Estuaries and Coasts (2014) 37:576–588
DOI 10.1007/s12237-013-9698-9

Trophic Links in the Plankton in the Low Salinity Zone of a Large Temperate Estuary: Top-down Effects of Introduced Copepods

Joanna K. York · George B. McManus · Wim J. Kimmerer · Anne M. Slaughter · Toni R. Ignoffo

Received: 31 May 2013 / Revised: 9 August 2013 / Accepted: 12 August 2013 / Published online: 20 September 2013

Abstract We investigated trophic relationships involving microzooplankton in the low salinity zone of the San Francisco Estuary (SFE) as part of a larger effort aimed at understanding the dynamics of the food web supporting the endangered delta smelt, *Hypomesus transpacificus*. We performed 14 cascade experiments in which we manipulated the biomass of a copepod (*Limnoithona tetraspina*, *Pseudodiaptomus forbesi*, or *Acartiella sinensis*) and quantified responses of lower trophic levels including bacterioplankton, phytoplankton, and microzooplankton. Microzooplankton comprised a major food source for copepods; 9 out of 14 experiments showed removal of at least one group of microzooplankton by copepods. In contrast, the impact of copepods on phytoplankton was indirect; increased copepod biomass led to greater growth of phytoplankton in 3 of 14 experiments. Estimated clearance rates on microzooplankton were 4 mL day^{-1} for *L. tetraspina* and 2–6 mL day^{-1} for *P. forbesi*, whereas *A. sinensis* consumed mainly copepod nauplii. Complex trophic interactions, including omnivory, among copepods, microzooplankton, and different components of the phytoplankton likely obscured clear trends. The food web of the SFE is probably less efficient than previously thought, providing poor support to higher trophic levels; this inefficient food web is almost certainly implicated in the continuing low abundance of fishes, including the delta smelt that use the low salinity zone of the San Francisco Estuary.

Keywords Food webs · Trophic cascades · Copepod feeding · Microzooplankton

Communicated by Darcy Lonsdale

J. K. York (✉)
School of Marine Science and Policy, University of Delaware, Newark, DE 19716, USA
e-mail: jyork@udel.edu

G. B. McManus
Department of Marine Sciences, University of Connecticut, Groton, CT 06340, USA

W. J. Kimmerer · A. M. Slaughter · T. R. Ignoffo
Romberg Tiburon Center for Environmental Studies, San Francisco State University, Tiburon, CA 94920, USA

Introduction

Estuarine food webs vary widely in structure and productivity, depending on size, depth, drainage area, climate, and diverse human influences (Nixon et al. 1986). Many estuaries have higher primary productivity than adjacent coastal waters, but production is often modulated by anthropogenic nutrient inputs, manipulations of freshwater flows, high sediment loading, and high grazing rates by benthic organisms (Boynton et al. 1996; Cloern 2001). In addition to autochthonous production, metabolism and secondary production in estuaries may depend heavily on organic matter inputs from rivers and marshes (Kraus et al. 2008; Mann 1988; Sobczak et al. 2002, 2005). Estuaries containing significant port cities can suffer from food web alterations due to nonnative species introduced via ballast water from ships (Williams et al. 1988; Pierce et al. 1997).

The San Francisco estuary (SFE) (see Fig. 1 in Kimmerer et al. 2012) has been heavily modified for human use. Its ports constitute an important center of trans-Pacific commerce, freshwater flow in its watershed is extensively manipulated for agriculture and urban use, and a large human population lives within a short distance of its shores (Conomos 1979). In recent years, the SFE food web has undergone a number of significant changes, especially at the base of the food web. These include decreases in phytoplankton biomass and a shift in phytoplankton community composition. The invasion of the estuary beginning in 1986 by the overbite clam *Potamocorbula amurensis* (Carlton et al. 1990; Alpine and Cloern 1992)

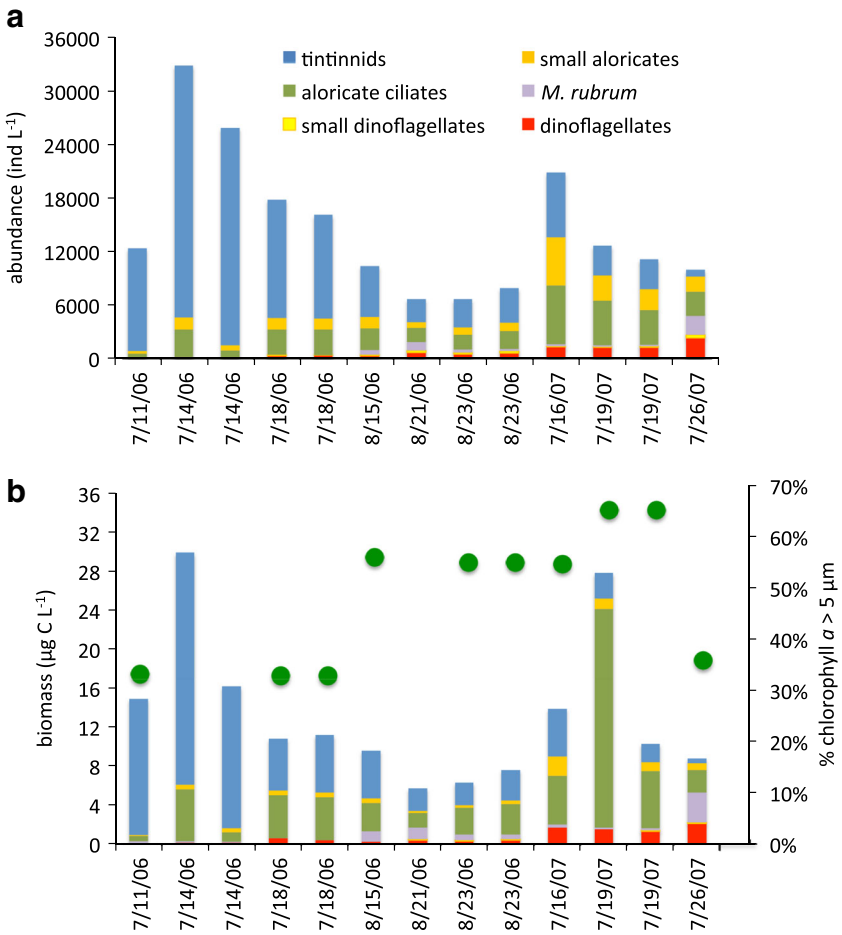

Fig. 1 Natural prey assemblages in the SFE during collections for cascade experiments including **a** microzooplankton abundance and **b** microzooplankton biomass (*bars*; primary *y*-axis) and percent of chlorophyll *a* in the >5 µm fraction (*symbols*; secondary *y*-axis). Chlorophyll *a* data from Kimmerer et al. 2012

caused a ~5-fold decline in phytoplankton biomass in the estuary's low salinity zone (LSZ), along with a shift from a diatom-dominated assemblage to one consisting of chlorophytes, small flagellates, and cyanobacteria (Alpine and Cloern 1992; Lehman 1996) and a nearly complete loss of diatom production (Kimmerer 2005). Increasing levels of ammonium have also been implicated in the decline of diatoms and in particular in the low frequency of spring diatom blooms that have occurred in some years since 1987 (Wilkerson et al. 2006; Dugdale et al. 2007; Parker et al. 2012a).

Higher trophic levels have responded to these changes. Copepods declined sharply and several newly introduced species appeared in the years after the invasion by *Potamocorbula* (Orsi and Walter 1990; Orsi and Ohtsuka 1999). Mysids declined precipitously (Orsi and Mecum 1996), as did several fish species (Kimmerer 2002). Anchovy biomass declined in the upper estuary, probably because the fish responded behaviorally to the decline in food. Because anchovies were the only abundant filter-feeding fish species in the LSZ, most of the planktivory by fish in the upper estuary is now done by visual planktivores (Kimmerer 2006).

In ~2002, several species of fish began to decline in the LSZ of the estuary, including the endangered delta smelt, *Hypomesus transpacificus* (Sommer et al. 2007; Thomson et al. 2010). Reasons for this decline are the subject of a substantial research effort, including the study reported here. Delta smelt reside in the LSZ during summer–fall, where they consume copepods, particularly the calanoid copepod *Pseudodiaptomus forbesi* (Lott 1998). Field studies, condition analyses, correlations with monitoring data, and modeling evidence all suggest that juvenile smelt have been strongly food-limited in recent years (Feyrer et al. 2003; Bennett 2005; Kimmerer 2008; Maunder and Deriso 2011; Rose et al. 2013). Declines and changes in composition at the base of the food web are at least a contributing factor to the decline in fish abundance (Sommer et al. 2007; Baxter et al. 2008).

Microzooplankton are a ubiquitous component of plankton communities and play a central role in estuarine food webs by facilitating the flows of material and energy from phytoplankton and bacterioplankton to copepods and other grazers that in turn provide food for larval and juvenile fish (McManus and Ederington-Cantrell 1992; Strom and Strom 1996; White and Roman 1992; Wiadnyana and Rassoulzadegan 1989; Wong et al. 2003). Although there are no long-term data on microzooplankton abundance with which to compare changes in other plankton in the SFE, there are some indications of

concomitant change. For example, a sharp decline in the abundance of rotifers in the low salinity zone of the estuary was observed at the same time as the introduction of *P. amurensis* (Kimmerer and Orsi 1996). In addition, ciliates larger than ~64 μm were much less abundant in 2008–2009 than had been reported in 1978–1981 for the low salinity zone (Ambler et al. 1985; Greene et al. 2011). Although Murrell and Hollibaugh (1998) observed low grazing rates by microzooplankton in the LSZ during 1993–1994, they were an important source of phytoplankton mortality in the same area during 2006–2008 (York et al. 2010).

The importance of microzooplankton as food for copepods in the SFE has been shown for both high salinity (Rollwagen-Bollens et al. 2006) and low salinity (Bouley and Kimmerer 2006; Gifford et al. 2007) regions. *P. amurensis* has also been shown to consume microzooplankton at a rate that may limit microzooplankton abundance, although it is not a major food source for the clams (Greene et al. 2011). The importance of this consumption in relation to that on phytoplankton and the energy sources for the microzooplankton in this region of low productivity are not well understood. We report here on trophic interactions involving microzooplankton in the low salinity zone of the SFE.

This study was part of a larger effort aimed at understanding the dynamics of the food web supporting the endangered delta smelt *H. transpacificus* (York et al. 2010; Gould and Kimmerer 2010; Greene et al. 2011; Kimmerer et al. 2012; Parker et al. 2012b). A key finding of that study was the persistently low phytoplankton biomass and productivity, of which only ~half was in cells larger than 5 μm and diatoms made up ~20 % (median of 111 samples) of the biomass (Kimmerer et al. 2012). Nutrient concentrations were always high, and productivity was persistently light limited (Kimmerer et al. 2012).

We focused on microzooplankton as food for three non-native species of copepods, all of which are significant components of the low-salinity zooplankton community of the SFE. *Limnoithona tetraspina* is a very small (c. 0.5 mm) cyclopoid copepod that was first observed in the estuary in 1993 (Orsi and Ohtsuka 1999). It consumes motile food including ciliates (Bouley and Kimmerer 2006). Its only known congener is *Limnoithona sinensis*, introduced to the estuary in 1979 (Ferrari and Orsi 1984). Although these species are difficult to distinguish as adults and impossible as earlier stages, *L. tetraspina* is about 40-fold more abundant than *L. sinensis* and concentrated in the LSZ, whereas *L. sinensis* is most abundant in freshwater (Ferrari and Orsi 1984). We therefore refer to these copepods as *L. tetraspina*, although a small fraction of individuals in our experiments may have been *L. sinensis*.

The calanoid copepod *P. forbesi* was introduced in the late 1980s (Orsi and Walter 1990). It is a generalist feeder, grazing on phytoplankton and probably microzooplankton (Bouley and Kimmerer 2006). *Acartiella sinensis* is another calanoid that appeared in the estuary at about the same time as *L. tetraspina* (Orsi and Ohtsuka 1999). Based on feeding appendage morphology, *Acartiella* species appear to be predators (Tranter and Abraham 1971), likely consuming other zooplankton and possibly large microzooplankton, although no experimental evidence of predatory feeding has previously been reported. Our model copepods thus represent putative omnivorous and carnivorous feeders, including an intraguild predator (*A. sinensis*).

We performed 14 cascade experiments (Lehman and Sandgren 1985; Calbet and Landry 1999) in which we manipulated the biomass of a top predator (one copepod species per experiment) and quantified differential responses of lower trophic levels including bacterioplankton, phytoplankton (as chlorophyll *a*), and microzooplankton comprising primarily tintinnid ciliates, other ciliates, and dinoflagellates. Our objectives were to characterize the trophic interactions between copepods, microzooplankton, and lower trophic levels in the food web of the low salinity zone of the San Francisco Estuary, and to determine the extent to which these groups are linked through manipulative cascade experiments.

Methods

Field Sampling

We conducted cascade experiments (Lehman and Sandgren 1985; Calbet and Landry 1999) to measure differences in the net growth rates of bacteria, phytoplankton, and microzooplankton while varying grazing pressure from copepods. Water samples for cascade experiments were collected from R/V Questuary in July and August 2006 and July 2007. Sampling locations varied with the location of the LSZ. We took all samples for cascade experiments at a surface salinity of 2, which was almost always found in Suisun Bay (Fig. 1 in Kimmerer et al. 2012). Suisun Bay is shallow, with about 30 % of its area 2 m or less in depth, with a narrow navigation channel (ca. 15 m). In situ temperatures ranged from 19.8 to 23.4 °C at the time of collection.

Mesozooplankton were collected by gentle horizontal net tows just below the surface using 53 and 150-μm mesh, 0.5-m diameter plankton nets. Plankton were diluted into 20-L insulated buckets containing surface water from the sampling site. Surface water for experiments was collected by submerging an inverted 20-L carboy vented by opening the spigot. Samples were typically collected before 1000 h and were transported in the dark to the laboratory at the Romberg Tiburon Center in Tiburon, CA, where experiments were set up by 1500 h. Additional samples were taken by vertical tows from near the bottom to the surface with the same net, equipped with a General Oceanics flowmeter. Microscopic

counts of copepods in subsamples were converted to abundance and then to biomass based on estimates of carbon per individual (Kimmerer, unpublished).

Cascade Experiments

Cascade experiments were performed using the dominant copepod species present. Adult females of *L. tetraspina* (four experiments), *P. forbesi* (four experiments), and *A. sinensis* (seven experiments) were used for these experiments.

L. tetraspina individuals were isolated by sequential size fractionation using 125 and 150-μm mesh sieves, which resulted in samples of mostly adult females. Three replicate samples of 200 mL from the 125–150-μm fraction were counted on a dissecting microscope to determine the copepod density of the size fractioned assemblage. Aliquots were taken to provide approximately 125, 250, and 500 *L. tetraspina* per incubation bottle. Aliquots were rinsed with 20-μm filtered sample water and added to 1 L polycarbonate bottles filled with sample water that had been reverse-filtered by siphoning through a submerged 100-μm sieve. The larger calanoid copepods were isolated under a dissecting microscope, then transferred individually by pipette into 1 L bottles filled with 200-μm reverse-filtered water to achieve densities of 8, 16, 24, 32, and 48 adult female copepods per bottle. The biomass of copepods in the high-density treatments averaged 10 times (minimum 3 times) the mean for June-August, based on field sampling for *L. tetraspina*, and over 20 times (minimum 14) the mean for the calanoid copepods. Bottles were sealed with Parafilm to eliminate destructive turbulence caused by bubbles and incubated on a plankton wheel rotating at 1 rpm for 24 h in an environmental chamber on a 12:12 light/dark cycle at 18 °C. Ambient light in the chamber during the light phase was approximately 17 μmol m^{-2} s^{-1}, which provided sufficient light to saturate phytoplankton primary productivity (Kimmerer et al. 2012). Incubation conditions were standardized across incubations and kept within the range observed in the field.

Analyses

Samples were collected at initial and final (24 h) time points to determine changes in chlorophyll *a* concentration and abundance and biomass of bacteria, microzooplankton, and copepods. At the conclusion of each experiment, 800 mL from the 1 L bottle was reverse-filtered (100-μm mesh for *Limnoithona*, 200-μm for calanoids) to separate copepods from microplankton. The filtered water was further processed for collection of potential prey (bacteria, phytoplankton, microzooplankton). The remaining 200 mL of water (predators) were concentrated onto a 53-μm mesh sieve and transferred to a 20-mL scintillation vial. Living copepods were verified with the vital stain Neutral Red, then fixed, and preserved with 5 % glutaraldehyde.

Twenty milliliter water samples were fixed with 1 % paraformaldehyde (final concentration) for bacteria counts. A 2-mL subsample was stained with DAPI and filtered onto a 0.2-μm pore-size black polycarbonate filter. The filter was mounted on a slide and stored frozen. Bacteria were counted from images taken with an Olympus Magnafire CCD camera mounted on an Olympus epifluorescence microscope, at ×1,250, using the proprietary Java-based image analysis program Skipper (P. Verity, personal communication).

One hundred milliliter water samples were filtered across 25-mm-diameter Whatman GF/F filters (0.7 μm nominal pore size) for chlorophyll *a*. Filters were immediately frozen and, later, pigments were extracted in 90 % acetone and analyzed on a Turner 10 fluorometer (Parsons et al. 1984). We also report size-fractionated chlorophyll *a* values from Kimmerer et al. (2012). These were filtered onto either 25-mm-diameter Whatman GF/F or 5.0 μm pore size polycarbonate filters and analyzed by fluorometry, as above.

Samples (500 mL) were preserved in 5 % acid Lugol's solution for counts of microzooplankton. Subsamples (50 mL) were settled down to 5 mL, transferred to tissue culture well plates, resettled, and counted on an inverted microscope. The total volume examined ranged from 7.5 to 50 mL; a minimum of 200 cells per sample was counted, corresponding to a coefficient of variation for the whole sample of 7 %. The smallest (15–20 μm) ciliates and dinoflagellates were counted and reported as small aloricate ciliates or small dinoflagellates (see "Results"). All other cells measured 20–200 μm. Nanoflagellates were not counted. Our microzooplankton counts, which focused on ciliates and copepod nauplii, thus provided a minimum estimate of microzooplankton abundance.

Two-dimensional shapes and linear dimensions were recorded for biovolume calculations, except for copepod nauplii, for which length–weight regressions from the literature were used to calculate biomass (Uye 1991; Mauchline 1998). A factor of 0.19 pg C μm^{-3} was used to convert non-tintinnid ciliate biovolume to carbon mass (Putt and Stoecker 1989). We measured tintinnid lorica volume and used a conversion factor of 0.072 pg C μm^{-3} to estimate its carbon mass. This is equal to the conversion factor 0.053 pg C μm^{-3} for tintinnids measured for formaldehyde-preserved samples (Verity and Langdon 1984), increased by 35 % to account for the greater shrinkage with Lugol's preservation (Putt and Stoecker 1989). We compared our biomass calculations with the regression approach in Menden-Deuer and Lessard (2000). Our approach to calculating tintinnid biomass provides a more conservative estimate than Menden-Deuer and Lessard (2000) because of assumptions regarding cell volumes and cell shrinkage due to Lugol's preservation. While the Menden-Deuer and Lessard (2000) method resulted in lower biomass estimates for aloricate (non-tintinnid) ciliates (30–40 % lower) and higher estimates for

loricate (tintinnid) ciliates (50–140 % higher), estimates of total ciliate biomass were largely equivalent between the two methods because assemblages were a mixture of these cell types. Dinoflagellates were a minor component of the microzooplankton community at all times, so they had a small effect on the biomass estimates, and values using the two methods were comparable. We used a factor of 0.14 pg C μm^{-3} to convert dinoflagellate biovolume to carbon mass (Lessard 1991). It is not possible with Lugol's preservation to discriminate between heterotrophs and autotrophs so dinoflagellate data are reported separately from the microzooplankton.

L. tetraspina was abundant during the cascade experiments performed with *A. sinensis*. Because all life stages of *L. tetraspina* are capable of passing through a 200-μm mesh sieve, those experiments contained both copepod species. Analysis of the 2006 experiments suggested that *A. sinensis* may have consumed *L. tetraspina*. We therefore quantified nauplii and copepodites of *L. tetraspina* separately in four experiments (2007 only) to get a first estimate of consumption by *A. sinensis*. *Limnoithona* copepods were identified to gross life stage (nauplii or copepodite) and counted.

Copepod biomass for all experiments were determined for individual species. All copepods were isolated from each preserved sample, rinsed with Milli-Q water, identified by life stage and counted, and transferred under a dissecting microscope to pre-weighed 8×5 mm tin capsules. Copepods were dried at 50 °C for at least 48 h, re-weighed using a Sartorius SE2 Ultra Microbalance, and analyzed for carbon and nitrogen content on a Costech Model 4010 Elemental Combustion System calibrated with Cystine OAS (Elementar Americas B2105).

Data Analysis

Data for each experimental replicate comprised numbers and biomass of copepods, and the expected response variables bacterial counts, chlorophyll *a* concentration, and counts and biomass of several microzooplankton taxa. Copepod species and microzooplankton taxa were included in calculations for a given experiment if at least 70 % of all samples in the experiment contained the taxon. For four experiments with *A. sinensis* in 2007, the microzooplankton prey included *L. tetraspina* nauplii and copepodites. We calculated a net population growth rate for each response variable; this growth rate was assumed to be constant for the 24-h incubation:

$$Y = Y_0 e^{-gt} \quad (1)$$

where Y is the value of the response variable (cells per liter or microgram chlorophyll per liter), Y_0 is the mean of the values in the initial samples, g is the specific growth rate (per day), and t is the duration of the experiment. Deviations of Y from constant growth during incubation do not matter if the deviation is similar for different copepod biomasses and the copepods are responsible for most of the consumption. However, constant growth does not apply where a trophic cascade causes one of the response variables to increase or decrease because its consumer is changing in abundance over time.

The model to be fitted to the data was

$$g = g_0 - g_1 M \quad (2)$$

where g is the specific growth rate in a sample calculated using Eq. (1), g_0 is the intercept, i.e., the growth rate with no copepods, g_1 is the negative slope, i.e., the change in growth rate per unit copepod biomass, and M is the biomass of the copepods per unit volume in the experimental containers. Inspection of the data for each experiment revealed no departure from the linearity of g with M in Eq. (2). With M expressed as milligram C per liter, the parameter g_1 has units of liter per milligram C per day and is a clearance rate per unit of copepod biomass. Clearance rate was calculated for both suspension feeding (*P. forbesi*) and raptorially feeding (*L. tetraspina* and *A. sinensis*) copepods, and can be interpreted as the ratio of grazing rate per unit copepod biomass to the ambient food concentration, which therefore has units of volume per biomass per time.

For *A. sinensis* feeding on *L. tetraspina*, we modeled clearance rate for each prey stage as

$$N = (N_0 f) e^{-CAt/V} \quad (3)$$

where N is the number of prey copepods remaining after incubation, N_0 is the initial number, f is the fraction of the experimental volume sampled for copepods, V is the container volume (=1 L), C is clearance rate (liter per day), A is the number of *A. sinensis* in each container, and t is the duration of the experiment (1 day). The initial number N_0 was unknown and treated as a free parameter in an analysis as discussed below.

Equation (2) was fitted by ordinary least squares for the bacterial and phytoplankton biomass data. Some of the microzooplankton counts were rather low, such that the normal approximation to a Poisson error distribution resulted in lower error bounds <0 for mean number of cells per liter. We therefore fitted Eq. (2) for various microzooplankton taxa using a Bayesian hierarchical model. This was the most straightforward way to obtain likelihood-based estimates of the clearance rates, and it also provides correct confidence intervals for the estimates. The response variable in this case was number per liter, and the model was fit to raw count data with a Poisson error distribution. Equation (3) was fitted similarly using the raw count data and combining control and experimental treatments to calculate C for each experiment. The analysis was run in WinBUGS 1.4.3 (Lunn et al. 2000; Gelman et al. 2004). Models were tested first with

simulated data, then fitted and tested using the procedures of Kimmerer and Gould (2010). Briefly, for each experiment, a WinBUGS simulation of three independent Markov chains was run with 10-fold thinning to reduce autocorrelation. After an initial 1,000 steps had been run to eliminate the effect of random initial conditions, the next 10,000 steps were used for parameter estimation. Results were checked by examining autocorrelation (generally none remaining), ensuring Monte Carlo errors were small compared to standard errors of parameters, checking Gelman–Rubin statistics (Gelman et al. 2004), and comparing parameter estimates from the first half and the second half of each Markov chain. This procedure gave estimates of the parameters g_0 and g_1 with confidence intervals for each microzooplankton taxon.

Results

Abundance and biomass of planktonic organisms in the low salinity zone of the San Francisco estuary varied during our experiments, resulting in variable initial conditions for each experiment. Chlorophyll *a* was higher in 2006 than in 2007 (Kimmerer et al. 2012). Dominant size classes shifted through time, with cells >5 μm making up a significant fraction of total phytoplankton biomass during most of our experiments (Fig. 1b). Of the microzooplankton, loricate ciliate abundance was extremely high in 2006, dominated by one tintinnid (*Tintinnopsis* sp.), which reached a maximum abundance of 28,000 cells L^{-1} (Fig. 1b). We also observed variations in copepod abundance and biomass over time. In July 2006, *L. tetraspina* was the numerically dominant copepod species in the estuary with maximum abundance of 184,000 copepods per cubic meter (all stages; Fig. 2a, secondary *y*-axis), of the three that were manipulated in this study. The numerically less abundant (11,800 copepods per cubic meter), but larger, *P. forbesi* dominated the biomass at that time. *A. sinensis* was absent during our July 2006 experiments, but increased by August 2006, during which time *P. forbesi* declined considerably. Both *P. forbesi* and *L. tetraspina* were much less abundant in 2007 than in 2006, while *A. sinensis* showed the opposite pattern.

There was a negative relationship between copepod biomass and apparent growth of at least one taxonomic group of microzooplankton in all but one of our experiments with *P. forbesi* or *L. tetraspina* (Table 1), indicating consumption by copepods. However, we typically did not find evidence of either direct or cascading effects of copepods on phytoplankton or bacteria.

L. tetraspina

Cascade experiments with *L. tetraspina* showed significant clearance of tintinnids in three out of four experiments with a maximum clearance rate of 10 mL(μg C)$^{-1}$day^{-1} (Table 1; Fig. 3). There were mixed impacts on other components of the microzooplankton, with aloricate ciliates sometimes being consumed and other times showing increased population growth with greater copepod abundance. In one experiment (14 July 2006), phytoplankton increased in an apparent cascading effect due to release from grazing pressure by tintinnids that had been removed by copepods.

P. forbesi

All four experiments conducted with *P. forbesi* showed a direct effect of increased copepod biomass (grazing) on tintinnids with clearance rates of 3–16 mL(μg C)$^{-1}$day^{-1} (Table 1; Fig. 4). Three out of four experiments also showed a positive clearance rate on aloricate ciliates, while one experiment showed an indirect (stimulatory) impact on very small ciliates (less than 20 μm in diameter). Although the grazing impact on tintinnids was consistent for all four experiments, phytoplankton biomass did not show a cascading impact from the presumed release of grazing pressure by the microzooplankton.

A. sinensis

Some experiments with *A. sinensis* showed a significant direct impact on groups of microzooplankton, with clearance rates of 3–5 mL(μg C)$^{-1}$day^{-1} (Fig. 5), but trends were inconsistent among experiments and almost half of the estimated clearance rates were negative (Table 1; Fig. 5). To determine if the lack of consistency in these experiments may have been the result of additional links in the food web, we analyzed all 2007 experiments for changes in abundance of early life-stage *L. tetraspina*, a potential food item for *A. sinensis*. One or the other life stage of *L. tetraspina* was consumed in all four experiments (Table 1, Fig. 6), presumably by *A. sinensis* as predator, with clearance rates up to 23 mL day^{-1}, confirming our suspicion that the food web in these experiments had an additional copepod–copepod trophic link between *Acartiella* and microzooplankton.

Discussion

Comparison with Other Cascade Experiments

Microzooplankton comprised a major food source for copepods in the low salinity zones of the San Francisco estuary. However, cascading impacts on lower trophic levels, including phytoplankton and bacterioplankton, were not as apparent in our experimental data set. The extent to which phytoplankton was consumed directly by zooplankton is less clear than the impact on microzooplankton, possibly because of the low biomass of large phytoplankton in the SFE (Kimmerer et al.

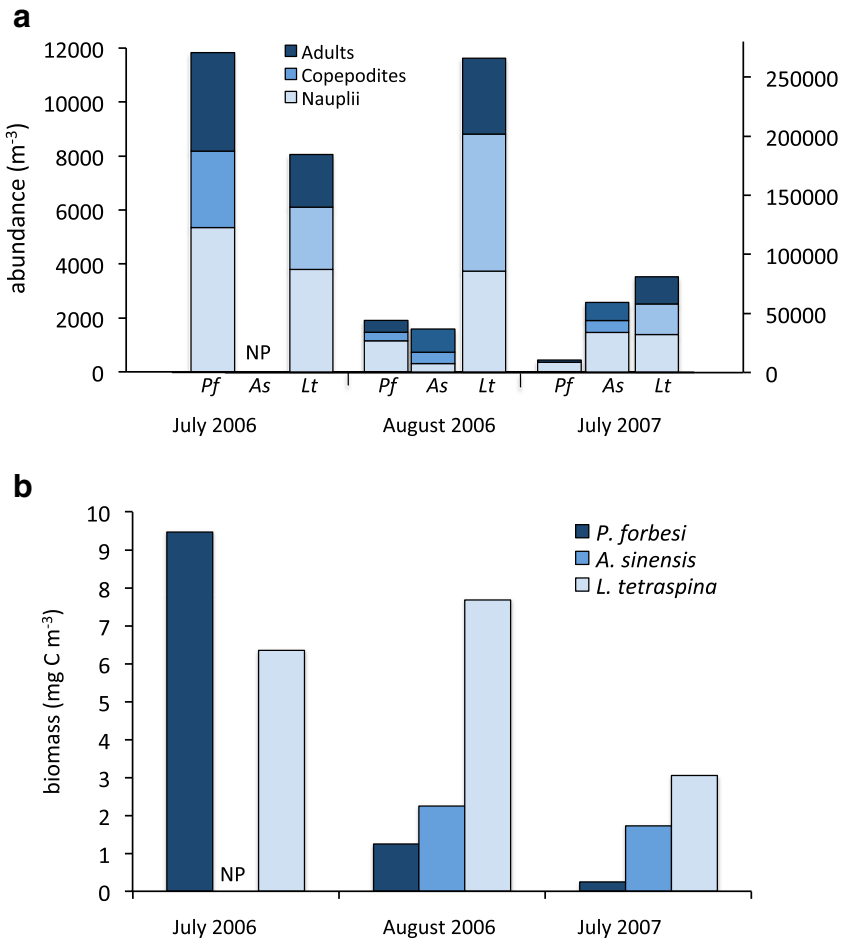

Fig. 2 **a** Abundance of *L. tetraspina* (*Lt*), *P. forbesi* (*Pf*), and *A. sinensis* (*As*) during July and August 2006 and July 2007. Note that bars for *L. tetraspina* are plotted on the right-hand *y*-axis. *NP* = not present. **b** Biomass of adult copepods by species

2012). Previous work showed that microzooplankton were an important source of phytoplankton mortality (York et al. 2010). However, only three experiments in our study showed statistically significant *indirect* impacts of copepods on phytoplankton; increasing copepod biomass led to greater growth of phytoplankton presumably due to release of grazing pressure from microzooplankton. It seems that complex trophic interactions among copepods, microzooplankton, and different components of the phytoplankton obscured clear trends in impacts on phytoplankton.

Cascading trophic pathways have been examined on a variety of scales and in diverse systems. Among freshwater studies, whole-lake and microcosm experiments have shown predation by top consumers produces indirect impacts at lower trophic levels by altering the biomass of intermediate consumers (Carpenter et al. 1985; Cottingham et al. 1997). This has been shown for bacterioplankton, phytoplankton, and heterotrophic nanoplankton (Vaqué and Pace 1992; Pace et al. 1998). Demonstration of such effects in marine systems has been less consistent. For example, Calbet and Landry (1999) showed statistically significant impacts of mesozooplankton on bacteria, small phytoplankton, and heterotrophic nanoplankton in an oligotrophic system, but only at very high additions of mesozooplankton biomass. They concluded that the cascading effect of mesozooplankton on bacterioplankton was very small at natural abundances. In a coastal environment, Schnetzer and Caron (2005) found that grazing pressure by copepods on ciliates resulted in a stimulation of growth in heterotrophic nanoplankton, but did not observe a consistent cascading effect on bacterioplankton, which presumably suffered heavier predation as heterotrophic nanoplankton became more abundant. Sipura et al. (2003) found variable cascading effects of copepod manipulations on bacterioplankton in an estuarine system. They suggested that omnivory and other complex trophic interactions made simple cascades difficult to quantify, which may have also been the case in our work. In week-long mesocosm experiments, Zöllner et al. (2009) found increases in bacterivorous flagellates due to copepod grazing on their predators, but the resulting increased bacterivory was expressed more strongly as an increase in diversity and a decrease in the metabolic activity of bacteria than as an increase in bacterial abundance. However, at that duration, the assemblage would have been very different from that in the initial sample, so these results are not directly comparable to

Table 1 Summary table of results from cascade experiments

	Date	Ba	Ch	Di	SD	Me	Al	SA	Ti	Li
L. tetraspina	14 July 2006		+				+		−	
	18 July 2006			−					−	
	23 August 2006									
	19 July 2007				+		−	−	−	
P. forbesi	11 July 2006							+	−	
	14 July 2006						−	−	−	
	18 July 2006				−		−		−	
	16 July 2007			−	−		−	−	−	
A. sinensis	15 August 2006							−	+	ND
	21 August 2006		+			+				ND
	23 August 2006			+						ND
	16 July 2007			−			+			−
	19 July 2007						−		−	−
	23 July 2007			ND	ND	ND	ND	ND	ND	−
	26 July 2007		+					+		−

(−) indicates direct relationship between copepod biomass and that potential food item. (+) indicates indirect relationship between copepod biomass and that potential food item. Only results with 95 % confidence limits that excluded zero are included here

Ba bacteria, *Ch* chlorophyll *a*, *Di* dinoflagellates, *SD* small dinoflagellates, *Me Mesodinium rubrum*, *Al* aloricate ciliates, *SA* small aloricate ciliates, *Ti* tintinnids, *Li* *L. tetraspina* nauplii, *ND* no data

those in short-term experiments such as ours. Given the complexity of the estuarine food web in the SFE, it is not surprising that we did not see unequivocal cacades in grazing pressure, or release of grazing pressure, to the level of bacterioplankton.

Some authors have suggested that variability in the structure of marine planktonic food webs can cause contrasting outcomes in trophic cascade experiments. Stibor et al. (2004) found that the cascading effects exerted by gelatinous zooplankton on phytoplankton were positive when large phytoplankton were dominant because the gelatinous zooplankton ate their grazers, but negative when small phytoplankton were dominant because an intermediate trophic step, ciliates, was the main source of mortality to small phytoplankton. In a study that focused on changes in field populations, Reaugh et al. (2007) found strong indications of cascading effects of copepods on phytoplankton. Their work showed that phytoplankton increased with copepod abundance due to the resulting drop in microzooplankton grazing during a wet year, when gelatinous predators of copepods were scarce, but not in a dry year, when gelatinous zooplankton were abundant (Reaugh et al. 2007). We conducted our study during two hydrologically very different years (Gould and Kimmerer 2010): 2006 was very wet while 2007 was dry. Although gelatinous zooplankton were not a factor at the low salinities of our experiments, this climatologic variation may have affected the structure of the planktonic community in other important ways, as for example, in the difference in dominant phytoplankton size class (Fig. 1b) or dominant copepod species (Fig. 2).

A number of studies have suggested that omnivory by copepods or switching between food types over time also complicates the interpretation of cascade experiments. Many small coastal and estuarine copepods are omnivores (Conley and Turner 1985; Dam et al. 1994; Atkinson 1995; Zeldis et al. 2002; Dam and Lopes 2003; Rollwagen-Bollens and Penry 2003) including two of the species examined here (Bouley and Kimmerer 2006). Omnivory can lead to simultaneous positive and negative effects of copepods on different components of the phytoplankton assemblage (Leising et al. 2005; Olson et al. 2006) and may explain the lack of clear response of phytoplankton to changes in copepod biomass in our experiments. In this situation, chlorophyll is not a useful surrogate for phytoplankton because it integrates across a diverse assemblage. Omnivory may also obscure impacts on other trophic levels. For example, Froneman (2006) found cascading effects of copepods on bacteria when phytoplankton were dominated by small forms and copepods were eating heterotrophic nanoflagellates and other bacterivores. This effect was not seen when copepods were feeding as herbivores. A similar observation by Goleski et al. (2010) indicated that copepod-induced cascades disappeared during diatom blooms, but occurred during non-bloom conditions, when heterotrophs became a larger component of the copepods' diet. Our results occurred during non-bloom conditions, and diatoms made up only a moderate proportion of the rather low phytoplankton biomass (Kimmerer et al. 2012).

Clearance Rates and Selective Feeding

Clearance rates have been previously reported for adult female *L. tetraspina* at a maximum of ~2–4 mL day^{-1} (Bouley and Kimmerer 2006) and at ~5–10 mL day^{-1} (Gifford et al. 2007). In our study, clearance rates by *L. tetraspina* were around 10 mL(μg C)$^{-1}$ day^{-1} on 18 July 2006 and lower on the other dates (Fig. 3). At an adult female body weight of 0.15 μg C, this would translate to about 2 mL day^{-1}. Maximum clearance

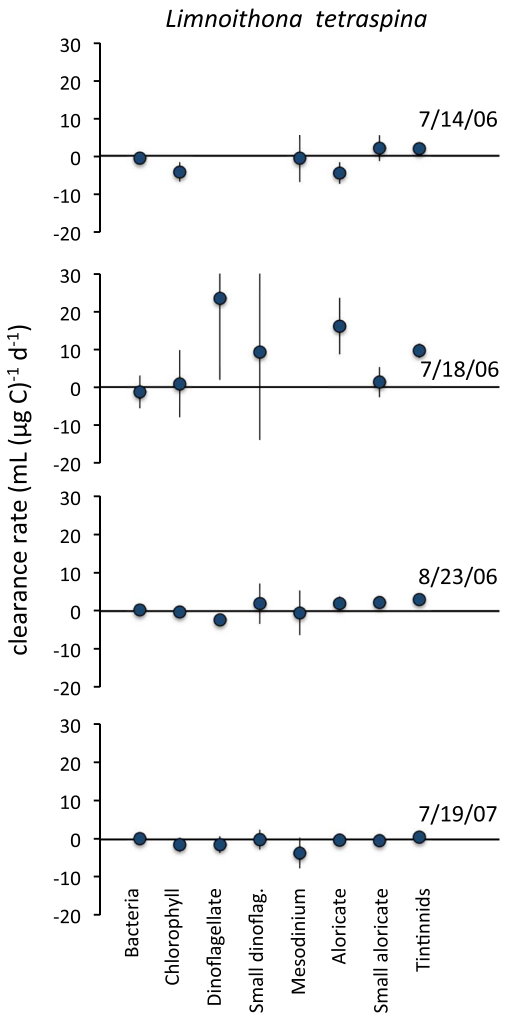

Fig. 3 Results from cascade experiments with *L. tetraspina*. *Error bars* are 95 % confidence intervals, where invisible they fall within the symbols. Some *error bars* are cutoff in one direction to maximize scaling. *Gaps* indicate taxa that were insufficiently abundant in a particular experiment

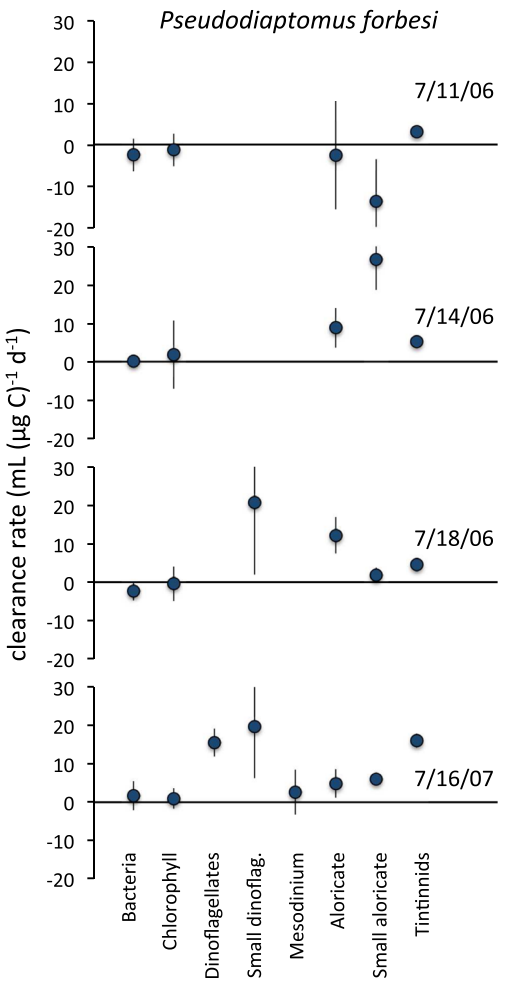

Fig. 4 Results from cascade experiments, as in Fig. 3, for *P. forbesi*

rates of planktonic organisms generally scale directly with body volume (Kiørboe 2011), with a mean scaling of ~2× 10^6 day^{-1} at 15 °C. With an adult female body carbon mass of ~0.15 µg C, a carbon density of the copepod of about 0.1 g C mL^{-1} (Hansen et al. 1997), and an ambient temperature of 19 °C, the clearance rate would be about 4 mL day^{-1}. This estimate based on a broad analysis of literature values is reasonably close to the experimental values from our study and others on this species in the SFE.

A previous study showed saturated feeding and declining clearance rate above ~2 cells mL^{-1} for *L. tetraspina* (Fig. 6 in Bouley and Kimmerer 2006). In our analyses, the data were rather noisy and there was no evidence of a declining clearance rate with increasing cell density as high as 50 cells mL^{-1} for tintinnids.

The only previous estimate of clearance rate for *P. forbesi* gave a value of 28–50 mL day^{-1} (Bouley and Kimmerer 2006). The body carbon of an adult female *P. forbesi* is around 3 µg C (Bouley and Kimmerer 2006; Kimmerer, unpublished), so this estimate of clearance rate was consistent with Kiørboe's (2011) scaling by body mass. However, our estimates of clearance rate on the more abundant cells were around 5–20 mL(µg C)$^{-1}$ day^{-1} (Fig. 4) which converts to about 2–6 mL day^{-1}. The low clearance rate for *P. forbesi* and to some extent *L. tetraspina* appears inconsistent with the finding of apparent food-limited growth and reproduction in these species (Gould and Kimmerer 2010; W. Kimmerer, unpublished). This result may be due to escape responses of ciliates to feeding currents of *P. forbesi* or attacks by *L. tetraspina* (Jakobsen 2001).

Clearance rate in copepods is generally highest at limiting food concentrations (Kiørboe 2011). Clearance rates of *P. forbesi* were at a maximum for less abundant cells, but with considerable variability possibly reflecting selective feeding. For example, in the experiment on 16 July 2007, clearance rates ranged from 3 to 20 mL(µg C)$^{-1}$ day^{-1} for the four prey taxa that were less abundant than 3 cells mL^{-1}. Clearance rate was below ~6 mL(µg C)$^{-1}$ day^{-1} when abundance exceeded 20 cells mL^{-1}, but those were tintinnids in every case so low

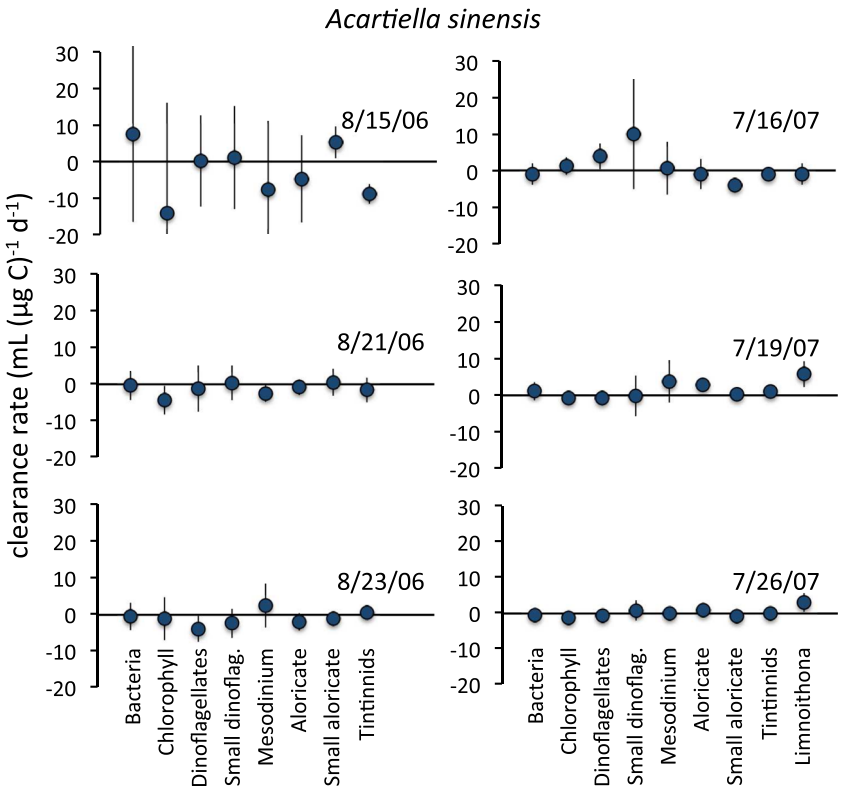

Fig. 5 Results from cascade experiments, as in Fig. 3, for *A. sinensis*. *Limnoithona* here refers to nauplii of *L. tetraspina*

selectivity for tintinnids, or strong escape responses, cannot be ruled out. *P. forbesi* either did not feed on phytoplankton, or fed at such a low rate that feeding was undetectable. Even at the upper confidence limit of the estimates (Fig. 4), the grazing rate by *P. forbesi* on phytoplankton was well below the grazing rate on microzooplankton. About half of the phytoplankton biomass was larger than 5 µm (Kimmerer et al. 2012, Fig. 2), which is an approximate cutoff for efficient feeding by small copepods (e.g., Bartram 1981). Therefore, some small amount of consumption of phytoplankton could have gone undetected. *P. forbesi* is capable of consuming phytoplankton and has been reared on an exclusive diet of phytoplankton (Ger et al. 2010); however, phytoplankton biomass in the LSZ is rather low. It is therefore likely that *P. forbesi* was actively selecting larger microzooplankton, perhaps as a way to maximize foraging efficiency.

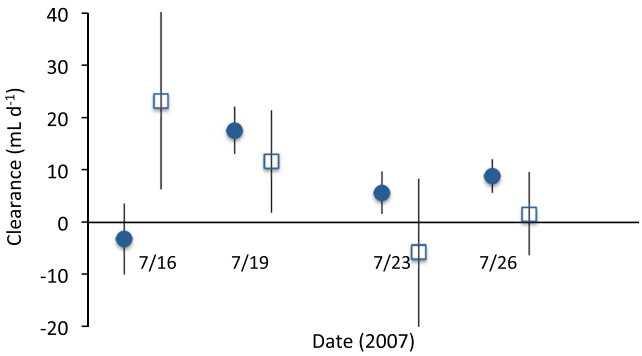

Fig. 6 Clearance rate of *A. sinensis* feeding on *L. tetraspina* nauplii (*filled circles*) and copepodites (*open squares*) with 95 % confidence limits. Data series are offset from actual date to avoid overlap of error bars

In contrast to the other two copepods, the experiments with *A. sinensis* revealed almost no evidence of feeding on protists (Fig. 5); rather, there were a few substantially negative estimates of clearance rate for the more abundant microzooplankton taxa. This suggests a positive cascading effect due to consumption of *L. tetraspina* copepodites and nauplii. Grazing by *L. tetraspina* nauplii has not been examined, but experiments with *Oithona davisae*, another cyclopoid of similar size and feeding mode as an adult, showed substantial overlap in feeding capabilities between adults and nauplii (Vogt et al. 2013). In the four experiments in which *L. tetraspina* individuals were counted, there was evidence for consumption of nauplii or copepodites or both by *A. sinensis* (Fig. 6, Table 1). Clearance rates in excess of 20 mL day^{-1} were observed, though this was quite variable, with three out of eight experiment/life stage combinations indicating no significant grazing. If *A. sinensis* is an important predator of *L. tetraspina*, then it would be expected to exert a cascading positive effect on the population growth of microzooplankton. On the other hand, some consumption of microzooplankton by *A. sinensis* cannot be ruled out by our results, since positive cascading effects were not observed in every experiment despite consistent consumption of at least one life stage of *L. tetraspina*.

In many estuaries, the low salinity zone is the site of intensive chemical and biological activity (Morris et al. 1978), although not necessarily a region of high phytoplankton production (David et al. 2006). The LSZ is also often a region where hydrodynamic conditions can cause physical retention of diatoms and other particles with high settling rates (Postma and Kalle 1955). This does not seem to be the case in the LSZ of the San Francisco Estuary because strong stratification and gravitational circulation, necessary to retain settling particles, are largely absent from the LSZ most of the time (Schoellhamer 1996). Primary production is low and about half is by particles smaller than 5 μm (Kimmerer et al. 2012), which settle slowly and are below the size threshold for feeding by the copepods found in this part of the estuary. Higher phytoplankton biomass in other regions, especially landward of the LSZ, provides a subsidy of organic matter including phytoplankton and zooplankton to the LSZ (Kimmerer 2004), and much of the food web energy reaches the metazoan food web through bacteria and small phytoplankton including cyanobacteria.

Implications for the Food Web

The principal implication of our results for this region of the estuary is that its food web is more reticulate and probably less efficient at transferring energy to higher trophic levels than previously thought. With copepods feeding mainly on ciliates or other copepods, and the ciliates getting at least some of their energy from bacteria, copepod consumers like the delta smelt are feeding at the 4th to 6th trophic level. Coupled with the low primary production of the LSZ (Kimmerer et al. 2012), this means that the food web of this region provides poor support to higher trophic levels. This is almost certainly implicated in the continuing low abundance of fishes that use this part of the estuary (Sommer et al. 2007; Thomson et al. 2010).

Acknowledgments We thank Don Schoener and Barbara Costas for help with the experiments, David Bell and David Morgan for vessel and logistic support, and our fellow CALFED Food Web investigators for ideas and discussion. Three anonymous reviewers provided helpful comments on this work. Funding was provided by the California Bay-Delta Authority (Award SCI05 C107 to W. Kimmerer).

References

Alpine, A.E., and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37: 946–955.

Ambler, J.W., J.E. Cloern, and A. Hutchinson. 1985. Seasonal cycles of zooplankton from San Francisco Bay. *Hydrobiologia* 129: 177–197.

Atkinson, A. 1995. Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. *ICES Journal of Marine Science: Journal du Conseil* 52: 385–396.

Bartram, W.C. 1981. Experimental development of a model for the feeding of neritic copepods on phytoplankton. *Journal of Plankton Research* 3: 25–52.

Baxter, R., R. Breuer, L. Brown, M. Chotkowski, F. Feyrer, M. Gingras, B. Herbold, A. Mueller-Solger, M. Nobriga, T. Sommer, and K. Souza. 2008. Pelagic organism decline progress report: 2007 Synthesis of results. Interagency Ecological Program for the San Francisco Estuary, Sacramento. Available at http://www.water.ca.gov/iep/docs/pod/synthesis_report_031408.pdf. Accessed 1 May 2012.

Bennett, W. A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3: Issue 2 Article 1.

Bouley, P., and W.J. Kimmerer. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. *Marine Ecology Progress Series* 324: 219–228.

Boynton, W.R., J.D. Hagy, L. Murray, C. Stokes, and W.M. Kemp. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries* 19: 408–421.

Calbet, A., and M.R. Landry. 1999. Mesozooplankton influences on the microbial food web: direct and indirect trophic interactions in the oligotrophic open ocean. *Limnology and Oceanography* 44: 1370–1380.

Carlton, J.T., J.K. Thompson, L.E. Schemel, and F.H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis.* I. Introduction and dispersal. *Marine Ecology Progress Series. Oldendorf* 66: 81–94.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake ecosystem productivity. *BioScience* 35: 634–639.

Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210: 223–253.

Conley, W.J., and J.T. Turner. 1985. Omnivory by the coastal marine copepods *Centropages hamatus* and *Labidocera aestiva*. *Marine Ecology Progress Series* 21: 113–120.

Conomos, T. J. 1979. San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

Cottingham, K.L., S.E. Knight, S.R. Carpenter, J.J. Cole, M.L. Pace, and A.E. Wagner. 1997. Response of phytoplankton and bacteria to nutrients and zooplankton: a mesocosm experiment. *Journal of Plankton Research* 19: 995–1010.

Dam, H.G., and R.M. Lopes. 2003. Omnivory in the calanoid copepod *Temora longicornis*: feeding, egg production and egg hatching rates. *Journal of Experimental Marine Biology and Ecology* 292: 119–137.

Dam, H.G., W.T. Peterson, and D.C. Bellantoni. 1994. Seasonal feeding and fecundity of the calanoid copepod *Acartia tonsa* in Long Island Sound: is omnivory important to egg production? *Hydrobiology* 292(293): 191–199.

David, V., B. Sautour, R. Galois, and P. Chardy. 2006. The paradox high zooplankton biomass-low vegetal particulate organic matter in high turbidity zones: what way for energy transfer? *Journal of Experimental Marine Biology and Ecology* 333: 202–218.

Dugdale, R.C., F.P. Wilkerson, V.E. Hogue, and A. Marchi. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuarine, Coastal and Shelf Science* 73: 17–29.

Ferrari, F.D., and J.J. Orsi. 1984. *Oithona davisae*, new species, and *Limnoithona sinensis* (Burkhardt, 1912) (Copepoda: Oithonidae) from the Sacramento-San Joaquin Estuary, California. *Journal of Crustacean Biology* 4: 106–126.

Feyrer, F., B. Herbold, S.A. Matern, and P.B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67: 277–288.

Froneman, P. 2006. The importance of phytoplankton size in mediating trophic interactions within the plankton of a southern African estuary. *Estuarine, Coastal and Shelf Science* 70: 693–700.

Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. *Bayesian data analysis*, 2nd ed. Boca Raton: CRC.

Ger, K.A., S.J. Teh, D.V. Baxa, S. Lesmeister, and C.R. Goldman. 2010. The effects of dietary *Microcystis aeruginoa* and microcystin on the copepods of the upper San Francisco Estuary. *Freshwater Biology* 55: 1548–1559.

Gifford, S.M., G.C. Rollwagen-Bollens, and S.M. Bollens. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. *Marine Ecology Progress Series* 348: 33–46.

Goleski, J.A., F. Koch, M.A. Marcoval, C.C. Wall, F.J. Jochem, B.J. Peterson, and C.J. Gobler. 2010. The role of zooplankton grazing and nutrient loading in the occurrence of harmful cyanobacterial blooms in Florida Bay, USA. *Estuaries and Coasts* 33: 1202–1215.

Gould, A.L., and W.J. Kimmerer. 2010. Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in the upper San Francisco Estuary. *Marine Ecology Progress Series* 412: 163–177.

Greene, V.E., L.J. Sullivan, J.K. Thomson, and W.J. Kimmerer. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. *Marine Ecology Progress Series* 431: 183–193.

Hansen, P.J., P.K. Bjornsen, and B.W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2–2000 μm body size range. *Limnology and Oceanography* 42: 687–704.

Jakobsen, H.H. 2001. Escape response of planktonic protists to fluid mechanical signals. *Marine Ecology Progress Series* 214: 67–78.

Kimmerer, W.J. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series* 243: 39–55.

Kimmerer, W. J. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science (Online Serial) 2: Issue 1, Article 1. http://repositories.cdlib.org/jmie/sfews/vol2/iss1/art1.

Kimmerer, W.J. 2005. Long-term changes in apparent uptake of silica in the San Francisco estuary. *Limnology and Oceanography* 50: 793–798.

Kimmerer, W.J. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. *Marine Ecology Progress Series* 324: 207–218.

Kimmerer, W. J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 6: Issue 2 Article 2.

Kimmerer, W.J., and A.L. Gould. 2010. A Bayesian approach to estimating copepod development times from stage frequency data. *Limnology and Oceanography: Methods* 8: 118–126.

Kimmerer, W.J., and J.J. Orsi. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In *San Francisco Bay: the ecosystem*, ed. J.T. Hollibaugh, 403–424. San Francisco: AAAS.

Kimmerer, W.J., A.E. Parker, U. Lidström, and E.J. Carpenter. 2012. Short-term and interannual variability in primary production in the low-salinity zone of the San Francisco Estuary. *Estuaries and Coasts*. doi:10.1007/s12237-012-9482-2.

Kiørboe, T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biological Reviews* 86: 311–339.

Kraus, T.E.C., B.A. Bergamaschi, P.J. Hernes, R.G.M. Spencer, R. Stepanauskas, C. Kendall, R.F. Losee, and R. Fujii. 2008. Assessing the contribution of wetlands and subsided islands to dissolved organic matter and disinfection byproduct precursors in the Sacramento-San Joaquin River Delta: a geochemical approach. *Organic Geochemistry* 39: 1302–1318.

Lehman, P.W. 1996. Changes in chlorophyll-a concentration and phytoplankton community composition with water-year type in the upper San Francisco Estuary. In *San Francisco Bay: the ecosystem*, ed. J.T. Hollibaugh, 351–374. San Francisco: AAAS.

Lehman, J.T., and C.D. Sandgren. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnology and Oceanography* 30: 34–46.

Leising, A.W., J.J. Pierson, C. Halsband-Lenk, R. Horner, and J. Postel. 2005. Copepod grazing during spring blooms: does *Calanus pacificus* avoid harmful diatoms? *Progress in Oceanography* 67: 384–405.

Lessard, E.J. 1991. The trophic role of heterotrophic dinoflagellates in diverse marine environments. *Marine Microbial Food Webs* 5: 49–58.

Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin River Estuary. *IEP Newsletter* 11(1): 14–19. Available at: http://www.water.ca.gov/iep/products/newsletterPrevious.cfm.

Lunn, D.J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10: 325–337.

Mann, K.H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography* 33: 910–930.

Mauchline, J. 1998. *The biology of calanoid copepods*. New York: Academic.

Maunder, M.N., and R.B. Deriso. 2011. A state-space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hypomesus transpacificus*). *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1285–1306.

McManus, G.B., and M.C. Ederington-Cantrell. 1992. Phytoplankton pigments and growth rates, and microzooplankton grazing in a large temperate estuary. *Marine Ecology Progress Series* 87: 77–85.

Menden-Deuer, S., and E.J. Lessard. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology & Oceanography* 45: 569–579.

Morris, A.W., R.F.C. Mantoura, A.J. Bale, and R.J.M. Howland. 1978. Very low salinity regions of estuaries: important sites for chemical and biological reactions. *Nature* 274: 678–680.

Murrell, M.C., and J.T. Hollibaugh. 1998. Microzooplankton grazing in northern San Francisco Bay measured by the dilution method. *Aquatic Microbial Ecology* 15: 53–63.

Nixon, S.W., C.A. Oviatt, J. Frithsen, and B. Sullivan. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. *Journal of the Limnological Society of Southern Africa* 12: 43–71.

Olson, M.B., E.J. Lessard, C.H.J. Wong, and M.J. Bernhardt. 2006. Copepod feeding selectivity on microplankton, including the toxigenic diatoms *Pseudo-nitzschia* spp., in the coastal Pacific Northwest. *Marine Ecology Progress Series* 326: 207–220.

Orsi, J.J., and W.L. Mecum. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary. In *San Francisco Bay: the ecosystem*, ed. J.T. Hollibaugh, 375–401. San Francisco: AAAS.

Orsi, J.J., and S. Ohtsuka. 1999. Introduction of the Asian copepods *Acartiella sinensis, Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. *Plankton Biology and Ecology* 46: 128–131.

Orsi, J. J., and T. C. Walter. 1990. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin estuary. Bulletin of the Plankton Society of Japan. Hiroshima. Bulletin of the Plankton Society of Japan Spec. Vol. 553–562.

Pace, M.L., J.J. Cole, and S.R. Carpenter. 1998. Trophic cascades and compensation: differential responses of microzooplankton in whole-lake experiments. *Ecology* 79: 138–152.

Parker, A.E., V.E. Hogue, F.P. Wilkerson, and R.C. Dugdale. 2012a. The effect of inorganic nitrogen speciation on primary production in the

San Francisco Estuary. *Estuarine, Coastal and Shelf Science* 104–105: 91–101.

Parker, A.E., W.J. Kimmerer, and U.E. Lidström. 2012b. Re-evaluating the generality of an empirical model for light-limited primary production in the San Francisco Estuary. *Estuaries and Coasts* 35: 930–942.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. *A manual of chemical and biological methods for seawater analysis*. New York: Pergamon.

Pierce, R. W., J. T. Carlton, D. A. Carlton, and J. B. Geller. 1997. Ballast water as a vector for tintinnid transport. *Marine Ecology-Progress Series* 149: 295–297.

Postma, V.H., and K. Kalle. 1955. On the development of turbid zones in the lower course of rivers with special consideration of conditions in the lower Elbe. *Deutsche Hydrographische Zeitschrift* 8: 137–144.

Putt, M., and D.K. Stoecker. 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34: 1097–1103.

Reaugh, M.L., M.R. Roman, and D.K. Stoecker. 2007. Changes in plankton community structure and function in response to variable freshwater flow in two tributaries of the Chesapeake Bay. *Estuaries and Coasts* 30: 403–417. doi:10.1007/BF02819387.

Rollwagen-Bollens, G., and D. Penry. 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). *Marine Ecology Progress Series* 257: 139–158.

Rollwagen-Bollens, G.C., S.M. Bollens, and D. Penry. 2006. Vertical distribution of micro- and nanoplankton in the San Francisco Estuary in relation to hydrography and predators. *Aquatic Microbial Ecology* 44: 143–163.

Rose, K. A., W. J. Kimmerer, K. P. Edwards, and W. A. Bennett. 2013. Individual-based modeling of delta smelt population dynamics in the upper San Francisco Estuary. II. Alternative baselines and good versus bad years. *Transactions of the American Fisheries Society* 142: 1260–1272.

Schnetzer, A., and D.A. Caron. 2005. Copepod grazing impact on the trophic structure of the microbial assemblage of the San Pedro Channel, California. *Journal of Plankton Research* 27: 959–971.

Schoellhamer, D.H. 1996. Factors affecting suspended-solids concentrations in south San Francisco Bay, California. *Journal of Geophysical Research* 101: 12087–12095.

Sipura, J., E. Lores, and R.A. Snyder. 2003. Effect of copepods on estuarine microbial plankton in short-term microcosms. *Aquatic Microbial Ecology* 33: 181–190.

Sobczak, W.V., J.E. Cloern, A.D. Jassby, and A.B. Muller-Solger. 2002. Bioavailability of organic matter in a highly disturbed estuary: the role of detrital and algal resources. *Proceedings of the National Academy of Sciences of the United States of America* 99: 8101–8105.

Sobczak, W.V., J.E. Cloern, A.D. Jassby, B.E. Cole, T.S. Schraga, and A. Arnsberg. 2005. Detritus fuels ecosystem metabolism but not metazoan foodwebs in San Francisco estuary's freshwater Delta. *Estuaries and Coasts* 28: 124–137.

Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32: 270–277.

Stibor, H., O. Vadstein, S. Diehl, A. Gelzleichter, T. Hansen, F. Hantzsche, A. Katechakis, B. Lippert, K. Loseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen, and Y. Olsen. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecology Letters* 7: 321–328.

Strom, S.L., and M.W. Strom. 1996. Microzooplankton growth, grazing, and community structure in the northern Gulf of Mexico. *Marine Ecology Progress Series* 130: 229–240.

Thomson, J.R., W.J. Kimmerer, L.R. Brown, K.B. Newman, R.M. Nally, W.A. Bennett, F. Feyrer, and E. Fleishman. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications* 20: 1431–1448.

Tranter, D.J., and S. Abraham. 1971. Coexistence of species of Acartiidae (Copepoda) in the Cochin Backwater, a monsoonal estuarine lagoon. *Marine Biology* 11: 222–241.

Uye, S. I. 1991. Temperature-dependent development and growth of the planktonic copepod *Paracalanus* sp. in the laboratory. Bulletin of Plankton Society, Japan. Special Volume: 627–636.

Vaqué, D., and M.L. Pace. 1992. Grazing on bacteria by flagellates and cladocerans in lakes of contrasting food-web structure. *Journal of Plankton Research* 14: 307–321.

Verity, P.G., and C. Langdon. 1984. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *Journal of Plankton Research* 6: 859–868.

Vogt, R., T. Ignoffo, L. Sullivan, J. Herndon, J. Stillman, and W. Kimmerer. 2013. Feeding capabilities and limitations in the nauplii of two pelagic estuarine copepods, *Pseudodiaptomus marinus* and *Oithona davisae*. Limnology and Oceanography (in press).

White, J.R., and M.R. Roman. 1992. Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Marine Ecology Progress Series* 86: 251–261.

Wiadnyana, N.N., and F. Rassoulzadegan. 1989. Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. *Marine Ecology Progress Series* 53: 37–45.

Wilkerson, F.P., R.C. Dugdale, V.E. Hogue, and A. Marchi. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. *Estuaries and Coasts* 29: 401–416.

Williams, R. J., F. B. Griffiths, E. J. Van der Wal, and J. Kelly. 1988. Cargo vessel ballast water as a vector for the transport of non-indigenous marine species. *Estuarine, Coastal and Shelf Science* 26: 409–420.

Wong, W.H., J.S. Levinton, B.S. Twining, and N. Fisher. 2003. Assimilation of micro- and mesozooplankton by zebra mussels: a demonstration of the foodweb link between zooplankton and benthic suspension feeders. *Limnology and Oceanography* 48: 308–312.

York, J.K., B.A. Costas, and G.B. McManus. 2010. Microzooplankton grazing in green water—results from two contrasting estuaries. *Estuaries and Coasts* 34: 373–385.

Zeldis, J., M. James, J. Grieve, and L. Richards. 2002. Omnivory by copepods in the New Zealand subtropical frontal zone. *Journal of Plankton Research* 24: 9–23.

Zöllner, E., H.G. Hoppe, U. Sommer, and K. Jürgens. 2009. Effect of zooplankton-mediated trophic cascades on marine microbial foodweb components (bacteria, nanoflagellates, ciliates). *Limnology and Oceanography* 54: 262–275.