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Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary

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ABSTRACT: Grazing by the overbite clam *Corbula amurensis* (formerly known as *Potamocorbula*) may be the cause of substantial declines in phytoplankton biomass and zooplankton in the San Francisco Estuary (SFE) following its introduction in 1986. While grazing rates have been examined on bacteria, phytoplankton, and copepod nauplii, the consumption of protistan microzooplankton by *C. amurensis* has not previously been measured. In this study, laboratory feeding experiments revealed that *C. amurensis* cleared 0.5 l ind^{-1} h^{-1} of microzooplankton (ciliates) and 0.2 l ind^{-1} h^{-1} of chlorophyll (chl) *a*. Despite the higher clearance rate on microzooplankton, clams obtained more of their carbon from phytoplankton, which dominated the prey assemblage on most dates. When the measured clearance rates are extrapolated to field populations of clams, fractional loss rates (50 to 90% d^{-1}) exceed the population growth capacity of microzooplankton. Although microzooplankton may not be a major component of the diet of these clams, *C. amurensis* may further alter food web dynamics through consumption of this important trophic intermediary, thus disrupting this link from bacteria and phytoplankton to higher trophic levels.

KEY WORDS: Bivalves · Benthic-pelagic coupling · Microzooplankton · Microphytoplankton · Low-salinity zone · Ciliates

INTRODUCTION

Benthic-pelagic coupling is a key process in shallow estuaries (Dame et al. 1980, Cloern 1982, Nichols et al. 1990) that links food web dynamics in several ways. Tidal or wind-driven mixing re-suspends nutrients from the benthos, stimulating bacterial and phytoplankton production in the water column. This production may be filtered directly from the water column by zooplankton and benthic grazers or can sink to the bottom to fuel benthic communities. Grazing by filter-feeding bivalves on phytoplankton, as well as on other pelagic organic particles including zooplankton and bacteria, has been described for freshwater clams (Vaughn & Hakenkamp 2001), freshwater mussels (MacIsaac et al. 1999), estuarine clams (Werner & Hollibaugh 1993), marine mussels (Noren et al. 1999, Davenport et al. 2000), oysters (Riisgard 1988, Baldwin & Newell 1991), and scallops (Lehane & Davenport 2002). By consuming phytoplankton, these bivalves divert resources from the water column to the sediments (Dame 1996) which depresses pelagic production. Control of phytoplankton biomass in the water column by both native and non-native bivalves has been reported to exert substantial influence on pelagic food webs (Cloern 1982, Officer et al. 1982, Miehls et al. 2009).

The clam *Corbula amurensis* (Family Corbulidae, formerly known as *Potamocorbula amurensis*; Coan 2002) was first discovered in Grizzly Bay (Fig. 1) in October 1986 and has persisted in the northern San Francisco Estuary (SFE) at densities exceeding 10 000 m^{-2} (Carlton et al. 1990). *C. amurensis* can burrow into most sediment and has the ability to withstand a wide range of

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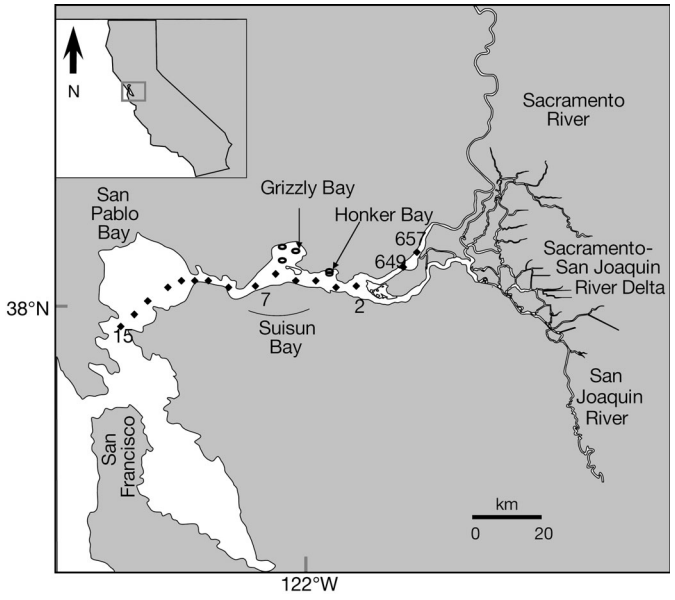

Fig. 1. The San Francisco Estuary. Solid black diamonds indicate US Geological Survey Water Quality Sampling Stations 2 to 15, 649 and 657, sampled for microplankton abundance from February 2008 to February 2009. Eight benthic stations were sampled monthly; not all stations were sampled on all dates. The 4 channel stations were adjacent to Water Quality Stations 2, 4, 6, and 8. The 4 shoal stations (408, 415, 417, and 433; represented by open circles) were located in Suisun Bay, Grizzly Bay and Honker Bay

salinities (~2 to 30, Nicolini & Penry 2000). As a result, *C. amurensis* can maintain high abundance year round in the northern SFE (Nichols et al. 1990) with peak abundance occurring in late summer (Thompson 2005).

Following the introduction of *Corbula amurensis* to the SFE, phytoplankton biomass in Suisun Bay (Fig. 1) dropped from a summer average of >20 to <2 mg chl *a* m^{-3} (Alpine & Cloern 1992, Jassby et al. 2002). This decline of phytoplankton biomass has been correlated with long-term declines of copepod and mysid shrimp populations (Orsi & Mecum 1996, Kimmerer 2006). The decline of several species of calanoid copepods was attributed to a combination of competition for food and direct consumption of copepod nauplii by clams (Kimmerer et al. 1994, Kimmerer 2006). Changes in the abundance of zooplankton and mysid shrimp (Orsi & Mecum 1996, Kimmerer 2006) have been further linked to declines in planktivorous fish (Feyrer et al. 2003, Sommer et al. 2007) including the endangered delta smelt *Hypomesus transpacificus*, threatened longfin smelt *Spirinchus thaleichthys*, threadfin shad *Dorosoma petenense*, and striped bass *Morone saxatilis*. Similarly, the decline of the northern anchovy *Engraulis mordax* in San Pablo and Suisun Bays may have been due to a behavioral response to the declines in phytoplankton and zooplankton (Kimmerer 2006).

Corbula amurensis grazing rates have been estimated in the SFE for bacterioplankton (Werner & Hollibaugh 1993), phytoplankton (Cole et al. 1992; Werner & Hollibaugh 1993), and copepod nauplii (Kimmerer et al. 1994). These studies have used measured clearance rates to estimate potential impact of clams on prey populations. However, nothing is known about consumption by *C. amurensis* of protistan microzooplankton (20 to 200 µm), including ciliates and heterotrophic flagellates. Microzooplankton are key components of pelagic food webs as they remineralize organic matter and nutrients (Goldman & Caron 1985, Goldman et al. 1985). Grazing microzooplankton can control the biomass of bacteria and phytoplankton (Fenchel 1982, McManus & Fuhrman 1988, York at al. 2010), and are in turn a main food source for mesozooplankton (Bouley & Kimmerer 2006, Gifford et al. 2007). Thus, microplankton are important trophic intermediaries between the microbial loop and the rest of the food web.

Our aim here is to understand the role of bivalve grazing on microplankton population dynamics and function in the aquatic food web. We quantified the abundance of microplankton, including both autotrophs and heterotrophs, during February 2008 to February 2009 in the northern SFE. We estimated clearance rates of *Corbula amurensis* on the microplankton community in the low-salinity zone (LSZ) and used *C. amurensis* biomass to estimate the potential impact of clam grazing on microplankton assemblages.

MATERIALS AND METHODS

Study area. The northern SFE includes the bays between the Sacramento-San Joaquin River Delta and central San Francisco Bay (Fig. 1). The focus for this study was in the LSZ, defined here to include salinities of 0.5 to 6 (Kimmerer 2004), usually located in Suisun Bay or the western Delta. This salinity range is summer-fall habitat for the threatened (federal) and endangered (state) delta smelt (Bennett 2005). It is turbid, well mixed, and has a bimodal depth distribution that includes extensive shoals (2 m) and deep channels (>10 m).

Field abundance. Samples were collected from R/V 'Polaris' in conjunction with the US Geological Survey (USGS) Water Quality Program which samples at fixed stations throughout the SFE (Fig. 1; http://sfbay.wr.usgs.gov/access/wqdata/). Microplankton were sampled monthly from February 2008 to February 2009 at Stations 2–15, 649, and 657 (Fig. 1); however, only samples from the LSZ were analyzed (Table 1). Salinity and temperature data were collected at each water quality sampling station using a submersible instru-

ment package (Sea-Bird 9plus CTD). We collected water samples using a 20 l bucket (surface) and a Niskin bottle (~1 m from the bottom). Samples were preserved by gently filling a 250 ml HDPE Nalgene® bottle containing 25 ml of acid Lugol's solution (10% final conc., vol/vol, Throndsen 1978).

Samples were stored for at least 48 h before processing to allow for complete fixation. Then each bottle was inverted a minimum of 50 times to ensure that the contents were homogenous and a 50 ml subsample was removed and settled for 24 h (Claessens & Prast 2008). The subsamples were then transferred to Utermöhl chambers (Lund et al. 1958) and microplankton were identified and counted with a Wild M40 inverted microscope at 100× magnification. A volume containing a minimum of 100 to 200 of the most abundant organisms was processed for each sample. Biovolume was estimated for representative cells of different shapes within each sampling period using measured lengths and widths. We calculated carbon biomass for each prey type using published relationships of volume to carbon. Aloricate ciliate carbon was calculated using the carbon:volume of 0.19 ± 0.01 (95% CL, confidence limits) pg μm^{-3} (Putt & Stoecker 1989) and adjusted for shrinkage during preservation (Stoecker et al. 1994). Tintinnid ciliate carbon was calculated using the carbon:lorica volume of 0.053 pg μm^{-3} (Verity & Langdon 1984). Diatom carbon was calculated using the algorithm pg C $cell^{-1}$ = 0.216 $volume^{0.939}$ (Menden-Deuer & Lessard 2000). Carbon content of copepod nauplii was estimated using carbon measurements for *Limnoithona tetraspina* (Gould & Kimmerer 2010). Counts and biomass from surface and bottom samples were averaged.

Feeding experiments. Clam feeding rates were quantified through disappearance of prey in incubation experiments. Six experiments were completed on board the R/V 'Polaris', once per month from July to December 2008 (Table 2). Clams and microplankton used in feeding experiments were collected from USGS benthic Station 2.1 (adjacent to Water Quality Station 2, Fig. 1). To ensure normal feeding, clams used in our experiments were collected immediately before incubations with a 0.05 m^2 Van Veen grab. Six clams were chosen at random from the grab sample and shell lengths were measured to the closest millimeter with calipers. Only clams with no visible epiphytes were used in experiments. All experiments were conducted at *in situ* temperature and salinity (Table 2) under low light (0.0015 µmol m^{-2} s^{-1}). Light levels were measured using a LI-COR Model LI-1400 Data logger with an LI-192SA Underwater Quantum Sensor.

In situ surface water containing the microplankton assemblage was collected with a 20 l bucket and poured gently through a 200 µm mesh screen to remove larger zooplankton. Nine 4 l Camwear® clear plastic containers were filled with 3 l of the *in situ* microplankton assemblage. Magnetic stir bars rotating at low speed kept the natural prey assemblage well mixed in experimental and control containers. Experimental duration (4 h) was estimated from preliminary experiments to ensure that clams did not clear more than 60% of the assemblage to avoid changes in feeding rate in response to decreases in food concentration. One clam was placed into a suspended tray filled with sand and 1 tray was suspended at the midpoint of each of 6 experimental containers (Werner & Hollibaugh 1993). Each experimental period began when 50% of the clams had buried themselves, opened their valves, and extended their siphons, at which point they were assumed to be filtering (~15 min). Three control containers with trays and sand but no clams accounted for growth or mortality of the prey assemblage not related to clam feeding.

Three 250 ml initial samples were taken immediately after size fractionating the entire water sample and preserved with 10% acid Lugol's solution to determine the initial *in situ* assemblage. Experiments were run for 4 h, after which a 250 ml sample was taken from

Table 1. Microplankton abundance survey. Stations sampled in the low-salinity zone of the northern San Francisco Estuary

Date	Stations in low-salinity zone	Salinity range
12 Feb 08	2–10	0.15–3.7
11 Mar 08	2–9	0.16–5.5
6 May 08	2–6	0.54–5.4
17 Jun 08	2–5, 649	0.5–4.7
15 Jul 08	2–3, 649, 657	1.9–5.7
19 Aug 08	2–4, 649, 657	0.09–5.7
16 Sep 08	2, 649, 657	0.16–4.7
15 Oct 08	649–657	0.5–6.4
19 Nov 08	2, 649, 657	0.11–3.9
16 Dec 08	649–657	0.3–5.7
13 Jan 09	2, 649, 657	0.25–5.9
10 Feb 09	2–3, 649, 657	0.15–4.7

Table 2. *Corbula amurensis* feeding experiments. Experimental conditions and mean clam length and ash-free dry weight (AFDW)

Expt. no.	Date	Temp. (°C)	Salinity	Mean length (mm)	Mean weight (g AFDW)
1	16 Jul 08	20.6	4.3	10.8	0.0061
2	20 Aug 08	20.4	5	13.8	0.0185
3	17 Sep 08	18.7	4.1	14.5	0.0201
4	16 Oct 08	16.9	4.8	15.0	0.0183
5	18 Nov 08	15.3	3	14.7	0.0170
6	17 Dec 08	9.6	3.4	13.2	0.0159

each control and experimental container and preserved in the same way as the initial samples. Samples were analyzed as described for the field abundance.

Chl *a* concentrations in experimental and control treatments were determined at $t = 0$ and $t = 4$ h. Samples (250 ml) were filtered onto 47 mm Whatman GF/F filters and extracted with 90% acetone. Chl *a* concentration was determined using a Turner Designs Model 10 Fluorometer.

Clam biomass. Clam biomass was measured from February 2008 through February 2009 at 4 channel stations (mean depth = 10 m) adjacent to water quality Stns 2, 4, 6, and 8; and 4 shoal stations (mean depth = 2 m) in Suisun Bay, Grizzly Bay and Honker Bay (Fig. 1). Three benthic samples were taken from each station from February 2008 to September 2008, and 1 sample per station was taken from October 2008 to February 2009. Samples were fixed in 10% buffered formalin, then preserved in 70% ethyl alcohol, and all bivalves were measured and counted. A subset of clams was measured, dried at 60°C, weighed (dry weight, DW), combusted at 500°C, and re-weighed (ash weight, AW); ash-free-dry weight (AFDW) was determined by difference (Crisp 1971). Length-weight regressions were determined monthly ($\ln \text{AFDW} = a\,(\ln \text{length}) - b$) and used to estimate bivalve biomass at each station.

We calculated ingestion rates at all water-quality monitoring stations in the LSZ as the product of prey biomass and the mean clearance rate. Additionally, clam biomass (g m^{-2}) was multiplied by weight-specific clearance rates (l g^{-1} h^{-1}) to estimate community clearance rate (l m^{-2} d^{-1}) which was divided by depth to calculate the daily fractional loss of prey (d^{-1}) due to grazing by clams.

Data analysis. Clearance rates were calculated as (Frost 1972):

$$g_i = \ln (N_c/N_i)\, V/t \quad (1)$$

where g_i is clearance rate for a single clam (l h^{-1}), N_i is the number of cells per liter of a given taxon counted in experimental sample i, N_c is the mean number of cells per liter counted in the corresponding controls, V is the volume of the experimental containers (l), and t is the incubation duration (h). This model assumes constant grazing and growth in the sample containers, and that the specific growth rate of microplankton in experimental containers was the same as that in the controls. All taxon combinations in each experiment were included if there were no zero abundances in the controls, mean abundance of controls (N_c) was at least 5, and no more than 2 zeros occurred in the experimental samples. This resulted in 29 experiment/taxon combinations in all 6 experiments.

The above model was fit to the count data using Bayesian hierarchical models (Lunn et al. 2000) with a Poisson error distribution under the assumption that subsampling was random. This results in decreasing uncertainty as the number of cells counted increases. Using Bayesian models allowed us to incorporate subsampling error and to readily determine differences in clearance rate among prey taxa and experiments. The Bayesian models were fit using WinBUGS 1.4.3 (Lunn et al. 2000) with triplicate Markov chains. Each chain was thinned 10-fold to reduce autocorrelation, and 10 000 samples were retained after the first 1000 samples were discarded to remove effects of initial values. Monte Carlo standard errors of the mean were much smaller than the standard deviations of the parameter estimates, also indicating good model performance. Gelman-Rubin statistics (Gelman et al. 2004) and plots of autocorrelation and time series of simulations demonstrated convergence of the model.

Prior distributions for grazing rates were uninformative and were normally distributed with a mean of 0 and a standard deviation of 10. These distributions were flat over the range of the results and therefore had no influence on the model results. Control means had normal prior distributions with a standard deviation of 1000, truncated to >0, which were also flat enough to have negligible influence on the results.

RESULTS

Field abundance

Diatoms were the numerically dominant microphytoplankton across all months sampled (Fig. 2). Total microphytoplankton abundances were higher than those of total microzooplankton, except in early spring. A bloom of *Nitzschia* sp. (unidentified pennate diatoms) was observed in late summer and a bloom of benthic pennate diatoms, mostly *Entomoneis* sp., occurred in winter. Aloricate and tintinnid (= loricate; i.e. *Codonellopsis* sp.) ciliates were the most abundant microzooplankton in all months. *Myrionecta rubra* (= *Mesodinium rubrum*), an aloricate ciliate, was present in every month sampled (= 1100 l^{-1}, range 160 to 4690 l^{-1}) with the highest abundance in May. Tintinnid ciliate abundance (= 940 l^{-1}, range 100 to 1200 l^{-1}) was usually less than aloricate ciliate abundance. Copepod nauplii, some identified as *Limnoithona tetraspina* nauplii, were also present in every month, except February 2009. No dinoflagellates (>20µm) were observed in our counts.

Feeding experiments

Ten prey taxa were abundant enough to count during the 6 feeding experiments (Table 3). Microphyto-

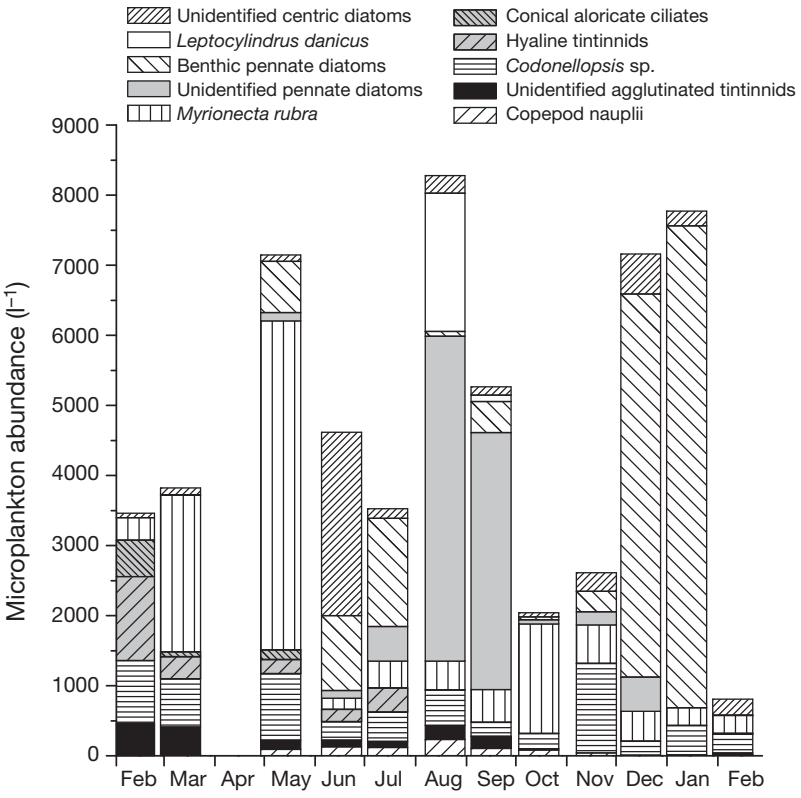

Fig. 2. Monthly abundance of microplankton in the low-salinity zone of the northern San Francisco Estuary from February 2008 to February 2009, averaged among stations

plankton were the most abundant in all experiments. Four categories of microphytoplankton were observed: unidentified centric diatoms, *Leptocylindrus danicus* (a chain-forming centric diatom), benthic pennate diatoms (including *Entomoneis* sp.), and unidentified pennate diatoms (most of which were *Nitzschia* spp.). The remaining 6 categories were microzooplankton: aloricate ciliates (*Myrionecta rubra* and conical ciliates), tintinnid ciliates (hyaline and agglutinated, including *Codonellopsis* sp.), and copepod nauplii. The copepod nauplii were the size of *Limnoithona tetraspina* nauplii but were not identified in all experiments. Only *M. rubra* and *Codonellopsis* sp. were observed in every experiment. Diatom and ciliate populations were sometimes lower in the control treatments than in the initial samples, indicating a decrease over the 4 h experimental duration, presumably from grazing by mesozooplankton not removed by the 200 µm size fractionation prior to incubations.

Prey biomass (Table 4) was dominated by copepod nauplii (~34 µg C l^{-1}). Ciliates (aloricate and loricate; ~4 µg C l^{-1}) and pennate diatoms (~2 µg C l^{-1}) made up most of the remainder, and centric diatoms contributed a negligible amount to the total prey biomass.

Clearance rates on individual microplankton taxa (Table 5) ranged from –0.6 to 1.1 l ind^{-1} h^{-1}. The highest mean rates in all experiments on microphytoplankton (0.7 to 0.8 l ind^{-1} h^{-1}) were on the 'unidentified pennate diatoms' and 'benthic pennate diatoms'. The lowest rates were on copepod nauplii (= 0.1 l ind^{-1} h^{-1}) and confidence limits included zero in every experiment. Rates on 'unidentified centric diatoms' were the most

Table 3. *Corbula amurensis* feeding experiments. Mean abundance of microplankton (number l^{-1} ± 95% CL) in initial samples (upper section) and final control samples (lower section). –: experiment/taxon combinations that did not meet criteria to be included in the calculations (see 'Materials and methods'). Microzooplankton are indicated in **bold**

Expt. no.	Unidentified centric diatoms	*Leptocylindrus danicus*	Benthic pennate diatoms	Unidentified pennate diatoms	***Myrionecta rubra***	**Conical aloricate ciliates**	**Hyaline tintinnids**	***Codonellopsis* sp.**	**Unidentified agglutinated tintinnids**	**Copepod nauplii**
Initial no. l^{-1}										
1	864 ± 218	–	–	–	489 ± 89	333 ± 62	504 ± 268	603 ± 146	93 ± 24	285 ± 36
2	390 ± 123	1149 ± 187	36 ± 23	7581 ± 875	435 ± 131	–	–	204 ± 90	495 ± 84	195 ± 150
3	126 ± 76	84 ± 53	–	9747 ± 969	156 ± 36	–	–	132 ± 64	504 ± 118	207 ± 81
4	228 ± 48	–	–	696 ± 150	1152 ± 352	–	–	288 ± 140	24 ± 27	144 ± 323
5	–	–	1104 ± 27	432 ± 186	336 ± 71	–	–	528 ± 27	–	12 ± 54
6	192 ± 54	–	20904 ± 2198	360 ± 186	204 ± 117	–	–	168 ± 54	–	–
Final no. l^{-1}										
1	606 ± 238	–	–	12 ± 6	483 ± 236	474 ± 74	411 ± 37	342 ± 104	108 ± 23	261 ± 160
2	441 ± 35	1299 ± 169	–	10290 ± 885	122 ± 158	–	–	204 ± 54	546 ± 60	306 ± 12
3	51 ± 36	48 ± 24	–	10266 ± 684	60 ± 78	–	–	24 ± 24	453 ± 55	177 ± 24
4	150 ± 75	–	–	720 ± 81	888 ± 210	–	–	156 ± 117	60 ± 27	33 ± 29
5	–	–	1380 ± 142	384 ± 220	144 ± 47	–	–	336 ± 117	–	–
6	60 ± 27	–	11916 ± 1556	–	216 ± 123	–	–	60 ± 27	–	–

Table 4. *Corbula amurensis* feeding experiments. Mean biomass of microplankton (µg C l^{-1} ± 95% CL) in initial control samples. –: experiment/taxon combinations that did not meet criteria to be included in the calculations (see 'Materials and methods'). Microzooplankton are indicated in **bold**

Expt. no.	Unidentified centric diatoms	*Leptocylindrus danicus*	Benthic pennate diatoms	Unidentified pennate diatoms	***Myrionecta rubra***	**Conical aloricate ciliates**	**Hyaline tintinnids**	***Codonellopsis* sp.**	**Unidentified agglutinated tintinnids**	**Copepod nauplii**	**Total microzooplankton carbon**
1	0.06 ± 0.01	–	–	–	3.6 ± 0.7	0.31 ± 0.06	0.38 ± 0.20	0.60 ± 0.15	0.07 ± 0.02	57.0 ± 7.2	61.96
2	0.03 ± 0.01	0.005 ± 0.004	0.04 ± 0.007	4.5 ± 0.52	3.2 ± 1.0	–	–	0.20 ± 0.09	0.39 ± 0.07	39.0 ± 30.0	42.79
3	0.01 ± 0.005	–	0.003 ± 0.002	5.9 ± 0.58	1.1 ± 0.3	–	–	0.13 ± 0.06	0.39 ± 0.09	41.4 ± 16.1	43.02
4	0.01 ± 0.003	–	–	0.42 ± 0.09	8.5 ± 2.6	–	–	0.29 ± 0.14	0.02 ± 0.02	28.8 ± 64.5	37.61
5	–	0.17 ± 0.004	–	0.26 ± 0.11	2.8 ± 0.5	–	–	0.53 ± 0.03	–	2.4 ± 10.8	5.73
6	0.01 ± 0.004	3.2 ± 0.33	–	0.04 ± 0.02	1.5 ± 0.9	–	–	0.17 ± 0.05	–	–	1.67

variable over experiments. The mean clearance rate for each month on *Myrionecta rubra* was always greater than or equal to that on any group of tintinnid ciliates (Table 5). Mean clearance rates on microplankton (Table 5) showed no seasonal trends.

Initial chl *a* concentrations ranged from 1 to 3 µg l^{-1}. A reduction in chl *a* was observed in every experiment. Clearance rates on chl *a* ranged from 0.1 to 0.4 l ind^{-1} h^{-1}, (Table 5). These rates were usually lower than rates on microzooplankton and, in most cases, on microphytoplankton (Table 5).

Ingestion of microzooplankton in the feeding experiments ranged from 10 to 240 µg C ind^{-1} d^{-1} (Table 6). Copepod nauplii were not included in these totals because they were not present in every experiment and when present their numbers were low. However, when present, copepod nauplii comprised the largest fraction of microplankton carbon ingested by clams (Table 6), despite the much lower clearance rates than for total microzooplankton (Table 5).

Population estimates

Corbula amurensis populations had seasonal peaks in biomass in late summer (Fig. 3A). Biomass began to

Table 5. *Corbula amurensis* feeding experiments. Clam clearance rates (l ind^{-1} h^{-1} ± 95% CL) on microplankton by experiment number and prey category. –: experiment/taxon combinations that did not meet criteria to be included in the calculations (see 'Materials and methods'). Microzooplankton are indicated in **bold**. MCR: mean clearance rate (microzooplankton excluding nauplii)

Expt. no.	Unidentified centric diatoms	*Leptocylindrus danicus*	Benthic pennate diatoms	Unidentified pennate diatoms	***Myrionecta rubra***	**Conical aloricate ciliates**	**Hyaline tintinnids**	***Codonellopsis* sp.**	**Unidentified agglutinated tintinnids**	**Copepod nauplii**	MCR	MCR chl *a*
1	0.1 ± 0.2	–	–	–	0.6 ± 0.2	0.7 ± 0.2	0.3 ± 0.2	–0.05 ± 0.2	0.4 ± 0.4	0.01 ± 0.3	0.4 ± 0.1	0.1 ± 0.1
2	0.8 ± 0.2	0.69 ± 0.1	–	0.8 ± 0.04	0.7 ± 0.2	–	–	0.5 ± 0.3	0.6 ± 0.2	0.2 ± 0.2	0.6 ± 0.1	0.4 ± 0.1
3	–0.6 ± 0.4	–	–	0.4 ± 0.03	0.2 ± 0.3	–	–	–	0.2 ± 0.2	0.1 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
4	1.1 ± 0.5	–	–	1.0 ± 0.2	1.1 ± 0.2	–	–	0.7 ± 0.4	–	–	1.0 ± 0.2	0.3 ± 0.2
5	–	–	0.9 ± 0.2	0.5 ± 0.3	0.7 ± 0.5	–	–	0.4 ± 0.3	–	–	0.5 ± 0.2	0.2 ± 0.1
6	–	–	0.6 ± 0.05	–	0.6 ± 0.3	–	–		–	–	0.6 ± 0.3	0.1 ± 0.1

Table 6. *Corbula amurensis* feeding experiments. Mean clam ingestion rate on microplankton (µg C ind^{-1} d^{-1} ± 95% CL). –: experiment/taxon combinations that did not meet criteria to be included in the calculations (see 'Materials and methods'). Microzooplankton are indicated in **bold**. TI: total ingestion of microzooplankton (excluding nauplii)

Expt. no.	Unidentified centric diatoms	*Leptocylindrus danicus*	Benthic pennate diatoms	Unidentified pennate diatoms	***Myrionecta rubra***	**Conical aloricate ciliates**	**Hyaline tintinnids**	***Codonellopsis* sp.**	**Unidentified agglutinated tintinnids**	**Copepod nauplii**	**TI**
1	0.2 ± 0.4	–	–	–	61.0 ± 31.0	5.3 ± 2.0	3.0 ± 2.0	–0.5 ± 3.0	0.7 ± 0.8	52.0 ± 326.0	69.5
2	0.3 ± 0.2	0.8 ± 0.3	–	89.0 ± 17.0	61.0 ± 38.0	–	–	2.8 ± 1.1	5.8 ± 1.8	296.0 ± 391.0	69.6
3	–0.1 ± 0.1	–	–	56.0 ± 25.0	9.5 ± 13.6	–	–	–	2.3 ± 2.5	147.0 ± 314.0	10.5
4	0.3 ± 0.1	–	–	10.5 ± 4.2	240.0 ± 70.0	–	–	4.3 ± 2.1	–	–	244.4
5	–	–	4.0 ± 1.0	3.5 ± 1.0	31.0 ± 28.0	–	–	7.5 ± 7.2	–	–	38.5
6	–	–	49.0 ± 9.0	–	23.0 ± 7.0	–	–	–	–	–	23.5

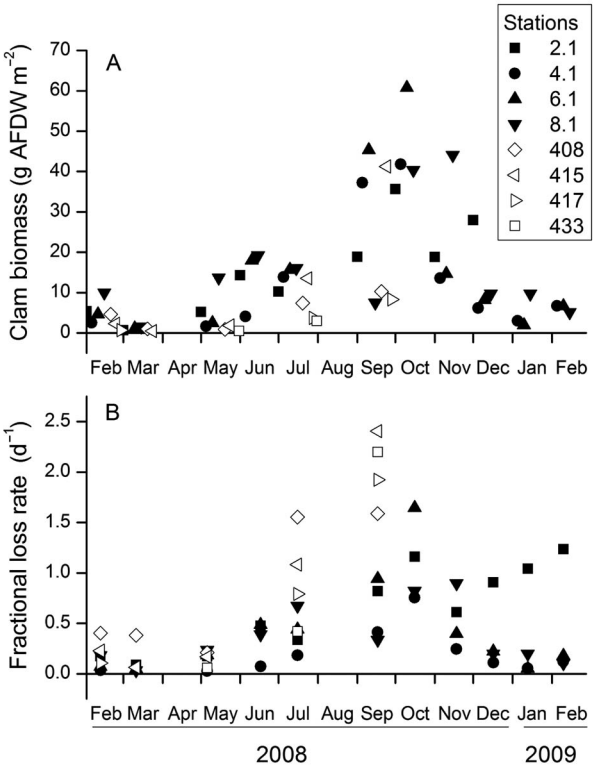

Fig. 3. *Corbula amurensis.* (A) Mean clam biomass from February 2008 to February 2009 in the low-salinity zone of the San Francisco Estuary. Stations 2.1, 4.1, 6.1 and 8.1 are adjacent to water quality stations 2, 4, 6, and 8, respectively. Points represent means of 3 replicates, except in June 2008 and October 2008 through February 2009 when only single grabs were taken. (B) Estimated fractional loss rate (d^{-1}) of microzooplankton resulting from grazing. In both panels, solid symbols indicate channel stations and open symbols indicate shoal stations

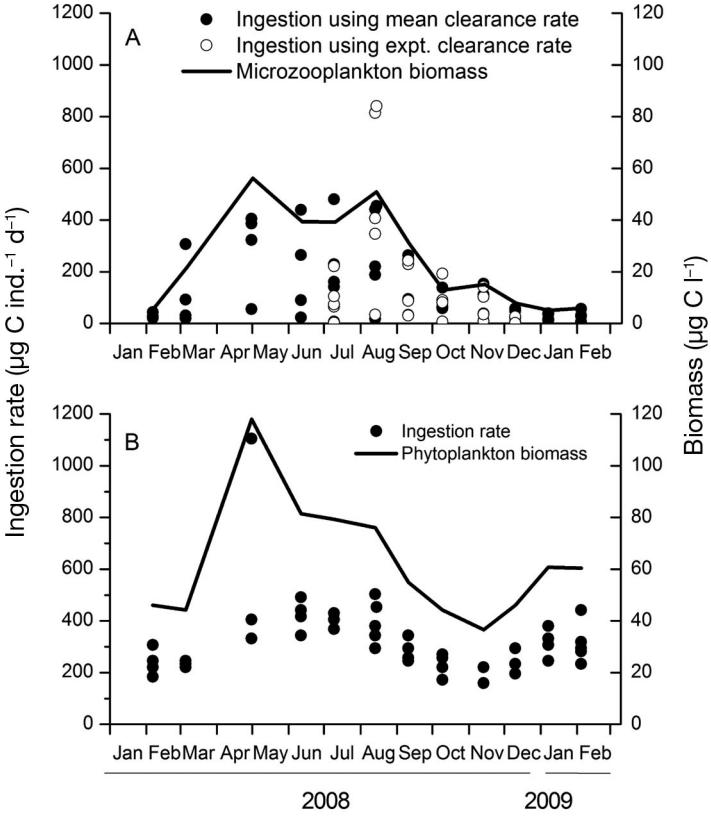

Fig. 4. *Corbula amurensis.* Ingestion by *C. amurensis* in the low salinity zone of the San Francisco Estuary from February 2008 to February 2009. (A) Ingestion by the clam was calculated using the overall mean calculated clearance rate for microzooplankton (solid circles) and the experimental (expt.) rate (open circles). The solid line represents mean standing stock (µg C l^{-1}) of microzooplankton on each date. (B) Ingestion of phytoplankton carbon by *C. amurensis* was calculated from chl *a* and standing stock of phytoplankton for all stations in the low-salinity zone from February 2008 to February 2009. Closed circles indicate ingestion of chl *a* and line shows the mean standing stock of phytoplankton carbon calculated from chl *a* (http://sfbay.wr.usgs.gov/access/wqdata/) on each date. Ingestion of phytoplankton carbon was calculated assuming a C:chl ratio of 23.6 (W.J. Kimmerer, A. Parker, U. Lidström unpubl.)

decline in the fall except at Stn 2.1 where it increased from October 2008 to February 2009. Clam biomass was always higher at the channel stations than at the shoal stations (Fig. 3A). *C. amurensis* cleared a mean of 20 to 50% d^{-1} of the microzooplankton from the water column in the channel and a mean of 80 to 90% d^{-1} in the shoals (Fig. 3B). Ingestion of microzooplankton increased as clam biomass increased in the late summer (Fig. 3). On most dates the ingestion of phytoplankton carbon was higher than ingestion of microzooplankton (Fig. 4). The mean ingestion rates of microzooplankton and phytoplankton (= chl *a*) by an individual *Corbula amurensis* varied in rough proportion to their respective standing stocks (Fig. 4).

DISCUSSION

This study reports the most comprehensive investigation of the clearance rates of bivalves on microzooplankton and the first measurements of clearance rates of an estuarine bivalve on ciliates. Most of the previous studies on bivalve clearance rates have focused on microphytoplankton using chl *a* as a proxy for all sizes of phytoplankton (e.g. Cole et al. 1992) and a few have examined other prey including bacterioplankton (e.g. Werner & Hollibaugh 1993), rotifers (e.g. MacIsaac et al. 1999), and crustaceans (e.g. Kimmerer et al. 1994, Pace et al. 1998, Davenport et al. 2000). The range of clearance rates on microzooplankton observed in this study were larger and the maxima higher than clearance rates previously determined on chl *a* and bacterioplankton (Table 7). However, microzooplankton provided a smaller portion of the clams' apparent

Table 7. *Corbula amurensis* clearance rates

Clearance rate	Prey category	Source
130–380 ml ind^{-1} h^{-1}	Chl *a*	This study
110–1050 ml ind^{-1} h^{-1}	Microphytoplankton	
170–970 ml ind^{-1} h^{-1}	Microzooplankton	
154–337 ml ind^{-1} h^{-1}	Chl *a*	Werner & Hollibaugh (1993)
45 ml ind^{-1} h^{-1}	Bacterioplankton	
3–200 ml ind^{-1} h^{-1}	Chl *a*	Cole et al. (1992)
4×10^{-3} l ind^{-1} h^{-1}	Copepod nauplii	Kimmerer et al. (1994)

ingestion than phytoplankton measured as chl *a* (Fig. 4) due to the lower biomass of microzooplankton than phytoplankton during the sample period.

Field abundance

The microplankton abundances observed in this study were similar to those reported previously for the SFE. Ambler et al. (1985) quantified estuary-wide distribution and abundance of zooplankton, including tintinnids, rotifers, and copepod nauplii, from 1978 to 1981, prior to the introduction of *Corbula amurensis*. However, the 64-µm mesh used in that study was most likely too large to capture small ciliates or they were not reported. Nevertheless, tintinnid ciliate abundances (≥80 µm) reported by Ambler et al. (1985) were generally >1000 l^{-1} and occasionally as great as 10^4 l^{-1} to 10^5 l^{-1} in the northern SFE (Ambler et al. 1985). Ciliates larger than 64 µm were rarely observed in the present study, and when present their abundances never exceeded 1000 l^{-1} (Fig. 2, unidentified agglutinated tintinnids).

Other, less spatially and temporally extensive studies (Rollwagen-Bollens et al. 2006, Gifford et al. 2007) conducted after the spread of *Corbula amurensis* have reported similar abundances of ciliates to those measured in this study. During 1998 and 1999, Rollwagen-Bollens et al. (2006) observed *Myrionecta rubra* and tintinnid ciliates in all samples, with mean abundances of ~1000 l^{-1} for each category. In 2004 and 2005, Gifford et al. (2007) observed mean abundances of aloricate and tintinnid ciliates of ~1500 l^{-1} and ~500 l^{-1}, respectively, at Stn 7, with lower abundances of tintinnids in the winter (~10 l^{-1}). We observed *M. rubra* in every month at almost every station in the LSZ at a mean abundance of ~1000 l^{-1} (range 0–8300 l^{-1}). Tintinnid ciliate abundance in this study averaged ~1100 l^{-1} (range 40–2600 l^{-1}), with the lowest values in winter (Fig. 2).

Dinoflagellates (>20µm) were not observed in any of our feeding experiments or in the abundance survey. Rollwagen-Bollens et al. (2006) and Gifford et al. (2007) reported overall lower dinoflagellate abundances in the LSZ than any other types of microplankton. Additionally, dinoflagellate biomass was much lower than microzooplankton biomass (York et al. 2010) and total phytoplankton biomass (Lidström 2009) in the LSZ in 2006 to 2008.

Feeding experiments

Clam clearance rates on chl *a* in this study (130 to 380 ml ind^{-1} h^{-1}) were similar to those reported in previous studies (Table 7). Clearance rates on microphytoplankton (110 to 1050 ml ind^{-1} h^{-1}; median 580 ml ind^{-1} h^{-1}) and microzooplankton (170 to 970 ml ind^{-1} h^{-1}; median 570 ml ind^{-1} h^{-1}) calculated from cell counts were similar and generally higher than those on chl *a*. Additionally, clearance rates on bacterioplankton (Werner & Hollibaugh 1993) were lower than those on chl *a* (their study) and on microzooplankton (this study), suggesting that *Corbula amurensis* has a lower clearance rate on smaller particles. Particle size influences filtration rates as gill ostia size controls the size range of particles that can be captured by bivalves (Riisgard 1988, Way 1989). The higher clearance rates observed in this study on microphytoplankton and microzooplankton than on chl *a* may be due to size-selective feeding, since much of the chl *a* in the SFE consists of cells less than 5 µm (Kimmerer 2004, Wilkerson et al. 2006).

Clearance rates on microphytoplankton were more variable than on microzooplankton or chl *a* and were sometimes negative (Table 5). All microphytoplankton were counted as individuals but some (i.e. *Thalassiosira* spp. and *Leptocylindrus danicus*) are chain-forming diatoms. The strength of the cell-to-cell connections or length of the diatom chains *in situ* may influence capture by clams; however, this could not be examined directly using the individual cell counts.

The highest clearance rates on microzooplankton were on the aloricate ciliate *Myrionecta rubra*. Apparent food selectivity by a clam may occur through the interaction of swimming behavior of the prey with the incurrent and excurrent flows of the clam siphons, through size selectivity (either pre-capture by active rejection by the clam or post-capture), or through active post-capture rejection. *M. rubra*'s high swimming speeds (Lindholm 1985) may increase the rate of encounters with potential predators and therefore lead to higher consumption rates (and clearance rates) by predators. Clearance rates by *Corbula amurensis* on tintinnid ciliates were lower than on aloricate ciliates, including *M. rubra*. The lower swimming speeds of tintinnid ciliates compared to aloricate ciliates and dif-

ferences in swimming behavior may affect their encounter rates with clams (Capriulo et al. 1982).

Clearance rates of *Corbula amurensis* on cyclopoid copepod nauplii (*Limnoithona tetraspina*) were lower than rates observed for all other prey categories (Table 5). Kimmerer et al. (1994) also reported low clearance rates for *C. amurensis* feeding on calanoid copepod nauplii (Table 7). Copepod nauplii have been observed to actively escape incurrent plumes of both *C. amurensis* (W.J. Kimmerer unpubl. data) and mussel (Jonsson et al. 2009) siphons. These reported escape responses may contribute to the lower clearance rates of bivalves on nauplii. Copepod nauplii, while not very abundant, were the largest prey organisms examined in this study and contained the most carbon per individual. As a result, ingestion of nauplii had the potential to contribute significantly to the diet of clams if nauplii were actually ingested and fully assimilated as shown in Davenport el al. (2000).

Bivalves reject unwanted particles through the production and ejection of pseudofeces (Beninger & St. Jean 1997), and prey, particularly tintinnd ciliates, may have been rejected by clams and entrained in pseudofeces. The equations used to calculate clearance rates in this study do not distinguish between particles that are ingested and those rejected in pseudofeces, since neither is assumed to reappear in the plankton. As a result, ingestion rates calculated from these clearance rates may be overestimates of what is actually available for assimilation. Additionally, ingestion rates reported in this study do not take into account assimilation efficiency, which has been observed to differ among prey types (Werner & Hollibaugh 1993). This may affect the contributions of various prey to the growth of clams.

Population estimates

Fractional loss rates of microzooplankton (Fig. 3) varied seasonally with clam biomass and station depth. The high *Corbula amurensis* biomass (16 g AFDW m^{-2}) in the channel during summer, combined with the measured clearance rates (= 0.55 l ind^{-1} h^{-1}; 34 l g $AFDW^{-1}$ h^{-1}) on microzooplankton, indicates the potential for *C. amurensis* to clear a mean of 50% of the water column d^{-1} of microplankton at channel stations. In the shoals, the calculated mean water column turnover is 80 to 90% d^{-1}. A Suisun Bay-wide (including both the channel and shoals) average depth of ~5 m gives a calculated maximum water column turnover of ~60% d^{-1}. However, these calculations do not take into account that benthic boundary layers may reduce the availability of prey to the benthos (Jones et al. 2009) and that clams do not filter water 100% of the time. As a result, the reported fractional loss rates likely overestimate clam clearance rates at individual stations.

The fractional loss rates of microzooplankton suggest that the impact of *Corbula amurensis* on plankton extends from phytoplankton to protistan microzooplankton, particularly ciliates. Population growth rates determined in the LSZ during 2006 to 2008 were –16 to 27% d^{-1} for tintinnid ciliates and –111 to 41% d^{-1} for *Myrionecta rubra* (J. York pers. comm.). If clam consumption in Suisun Bay is as high as 60% d^{-1} then a subsidy of ciliates is required from the more saline regions downstream via dispersion in order to maintain ciliate populations in this region. These estimates of fractional loss rates support previous studies attributing declines in pelagic production to grazing by *C. amurensis* (Alpine & Cloern 1992, Kimmerer et al. 1994, Jassby et al. 2002, Kimmerer 2006).

The ingestion of phytoplankton carbon was higher than the ingestion of microzooplankton carbon in most cases (Fig. 4), and no seasonal trends were observed in the relative proportions of phytoplankton carbon to microzooplankton carbon consumed. The mean ingestion of microzooplankton was 130 µg C ind^{-1} d^{-1} (Fig. 4). Using an average AFDW of 0.016 g per clam and assuming carbon is 41% of AFDW (Cloern et al. 1993), each clam in this study consumed <1.6% of its body carbon per day as microzooplankton. Mean ingestion of chl *a* as carbon was equivalent to ~300 µg C ind^{-1} d^{-1} (Fig. 4), approximately 4.5% of each clams' body carbon per day as chl *a*.

Oxygen consumption, when represented in units of carbon, can be used to calculate the carbon requirement for metabolism (Ikeda et al. 2000). Paganini et al. (2010) reported respiration rates of 34 µmol O_2 g dry wt^{-1} h^{-1} for *Corbula amurensis*. Using a respiratory quotient of 0.61 for *Corbula gibba* (Holmes & Miller 2006) and this study's proxy for estimating dry weight of *C. amurensis* (0.016 g AFDW ind^{-1}) we estimate base metabolic carbon demand per individual clam as 95 µg C ind^{-1} d^{-1}. Thus, *C. amurensis* could meet its base metabolic carbon demand by ingesting microzooplankton alone.

Previous studies of bivalve grazing have focused primarily on phytoplankton and mesozooplankton consumption (Riisgard 1988, Hebert et al. 1991, Cahoon & Owen 1996, Lehane & Davenport 2002). The observed consumption of microzooplankton by *Corbula amurensis* suggests that these studies may underestimate the impact of bivalves on aquatic food webs. Additionally, the ability of *C. amurensis* to utilize microzooplankton as a carbon source may contribute to its success in the SFE.

In the future, studies assessing the impacts of benthic grazing on the overlying water column should include all planktonic functional groups including bac-

teria, phytoplankton, and protistan and metazoan microzooplankton. Apparent changes in the abundance and size distribution of tintinnid ciliates suggest that ciliate biomass has declined following the introduction of *Corbula amurensis*. This seems likely given the decline in primary productivity of this region (Alpine & Cloern 1992, Jassby et al. 2002) and the high clearance rate of clams on ciliates (this study).

Large-scale changes in food web dynamics can occur as a result of an invasion by a single species (Petersen et al. 2008). The introduction of the suspension feeding clam *Mya arenaria* and the zebra mussel *Dreissena polymorpha* serve as important examples of these kinds of ecosystem transformations (Petersen et al. 2008, Higgins & Vander Zanden 2010). Rapid filter feeding by benthic bivalves can have devastating 'top down' effects on cladoceran, copepod, and rotifer populations (Higgins & Vander Zanden 2010). Information on the contribution of bivalve grazing to mortality rates of all functional groups will help researchers understand the full role of bivalves in aquatic systems and will allow for better management of systems impacted by bivalve invasions.

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