here for *U. pugettensis.*

In summary, the shrimp-burrow complex may be responsible for removing large proportions of the total available phytoplankton over tide flats of the lower Yaquina Bay (see Figure 2.6). This indicates that the complex is important in estuarine trophodynamics, and may be capable of reducing, or even depleting, suspended food in some areas of the estuary. Also, the similarity of relative retention efficiencies of shrimp and the Pacific oyster (Griffen et al. 2002) indicates that the potential for food competition exists in areas where shrimp remove a significant proportion of available food.

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SUMMARY

Based on filtration rates measured in our experiments and estimated tidal flow, we have shown that shrimp populations and associated shrimp-burrow complexes at current densities, are capable of depleting, or significantly reducing, phytoplankton abundance in the lower Yaquina Bay, Oregon.

We have also shown that shrimp have similar relative retention efficiencies to those of the Pacific oyster, for the size range of particles predominantly found in the lower Yaquina. This indicates that food competition is likely to occur between shrimp and other suspension feeders in areas of Yaquina Bay where shrimp deplete available food resources.

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APPENDICES

APPENDIX 1

Artificial Burrow Experiment

Introduction

Several researchers have looked at various aspects of thalassinid behavior using artificial burrows. Dworschak (1981) determined pumping rates of *Upogebia pusilla* using an acrylic-glass, U-shaped tube. Stamhuis & Videler (1998) looked at dynamics of flow around the shrimp, as well as pleopod motion in *Callianassa subterranea*, using a U-shaped glass tube. Because of the intensive labor and time required to transport sediment to the laboratory, and sieve it to remove other suspension feeders, we carried out an experiment to examine the feasibility of using artificial burrows. We also hoped to use artificial burrows to separate filtration by the shrimp from particle losses by attachment to the mucus-lined burrow wall of burrows in natural sediment.

Methods

The experiment included eight replicates of each of three treatments: 1) shrimp in chambers containing 17 cm of sediment in which shrimp developed burrows, 2) shrimp in opaque artificial burrows (to determine whether any effect of the artificial burrow was due to light rather than a property of the burrow itself),

and 3) shrimp in transparent artificial burrows. Eight controls of each treatment consisted of an identical set-up, without shrimp. Transparent burrows were made from Plexiglas tubes. Opaque burrows were made from Plexiglas tubes wrapped in thick black plastic (held in place with rubber bands). Thirty cm-long sections of tubes were bent into a U-shape and submerged in buckets of seawater. Only shrimp with carapace lengths between 21 and 25 mm (mean ± S.D.: 22.46 ± 1.20) were used in the experiment. Because the diameter of natural burrows vary with shrimp carapace length (carapace length = 1.1 x burrow diameter, Thompson 1972), we constructed artificial burrows from three different tube sizes in an effort to maintain this relationship. Both opaque and transparent burrows were constructed from 25, 22, and 19-mm (inside diameter) tubing.

Shrimp were collected and separated into three size classes that were based on the burrow sizes available and the equation relating burrow diameter to carapace length. Shrimp from each size class were then randomly assigned to one of the three treatments. In artificial burrows, there was an average relationship of carapace length = 1.13 x burrow diameter, similar to that found by Thompson (1972) in natural burrows.

Shrimp for the sediment treatment were allowed to establish burrows in 19-l chambers containing 10-l of sediment for two weeks prior to experimentation. Shrimp for the artificial tube treatments were stored in 1-l containers with 0.5 l of sediment, where they established burrows for two weeks prior to experimentation. Twenty-four hours before the experiment began, they were removed from these

burrows and introduced into artificial burrows. This was done in an effort to treat all shrimp the same (by maintaining equal time in the laboratory and by allowing them all to establish burrows in the lab) prior to different treatments in the experiment.

During the experiment, water-flow was turned off and the volume of water in each chamber was adjusted to eight liters. Algae (*Rhodomonas salina*) were added to each chamber to bring the cell concentration to 35,000 cells/ml. Water was constantly aerated throughout the experiment to maintain adequate mixing. Twenty-ml samples were taken hourly for nine hours (after this time, shrimp that actively fed had depleted the supply of algae to < 1,000 cells/ml). Samples were analyzed using a Coulter Counter for one size range of particles, corresponding to the size of algal cells (5.97 to 10.7 μm). After the experiment, shrimp were removed from their burrows and were dried and weighed.

From the sediment, transparent tube, and opaque tube treatments, six, five, and seven shrimp fed respectively. Only these shrimp were used in the analysis. Clearance rates were calculated for each time interval over the nine-hour experiment using methods by Coughlan (1969), and were then standardized to an animal of one-gram dry organic weight (using methods outlined in the methods section of Chapter 1). The average concentration over the time interval between samplings was calculated as follows:

$$\text{Concentration} = e\left(\frac{\ln(R_0)+\ln(R_1)}{2}\right)$$

Where R_0 is the concentration of particles at time zero, and R_1 is the concentration of particles at time one. In order to compare the shapes of the curves, clearance rates were then plotted against concentrations.

The maximum standardized clearance rate for each shrimp was used as a statistic for comparison between the three treatments. One-way ANOVA was used to test for differences among treatments.

Results and Discussion

Results for sediment, clear, and opaque burrow treatments are shown in Figure A-1. No significant difference in maximum clearance rate was found (ANOVA, $p = 0.10$). However, visual inspection of the graphs (see Fig. A-1) revealed differently shaped curves for shrimp in sediment as opposed to those in artificial tubes. Also, there were five separate instances during the experiment when shrimp with the artificial burrow treatment (both transparent and opaque), left the burrow and were found swimming or on the bottom of the experimental chamber. In each case the shrimp was placed back in the burrow. However, stress for the shrimp due to frequent handling adds an additional unknown factor in the experiment. Also, the shrimp presumably experienced some level of stress in the artificial burrow that stimulated it to leave the burrow in the first place.

For these reasons, and to attempt to simulate field conditions as much as possible, we decided to conduct all feeding experiments in sediment burrows that had been constructed by the shrimp in the laboratory. The above-mentioned concerns may also indicate a need for caution in interpreting other studies that examine shrimp behavior using artificial burrows.

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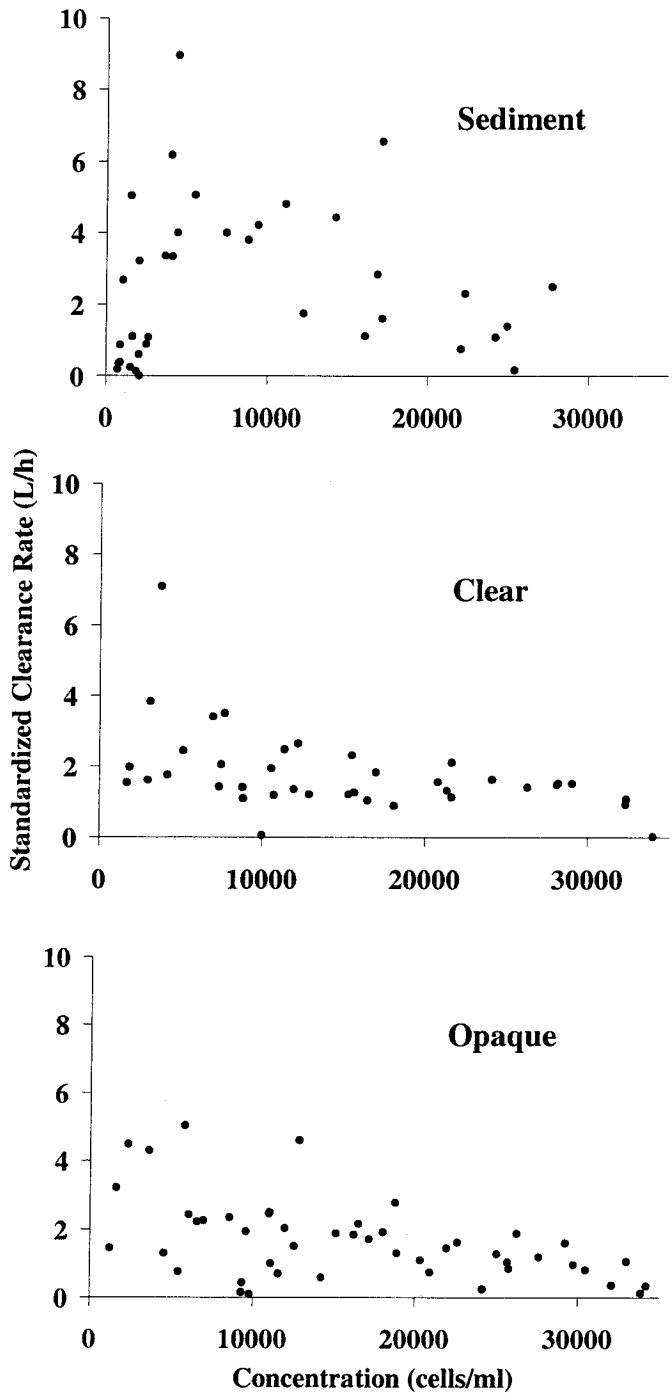

Figure A1-1 Standardized clearance rate of *Upogebia pugettensis* vs. algal cell concentration in sediment, artificial clear, and artificial opaque burrows at 12°C and 34 ppt salinity

APPENDIX 2

Test for Additivity of Shrimp and *Cryptomya* Filtration

Introduction

We compared filtration rates of the same individuals together, and separately, to determine whether the filtration rates of shrimp + burrow and *Cryptomya* are additive, i.e. whether the sum of the feeding activities of the two species when separate is the same as that of the two species when they physically co-occur (i.e. when *Cryptomya* are present in the shrimp's burrow). This was important to determine whether we could add the filtration rates observed for each species separately in the laboratory to predict the effects of the shrimp-burrow complexes on phytoplankton abundance in the lower Yaquina Bay.

Methods

After completion of feeding experiments with the shrimp alone (see chapter one for description of flow-through experimental techniques used), groups of 13 *Cryptomya,* with a range of sizes (1-25 mg dry organic weight; all groups had similar size ranges and distribution of *Cryptomya*), were added to each of 14 chambers. The clams were allowed two weeks to adjust to experimental conditions. Some clams remained just below the surface of the sediment, while

others established themselves in the shrimp burrow, as determined upon excavation at the end of the experiment.

The flow-through filtration rate experiment at low algal concentration (5-8,000 cells/ml) was then repeated. Following the experiment, *Cryptomya* were removed and filtration rates for each group of 13 bivalves were determined in the absence of shrimp. Standardized filtration rates for the shrimp and *Cryptomya* alone, at low algal concentrations (5-8,000 cells/ml) were then summed and compared (paired, two-tailed t-tests, assuming unequal variance, $\alpha = 0.05$) with standardized filtration rates for the two species together in the same chamber. Because we were unable to determine what portion of the filtration was attributable to individual clams, no distinction was made in our analysis between clams that established themselves in the burrows and those that remained just below the sediment surface.

Results and Discussion

There was no difference in filtration rates (paired, two-tailed t-test, $p = 0.29$) between shrimp and *Cryptomya* in the same chamber (0.584 ± 0.243 mg C/h/g shrimp DOW), and the sum of the filtration rates for the same individuals (0.486 ± 0.110 mg C/h/g shrimp DOW, the sum of the unstandardized filtration rates of shrimp and clams were standardized) tested separately, indicating that the filtration rates of the two species are additive.

APPENDIX 3

Feeding Rate Graphs

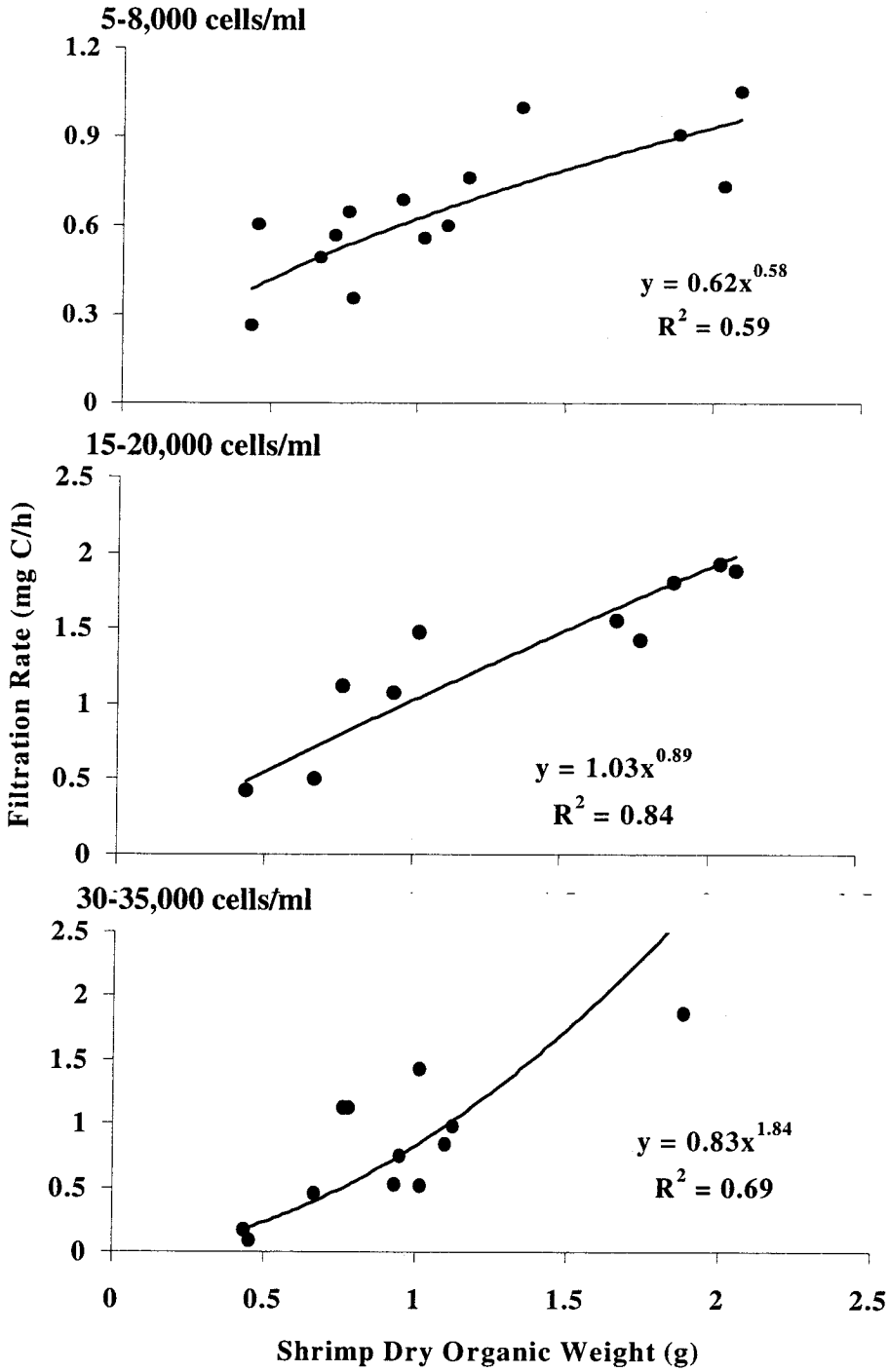

Figure A3-1 Allometric relationship between filtration rates of *Upogebia pugettensis* (based on shrimp DOW) at different food concentrations, at 12-13°C and 34-35 ppt salinity. Relationship was obtained using the clearance rates of the 8.5 μm particle size class because this size class gave the highest R^2 values.

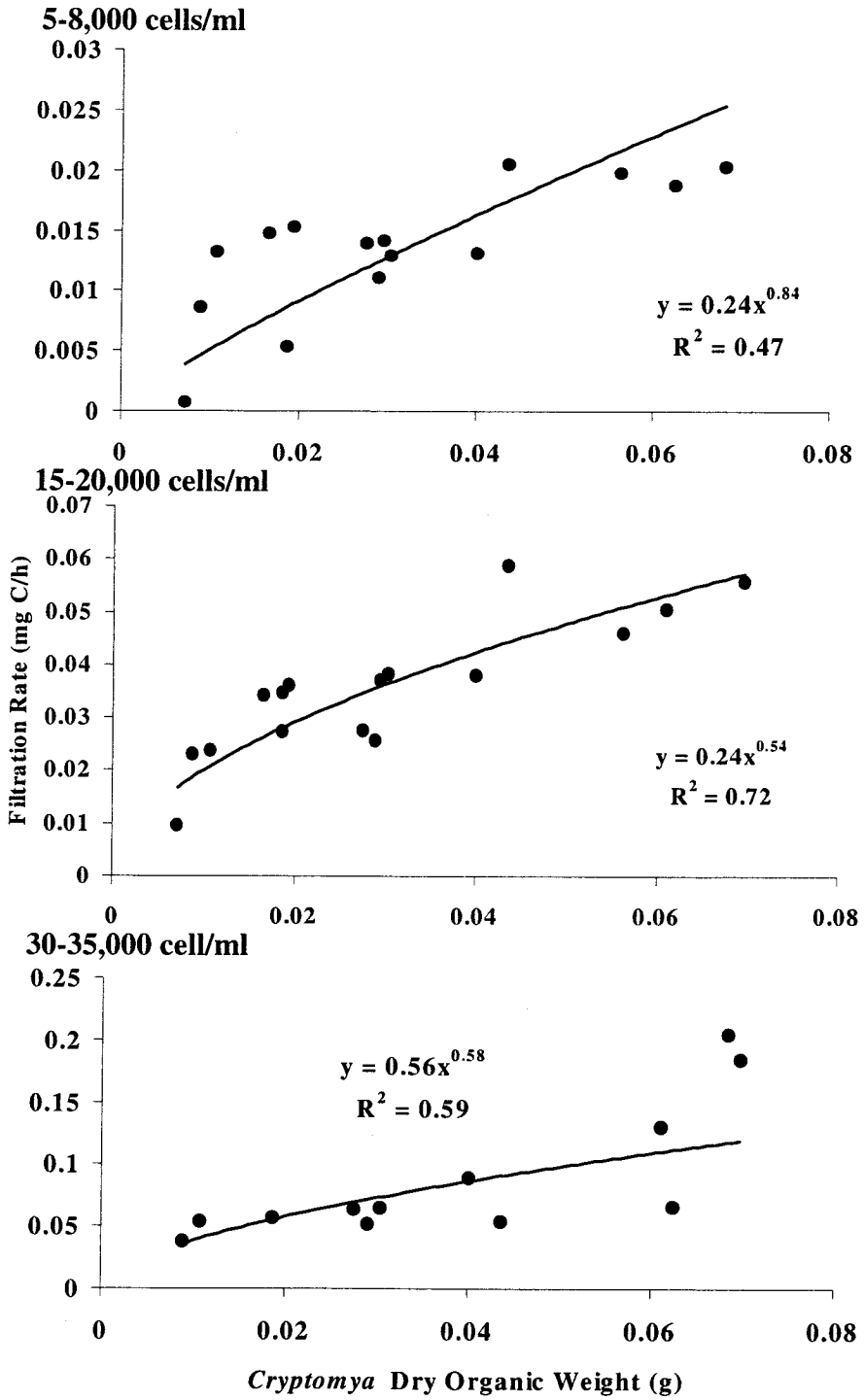

Figure A3-2 Allometric relationship between filtration rate of *Cryptomya californica* (based on DOW) at 13°C and 35 ppt salinity. Relationship was obtained using the clearance rates of the 5.5 μm particle size class because this size class gave the highest R^2 values.

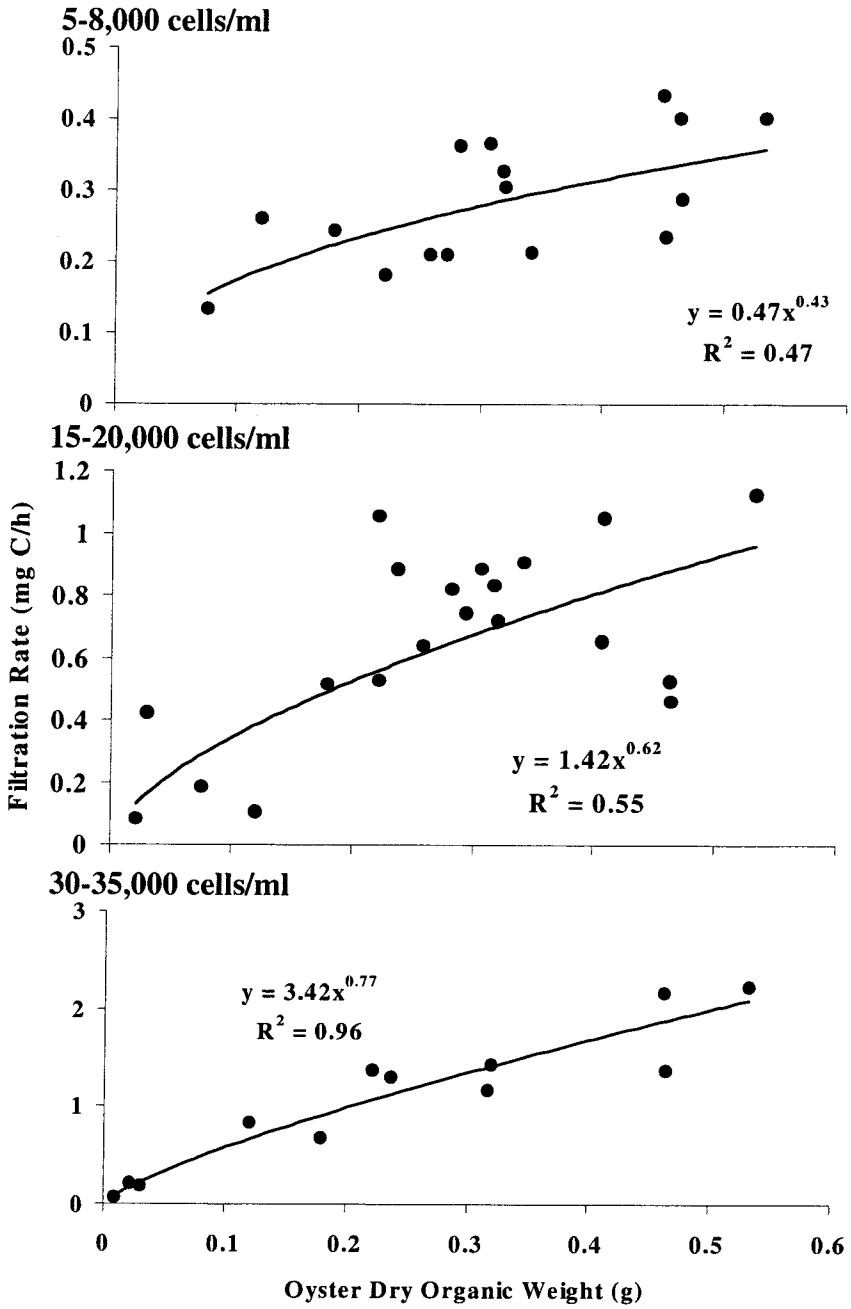

Figure A3-3 Allometric relationship between filtration rate of *Crassostrea gigas* (based on DOW) at different algal concentrations in laboratory experiments at 13°C, 35 ppt salinity. Relationship was obtained using the clearance rates of the 8.5 μm size class because this size class gave the highest R^2 values.

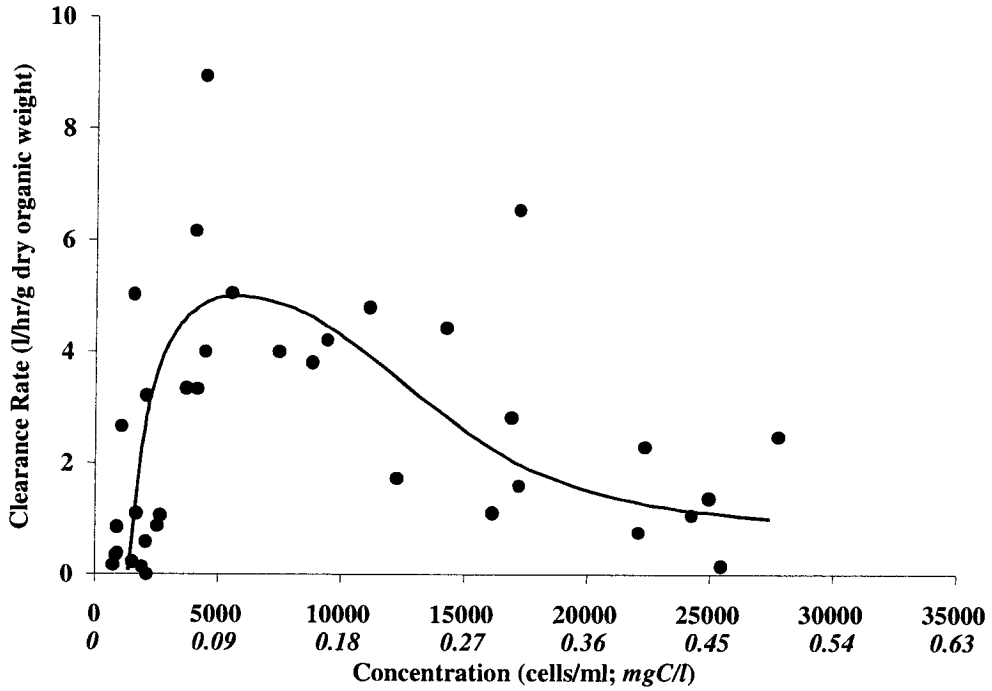

Figure A3-4 Change in standardized clearance rate (standardized to an animal of one-gram dry organic weight) of *Upogebia pugettensis* + burrow with change in food concentration at 12°C and 34 ppt salinity. The curve was drawn by hand to illustrate the trend. Results of experiment used to determine the concentrations to use in feeding rate experiments. Concentrations were chosen to represent each area of the curve (5-8,000 cells/ml, 15-20,000 cells/ml, and 30-35,000 cells/ml)

APPENDIX 4

Determination of Pumping Rates

Introduction

The burrow wall represents a topological extension of the sediment-water interface. Burrowing shrimp effectively increase the surface area of this interface by as much as 36 times that of areas not inhabited by shrimp (DeWitt, unpubl. Data). Knowledge of the rate of water flow through the burrows is important because of the effect that flow has on nutrient exchange across the sediment water interface (Forster and Graf 1995). The pumping rate (the rate at which shrimp move water through their burrow) is therefore an important value to determine.

Methods

By assuming that the size of particles that were retained with the greatest efficiency in our experiments were retained with 100% efficiency, the pumping rate can then be calculated as follows:

$$P = D \times [(V^* - V)/V^*] \qquad (1.5)$$

Where P is the pumping rate, and other symbols are as indicated above. Equation 1.5 was used to calculate P for each particle size tested. Pumping rate was then

determined by averaging P for all particle sizes with values within 5% of the maximum P.

Results and Discussion

Pumping rates as a function of ash-free dry weight are given in Figure A4-1.

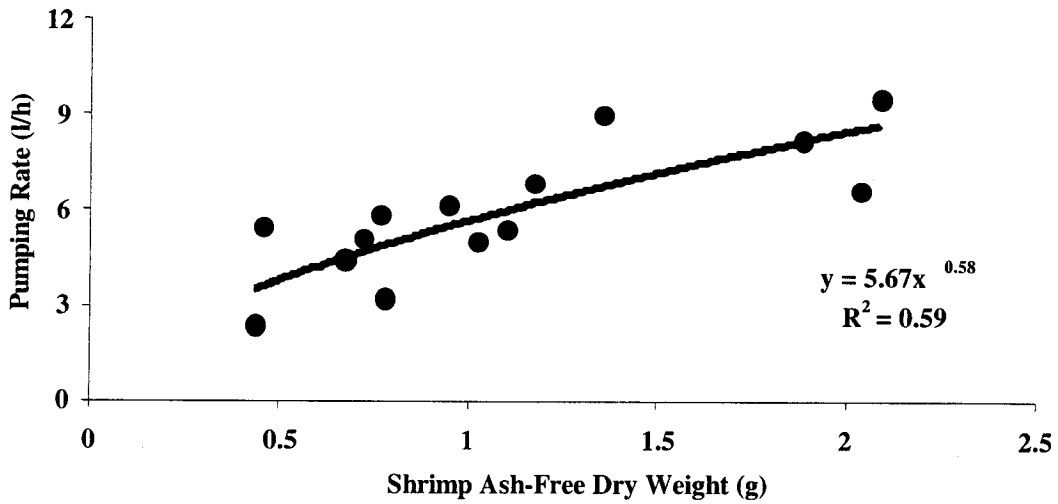

Figure A4.1 Pumping rate of *Upogebia pugettinsis* vs. dry organic weight (g) at 13°C, 35 ppt salinity, and an algal concentration of 5-8,000 cells/ml.

The pumping rates given here are somewhat higher than reported values for other suspension-feeding burrowing shrimp. For example, using the equation given here, a 0.6 g shrimp has a pumping rate of 1.17 ml/s. Dworschak (1981) reported a pumping rate of 0.34 ml/s for a similar sized individual of the species *Upogebia pusilla.*

APPENDIX 5

Data From Experiments

Table A5-1 Data from laboratory, static (non-flow-through) experiment to determine the amount of algae that settles on the burrow wall. Altering the volume of sediment in which *Upogebia pugettensis* were allowed to burrow controlled burrow length. *Rhodomonas salina* was introduced and a time series of samples was taken and analyzed with a Coulter Counter (one size range of particles was analyzed from 5.4 - 9.4 μm). Filtration rates were calculated for each shrimp for the time interval during which the algal concentration was from 5-8,000 cells/ml. Burrow casts were then made with plaster and the burrow wall surface area was calculated by assuming the burrow was a cylinder. Results of the experiment are shown in Figure 1.2. SA is surface area, and Std FR is filtration rate in mg C/h standardized to an animal of one-gram dry organic weight (determined using the relationship: dry organic weight = $0.00005 \times (\text{carapace length})^{3.168}$.

Treatment	Shrimp Carapace Length (mm)	Burrow SA (cm^2)	Std CR at 5-8,000 cells/ml
10 liter	22.8	427.66	0.59
10 liter	22.6	567.75	0.94
10 liter	20.1	476.36	0.84
10 liter	21.7	377.19	1.07
10 liter	21.0	446.2	0.81
5 liter	22.2	413.21	0.89
5 liter	20.2	313.3	1.02
5 liter	21.8	400.97	0.82
5 liter	20.3	334.24	0.92
5 liter	23.4	424.26	0.86
0.5 liter	22.0	174.77	0.83
0.5 liter	19.7	146.07	0.54
0.5 liter	20.4	188.86	0.83
0.5 liter	23.5	147.05	0.56
0.5 liter	21.3	194.62	0.44

Table A5-2 Data from the laboratory, non-flow-through experiment to examine the feasibility of using artificial burrows in feeding experiments on *Upogebia pugettensis*. Three treatments included shrimp burrowed in sediment, shrimp placed in opaque artificial tubes, and shrimp placed in transparent artificial tubes. DW is dry organic weight, and Max SCR is standardized (to an animal of one-gram dry organic weight) maximum clearance rate (volume of water cleared of particles per unit time).

Treatment	DW (g)	Max SCR (L/h)
opaque	1.65	5.42
opaque	1.15	2.59
opaque	1.15	2.41
opaque	1.53	6.14
opaque	0.96	4.52
opaque	1.97	1.78
opaque	1.66	2.37
mud	1.49	4.59
mud	1.95	5.33
mud	1.33	7.04
mud	1.52	10.86
mud	1.48	5.75
mud	1.44	4.74
clear	1.32	4.36
clear	1.28	7.95
clear	1.00	1.42
clear	1.46	4.05
clear	1.44	1.83

Table A5-3 Data from flow-through laboratory feeding experiments with *Upogebia pugettensis* at three different algal concentrations. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure 1.5. SFR is standardized filtration rate in mg C/h. Values were standardized to a 0.6 g animal, the average size *Upogebia pugentensis* in Yaquina Bay (DeWitt, unpubl. data)

Shrimp Dry Organic Weight (g)	SFR at 5-8,000 cells/ml	SFR at 15-20,000 cells/ml	SFR at 30-35,000 cells/ml
1.13			0.27
0.72	0.53		
0.78	0.31		0.27
1.69	0.54	0.52	0.20
1.77	0.53	0.51	0.12
0.76	0.57	0.55	0.53
1.88	0.39	0.41	0.15
0.95	0.52		0.34
1.10	0.51		0.25
1.02	0.33	0.80	0.19
0.44	0.27	0.53	0.26
0.67	0.46	0.37	0.26
0.93	0.50	0.73	
1.35	0.60	0.75	
0.45	1.07		0.11
1.17	0.62		
2.09	0.46	0.49	
2.03	0.42	0.70	
0.93			0.19

Table A5-4 Data from flow-through laboratory particle retention efficiency experiments with *Upogebia pugettensis* at algal concentrations from 5-8,000 cells/ml. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, as well as background particles present in the incoming seawater system, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure 1.3. Values in columns 2.5 through 9.5 are the efficiencies (relative to some maximum for each individual) of particle retention. Blank spaces represent negative values that were removed. Data are retention efficiencies, relative to a maximum value (obtained from the average of all values within 5% of the maximum) for each animal.

	Mean Particle Diameter (μm)							
	Retention Efficiencies							
Dry Organic Weight (g)	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
0.72	0.29	0.43	0.80	0.85	0.89	0.93	1.02	0.98
0.78		0.10	0.77	0.88	0.94	0.92	1.00	0.88
1.69	0.72	0.87	0.72	0.69	0.68	0.66	0.77	1.00
1.77	0.82	1.00	0.62	0.63	0.62	0.66	0.74	0.65
0.76	0.48	0.80	0.82	0.93	0.83	0.97	1.01	1.02
1.88	0.16	0.61	0.66	0.81	0.65	0.79	1.00	0.70
0.95	0.08	0.29	0.74	0.79	0.88	0.92	1.00	0.77
1.10			0.73	0.90	0.95	0.95	1.00	1.00
1.02		0.04	0.68	0.89	0.98	1.00	1.02	0.83
0.44	0.02	0.42	0.78	0.89	0.87	1.00	0.93	0.89
0.67	0.28	0.47	0.77	0.84	0.73	0.81	0.88	1.00
0.93	0.01	0.32	0.60	0.69	1.00	0.81	0.13	
1.35		0.25	0.60	0.77	0.81	0.83	0.95	1.00
0.45	0.82	0.88	0.92	0.95	0.95	1.00	1.01	0.98
1.17	0.26	0.54	0.72	0.89	0.99	1.01	0.86	0.67
2.09	0.09	0.41	0.46	0.60	0.64	0.77	0.93	1.00
2.03	0.66	0.71	0.67	0.88	0.90	0.98	1.02	0.94

Table A5-5 Data from flow-through laboratory feeding experiments with *Cryptomya californica* at three different algal concentration. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure 1.5. SFR is standardized filtration rate in mg C/h. Values were standardized to a 0.019 g animal, the average size *Cryptomya* in the lower Yaquina Bay (DeWitt, unpubl. data). Values in Figure 1.5 were multiplied by eight because there are an average of eight *Cryptomya* per shrimp-burrow complex in the lower Yaquina (DeWitt, unpubl. data).

Cryptomya Dry Organic Weight (g)	SFR at 5-8,000 cells/ml	SFR at 15-20,000 cells/ml	SRF at 30-35,000 cells/ml
0.056	0.005	0.017	0.013
0.040	0.006	0.017	0.029
0.030	0.008	0.020	0.024
0.028	0.005	0.012	0.028
0.062	0.004	0.006	0.020
0.029	0.004	0.012	0.019
0.011	0.011	0.022	0.034
0.009	0.010	0.022	0.032
0.042	0.002		
0.061	0.008	0.002	0.020
0.068	0.004		0.025
0.019	0.020	0.032	0.075
0.019	0.010	0.040	
0.030	0.001	0.015	
0.017	0.007	0.006	
0.019	0.008	0.018	

Table A5-6 Data from flow-through laboratory particle retention efficiency experiments with *Cryptomya californica* at algal concentrations from 5-8,000 cells/ml. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, as well as background particles present in the incoming seawater system, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure 1.3. Values in columns 2.5 through 9.5 are the efficiencies (relative to some maximum for each individual) of particle retention. Blank spaces represent negative values that were removed. Data are retention efficiencies, relative to a maximum value (obtained from the average of all values within 5% of the maximum) for each animal.

	Mean Particle Diameter (μm)							
	Retention Efficiencies							
Dry Organic Weight (g)	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
0.056	0.43	0.70	0.81	1.03	0.85	0.97	0.78	0.38
0.040	0.45	0.73	0.93	0.94	1.00	0.94	1.27	0.99
0.030	0.36	0.52	0.67	0.62	0.67	0.56	1.00	0.58
0.028			0.64	0.72	0.99	1.03	0.98	0.28
0.062	0.46	0.21	0.33	0.53	0.21	0.52	0.40	1.00
0.029	0.22		0.74	0.86	0.40	0.86	0.45	1.00
0.011			0.76	0.87	0.64	1.01	0.72	0.99
0.009	0.43	0.39	0.92	1.01	0.93	1.00	0.99	0.62
0.042	0.64	0.70	0.40	0.48	0.71	0.14	0.54	1.00
0.044	0.80	0.66	0.67	0.85	0.71	0.51	0.82	1.00
0.061	0.21	0.28	0.72	0.90	1.00	0.37	0.79	0.78
0.068	0.86	1.01	0.93	0.94	0.99	0.70	0.84	0.99
0.019	0.77	0.99	0.60	0.48	0.80	0.22	0.29	1.01
0.019	0.54	0.84	1.00		0.69			
0.030	0.13	0.78	0.94	0.69	1.00	0.72	0.45	
0.017	1.00	0.92	0.85	0.75	0.90	0.54	0.70	0.75
0.019	0.13	0.68	1.00	0.93	1.00	0.91	0.73	0.56
0.070	0.90	0.48	0.35	0.53	0.20	0.41	0.73	1.00

Table A5-7 Data from flow-through laboratory feeding experiments with *Crassostrea gigas* at three different algal concentrations. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure 1.5. SFR is standardized filtration rate in mg C/h. Values were standardized to a 0.752 g animal, which equals the biomass of the average shrimp-burrow complex.

Oyster Dry Tissue Weight (g)	SFR at 5-8,000 cells/ml	SFR at 15-20,000 cells/ml	SFR at 30-35,000 cells/ml
0.31	0.33	1.05	
0.18	0.37	0.78	1.11
0.12	0.42	1.05	1.80
0.39		0.73	
0.32	0.33	1.01	1.61
0.46	0.31	0.64	0.03
0.45	0.45		
0.53	0.38	1.14	1.92
0.27	0.27	0.76	
0.32	0.42	1.16	1.55
0.24	0.53	1.24	2.03
0.26	0.24	0.90	
0.41	0.22	1.17	0.05
0.01			
0.45	0.04		
0.34	0.10	1.52	
0.28	0.69	1.64	
0.22		1.02	
0.46	0.31	1.29	2.78
0.22	0.75	1.71	
0.29		0.81	
0.08	0.73		
0.02			
0.03			

Table A5-8 Data from flow-through laboratory particle retention efficiency experiments with *Crassostrea gigas* at algal concentrations from 5-8,000 cells/ml. Two species of algae, *Isochrysis galbana* (Tahaitian strain) and *Rhodomonas salina*, as well as background particles present in the incoming seawater system, were used. The experimental design is shown in Figure 1.1, and the results of the experiment are shown in Figure1.3. Values in columns 2.5 through 9.5 are the efficiencies (relative to some maximum for each individual) of particle retention. Blank spaces represent negative values that were removed. Data are retention efficiencies, relative to a maximum value (obtained from the average of all values within 5% of the maximum) for each animal.

	Mean Particle Diameter (μm)							
	Retention Efficiencies							
Dry Tissue Weight (g)	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
0.31		0.03	0.50	0.52	0.94	1.00	0.91	0.21
0.18	0.52	0.63	0.56	0.65	0.89	0.73	1.00	0.43
0.12	0.23	0.38	0.59	0.57	0.98	0.90	1.02	0.97
0.32	0.23	0.36	0.79	0.86	1.00	0.92	0.88	0.32
0.45		0.39	0.65	0.76	0.93	1.00	0.92	0.78
0.53	0.24	0.63	0.72	0.76	1.03	0.98	0.99	0.76
0.27	0.38	0.67	0.83	0.82	1.00	1.00	1.00	0.73
0.32	0.74	0.68	0.67	0.75	1.02	0.96	0.98	
0.24	0.63	0.54	0.67	0.82	1.00	0.96	1.00	0.88
0.25	0.33	0.45	0.60	0.69	0.85	0.99	1.01	0.91
0.41	0.54	0.70	0.82	0.88	0.92	0.93	0.98	1.02
0.01		0.50	0.77	0.78	0.81	0.90	1.00	0.76
0.45	0.35	0.57	0.55	0.43	0.99	0.93	0.90	0.80
0.34	0.37	0.59	0.69	0.80	1.01	0.99	0.95	0.94
0.28	0.47	0.52	0.64	0.79	0.67	1.00	1.00	0.93
0.46	0.60	0.60	0.48	0.73	0.93	1.01	0.98	1.00
0.22	0.67	0.73	0.83	0.88	0.92	1.00	0.99	1.01
0.29		0.46	0.64	0.76	0.77	0.98	1.02	0.96
0.08	0.45	0.51	0.72	0.79	0.82	0.92	1.00	0.87
0.02	0.17	0.52	0.77	0.75	0.82	0.70	1.00	0.78
0.03	0.26	0.70	0.78	0.86	0.83	0.85	1.00	0.88

Table A5-9 Data from field experiments on filtration rates of shrimp-burrow complexes on Idaho Flat in Yaquina Bay, OR and model results of predicted filtration rates. Temperatures ranged from 12-18°C and salinities from 34-36 ppt. Field experiments used the alga *Rhodomonas salina*. Results shown in Figure 2.3.

Model Predictions (mg C removed)	Field Results (mg C removed)	Algae Concentration	Shrimp Density	Site
2.3	1.0	Low	High	2
4.4	2.1	Low	High	3
2.4	1.1	Low	Medium	2
7.0	0.1	Low	Medium	1
3.6	1.1	Low	Low	1
3.3	4.1	Medium	High	3
3.4	4.4	Medium	High	2
2.8	5.0	Medium	High	1
1.9	4.4	Medium	Medium	3
2.6	4.3	Medium	Medium	2
2.6	5.3	Medium	Medium	1
3.0	2.7	Medium	Low	3
5.8	1.3	Medium	Low	2
2.1	1.1	Medium	Low	1
2.3	6.6	High	High	3
2.3	9.4	High	High	2
2.1	9.5	High	High	1
4.9	4.4	High	Medium	3
5.7	3.7	High	Medium	2
8.5	6.0	High	Medium	1
2.6	4.9	High	Low	3
3.2	1.3	High	Low	2
4.7	2.4	High	Low	1

APPENDIX 6

Equations

Feeding Rate Equations

The equation used to calculate retention efficiency is as follows:

$$R_s = (V_s^* - V_s)/V_s^* \, R_{s(max)}$$

Where R_s is percentage of particles in a given size range removed, V_s^* is volume of particles of a given size range from the outflow of the control chamber (μm^3/ml), and V_s is volume of particles of a given size range from the outflow of the experimental chamber (μm^3/ml).

The equation used to calculate filtration rate is as follows:

$$F = D\,(V^* - V)$$

Where F is filtration rate of the suspended particulate matter removed in $\mu m^3\ hr^{-1}$, D is flow rate of water through the experimental chamber (liters hr^{-1}) and other symbols as indicated above.

The equation by Strathman (1967) was used to convert phytoplankton cell volume to mass of carbon:

$$\log_{10} Carbon(pg) = -0.314 + 0.712 \times \log_{10} Volume(\mu m^3)$$

The equation used to standardize feeding rates to a standard sized animal is as follows:

$$C^* = C_e^* \, (W_s/W_e)^b$$

Where C* is the clearance or filtration rate of the standard animal, C_e* is the uncorrected clearance or filtration rate of the experimental animal, W_s is the dry organic weight of the standard animal, W_e is the measured dry organic weight of the experimental animal, and *b* is the allometric coefficient obtained by plotting feeding rate vs. dry tissue weight of the animal.

Model Equations

The equations used in the model are as follows:

$$\%R_{total} = \sum \%R_{shrimp\ +\ burrow} + \%R_{Cryptomya}$$

Where *%R* is the percent of total available carbon consumed. Only the consumption by shrimp and the burrow ($\%R_{shrimp\ +\ burrow}$) is shown here, as the development of the model for *Cryptomya* ($\%R_{Cryptomya}$) is the same as that of the shrimp and burrow:

$$\%R_{\text{shrimp + burrow}} = \frac{\text{Mass of carbon consumed}}{\text{Mass of carbon available in box}}$$

$$= \frac{\sum\{M_i \times F_i\} \times T}{C \times V}$$

Where M_i is the biomass (g) of shrimp of size class *i* in the box; F_i is the filtration rate (mg C/h/g dry organic weight) of shrimp in size class *i*; *T* is half of the submergence time; *C* is concentration of carbon (mg/l) in the box; and *V* is volume of water (l) in the box.

The equations for F_i are as follows:

$$F_{shrimp} = -0.2667W + 0.9896 \qquad R^2 = 0.84$$

$$F_{Cryptomya} = -0.5515 - 0.6229(\ln W) + 0.5848(\ln C) \qquad R^2 = 0.64$$

where W is ash-free dry weight (g), and C is concentration of suspended carbon (mg/l) available for food.