Limnol. Oceanogr., 38(5), 1993, 949–964

Potamocorbula amurensis: Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton

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Abstract

This study compared clearance and assimilation of natural bacterioplankton (<1.2 μm) and cultured phytoplankton by an Asian bivalve, *Potamocorbula amurensis*. The average clearance rate for bacterioplankton was 45 ml h^{-1} $clam^{-1}$ and was independent of the size (shell length, wet wt including shell, or dry tissue wt) of the clam. The clearance rate for phytoplankton is given by $f = 162 + 166 \times WW$ or $f = -40 + 199 \times L$ where f, WW, and L are clearance rate (ml h^{-1}), wet weight including shell (g), and shell length (cm).

Bacteria were readily assimilated by *P. amurensis*. Gross assimilation was 73% after 49 h compared to 90% for *Isochrysis galbana*. Net assimilation was 45 and 53% for bacterioplankton and *I. galbana*, respectively. Bacterial carbon appeared to be respired faster than algal carbon. As seen in other bivalves, feces production increased and assimilation efficiency decreased at higher food concentrations.

At the mean bacterioplankton and phytoplankton standing stocks found in northern San Francisco Bay, bacteria supplied ~13 and 16% of the sum of bacteria and phytoplankton C and N, respectively, consumed by a 1-cm *P. amurensis*. We calculate that a 1-cm clam could double its C biomass in 221 d by feeding on bacterioplankton and in 26 d by feeding on phytoplankton.

San Francisco Bay has been the site of numerous invasions by exotic species (Carlton 1979; Nichols et al. 1986). In recent years, transport and release of seawater ballast from cargo vessels has become a major source of introduced species (Carlton 1985). Improved relations with the People's Republic of China and the opening up of new Chinese ports in the mid-1980s coincides with the appearance of the Asian bivalve mollusc *Potamocorbula amurensis* (Fam: Corbulidae), which was first discovered in Grizzly Bay in October 1986 (Carlton et al. 1990). From one specimen reported late in 1986, the population of *P. amurensis* has increased to peak densities of >12,000 animals m^{-2} (Carlton et al. 1990). It is now the dominant species in northern San Francisco Bay benthos, particularly in Suisun Bay, and has become established throughout San Francisco Bay (Nichols et al. 1990).

A significant drop in the Suisun Bay phytoplankton standing crop, from a summer average of >20 to <2 mg Chl *a* m^{-3}, coincided with the increase of *P. amurensis* populations (Alpine and Cloern 1992). Although specific growth rates remain unchanged, phytoplankton production declined fivefold from an average of 106 to 20 g C m^{-2} yr^{-1} in 1988. The decline in phytoplankton standing crop has been attributed to increased benthic grazing (Alpine and Cloern 1992).

Despite considerable reduction in phytoplankton standing crop and production, the *Potamocorbula* population continued to increase at a rapid rate, suggesting that organic carbon sources other than phytoplankton might be significant components of the diet of *P. amurensis*. Bacteria are abundant in estuaries and bacterial production is often high (Ducklow 1983; Coffin and Sharp 1987). Bacterial production now greatly exceeds phytoplankton production in Suisun Bay and the western delta (Hollibaugh unpubl. data). Bacteria are important agents of organic matter decomposition and nutrient regeneration as well as food for higher organisms (Wright 1978). Recent work (Wright et al. 1982;

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Acknowledgments

The State of California, Department of Water Resources funded this study through contract B-57360 to J.T.H. I.W. was supported by Studienstiftung des Deutschen Volkes.

We thank Jan Thompson, Pat Wong, and S. Obrebski for help and advice and Z. Hymanson, D. Kirchman, J. Orsi, and an anonymous reviewer for comments on an earlier draft.

Langdon and Newell 1990) demonstrates that bacteria can be an important food source for bivalves, depending on the efficiency with which its biomass can be used and the availability of phytoplankton and detritus. In addition, bacteria may provide nutrients that are deficient in detrital diets. These considerations raise the following questions: What are the relative clearance rates for phytoplankton and bacterioplankton by *P. amurensis*? What are the assimilation efficiencies of *P. amurensis* for bacterioplankton and phytoplankton?

These questions were addressed in a series of laboratory experiments. The primary goal of the study was to obtain comparative data on clearance rates and assimilation efficiencies under controlled conditions as a first step toward understanding the autecology of *P. amurensis,* rather than to measure in situ rates and efficiencies. The relationships between clearance rates for phytoplankton, primarily *Isochrysis galbana,* and natural bacterioplankton and animal size and weight were examined. We found that *P. amurensis* is capable of retaining natural bacterioplankton, albeit at a lower efficiency than phytoplankton. We also examined the ability of *P. amurensis* to assimilate phytoplankton and bacterial C. We found that both bacterioplankton and phytoplankton C are assimilated with high efficiency.

Methods

Clams—Animals were collected from various sites in northern San Francisco Bay. They were held in tanks at the Tiburon Center for at least 2 months to acclimate before being used in experiments. Water flowing through the tanks was pumped from ~15 m offshore and a depth of ~3.5 m (bottom). The flow rate was ~18 liters h^{-1} resulting in a tank residence time of ~0.5 h. The water was not filtered and no additional food was added. The animals buried themselves in mud that settled out of the inflowing bay water. Chlorophyll *a* concentrations off the Tiburon Center are 1–2 μg $liter^{-1}$, similar to concentrations elsewhere in northern San Francisco Bay. Clams increased in size under these conditions, indicating that they were obtaining an adequate ration from material in the inflowing water. One to two days before the experiments the clams were measured, weighed, and placed in small, clean Petri dishes in the tanks to acclimate to not being buried. We found that animals so treated did not move as much during the experiments and began feeding sooner than animals removed from sediment immediately before commencing the experiment.

Morphometrics—In order to facilitate comparison between studies, we determined shell lengths and widths and wet and dry weights for a number of clams. These data can be used to convert clearance rates into various units, for identifying the clam, or for setting up automated counting procedures.

The lengths and widths of clams were measured to 1 mm with calipers. Weights were determined to 0.1 mg with a Mettler balance. Clams were blotted dry on paper toweling; wet weights, including shell, were then measured. Clam tissue was carefully removed from the shell with a scalpel; the shell was blotted dry and then weighed. The tissue was then lyophilized and weighed. Conversion to ash-free dry weight (AFDW, mg) was accomplished by regressing AFDW against shell length (L, mm) as reported by Cole et al. (1992): $\ln(\text{AFDW}) = -4.81 + 2.81 \times \ln(\text{L})$. It should be noted that the units for this regression (g, cm) given by Cole et al. were reported incorrectly; the correct units are mg and mm (B. E. Cole and J. K. Thompson pers. comm.).

Phytoplankton—Unialgal, axenic cultures of *Skeletonema costatum* (Grev.) Cleve, *Phaeodactylum tricornutum* Bohlin, *Platymonas subcordiformis* (Wille) Hazen, and *I. galbana* Parke were obtained from the UTEX Culture Collection of Algae, Austin, Texas, and maintained under unialgal but not axenic conditions in f/2 medium (Guillard and Ryther 1962). Pilot experiments were performed with each of these species. Of the species we tested, *I. galbana,* a marine flagellate (Fam.: Prymnesiophyceae), was found to be best suited for this study. It is a flagellated, spherical cell ~5 μm in diameter that grows slowly and does not form chains or clumps.

Phytoplankton were washed on 3-μm pore-size Nuclepore filters (3.0 NF) with particle-free bay water (filtered through a 0.45-μm pore-size Millipore filter, HAMF) to remove most of the bacteria growing in the culture (which are larger than natural bacterioplankton), then resuspended in a small volume of particle-free water. The volume filtered depended on the concentration of phytoplankton in the culture.

All filtrations, except those used to prepare particle-free water, were performed with gravity or <20-kPa vacuum. Microscopic examination of washed cultures revealed no lysed phytoplankton cells. The washed phytoplankton suspension was added to glass-fiber-filtered (GF/C) bay water to yield final concentrations of 4,000–12,000 cells ml^{-1} or 52–160 μg C $liter^{-1}$ of *I. galbana* calculated from Strathmann's (1967) equations relating biovolume to C content (13 ng C $cell^{-1}$). The final concentrations of *Phaeodactylum* and *Skeletonema* were 25,000 and 8,000 cells ml^{-1}. These concentrations are similar to phytoplankton standing crops currently found in San Francisco Bay.

Bacterioplankton—Clearance rates on natural bacterioplankton were measured in the presence and absence of *I. galbana, Phaeodactylum,* and *Skeletonema* to determine whether bacteria were retained more efficiently when phytoplankton were present. The bacterioplankton suspension was prepared by filtering San Francisco Bay seawater through Whatman GF/C filters (nominal pore size, 1.2 μm) to remove large particles. From 75 to 90% of the bacterioplankton passed through the GF/C filters, resulting in initial abundances of 0.5–1.5 ($x = 0.9$) $\times 10^6$ cells ml^{-1} or 10–30 μg C $liter^{-1}$ calculated with Lee and Fuhrman's (1986) conversion factor of 20 fg C $cell^{-1}$. The suspensions were used within 2 h of collection.

Clearance rate measurements—Clearance rates were determined at in situ temperature and salinity (September 1989–January 1990; 12–25°C, 25–34‰) in a shaded greenhouse. The temperature change during an experiment was never >2°C.

The measurements were conducted in 1,000-ml Pyrex beakers containing 500 ml of the food suspension. Magnetic stir bars, rotating at the slowest possible speed (<120 rpm), kept the suspension well mixed. Stirring bars were enclosed in perforated, inverted Petri dishes attached to the bottom of the beaker to dampen water flow and prevent formation of vortices that might disturb the animals. Three rinsed clams of similar shell length (±1 mm) were placed in a perforated plastic cup suspended in the beaker.

Each experiment consisted of five replicate beakers containing clams and one control with no clams. Experiments were run with food suspensions containing bacterioplankton alone or with bacterioplankton plus cultured phytoplankton. The control was used to assess changes in bacterial and algal concentration due to growth, contamination, lysis, or attachment of the cells to the glass or plastic. We also ran separate experiments to determine whether clams released bacteria into the experiments (clams placed in particle-free water) or whether bacterioplankton attached to clams independently of grazing (clams killed with NaN_3, rinsed, and then placed in bacterioplankton suspension). Neither of these potential experimental artifacts was significant.

Clams were allowed to acclimate for 15 min before sampling began, long enough for most to resume filtering. Clams that did not open their valves at all during the experiment were considered nonfeeding and were not counted when calculating mean rates. Actively feeding clams opened and closed their valves at varying frequencies. We did not correct our data for this, which accounts for some of the variance in clearance rates.

Enumeration of microorganisms—Water samples (4 ml) were removed from the beakers every 15 min for 75–105 min, placed in plastic vials, and preserved with 0.2 ml borate-buffered formaldehyde (bacteria) or 0.4 ml of Lugol's solution (algae). Bacteria concentrations were determined by enumerating samples stained with DAPI (4′,6′-diamidino-2-phenylindole) with an epi-illuminated fluorescence microscope (Porter and Feig 1980). The average C.V. of the counts in 10 fields was 17%. Phytoplankton concentrations were determined by counting the cells with an inverted microscope and Utermöhl chambers (Utermöhl 1958). The average C.V. of the counts was 15%.

Assimilation measurements—Four (*I. galbana*) or three (bacteria) complete experiments, each containing five replicates plus one control, were conducted with radiolabeled food suspensions. Five additional measurements were made with only radiolabeled bacterioplankton, however respired ^{14}C was not determined. *I. galbana* was cultured in 200 ml of f/2 medium (Guillard and Ryther 1962) with 8.0 μCi of $NaH^{14}CO_3$ added 3–4 d before the experiments. Cultures were harvested, washed, and resuspended as described above. Final concentrations of radiolabeled *I. galbana* were

180,000 cells ml^{-1} or 2,300 μg C $liter^{-1}$ in one experiment; 47,000 cells ml^{-1} or 600 μg C $liter^{-1}$ in all others with specific activities ranging from 0.7 to 2.4 $\times 10^{-3}$ dpm $cell^{-1}$. The bacteria concentration was $\sim 10^6$ cells ml^{-1} or 20 μg C $liter^{-1}$.

The protocol for preparing radiolabeled bacteria is essentially that of Hollibaugh et al. (1980) except that ^{14}C amino acids were used instead of [*methyl*-^{3}H]thymidine. An amino acid mixture was used rather than one specific compound to provide the highest probability of achieving uniform ^{14}C labeling of the cells. Twenty-five microCuries of algal protein hydrolysate (ICN, sp act: 50 μCi μg-atoms C^{-1}) was added to 1.5 liters of GF/C-filtered bay water (0.33 μg-atoms C $liter^{-1}$ or 83 nM assuming an average of 4 g-atoms C mol^{-1} of algal hydrolysate amino acid). The flask was incubated for $\sim$18 h, then ^{14}C-labeled bacteria were washed and concentrated to a small volume by filtration through 0.2-μm pore-size Nuclepore filters (0.2 NF). Next, the suspension of bacteria was filtered through a 1.0-μm pore-size Nuclepore filter (1.0 NF) to remove any clumps of bacteria that may have formed during the concentration and washing steps. Approximately 15% of the added ^{14}C remained on the Nuclepore filters used in the concentration and screening steps while the 0.2 NF filtrate contained 65$\pm$15%. The resulting ^{14}C-labeled bacterioplankton suspension was added to GF/C-filtered bay water containing 0 or 20,000 cells ml^{-1} (0 or 300 μg C $liter^{-1}$) of unlabeled *I. galbana*. The final bacterioplankton concentration was $\sim 2 \times 10^6$ cells ml^{-1} or 40 μg C $liter^{-1}$, with a specific activity of 1–4 $\times 10^{-3}$ dpm $cell^{-1}$.

I. galbana experiments used two large or three smaller clams of similar size per beaker containing 500 ml of food suspension. Bacterioplankton experiments used three or four clams per beaker containing 500 ml of food suspension. Each measurement (ingestion, gross or net assimilation, excretion, egestion, respiration) reported is therefore the mean of two–three (*I. galbana*) or three–four (bacteria) clams, if all animals were feeding.

The experiments were run in the laboratory in dim light or darkness at temperatures of 19–22°C. Clams were allowed to feed for 1.0 (*I. galbana*) or 1.5 h (bacteria) and then transferred to beakers containing 250 ml of unlabeled *I. galbana* and bacteria suspension, prepared as described above, at about the same concentration as the radiolabeled food. They remained in the unlabeled food suspension for 1.5 h, after which they were radioassayed (*see below*). Particulate ^{14}C, dissolved inorganic ^{14}C ([^{14}C]DIC), dissolved organic ^{14}C ([^{14}C]DOC), and ^{14}C in feces were determined periodically as described below.

^{14}C in clam tissue—Clams were rinsed in particle-free seawater, cut open, the soft tissue was removed, lyophilized, ground with a mortar and pestle (large clams only), and then placed in small centrifuge tubes. A hypotonic solution of NaCl was added (1.5 ml of 0.08 M NaCl, 0.01 M EDTA-Na_2, pH 8) to lyse cells. After 1 h, the mixture was centrifuged (5 min, 5,000 $\times$ *g*). The supernatant was removed and placed in a scintillation vial. The pellet was digested for 2 d at 38°C in 1 ml of a 10 mg ml^{-1} protease solution (Pronase E; Sigma Chemical Co.) containing 1 mM NaN_3 to inhibit bacterial growth. Digested tissue and rinse water were combined with the hypotonic solution and radioassayed.

Ingested, egested, excreted, and respired ^{14}C—At the beginning and end of the feeding and rinse periods of each experiment, three 50-ml samples (later one) of the food suspension were analyzed (*see below*) to determine the amounts of ^{14}C in particulate ^{14}C, [^{14}C]DIC, and [^{14}C]DOC. During initial experiments, two sets of samples (2 ml) were taken every 15 min throughout the feeding period. In later experiments sampling was limited to the beginning and end of the feeding and rinse phases. One set of samples was fixed in buffered formaldehyde (2% final concn) for enumeration of bacteria or phytoplankton as described above. The second sample was filtered through 3.0 NF (^{14}C *I. galbana*) or HAMF (^{14}C bacteria). The filtrate was collected and acidified to volatilize [^{14}C]DIC so that only [^{14}C]DOC remained in the filtrate. Both the filter and the filtrate were radioassayed.

Feces produced during the feeding and rinse phases were collected with a Pasteur pipette, placed on a 3-μm Nuclepore filter, and then sucked dry. The gut passage time of *P. amurensis* is 37.6$\pm$16 min under experimental conditions similar to ours (A. W. Decho pers. comm.), thus we expect clams to have egested any unassimilated radiolabeled food during the

rinse period. Radiolabel, presumably from fecal material, dispersed rapidly into fine particles when clams were feeding on ^{14}C bacteria, so a pipette was not effective at collecting all of the egested fecal material produced in these experiments. Dispersed fecal particles were collected as particulate ^{14}C on an HAMF. We assume that water-soluble radiolabeled organic material leached out of the fecal material into the [^{14}C]DOC pool, thus this pool (which was a small fraction of the total label and not routinely quantified because it was at the limit of radiolabel detection) contains organic C that was both egested and excreted.

[^{14}C]DIC and [^{14}C]DOC were determined as described by Hobbie and Crawford (1969) and modified by Hollibaugh (1979). Samples (50 ml) were filtered through HAMF to remove bacteria and dispersed egested material. Following acidification and trapping of [^{14}C]DIC in phenethylamine-soaked glass-fiber filters, 2.0 ml of the acidified filtrate was radioassayed to measure [^{14}C]DOC. The efficiency of the [^{14}C]DIC trapping method is reported to be 100% (Hollibaugh 1979), confirmed by tests (not reported) that also showed loss of [^{14}C]DIC during filtration to be negligible.

For experiments with *I. galbana,* clam respiration was determined in both the feeding and rinse phases from the change in [^{14}C]DIC content of the suspensions. Variable [^{14}C]DIC production in controls prevented us from measuring clam respiration during the feeding phase in experiments with ^{14}C bacteria. Time-course experiments with *I. galbana* showed that [^{14}C]DIC was produced at a slightly faster rate immediately before than immediately after transfer into unlabeled food and that there was a slight lag before [^{14}C]DIC was produced once the clams started feeding on labeled food. Given these considerations, we calculated respiration rates during the feeding phase of experiments with ^{14}C bacterioplankton by extrapolating the rate of [^{14}C]DIC production during the rinse period to the feeding period.

Two experiments were carried out to investigate egestion and respiration of labeled food over a period of days. In one of them, ^{14}C-labeled *I. galbana* (50,000 cells ml^{-1} or 650 μg C liter^{-1}) and unlabeled bacteria (1×10^6 cells ml^{-1} or 20 μg C liter^{-1}) were fed to the animals. The second used ^{14}C-labeled bacteria (2×10^6 cells ml^{-1} or 40 μg C liter^{-1}) and unlabeled *I. galbana* (30,000 cells ml^{-1} or 400 μg C liter^{-1}). The experiments were conducted as described above except that after being fed radiolabeled food, all of the clams from the five replicates were transferred to one vessel containing 1 liter of unlabeled food suspension of about the same composition as the radiolabeled food suspension. Care was taken to maintain relatively constant food concentrations throughout the rinse phase by continuously adding food with a peristaltic pump and by transferring the animals into fresh, unlabeled food suspension every time samples were taken. Clams were held in unlabeled food for 48 h (^{14}C *I. galbana*) or 68 h (^{14}C bacteria), after which they were radioassayed. Particulate ^{14}C, [^{14}C]DIC, [^{14}C]DOC, and ^{14}C in feces were determined periodically during the rinse phase.

Control experiments—We performed several control experiments to evaluate the potential for experimental artifacts due to the exchange of ^{14}C between compartments of the experiment that were not mediated by grazing and clam metabolism. These experiments included tests for production of [^{14}C]DIC by radiolabeled food during the feeding phase, production and uptake of [^{14}C]DOC during both feeding and rinse phases, production and uptake of [^{14}C]DIC during the rinse phase, production of [^{14}C]DIC and [^{14}C]DOC by radiolabeled fecal material, changes in the specific activity of food during experiments, and attachment of ^{14}C bacteria to clams.

Calculations—Clearance rates were obtained by applying the equation

$$\ln(C_t) = \ln(C_0) - f \times t. \qquad (1)$$

C_t and C_0 are the concentrations of particles at the beginning of the experiment and after t minutes, f is clearance rate in volume time^{-1}, and t is incubation time in minutes.

In practice, f was calculated from model 1 least-squares linear regressions of $\ln(C_t)$ against t. To obtain f in ml h^{-1} clam^{-1} or ml h^{-1} (g wet wt)$^{-1}$, we multiplied f by the volume of water in the container (500 ml) and divided by the number of feeding clams (3–5) or by the sum of their weights. Based on the results of control experiments, we excluded clams that did not open their valves during the feeding period or which contained <500 dpm from the calculations. Each clearance rate estimate therefore represents the mean clearance rate of

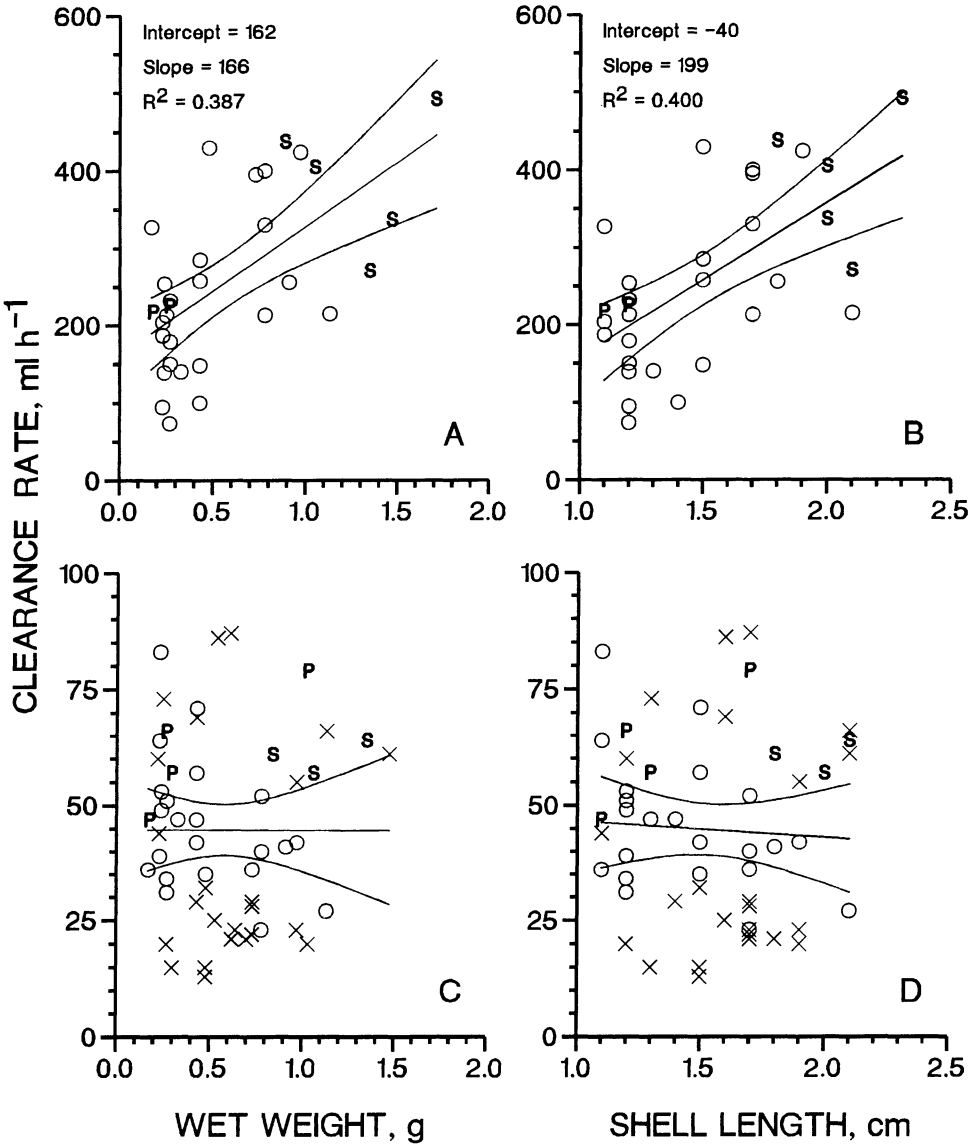

Fig. 1. Relationship between clearance rate and *Potamocorbula amurensis* size expressed as shell length or wet weight (including shell). Symbols: ×—no added algae; O—*Isochrysis galbana*; S—*Skeletonema costatum*; P—*Phaeodactylum tricornutum*. Rates, weights, and lengths are means of 2–4 clams per container. Panels A and B are clearance rates on phytoplankton; C and D are clearance rates on bacterioplankton. Model 1 linear regressions of clearance rate against clam size and 95% confidence belts for the regressions are shown. Regression slopes were not significantly different from 0 for bacterioplankton clearance rates.

the actively feeding clams in one beaker. Where f in controls was significantly different from zero ($P < 0.05$), the slope was subtracted from the slope for beakers containing clams.

Ingestion was calculated in assimilation experiments by adding the radiolabel found in the feces and the [^{14}C]DIC respired during the experiment to the radiolabel found in the clam tissue according to the mass balance equation:

$$I = A_N + R + E. \quad (2)$$

I is ingestion, A_N is net assimilation, R is respiration, and E is egestion. Gross assimilation (A_G) was calculated as

$$A_G = A_N + R. \quad (3)$$

Gross and net assimilation, respiration, and egestion were determined as percentages of ingestion or gross assimilation with the equations given above. The arithmetic means and standard deviations of the results obtained in the different experimental groups were tested for statistical significance by one-way ANOVA or one-tailed *t*-tests.

Results

Morphometrics of P. amurensis—Shell width (W, cm) was linearly related to shell length (L, cm) by the equation $W = -0.028 + 0.64 \times L$ ($P < 0.001$). Wet weight, including shell (WW, g), was related to shell length by $\ln(WW) = -3.91 + 2.03 \times L$ ($P < 0.001$). Shell weight (SW, g) was related to shell length by $\ln(SW) = -4.91 + 2.19 \times L$ ($P < 0.001$). The relationship between dry tissue weight (DTW, g) and shell length was more variable than other relationships. There was a clear difference between the relationship for clams collected in fall and those collected in spring, probably because spring clams had recently spawned (J. K. Thompson pers. comm.). All clams used in clearance rate measurements were collected in fall 1989. The regression for all clams was $\ln(DTW) = -6.81 + 2.09 \times L$ ($P < 0.001$).

Clearance rates on phytoplankton—Clearance rates on *P. tricornutum* and *S. costatum* were not significantly different from clearance rates determined for *I. galbana* ($P > 0.1$) as tested by a one-way ANOVA and a *t*-test, suggesting that *I. galbana* (5 μm) is filtered with the same efficiency as *S. costatum* (15 μm) and *P. tricornutum* (10 μm). Clearance rates (f) were highly correlated with the size (L, WW) of the clams (Fig. 1A,B) and with temperature (T, °C; data not shown):

$$f = -40 + 199 \times L \qquad P < 0.001, \quad (4)$$

$$f = 162 + 166 \times WW \qquad P < 0.001, \quad (5)$$

$$f = -120 + 20.6 \times T \qquad P < 0.001. \quad (6)$$

Data from experiments where regression slopes were not significantly different from 0 ($P > 0.1$, two experiments) were not included in regression calculations. Including temperature in a multiple linear-regression model with shell length increased the amount of variance explained by 5%. The relationship between phytoplankton clearance rate, temperature and shell length is

$$f = -162 + 10.3 \times T + 154 \times L r^2 = 0.450, \; P < 0.0001. \quad (7)$$

Table 1. Clearance rates of *Potamocorbula amurensis* on *Isochrysis galbana* and bacterioplankton. Clearance rates for 1.0- and 2.0-cm clams are given in various units for modeling purposes (*see text*) and to facilitate comparison with other bivalves. Shell length (cm)—L; clearance rate per individual (ml h^{-1})—f; clearance rate per unit wet weight including shell—WW; clearance rate per unit dry weight including shell—DW; clearance rate per unit dry tissue weight—DTW; clearance rate per unit ash-free dry weight—AFDW.

		WW	DW	DTW	AFDW
L	f	(ml h^{-1} mg^{-1})			
		I. galbana			
1.0	159	1.04	2.13	17.8	30.2
2.0	358	0.31	0.54	4.97	9.70
		Bacterioplankton			
1.0	45	0.30	0.60	5.05	8.55
2.0	45	0.04	0.07	0.62	1.22

The clearance rates of 1- and 2-cm clams are 159 and 358 ml h^{-1} $clam^{-1}$. These clearance rates were converted to dry weight equivalents with morphometric relationships and Eq. 2 and 3 (Table 1). Animals 1–2 cm long comprise the bulk of the population biomass and these rates are used for modeling purposes elsewhere in the text. It is apparent that smaller clams have higher clearance rates per unit biomass than larger clams (Table 1).

Clearance rates of bacteria—The presence or absence of phytoplankton cells had no significant effect on the ability of *P. amurensis* to retain bacteria (one-way ANOVA and *t*-test, $P > 0.1$). Clearance rate was not related to animal size as shell length, wet weight (Fig. 1C,D), or dry tissue weight (data not shown). The mean clearance rate for all experiments was 45 ml h^{-1} $clam^{-1}$. As was found with phytoplankton, bacterioplankton clearance rates were strongly temperature-dependent:

$$f = -18.5 + 3.5 \times T \qquad P < 0.001. \quad (8)$$

Including shell length in a multiple linear-regression model with temperature increased the amount of variance explained by only 1.5%. The relationship between bacterioplankton clearance rate, shell length, and temperature is

$$f = -8.1 - 8.1 \times L + 3.6 \times T$$
$$r^2 = 0.264, P < 0.0001. \quad (9)$$

Clearance rates on bacterioplankton for clams 1 and 2 cm long were also converted to dry weight equivalents with morphometric relationships and Eq. 2 and 3 (Table 1). Because clearance rate does not change significantly with animal size, smaller clams exert greater grazing pressure per unit biomass than larger clams [5.05 vs. 0.62 ml h^{-1} (mg DTW)$^{-1}$ for 1.0- and 2.0-cm clams]. Compared to *I. galbana,* bacteria were retained with 28–13% efficiency (1- and 2-cm clams, respectively).

Assimilation efficiencies–control experiments—The control experiments we performed indicated that artifacts arising from exchange of ^{14}C between system components not mediated by grazing and clam metabolism were negligible. Specific activity of radiolabeled food changed by <10% during the feeding period. Uptake of [^{14}C]DOC by clams was negligible. Some [^{14}C]DIC was released to the rinse water by radiolabeled fecal material, but it was <6% of total [^{14}C]DIC production. [^{14}C]DIC was produced prior to egestion in experiments with *I. galbana,* suggesting that it was not produced by bacterial metabolism of egested fecal material. Attachment of radiolabeled bacteria to clams resulted in a blank of ~500 dpm clam^{-1}—a small fraction of the label consumed by actively feeding clams (>5,000 dpm clam^{-1}).

Assimilation of ^{14}C I. galbana—Net assimilation, determined 2.5 h after feeding on ^{14}C-labeled algal cells began, was 82.9±3.4% ($x \pm$ SD, $n = 10$) of ingestion (Table 2, data from experiments where food concentrations were high or were not measured are not included in means). Gross assimilation was 94.2±3.1% of ingestion. Respiration and egestion were 12.1±1.4% and 5.8±3.1% of the total ingestion. There was no relationship between animal size (L) and any of these parameters (model 1 linear regression, $P > 0.1$).

Table 3 compares the results of experiments with high and low cell concentrations (180,000 and 47,000 cells ml^{-1}). Gross and net assimilation were significantly lower and feces production and the amount of radioactivity detected in the feces was significantly higher in experiments with high cell concentrations. Pseudofeces production was not observed, even at the highest concentration of *I. galbana.* Respiration as percentage of ingestion and gross assimilation was also lower at high concentrations of *I. galbana.*

Production of [^{14}C]DIC and ^{14}C-labeled feces declined rapidly once the clams were transferred to unlabeled food suspension (Fig. 2A,B). A low peak in labeled feces production was observed ~24 h after feeding the clams radiolabeled *I. galbana.* Following this peak, only small quantities of radiolabel were found in the feces, but radiolabel continued to be excreted. Particulate radiolabel collected during the rinse period was negligible (data not shown). Release of [^{14}C]DOC coincided with egestion of labeled feces, but the amount produced was at the limit of detection (data not shown).

After 49 h, the radiolabel collected as feces was 10% of ingestion and gross assimilation was 90% (Table 4). Respired [^{14}C]DIC was 41.6% of gross assimilation and net assimilation was 52.6% of ingestion, in contrast to net assimilation values of 82.9 (47,000 cells ml^{-1}) and 75% (180,000 cells ml^{-1}) seen in the 2.5-h experiments.

Assimilation of bacterioplankton—Gross assimilation of bacteria in the presence of unlabeled *I. galbana* was 85.8±8.8% ($x \pm$ SD, $n =$ 14, Table 2). Respired [^{14}C]DIC was 25.2±5.6% of gross assimilation and 21.4±4.7% of ingestion; net assimilation was 64.4±9.4% and egestion was 14.2±8.9% of ingestion after 3 h. There was no correlation between animal size (L) and any of these parameters (model 1 linear regression, $P > 0.1$). If we assume that respiration is the same percentage of ingestion in the presence and absence of *I. galbana,* gross and net assimilation and egestion were the same in experiments where clams were fed only ^{14}C bacterioplankton ($n = 19$, data not shown) as in experiments where clams were fed ^{14}C bacteria and unlabeled phytoplankton (t-test, $P > 0.1$).

Production of [^{14}C]DIC and ^{14}C-labeled feces declined rapidly once the clams were transferred to unlabeled food suspension (Fig. 2C,D). A peak in egested ^{14}C was observed about 24 h after feeding on labeled bacterioplankton, as was observed with *I. galbana* (Fig. 2). After 69.5 h, gross assimilation of bacterioplankton ^{14}C was 69.1% of ingestion, net assimilation was 39.2% of ingestion, and respiration was 43.3% of ingestion (Table 4).

In contrast to *I. galbana* experiments, a large

Table 2. Assimilation of radiolabeled *Isochrysis galbana* and bacterioplankton by *Potamocorbula amurensis*. Temperature (°C)—T; *I. galbana* concentration (cells ml^{-1})—concn; duration of experiment, sum of feeding + rinse periods (h)—duration; average shell length of clams in a replicate (cm)—L; gross and net ^{14}C assimilation as percentages of ingestion—A_G and A_N; respiration as percentages of ingestion and gross assimilation—R_I and R_A; egestion as percentage of ingestion—E_I.

1990	T	Concn	Duration	L	A_G	A_N	R_I	R_A	E_I
				I. galbana					
7 May	20–22	unknown	3	1.9	86.6	70.4	16.2	19	13.4
				1.25	95.8	72.1	21	22.5	7.1
				1.65	90.6	71.4	19.2	21	9.4
				1.05	95.4	78.5	17	18	4.6
				1.2	95.8	76.8	19	20	4.2
24 May	19–20	180,000	2.5	1.3	88	79.4	8.6	9.7	12
				1.2	84.3	75.4	8.9	10.5	15.7
				0.9	76.6	67.1	9.4	12.3	23.4
				1.5	83.3	73.5	9.8	11.8	16.7
				2.0	87.6	79.5	8.5	9.7	12.0
1 Jun	19–20	46,400	2.5	1.2	96	85.2	10.8	11.2	4.0
10 Jun	21–22	47,000	2.5	1.15	95.2	86.6	8.6	9.1	4.8
				1.0	92.8	81.1	11.7	12.6	7.2
				1.45	92.2	80.9	11.3	12.2	7.8
				1.3	95.9	85.8	10.1	10.6	4.1
				1.1	94.5	82.1	12.4	13.1	5.5
				Bacterioplankton					
2 Apr	18–20	20,000	3.0	1.9	87.1	51.8	35.3	40.5	12.8
				1.7	85.2	63.3	21.9	25.7	14.8
				1.6	96.7	70.9	25.8	26.6	3.3
				1.3	97.5	78.2	19.3	19.8	2.5
				1.5	96.4	74.5	21.9	22.7	3.6
10 Apr	20–22	20,000	3.0	1.7	92.9	71.3	21.6	23.3	7.1
				1.0	82.3	65.4	16.9	20.6	17.7
				2.1	79.5	61.1	18.4	23.2	20.5
				2.2	73.8	51.7	22.1	30.0	26.3
				2.15	86.6	67.1	19.5	22.5	13.4
17 Apr	19–21	20,000	3.0	1.3	83.4	65.2	18.2	21.9	16.6
				1.0	67.6	45.2	22.4	33.1	32.5
				2.2	80.6	62.9	17.7	22.0	19.4

amount of particulate ^{14}C was produced by clams fed ^{14}C-labeled bacterioplankton. Production of this material coincided with peaks in egestion. We conclude that this material was derived from feces and have included it as egested ^{14}C in calculations of assimilation efficiencies. As with [^{14}C]DIC production, we have extrapolated production of ^{14}C particulate material during the rinse phase to the feeding phase and included it in the inventory of ^{14}C egested during the feeding phase of the experiments.

Discussion

Clearance rates—The lack of a statistically significant relationship between bacterioplankton clearance rate and animal size was unexpected. The method we used measures net clearance rate: if clams were releasing bacteria at the same time that they were removing them from suspension, the clearance rate would be underestimated. However controls (fed clams placed in filtered water) showed that few bacteria were released by the clams. In contrast, experiments where *P. amurensis* was fed radiolabeled bacteria suggest rapid release of small particles, presumably bacteria from fecal material, perhaps partially compensating for bacterioplankton consumption. Clearance rates calculated from the loss of particulate ^{14}C during the feeding phase of these experiments agreed well with clearance rates calculated from changes in cell numbers. If bacterioplankton are retained with low efficiency, as appears to

Table 3. Effect of cell concentration on assimilation efficiencies of *Isochrysis galbana*. Means and standard deviations of data from Table 2. Concn, A_G, A_N, R_I, R_G, and E_I as in Table 2; number of replicates—n; statistical significance of a t-test of the difference between parameters—P.

Concn	A_G	A_N	R_I	R_G	E_I	n
180,000	84.0±4.6	75.0±5.1	9.0±0.6	10.8±1.2	16.0±4.7	5
47,000	94.2±3.1	82.9±3.4	11.4±1.2	12.1±1.4	5.8±3.1	10
$P <$	0.028	0.002	0.001	0.007	0.0001	

be the case, the slope of the clearance rate–animal size relationship would be low and obscured by experimental variability.

We chose to calculate clearance rates in units of ml h^{-1} individual^{-1} rather than to normalize the rates against biomass (ml h^{-1} g^{-1}) because the former units are more directly related to the measurements we made. Weight-specific clearance rates are higher in smaller than in larger *P. amurensis* (Table 1). They are up to two orders of magnitude higher than weight-specific rates reported for *Mya arenaria* by Wright et al. (1982). The animals used by Wright et al. were probably much larger than most of the clams we used, because adult *M. arenaria* are larger than *P. amurensis*. Bacte-

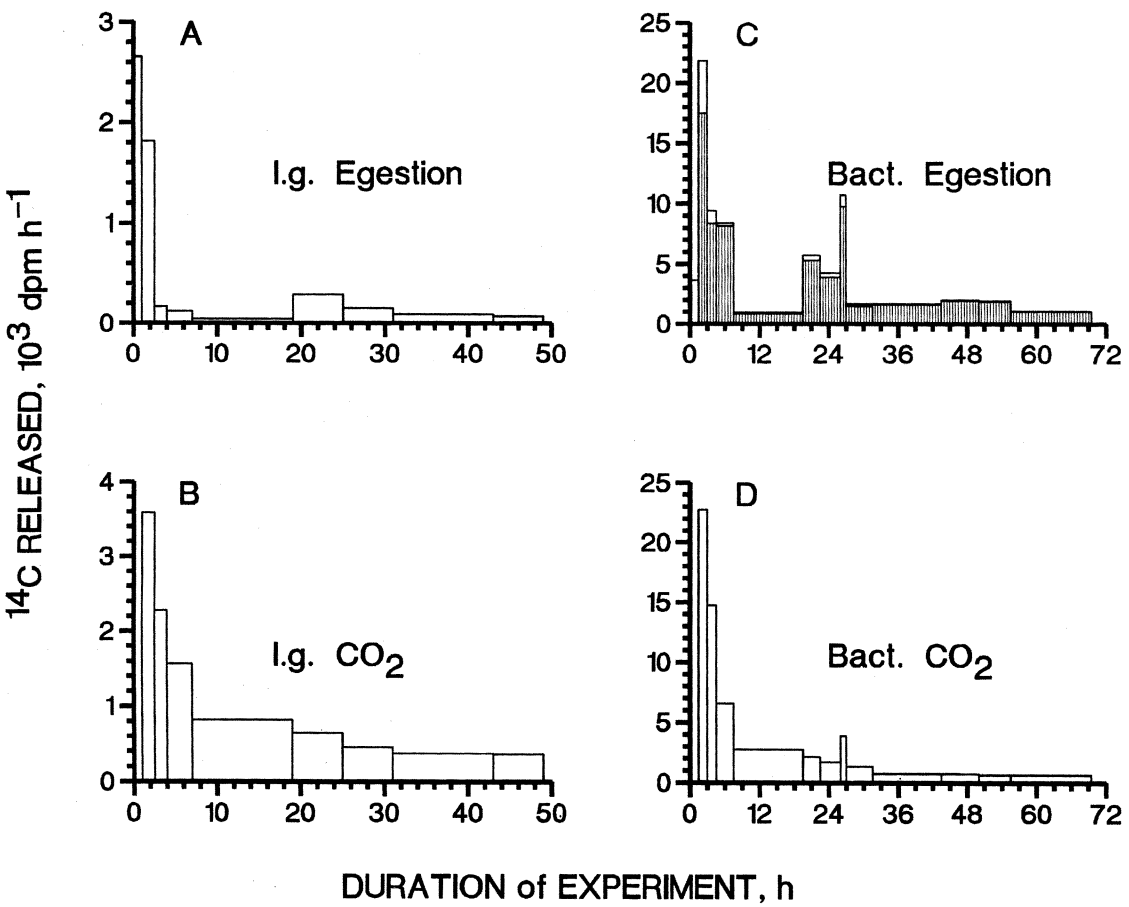

Fig. 2. Time-course of egestion and respiration of ^{14}C by *Potamocorbula amurensis* fed on ^{14}C-labeled *Isochrysis galbana* (l.g.) or bacteria (Bact). Data are pooled totals for all clams; shaded portions of bars in panel C show ^{14}C released as fine particles.

rioplankton clearance rates per animal are in the same range, but are higher for *P. amurensis*.

Retention efficiency of *P. amurensis* for natural bacteria <1.2 μm (free-living bacteria in San Francisco Bay are in the 0.4–1-μm size range) was 28–13% for clams 1–2 cm long, compared to retention of *I. galbana* cells which are assumed to be retained with 100% efficiency. Langdon and Newell (1990) reported retention efficiencies of mussels (*Geukensia demissa*) for unattached natural bacteria to be 15.8% of the efficiency of removal for 3.9-μm-diameter microspheres. Wright et al. (1982) found comparable values of 18.4% retention efficiency for natural bacteria by *G. demissa* when compared to graphite particles of 1–2.5-μm diameter.

Doering and Oviatt (1986) suggested that clearance rates for *Mercenaria mercenaria* obtained with algal cultures can be much higher than those obtained with natural seston. This discrepancy can be explained in part by the difference in the size distribution of ^{14}C-labeled particles used in their experiments vs. particle sizes in experiments with algal cultures. Doering and Oviatt's experiments used labeled particles generated by adding Na $H^{14}CO_3$ to a mesocosm run for at least 14 and up to 120 d. The amount of ^{14}C in particles assumed to be available to grazers was determined with a glass-fiber filter with a nominal pore size of 0.4 μm. This filter would have retained an unknown proportion of radiolabeled bacteria and other particles too small to have been grazed effectively by *Mercenaria,* as well as larger phytoplankton cells.

The impact of benthic filter feeders on plankton can be significant. Cloern (1982) attributed the control of phytoplankton biomass in south San Francisco Bay to benthic grazing. Alpine and Cloern (1992) reach the same conclusion for northern San Francisco Bay, now that it is dominated by *P. amurensis.* Cohen et al. (1984) presented another example of the control of phytoplankton standing crops by filter-feeding macrobenthos. They attributed a minimum in phytoplankton concentrations in one stretch of the Potomac River, Maryland, to high densities of the Asiatic clam *Corbicula fluminea,* which was introduced in 1977.

Our data also suggest that the grazing impact of *P. amurensis* can be substantial. At its present density in northern San Francisco Bay (>2,000 animals m^{-2}) and an average clearance rate of 267 ml h^{-1} $clam^{-1}$, the entire water column can be filtered 1.28 times per day in deeper areas (10 m) and 12.8 times per day in shallow areas (1 m). This turnover rate exceeds phytoplankton specific growth rates (Alpine and Cloern 1992) and, even when retention efficiency is considered, approaches or exceeds the growth rate of bacterioplankton populations (Hollibaugh unpubl. data). Since the water column is generally well mixed to the bottom in San Francisco Bay, all the food in it is potentially available to the benthos (Wolff 1977). How food availability is affected by stratification patterns, water movement, and food depletion within the benthic boundary layer (Frechette and Bourget 1985*a,b*; Frechette et al. 1989) is unknown; however, the *P. amurensis* clearance rates we measured are comparable to those measured by Cole et al. (1992) with a flume system that more closely simulates in situ conditions.

Table 4. Change in assimilation efficiencies of *Isochrysis galbana* and bacterioplankton with time. Time after feeding period began (h)—duration; A_G, A_N, R_G, and E_I as in Table 2.

Duration	A_G	A_N	R_G	E_I
		I. galbana		
2.5	95	85.2	8.8	5.0
49	90	52.6	41.6	10.0
		Bacterioplankton		
3	90	79.6	11.7	8.1
49.5	73	44.7	38.6	23.8
69.5	69	39.2	43.3	27.4

Assimilation efficiencies—The experiments described above show that both *I. galbana* and bacterial C are readily assimilated by *P. amurensis.* Gross assimilation efficiencies were similar for both bacteria and *I. galbana* in short experiments (Table 2). Most of the respiration and egestion occurred during the first few hours after transfer to unlabeled food suspension (Fig. 2). Assimilation efficiencies were calculated for the first few hours of the prolonged experiments with ^{14}C mass balance constrained by net assimilation determined at the end of the experiment and respired, excreted, and egested ^{14}C measurements (Table 4). Assimilation efficiencies for the first few hours were comparable to those obtained from short experiments

(cf. Tables 2 and 4). During the first few hours of the experiments, more [^{14}C]DIC was respired when the clams were fed ^{14}C-labeled bacteria than in experiments with ^{14}C-labeled *I. galbana* as food, suggesting that bacterial C is metabolized more readily. This difference may have been due to differences in the labeling patterns resulting from the use of ^{14}C amino acids vs. $NaH^{14}CO_3$ or due to differences in the composition and digestibility of truly uniformly labeled bacterioplankton and algae.

Prolonged experiments (Fig. 2, Table 4) showed that assimilation decreased with time due to respiration and egestion, as expected. Our observations of a peak in egestion after 24 h are consistent with Allen's (1962) and Dinamani's (1969) observations that this "secondary egestion" of material from the digestive gland occurs after ~24 h. The fractions of bacterial and algal ^{14}C that were respired after 49 h were similar; however, the gross assimilation efficiency for bacteria is lower than for *I. galbana* due to greater egestion. Net assimilation efficiencies for *I. galbana* and bacterial ^{14}C after 49 h are probably close to true net assimilation rates, since loss of ^{14}C by both respiration and egestion was small after ~26 h. Net assimilation efficiency of bacterial ^{14}C decreased to 39.2% after 71 h.

Amouroux (1986) reported a net assimilation efficiency of 40–50% for *Venus verrucosa* fed with cultured *Lactobacillus* sp. Langdon and Newell (1990) cited Crosby, who found a net assimilation efficiency of 52% for *Crassostrea virginica* fed cultured cellulolytic bacteria. Saunders (1969) reported assimilation efficiencies between 52 and 14% for *Daphnia* fed cultured bacteria. The net assimilation efficiency for natural bacterioplankton (44.7%, this study) is thus comparable to reported assimilation efficiencies for cultured bacteria. Cultured bacteria are much larger than bacterioplankton (1–2 vs. 0.4–0.6 μm), may contain large amounts of storage products, and may differ in composition with regard to C cell^{-1}, C:N:P ratio, and the ratios of major classes of macromolecules (Lee and Fuhrman 1986; Simon and Azam 1989; Hollibaugh et al. 1991). Given these differences, it could not be assumed a priori that assimilation efficiencies determined with cultured cells could be applied to natural bacterioplankton.

Although only one experiment (five replicates with three clams each) used high concentrations of *I. galbana,* it was obvious that assimilation efficiency decreased and egestion increased with increasing food concentration (Table 3). Both ^{14}C-labeled feces production and [^{14}C]DOC egestion increased with higher food concentration, suggesting more efficient utilization when food is scarce. Pseudofeces production was not observed in any of the experiments we performed. *C. virginica* begins to produce pseudofeces at a *Chlorella* (5 μm, about the same size as *I. galbana*) cell density of 450,000 cells ml^{-1} (Winter 1978).

Interestingly, our results indicate that very little [^{14}C]DOC is released on a short time scale (up to 3 d) by *P. amurensis,* either as excretory products or directly from food particles as a result of the feeding activities of bivalves, in marked contrast to the large percentage of organic matter released by the activities of planktonic grazers (Lampert 1978; Jumars et al. 1989). If this is a common feature of grazing by suspension-feeding macrobenthos, it may result in differences in food webs and biogeochemical cycling between systems that are dominated by planktonic crustacean grazers vs. those dominated by macrobenthos because "sloppy feeding" is an important source of organic matter for microbial loop processes in systems dominated by planktonic crustacean grazers (Williams 1981; Azam et al. 1983).

Relative importance of phytoplankton and bacterioplankton to the diet of P. amurensis *in Suisun Bay*—Although the primary focus of this study was to compare clearance rates and assimilation of phytoplankton and bacterioplankton, it is instructive to extrapolate these results to the field. We do this with reasonable confidence because the clearance rates for *I. galbana* that we measured are comparable to those for *Chroomonas salina* (a flagellate similar in size and morphology to *I. galbana*) measured by Cole et al. (1992) with a flume system that more nearly duplicates in situ conditions.

We compared the potential contribution of bacterioplankton and phytoplankton C and N to the daily ration of *P. amurensis* with observations of bacterioplankton abundance (Hollibaugh unpubl. data) and chlorophyll concentration (J. E. Cloern pers. comm.) made in Suisun Bay from July 1988 to July 1990. Bacterioplankton C and N standing crop was

Table 5. Calculated C and N ration supplied to 1.0- and 2.0-cm *Potamocorbula amurensis* by bacterioplankton and phytoplankton standing crops in Suisun Bay water. Standing crops, rations, assimilated C, and biomass doubling times calculated as indicated in text; totals do not include other C and N sources such as detritus.

Standing crop (μg liter^{-1})	Mean	Range
Phytoplankton C	80	11–500
Phytoplankton N	14	1.9–88
Bacteria C	31	11–71
Bacteria N	7	2.6–17
Total available C	111	36–556
Total available N	21	7.2–101

	1.0-cm *P. amurensis*		2.0-cm *P. amurensis*	
Parameter	Mean	Range	Mean	Range
Ingested (μg d^{-1})				
Phytoplankton C	305	42–1,910	686	95–4,300
Phytoplankton N	53	7.3–336	121	16–757
Bacteria C	33	12–77	33	12–77
Bacteria N	7.8	2.8–18	7.8	2.8–18
Total C consumed	338	72–1,970	720	125–4,362
Total N consumed	61	14–350	129	24–771
Bacteria C (% of total)	13	3.1–49	6.3	1.4–30.3
Bacteria N (% of total)	16	4.0–57	8.1	1.8–37
Assimilated (μg d^{-1})				
Phytoplankton C	160	22–1,000	361	50–2,260
Bacteria C	15	5.3–34	15	5.3–34
Bacteria C (% of total)	11	2.6–45	5.5	1.2–27
Clam biomass C doubling time (d)				
On phytoplankton	26	2.6–119	83	8.2–371
On bacteria	221	76–496	1,550	536–3,480

calculated from abundance data with a conversion factor of 20 fg C cell^{-1} (Lee and Fuhrman 1986) and a C : N ratio (by atoms) of 5.00 (Goldman et al. 1987; Hollibaugh et al. 1991). Phytoplankton C and N standing crops were calculated with a C : Chl ratio of 55 (Wienke and Cloern 1987) and a C : N ratio (by atoms) of 6.63 (Redfield 1934). Calculations were performed for 1.0- and 2.0-cm clams with the clearance rates given in Table 1. Ingestion rates of phytoplankton and bacterioplankton C and N were calculated; the contribution of bacterial C and N to the daily ration (clams assumed to feed only on bacterioplankton and phytoplankton) was then expressed as a percentage (Table 5).

We used the C net assimilation efficiencies after 49 h of rinse (Table 4) and the daily ration from above to calculate daily net assimilation of bacterioplankton and phytoplankton C. We are unable to make similar calculations for N because we have no estimates of N net assimilation efficiency. The contribution of bacterioplankton C to daily net assimilation was expressed as a percentage of the total. We also used daily net assimilation estimates to calculate the length of time it would take to double the C biomass of clams with shells 1.0 and 2.0 cm long. Clam biomass was calculated by assuming that 50% of AFDW is C. The doubling time in days was approximated by dividing clam biomass by daily net assimilation (Table 5).

These calculations suggest that bacteria contributed 13 and 6.3% of the C and 16 and 8.1% of the N consumed by 1.0- and 2.0-cm clams on the average. However, bacteria could contribute up to 49 and 30% of the C and 57 and 37% of the N consumed by these clams, depending on the relative proportions of bacteria and phytoplankton in a given sample. Phytoplankton biomass is greater and more variable than bacterioplankton biomass; thus increases in the relative contribution of bacterial biomass to the diet of *P. amurensis* are accompanied by an overall decrease in the amount

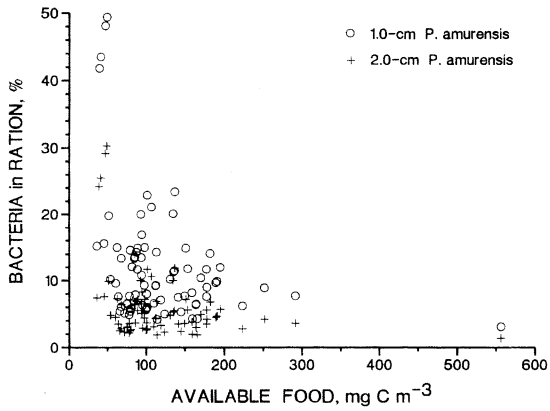

Fig. 3. Relationship between available food (in C equivalents) and the percentage of the C ration supplied to 1.0- and 2.0-cm *Potamocorbula amurensis* by bacterioplankton in Suisun Bay. Available food is calculated from standing crops of phytoplankton and bacterioplankton and excludes other C sources such as detritus.

of food available, as shown in Table 5 and Fig. 3.

This point is further emphasized by considering the contribution of bacterial C to the growth of *P. amurensis* (Table 5). Our calculations suggest that, on average, bacteria contribute 11 and 5.5% of the C assimilated into biomass by 1.0- and 2.0-cm clams. The contribution of bacteria could be as great as 45 and 27% of net C assimilation. The calculated C doubling times for clams feeding on phytoplankton, 26 and 83 d for 1.0- and 2.0-cm clams, suggest that the phytoplankton concentrations presently found in Suisun Bay are adequate to maintain the growth of *P. amurensis*. Calculated C doubling times of 221 and 1,550 d on bacteria suggest that bacteria contribute relatively little to the growth of clams in the 1–2-cm size range. However, given the relatively greater ability of small clams to retain them (Table 1), bacteria are likely to be a more important component of the nutrition of very small clams (Fig. 3).

The calculations discussed above are based on clearance rates for free-living bacteria, which account for most bacteria in San Francisco Bay (Hollibaugh unpubl. data) and other estuaries. In Suisun Bay, bacteria that are attached to or associated with particles represent 20–25% of the population of bacterioplankton. Association with particles may increase the availability of bacteria as a food source for suspension feeders because retention is facilitated. Attached bacteria are also often larger than their free-living counterparts. Kirboe et al. (1980) reported that suspended bottom material serves as an additional food source to *Mytilus edulis*. Grant et al. (1990) obtained similar results with *Ostrea edulis*. Most of the suspended sediment in San Francisco Bay is resuspended and thus possibly enriched with benthic microbes. Although we did not investigate the role of attached bacteria in the nutrition of *P. amurensis*, a simple calculation suggests that including attached bacteria could double the significance of bacteria as a food source for *P. amurensis* (20% of the bacterioplankton population grazed with 100% efficiency for attached bacteria vs. 80% of the population grazed with 20% efficiency for free-living bacteria).

Our calculations suggest that the direct contribution of free-living bacterioplankton to *P. amurensis* production in Suisun Bay is limited; however, bacterioplankton production could be available indirectly via processing through the microbial loop (Azam et al. 1983). If it is assumed that nanoflagellates and ciliates can be grazed and assimilated by *P. amurensis* with the same efficiencies as *I. galbana*, and that nanoflagellates and ciliates assimilate bacterioplankton biomass with a net efficiency of 50%, about half of the bacterioplankton production in Suisun Bay (0.5×100 g C m^{-2} yr^{-1} or 50 g C m^{-2} yr^{-1}) is available to *P. amurensis* indirectly. Bacterioplankton production presently is 2.5 times the phytoplankton production in Suisun Bay, suggesting that 56% [$1.25 \div (1 + 1.25)$] of the biomass ultimately available to consumers like *P. amurensis* is derived from bacterioplankton production. Heterotrophic processes driven by allochthonous C are extremely important in northern San Francisco Bay, and bacterioplankton are a key link in the food web of this and similar turbid estuaries.

References

ALLEN, J. A. 1962. Preliminary experiments on the feeding and excretion of bivalves using *Phaeodactylum* labeled with (32)P. J. Mar. Biol. Assoc. U.K. **42:** 609–623.

ALPINE, A. E., AND J. E. CLOERN. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol. Oceanogr. **37:** 946–955.

AMOUROUX, J. M. 1986. Comparative study of the car-

bon cycle in *Venus verrucosa* fed on bacteria and phytoplankton. Mar. Biol. **90:** 237–241.

AZAM, F., AND OTHERS. 1983. Ecological role of water column microbes in the sea. Mar. Ecol. Prog. Ser. **10:** 257–263.

CARLTON, J. T. 1979. Introduced invertebrates of San Francisco Bay, p. 427–443. *In* T. J. Conomos [ed.], San Francisco Bay: The urbanized estuary. AAAS.

———. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. Oceanogr. Mar. Biol. Annu. Rev. **23:** 313–371.

———, J. K. THOMPSON, L. E. SCHEMEL, AND F. H. NICHOLS. 1990. The remarkable invasion of San Francisco Bay, California (USA) by the Asian clam *Potamocorbula amurensis.* 1. Introduction and dispersal. Mar. Ecol. Prog. Ser. **66:** 81–94.

CLOERN, J. E. 1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? Mar. Ecol. Prog. Ser. **9:** 191–202.

COFFIN, R. B., AND J. H. SHARP. 1987. Microbial trophodynamics in the Delaware estuary. Mar. Ecol. Prog. Ser. **41:** 253–266.

COHEN, R. R. H., P. V. DRESLER, J. P. PHILLIPS, AND R. L. CORY. 1984. The effect of the Asiatic clam, *Corbicula fluminea,* on phytoplankton of the Potomac River, Maryland. Limnol. Oceanogr. **29:** 170–180.

COLE, B. E., J. K. THOMPSON, AND J. E. CLOERN. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. Mar. Biol. **113:** 219–225.

DINAMANI, P. 1969. A note on feeding and excretion in bivalves. Veliger **11:** 198–199.

DOERING, P. H., AND C. A. OVIATT. 1986. Application of filtration rate models to field populations of bivalves: An assessment using experimental mesocosms. Mar. Ecol. Prog. Ser. **31:** 265–275.

DUCKLOW, H. W. 1983. Production and fate of bacteria in the oceans. BioScience **33:** 494–499.

FRECHETTE, M., AND E. BOURGET. 1985*a*. Energy flow between the pelagic and benthic zones: Factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. Aquat. Sci. **42:** 1158–1165.

———, AND ———. 1985*b*. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer. Can. J. Fish. Aquat. Sci. **42:** 1166–1170.

———, C. A. BUTMAN, AND R. G. GEYER. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol. Oceanogr. **34:** 19–36.

GOLDMAN, J. C., D. A. CARON, AND M. R. DENNETT. 1987. Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C : N ratio. Limnol. Oceanogr. **32:** 1239–1252.

GRANT, J., C. T. ENRIGHT, AND A. GRISWOLD. 1990. Resuspension and growth of *Ostrea edulis*: A field experiment. Mar. Biol. **104:** 51–59.

GUILLIARD, R. R. L., AND J. H. RYTHER. 1962. Studies on marine planktonic diatoms. 1. *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can. J. Microbiol. **8:** 229–239.

HOBBIE, J. E., AND C. C. CRAWFORD. 1969. Respiration corrections for bacterial uptake of dissolved organic compounds in natural water. Limnol. Oceanogr. **14:** 528–532.

HOLLIBAUGH, J. T. 1979. Metabolic adaptation in natural bacterial populations supplemented with selected amino acids. Estuarine Coastal Mar. Sci. **9:** 215–230.

———, R. W. BUDDEMEIER, AND S. V. SMITH. 1991. Contributions of colloidal and high molecular weight dissolved material to alkalinity and nutrient concentrations in shallow marine and estuarine systems. Mar. Chem. **34:** 1–27.

———, J. A. FUHRMAN, AND F. AZAM. 1980. Radioactive labeling of natural assemblages of bacterioplankton for use in trophic studies. Limnol. Oceanogr. **25:** 172–181.

JUMARS, P., D. PENRY, J. BAROSS, M. PERRY, AND B. FROST. 1989. Closing the microbial loop: Dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res. **36:** 483–495.

KIRBOE, T., F. MOHLENBERG, AND O. NOHR. 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia **19:** 193–205.

LAMPERT, W. 1978. Release of dissolved organic carbon by grazing zooplankton. Limnol. Oceanogr. **23:** 831–834.

LANGDON, C. J., AND R. I. E. NEWELL. 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa.* Mar. Ecol. Prog. Ser. **58:** 299–310.

LEE, S., AND J. A. FUHRMAN. 1986. Relationships between biovolume and biomass of naturally derived marine bacterioplankton. Appl. Environ. Microbiol. **53:** 1298–1303.

NICHOLS, F. H., J. E. CLOERN, S. N. LUOMA, AND D. H. PETERSON. 1986. The modification of an estuary. Science **231:** 567–573.

———, J. K. THOMPSON, AND L. E. SCHEMEL. 1990. The remarkable invasion of San Francisco Bay, California, USA by the Asian clam *Potamocorbula amurensis.* 2. Displacement of a former community. Mar. Ecol. Prog. Ser. **66:** 95–101.

PORTER, K. G., AND Y. S. FEIG. 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. **25:** 943–948.

REDFIELD, A. C. 1934. On the proportions of organic derivatives in seawater and their relation to the composition of plankton, p. 177–192. *In* James Johnstone Mem. Vol. Univ. Liverpool.

SAUNDERS, G. W., JR. 1969. Some aspects of feeding in zooplankton, p. 556–573. *In* Eutrophication: Causes, consequences, correctives. Natl. Acad. Sci. Publ. 1700.

SIMON, M., AND F. AZAM. 1989. Protein content and protein synthesis rates of planktonic marine bacteria. Mar. Ecol. Prog. Ser. **51:** 201–213.

STRATHMANN, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. **12:** 411–418.

UTERMOHL, H. 1958. Zur Vervollkommung der quantitativen Phytoplankton Methodik. Mitt. Int. Ver. Theor. Angew. Limnol. 9. 38 p.

WIENKE, S. M., AND J. E. CLOERN. 1987. The phytoplankton component of seston in San Francisco Bay. Neth. J. Sea Res. **21:** 25–33.

WILLIAMS, P. J. LEB. 1981. Incorporation of microhet-

erotrophic processes into the classical paradigm of the planktonic food web. Kiel. Meeresforsch. **5:** 1–28.

WINTER, J. E. 1978. A review on the knowledge of suspension feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture **13:** 1–33.

WOLFF, W. J. 1977. A benthic food budget for the Grevelingen estuary, The Netherlands, and a consideration of the mechanisms causing high benthic secondary production in estuaries, p. 267–280. *In* B. C. Coull [ed.], Ecology of marine benthos. V. 6. Univ. South Carolina.

WRIGHT, R. T. 1978. Measurement and significance of specific activity in the heterotrophic bacteria of natural waters. Appl. Environ. Microbiol. **36:** 297–305.

———, R. B. COFFIN, C. P. ERSING, AND D. PEARSON. 1982. Field and laboratory measurements of bivalve filtration of natural bacterioplankton. Limnol. Oceanogr. **27:** 91–98.

Submitted: 11 June 1991
Accepted: 20 October 1992
Revised: 29 December 1992