Journal of
Plankton Research

plankt.oxfordjournals.org

J. Plankton Res. (2014) 36(3): 722–735. First published online January 7, 2014 doi:10.1093/plankt/fbt128

Food-limited reproduction and growth of three copepod species in the low-salinity zone of the San Francisco Estuary

WIM J. KIMMERER[1]*, TONI R. IGNOFFO[1], ANNE M. SLAUGHTER[1] AND ALISON L. GOULD[2]

[1]ROMBERG TIBURON CENTER, SAN FRANCISCO STATE UNIVERSITY, 3152 PARADISE DRIVE, TIBURON, CA 94920, USA AND [2]DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY, UNIVERSITY OF MICHIGAN, ANN ARBOR, MI 48109, USA

*CORRESPONDING AUTHOR: kimmerer@sfsu.edu

Received August 10, 2013; accepted November 26, 2013

Corresponding editor: Marja Koski

We determined reproductive and growth rates of three common copepods in the low-salinity zone of the San Francisco Estuary during spring–summer of 2006 and 2007. Rates were low, particularly during summer. The egg production rate of *Eurytemora affinis* in spring averaged ~3 eggs female^{-1} day^{-1} or 0.04 day^{-1}, while that of *Pseudodiaptomus forbesi* in summer averaged ~1 egg female^{-1} day^{-1} or 0.02 day^{-1}. Specific growth rates of copepodites were moderate for *E. affinis* in spring (0.23 and 0.15 day^{-1} for early and late stages, respectively) and low for *P. forbesi* in summer (0.15 and 0.03 day^{-1}, respectively). Growth and egg production rates of both species were generally lower than rates predicted from temperature for well-fed copepods, suggesting chronic food limitation. Previously published estimates for the small cyclopoid *Limnoithona tetraspina* were also low. None of the measures of growth of any species was related to phytoplankton biomass, primary production or abundance of the species, nor did they differ between the 2 years despite large differences in hydrology. To understand patterns of abundance will require investigation of differential mortality rates.

KEYWORDS: *Eurytemora affinis*; *Pseudodiaptomus forbesi*; *Limnoithona tetraspina*; food limitation; sac spawners

available online at www.plankt.oxfordjournals.org

INTRODUCTION

Endemic populations of plankton can be maintained in estuaries through some combination of high reproductive rate and short generation time (Ketchum, 1954). Highly productive estuaries offer opportunities for species capable of rapid population growth to offset losses to transport from the estuary, predation and other causes of mortality. Estuaries have generally been considered highly productive systems, with high primary production coupled to high fishery yield (Nixon, 1988). However, not all estuaries are productive: for example, median total chlorophyll concentrations were under 3 mg Chl m^{-3} in 50% of estuaries with long monitoring records (Cloern and Jassby, 2008).

What happens when productivity is low? Generally, primary productivity is positively related to growth and reproductive rates of zooplankton, but that link depends on foodweb efficiency, the food sources of the zooplankton and the dominant species of zooplankton (Nixon, 1988; Runge, 1988; Saiz and Calbet, 2011). If population growth rates of zooplankton in unproductive estuaries are generally low, these populations must have alternative ways of offsetting losses. Thus, a key question for understanding maintenance of plankton species in estuaries is the degree to which reproduction, growth and development are limited under ambient feeding conditions.

Primary production in the northern San Francisco Estuary falls at the lower end of the scale for estuaries (Alpine and Cloern, 1992; Jassby, 2008) and this estuary is therefore suitable for examining the response of zooplankton to variation in food supply. In this paper we determine the reproductive and growth rates of copepods common in the low-salinity zone (LSZ) of the San Francisco Estuary during spring–summer of 2006 and 2007.

Concerns over environmental degradation and conflicts over the diversion of freshwater from the basin have led to substantial monitoring efforts and recent investments in research on this estuarine ecosystem. In particular, declines in the abundance of several fish species, including the endangered, endemic delta smelt, *Hypomesus transpacificus*, in ~2002 (Sommer *et al.*, 2007), have led to increased efforts to understand the various factors affecting these species, including changes in the foodweb.

This study was part of a larger examination of the foodweb supporting the endangered delta smelt, which occurs in brackish water from late spring until winter and is probably food limited in spring–summer (Bennett, 2005). The study therefore focused on the LSZ, defined here to include a salinity range of 0.5 to ~5, from March to August. The LSZ is an unproductive region: estimates of primary production were only 25 and 31 gC m^{-2} $year^{-1}$ during 2006 and 2007, respectively and only half of the production was in cells >5 μm (Kimmerer *et al.*, 2012), roughly the size above which particles are available as food for zooplankton (Bartram, 1981). Calanoid copepods that provide much of the food for planktivorous fish (Nobriga, 2002; Bryant and Arnold, 2007) are less abundant than small cyclopoids, but their growth and development rates have not been measured.

We examined abundance, egg production rate and somatic growth rate of the calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi*, and combined these with previously published data on the small (0.45 mm total length) oithonid *Limnoithona tetraspina* (Gould and Kimmerer, 2010) for an overall examination of growth and reproduction of the three most common copepods of this region. *Limnoithona tetraspina* feeds, grows and reproduces slowly at levels indicating food limitation nearly all the time (Bouley and Kimmerer, 2006; Gould and Kimmerer, 2010). Our objective was to determine whether growth and reproductive rates of all common copepods in this region were low, linking low primary production to poor feeding conditions for delta smelt and other fishes.

METHOD

Study area and species

The San Francisco Estuary (SFE) is a large, turbid estuary with a lagoonal South Bay and a river-dominated northern reach (Fig. 1). The California Delta is a network of tidal channels, usually freshwater, formed by the confluence of the Sacramento and San Joaquin Rivers and some smaller rivers. Suisun and San Pablo Bays are both broad, shallow (5 m mean depth), turbid bays with deep, narrow channels. The climate is Mediterranean, and nearly all of the precipitation occurs during the wet season from ~ November to April. Interannual variability in freshwater discharge is very high: annual mean discharge from 1970 to 2010 varied ~25-fold. High freshwater flow has a strong positive effect on populations of some species of fish and macroinvertebrates (Jassby *et al.*, 1995), but effects on lower trophic levels are mixed (Jassby *et al.*, 2002; Kimmerer, 2002).

Many of the functional groups of organisms in the estuary are dominated by introduced species, including the zooplankton of the upper estuary (Orsi and Ohtsuka, 1999). *Eurytemora affinis* has been present since before sampling began, but the SFE population is closely related to populations from eastern North America (Lee, 2000)

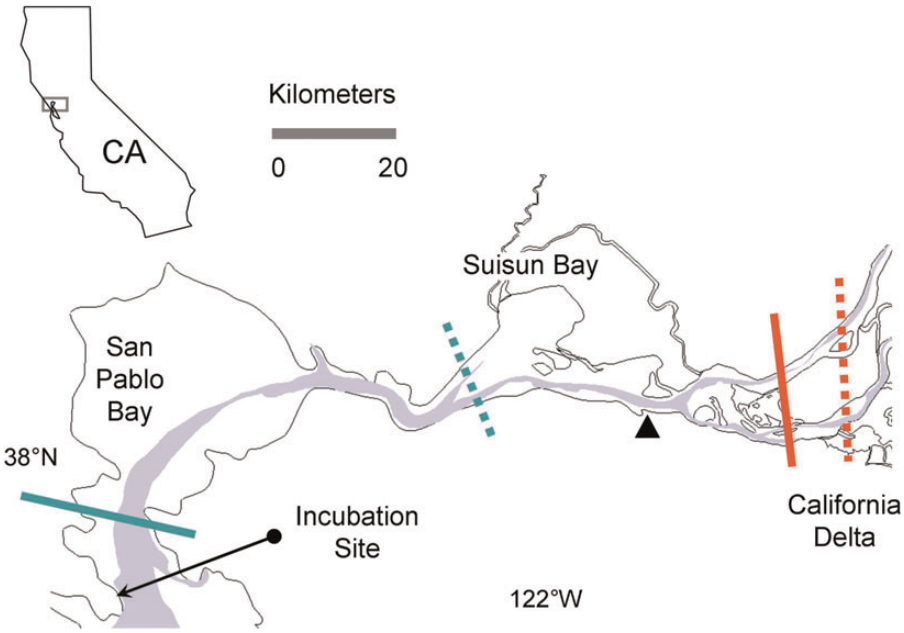

Fig. 1. Map of the northern San Francisco Estuary showing the 10-m isobath (gray). The range of sampling stations is indicated by a pair of solid lines for 2006 and dashed lines for 2007. The arrow shows the location of the incubation site at the Romberg Tiburon Center and the triangle indicates the continuous monitoring station (MAL) used for temperature.

suggesting this population was introduced. *Pseudodiaptomus forbesi* was introduced in ~1988 and became abundant in 1989 (Orsi and Walter, 1991). Since that time *E. affinis* has been abundant only during winter–spring, and has been replaced by *P. forbesi* during summer–autumn. *Limnoithona tetraspina* was introduced in 1993 (Orsi and Ohtsuka, 1999).

Sampling and data sources

Freshwater flow data were obtained from the Dayflow program (http://www.water.ca.gov/dayflow/) as net Delta outflow, the calculated flow out from the Delta to Suisun Bay at river kilometer 75. The daily mean distance of the 2-psu isohaline from the mouth of the estuary was calculated from outflow using the equations of Jassby *et al.* (Jassby *et al.*, 1995). This distance is used as a regulatory standard in the estuary and as a measure of the physical response of the estuary to freshwater flow. It indexes the approximate center of the LSZ, which was the target of our sampling.

Sampling cruises were conducted weekly during 2006 and biweekly to weekly during 2007, from March to August. Samples were taken at stations defined and identified by surface salinity: the key station was at a nominal salinity of 2 and two additional stations were at 0.5 and 5. Because the boat drifted during sampling, actual salinities varied by ±25% (10th and 90th percentiles) from the nominal values. Vertical profiles of salinity and temperature were taken with a Seabird SBE-19 CTD upon arriving at each station and just before departing. On four sampling dates, salinity and temperature were determined instead with a YSI Model 30 handheld conductivity meter.

At each station vertical plankton samples were taken for copepod abundance with 53- and 150-μm mesh, 0.5-m diameter nets. Samples were taken from 1 m off the bottom or a maximum of 10 m to the surface (mean 9 m); volume filtered for the 53-μm mesh net was 1.4 m^3 for a 10-m tow. These samples were placed on ice and preserved in 4% buffered formaldehyde upon return to the laboratory. Samples for live plankton were taken with the 150-μm net towed horizontally at slow speed just below the surface of the water. At the end of these tows the net was brought on board and the contents of the cod end jar were gently diluted into an insulated bucket containing surface water.

Preserved samples from vertical tows were subsampled and at least 100 organisms (median 290 copepods) were counted; only data from the 53-μm mesh net are reported here because counts of adult copepods were similar between the two net mesh sizes employed, and the finer net collected earlier stages quantitatively. Ovigerous adult female calanoid copepods were separated and their eggs were counted. Unattached egg sacs were readily identifiable to species by their shape and size, so eggs in unattached sacs were included in the counts of eggs of each species.

Additional samples were taken for chlorophyll, phytoplankton counts for biomass estimates and primary production (Lidström, 2009, Kimmerer *et al.*, 2012). Chlorophyll and primary production were determined using both 5 and 0.7-μm ("whole water") filters, and biomass based on counts was determined for cells larger and smaller than 5 μm (Lidström, 2009), because particles smaller than ~5 μm are less available to copepods than are larger particles (Bartram, 1981). Primary production was measured in simulated *in situ* incubations (Kimmerer *et al.*, 2012).

Rate estimates

Growth rates of *E. affinis* (spring) and *P. forbesi* (summer) were determined by the artificial-cohort method (Kimmerer and McKinnon, 1987). Live zooplankton samples were size fractionated into two classes, 200–250 and 250–300 μm, by reverse filtration through a clean PVC cylinder with mesh glued to one end. Samples were incubated in 4-L Cubitainers® suspended in a bath of flowing water at the Romberg Tiburon Center at a temperature close to ambient and shaded to ~50% ambient light. Incubation times were 48 or 72 h. Three or four (sometimes six) initial and final samples were taken, and in some experiments additional samples were taken at intermediate times to check for constancy of growth rate (Table I).

Initial samples and each incubated sample were concentrated onto a 35-μm mesh strainer, transferred to a 20-mL glass scintillation vial with filtered water of the same salinity, stained with neutral red for 30 min and preserved in 2% glutaraldehyde, which minimizes loss of carbon and dry weight in copepods (Kimmerer and McKinnon, 1986). After at least 1 month of preservation, copepods of the more abundant of the two species were separated and, in some cases, identified to stage. We used actual mass of copepods in each replicate sample rather than mass calculated from separate analyses (Kimmerer *et al.*, 2007). All copepods from each sample were counted and placed in a weighed tin capsule and dried for 48 h at 50°C. The capsules were then weighed again on a Sartorius SE2 Ultra Microbalance and analyzed for carbon on a Costech Model 4010 Elemental Combustion System calibrated with Cystine OAS (Elementar Americas B2105).

Table I. Summary of artificial-cohort experiments

Species	Year	Duration (days)	*n* total	*n* with intermediate	*n* with full replication
E. affinis	2006	3	12	0	0
	2007	3	6	6	6
P. forbesi	2006	3	6	0	0
		2	10	10	0
	2007	2	6	6	5
		3	2	2	2

Duration is the maximum for a given set of experiments. *n* total is the total number of individual measurements (i.e. slopes of log mass vs. time) for that species, year and duration; *n* with intermediate is the total number for which at least some samples were taken on Days 1 and (for 4-day experiments) 2 and *n* with full replication is the total number for which the samples on Days 1 and 2 had three or four replicates.

Dry weight and carbon were used separately to estimate the growth rate as the slope of log mass per individual over time. The residuals from these regressions contained some apparent outliers. To reduce the influence of these outliers we used robust regressions (function *rlm* in S-Plus, Venables and Ripley, 2003) to estimate slopes and confidence intervals.

The maximum growth rates of *E. affinis* and *P. forbesi* copepodites were estimated from laboratory-determined development times at 15 and 22°C, respectively, and stage-specific carbon content and dry weight for copepodites and adults (Gould and Kimmerer, 2010; Kimmerer and Gould, 2010; T. Ignoffo, unpublished data). The maximum growth rates were constant with stage in *E. affinis* but lower in late than early copepodites in *P. forbesi*, so the maximum growth of *P. forbesi* was determined separately for early and late copepodites. Temperature was obtained from a continuous monitoring station (Fig. 1; Station MAL, http://cdec.water.ca.gov), and maximum growth rates in the field were determined by adjusting laboratory rates to field temperature using the regressions of egg development time on temperature for these species (Sullivan and Kimmerer, 2013).

Carbon and dry weight of copepodite and adult stages for estimating maximum growth rates were determined from samples taken during March 2012 (*E. affinis*) and July 2009 (*P. forbesi*), i.e. during the seasons of maximum abundance of each species. An assumption of this method was that no bias would be introduced by the seasonal change in the sizes of copepods. Growth rates are determined essentially from the log ratios of masses of successive copepod life stages (Gould and Kimmerer, 2010). We tested whether these ratios varied with temperature using data from Durbin and Durbin (Durbin and Durbin, 1978, Table 2) for *Acartia hudsonica*. Analysis of covariance of the log ratio of successive dry weights with temperature and life stage showed that the effect of temperature was small and not significant. Thus, while temperature affects growth rate through its influence on development time, the effect of temperature on body size does not affect growth rate, and we are justified in estimating the maximum growth rate using stage-specific mass from a single date for each species.

Egg production was determined by the egg ratio method (Edmondson *et al.*, 1962) using egg development times as a function of temperature from Sullivan and

Kimmerer (Sullivan and Kimmerer, 2013). We lacked the data to correct for mortality as recommended by Ohman *et al.* (Ohman *et al.*, 1996). Specific production of adult females was determined by multiplying egg production rate by the ratio of carbon content of eggs to that of females. Egg carbon was determined from the mean diameter of eggs collected during our sampling program, using a value of 0.13 pgC μm^{-3} based on data summarized by Kiørboe and Sabatini (Kiørboe and Sabatini, 1995) and Uye and Sano (Uye and Sano, 1995).

Maximum egg production rates were estimated from the maximum growth rate of late female copepodites for *P. forbesi* and all copepodites for *E. affinis*, whose growth rate appeared constant with stage. For comparison we used the maximum egg production rates for *E. affinis* (Table 3 in Ban, 1994) at three temperatures and a relationship of specific egg production to temperature for *Pseudodiaptomus marinus* (Fig. 6 in Liang and Uye, 1997).

Data on egg production and growth rate of the cyclopoid copepod *L. tetraspina* were obtained from Gould and Kimmerer (Gould and Kimmerer, 2010). Methods were similar to those above, except that in 2007 copepods were also collected with Niskin bottles for egg ratios, because it became apparent that net sampling was dislodging a portion of the egg sacs from these small copepods. This did not appear to be a problem for the larger calanoids.

Monitoring data

We used data from a long-term monitoring program of the Interagency Ecological Program (Orsi and Mecum, 1986) as a basis for comparison with our abundance data. The samples analyzed here were collected with a 150-μm mesh, 10-cm diameter Clarke-Bumpus net towed for 10 min obliquely from near the bottom to the surface. Original reports (Orsi and Mecum, 1986) and electronic databases provide the calculated abundance m^{-3} based on the flowmeter in the net and the aliquot sampled. We selected data from samples taken at salinity 0.5–5 over the same time period as our study.

Samples from the monitoring program have been archived since the early 1990s. We re-analyzed a selection of archived net samples from July and August 1991, 1992 and 1996–2007 for egg ratios and abundance by life stage of *P. forbesi*. For the purposes of this paper we present egg production rate calculated as above from egg ratios for salinity 0.5–5 for 1996–2007, during which no new introductions had occurred (Winder and Jassby, 2011). Subsamples were taken and adult female copepods and eggs were counted as described above. Eggs were counted for a subsample of 20–50 females and the median eggs per sac were used to determine the egg ratios of the remaining ovigerous females. Unattached egg sacs of similar appearance to those of *P. forbesi* were also counted; ~10% (median) of the eggs were in unattached sacs. About 400 adult females and 300 eggs (medians) were counted per sample. A comparison of eggs per female in pairs of samples taken with 53- and 150-μm mesh nets in 2006–2007 gave a median difference of zero, suggesting that losses of eggs from the larger mesh net, and therefore the net used to collect the archived samples, were likely small.

All analyses were conducted in S-Plus v. 6.2 (Venables and Ripley, 2003). Error terms are reported as 95% confidence intervals throughout.

RESULTS

Freshwater flow varied markedly between the 2 years: 2006 was a very wet year, with the highest mean flow for April in the 55-year record, while 2007 was classified as a dry year, with a 7-fold lower annual mean flow than 2006 (Fig. 2A). The difference between the 2 years in position

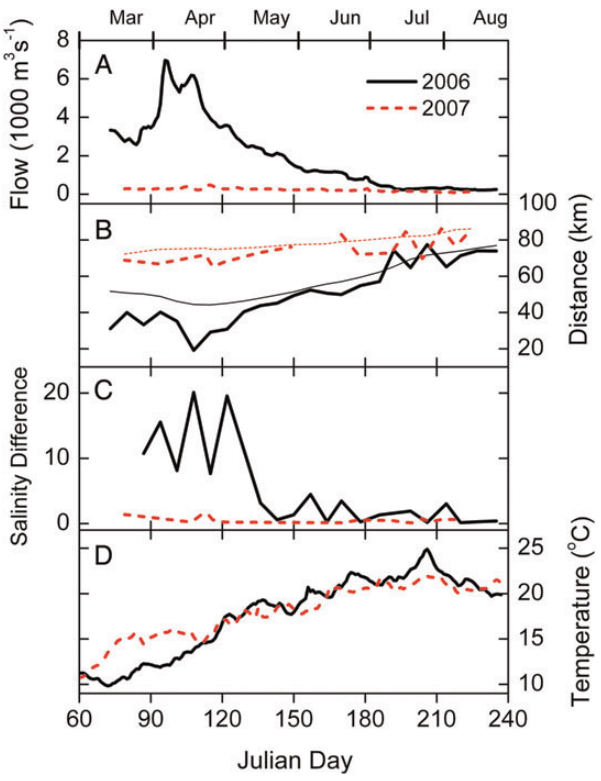

Fig. 2. Conditions during field studies in 2006 (solid lines) and 2007 (dashed lines). (**A**) Daily net Delta outflow. (**B**) Position of the 2-psu surface salinity station during cruises (heavy lines) and calculated daily position of the 2-psu near-bottom isohaline (thin lines). (**C**) Salinity difference between 10-m depth (or the deepest sample if <10 m) and the surface. (**D**) Daily medians of near-surface temperature from a continuous monitoring station at Port Chicago, River Kilometer 64 (CA Data Exchange Center, http://cdec.water.ca.gov/).

of the salinity field and therefore the sampling stations was equally striking, especially during spring (Fig. 2B). The strong compression of the salinity field during spring 2006 was accompanied by strong stratification in the deeper, wider channels of the lower estuary so that the salinity difference between near-surface and near-bottom was up to 20 (Fig. 2C). For the remainder of 2006 and all of 2007 stratification was negligible. Temperature (Fig. 2D) varied between 10 and 25°C in 2006; the range was somewhat narrower in 2007, but summer means in both years were 21°C. The gradient in temperature across the three stations was also stronger in summer of 2006 (−0.8°C from station 0.5 to station 5) than in summer of 2007 (−0.3°C).

Abundance of the three copepod species in our study was similar to that determined in the monitoring programs during the same years, with some differences from the long-term mean during 1994–2009 (Fig. 3). *Eurytemora affinis* abundance was moderately high in spring, but declined sharply in May–June until this copepod was effectively absent from the plankton during July–August. Abundance of *E. affinis* in late spring 2006 was substantially higher than the long-term mean, particularly at stations 0.5 and 2 (Fig. 3A), whereas abundance in 2007 was close to the long-term mean (Fig. 3B). Abundance of *P. forbesi* was initially low, increased to a peak in July, and declined slightly in summer–autumn. Abundance patterns for both 2006 (Fig. 3C) and 2007 (Fig. 3D) were similar to the long-term mean except for the July peak in abundance, and abundance was consistently highest at the 0.5-psu station and lowest at the 5-psu station. *Limnoithona tetraspina* increased in abundance through spring–summer (Fig. 3E and F).

Growth rate, determined as the slope of log biomass per individual with time, was usually constant during the 3-day incubation on the occasions when incubation samples were taken at 1 and 2 days (Fig. 4). Experiments with at least three data points for 1 and 2 days (Table I) gave growth rate estimates for each duration that had overlapping confidence intervals, and there was no general trend in the growth rate with experimental duration (Fig. 5). Growth measured using dry weight was closely correlated with growth measured using carbon for both *E. affinis* ($r = 0.99$) and *P. forbesi* ($r = 0.92$); we therefore used growth based on carbon determined over the entire incubation period for the remaining analyses.

Growth rates of *E. affinis* in spring and *P. forbesi* in summer during both years were nearly always greater in

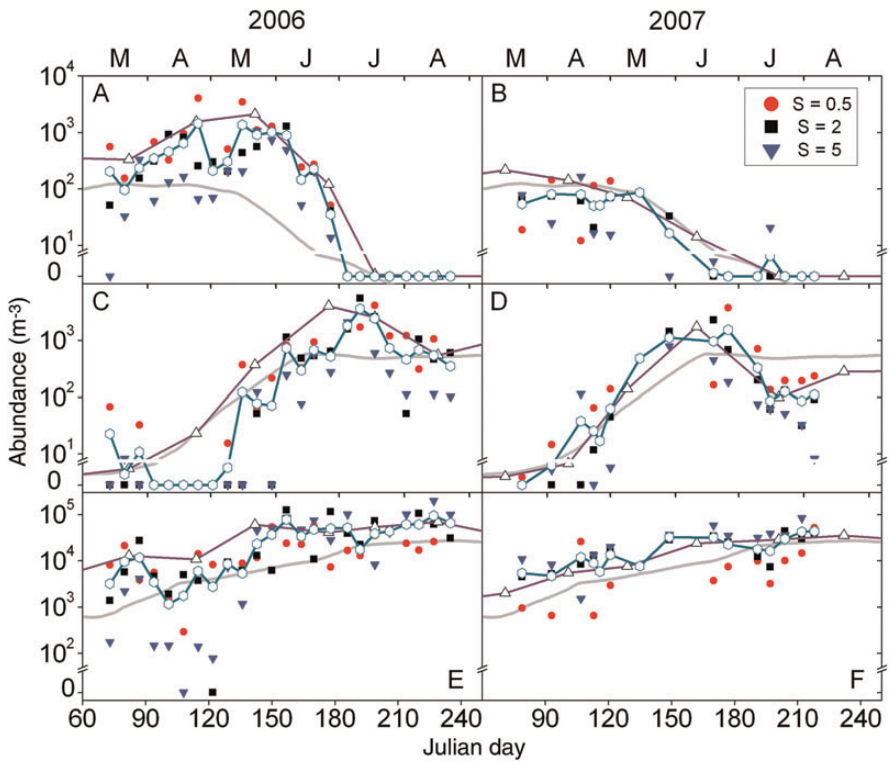

Fig. 3. Time series of abundance of adult copepods during 2006 (left column) and 2007 (right column). (**A** and **B**) *Eurytemora affinis*; (**C** and **D**) *Pseudodiaptomus forbesi* and (**E** and **F**) *Limnoithona tetraspina*. Symbols give individual values from stations defined by salinity (see legend). Line with open circles, mean of individual values. Line with open triangles, means from monitoring program for salinity 0.5–6. Thick gray line indicates data from long-term monitoring program from 1994 through 2009 smoothed with a generalized additive model with a loess smoother.

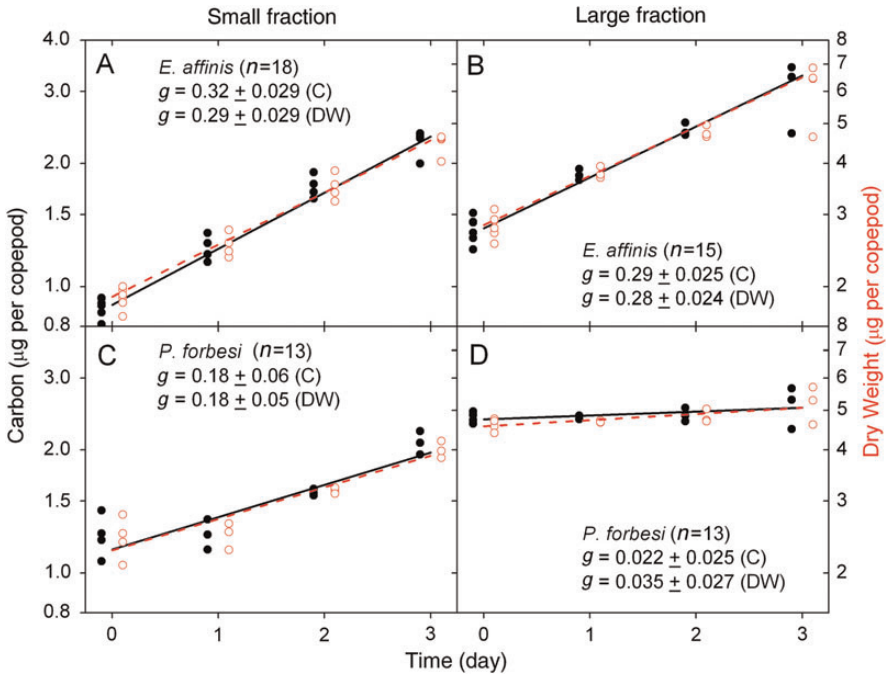

Fig. 4. Example results of growth rate measurements with full replication. (**A** and **B**) *Eurytemora affinis*; (**C** and **D**) *Pseudodiaptomus forbesi*. (**A** and **C**) Small (200–250 µm) fraction; (**B** and **D**) and large (250–300 µm) fraction. Filled symbols and solid line (left *y*-axis) represent mean carbon per copepod; open symbols and dashed line (right *y*-axis) represent the mean dry weight per copepod. Slopes with 95% confidence intervals based on carbon (C) and dry weight (DW) are given in each panel.

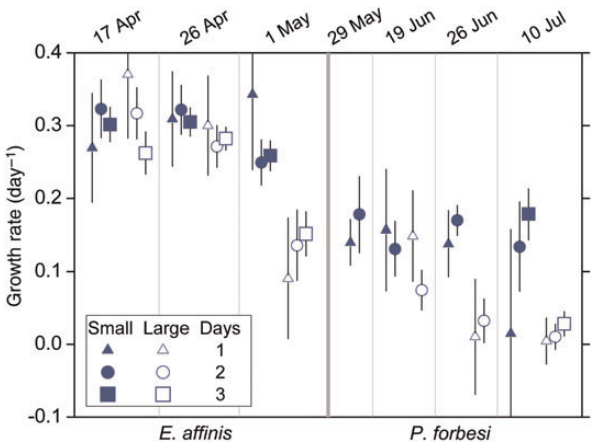

Fig. 5. Growth rate estimates with 95% confidence intervals based on 1, 2 or 3 days' incubation for measurements with full replication. Filled symbols, small size class; open symbols, large size class; symbol shapes and sizes indicate number of days. Dates at top are in 2007.

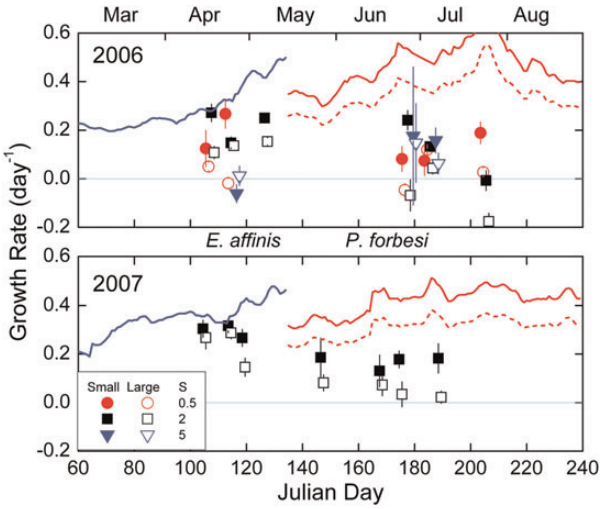

Fig. 6. Growth rate estimates for 2006 (top) and 2007 (bottom) with 95% confidence intervals. Data before mid-May are for *Eurytemora affinis*; data after mid-May are for *Pseudodiaptomus forbesi*. Salinity stations indicated by symbol shape; only salinity 2 was sampled in 2007. Filled symbols indicate small size class and open symbols large size class; symbols have been shifted slightly on the *x*-axis to minimize overlap. Solid lines represent the maximum growth rate under food-saturated conditions for *E. affinis* and for small fraction of *P. forbesi* (maximum 0.75 on 25 July 2006); dashed line indicates the maximum growth rate for large fraction of *P. forbesi*.

the small fraction than the large fraction and well below the maxima estimated from laboratory development times and field temperature (Fig. 6). The growth rate of *E. affinis* was lower relative to the maximum in 2006 than in 2007 (Fig. 6). The growth rate of *P. forbesi* was lower than that of *E. affinis* and in some cases negative. Growth rates differed among stations on individual days (e.g. day 115, 25 April 2006, Fig. 6, confidence intervals do not overlap for the small fraction) but these differences were not consistent among dates.

Egg production rates of the two species were persistently low, particularly for *P. forbesi* (Fig. 7), and rather similar between years. Estimates of maximum egg production for the two species showed that egg production in individual samples were almost always well below the maximum (Fig. 7).

Neither egg production nor growth rate of either calanoid species was related to measures of food availability, which included chlorophyll concentration, phytoplankton carbon based on counts and primary production (by graphical analysis and regression, Fig. 8, Table II). Furthermore, analysis of covariance with size fraction as a blocking variable showed that egg production had no positive relationship to growth rate for either species (slope with egg production -0.01 ± 0.006, $n = 16$, for *E. affinis* and 0.0004 ± 0.004, $n = 22$, for *P. forbesi*). The specific egg production rate was less than the specific growth rate of the small fraction of *P. forbesi* (difference $= -0.11 \pm 0.05$ day^{-1}, $n = 12$) but not for the large fraction or for either size fraction of *E. affinis* (confidence intervals included zero).

Re-analysis of samples from the long-term monitoring program gave egg production rates for *P. forbesi* in July–August that were slightly higher than those determined from our more temporally intensive sampling (Table III). Regression analysis of the egg production rate on log of freshwater flow during the months when the samples were taken gave slopes of -0.5 ± 0.8 ($n = 24$) for monthly means and -0.7 ± 1.0 ($n = 12$) for annual means. Averaging flow over the year to date or over the entire water year beginning the previous October gave similar results: in all cases the estimated slope was negative but the confidence intervals included zero.

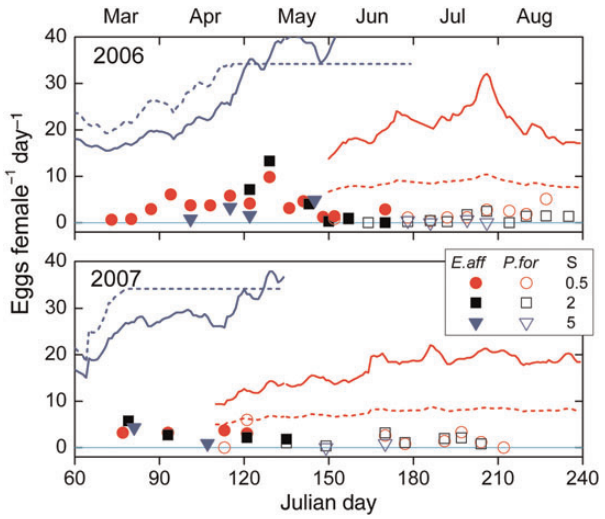

Fig. 7. Egg production rates of copepods in 2006 (top) and 2007 (bottom). Filled symbols, *Eurytemora affinis*; open symbols, *Pseudodiaptomus forbesi*. Salinity stations indicated by symbol shape. Some symbols have been shifted slightly on the *x*-axis to minimize overlap. Lines show the estimated maximum rates using literature values (dashed lines) or growth of stage C5 (solid lines; maximum of 60 on 23 June 2006).

DISCUSSION

Our results, together with previous reports (Gould and Kimmerer, 2010; Kimmerer *et al.*, 2012), reinforce the picture of the low-salinity region of the SFE as a low-productivity environment. Copepod growth and reproductive rates were persistently low, almost always well below the maxima determined for each species (Table III). However, growth rates in particular were also strikingly variable; on a few occasions values close to the maximum were measured at one station, while the growth rate was zero at another station (Fig. 6), and these differences were not consistently associated with any one station. Furthermore, freshwater flow had little effect on copepod growth and reproductive rates.

How can estuarine plankton maintain populations against losses to advection and dispersion if growth and reproductive rates are low? First, behavior that maintains position in the estuary can offset hydrodynamic losses. Both *E. affinis* and *P. forbesi* migrated vertically on a tidally-timed cycle so as to minimize seaward losses, although the migration of *L. tetraspina* was not examined (Kimmerer *et al.*, 2002). Second, a population can be maintained despite low reproductive and growth rates if mortality including any transport losses is sufficiently low. Mortality probably is low for at least the larger life stages of the copepods, because the abundance of planktivores in this part of the system is low (Kimmerer, 2006).

Methodological details

The mean mass of copepods was determined directly, as carbon or dry weight, in the growth rate experiments. This recommendation was based on the finding of bias introduced by using mean mass determined by counts by stage with standard mass per stage determined from separate samples (Kimmerer *et al.*, 2007). One concern with this approach was the error and possible bias introduced by a small number of large individuals that can occur with the artificial-cohort method. The use of robust regressions helped to minimize the effects of some over-dispersion of the residuals. The distributions of mean masses at each time point were generally symmetrical, indicating any bias was small. In addition, the weights determined in the robust regressions were distributed similarly between the two size classes in the experiments, indicating that the few large copepods were not biasing the results.

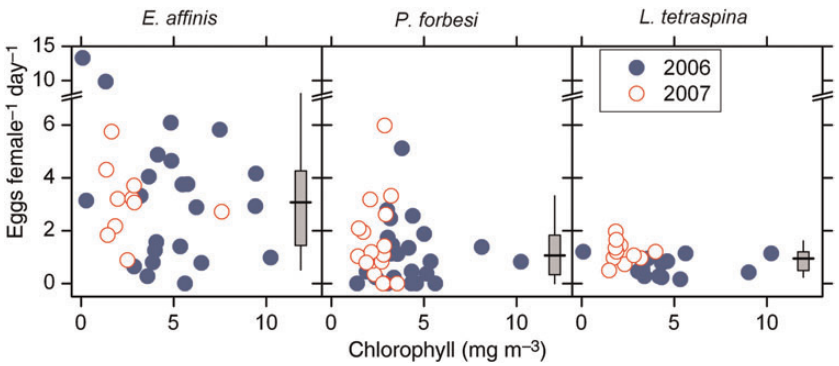

Fig. 8. Egg production rate vs. chlorophyll concentration for three copepod species. Boxplots in each panel give medians (horizontal lines), quartiles (boxes) and 5th and 95th percentiles (whiskers) for all data (see Table II for regression statistics).

Table II. Relationships of egg production and growth rates of the three copepod species to three measures of food availability (from Kimmerer et al., 2012: phytoplankton carbon from counts, chlorophyll and primary productivity) each based on whole-water samples or samples size fractionated to >5 μm

	Egg production rate			Growth rate		
Covariate	*E. affinis*	*P. forbesi*	*L. tetraspina*	*E. affinis*	*P. forbesi*	*L. tetraspina*
Carbon whole	−0.02 ± 0.044	−0.003 ± 0.023	−0.001 ± 0.007	0.001 ± 0.005	0.000 ± 0.002	0
Carbon >5 μm	−0.02 ± 0.052	0	−0.002 ± 0.008	0	0.001 ± 0.003	0.000 ± 0.001
Chl whole	−0.28 ± 0.372	−0.06 ± 0.25	−0.001 ± 0.09	−0.001 ± 0.023	−0.01 ± 0.04	−0.002 ± 0.003
Chl >5 μm	−0.35 ± 0.69	0.24 ± 0.46	−0.08 ± 0.12	0.002 ± 0.040	−0.036 ± 0.048	−0.005 ± 0.006
Primary prod. whole	0.007 ± 0.013	−0.004 ± 0.01	0.002 ± 0.002	0.001 ± 0.001	0.000 ± 0.001	0
Primary prod. >5 μm	0.020 ± 0.023	−0.004 ± 0.013	0.001 ± 0.005	0.001 ± 0.002	−0.001 ± 0.001	0

Data given are slopes ± 95% confidence intervals for each covariate independently; values of zero were <0.001 and smaller than the confidence interval in absolute value. Models were linear regressions except that growth rate of the two calanoid copepods had the size fraction as an additional covariate.

Table III. Summary of growth and production measurements for Eurytemora affinis *and* Pseudodiaptomus forbesi *(this study) and* Limnoithona tetraspina *(Gould and Kimmerer, 2010)*

					L. tetraspina	
Measurement	Year	Size fraction	*E. affinis* March–June	*P. forbesi* April–August	March–May	June–August
Length ♀ (mm)	2007		1.2 ± 0.1 (total)	1.1 ± 0.1 (total)	0.29 (prosome)	
Egg diameter (μm)	2007		87	97	50	
Egg production (eggs female^{-1} day^{-1})	1996–2007		—	2.2 ± 0.3	—	—
Egg production (eggs female^{-1} day^{-1})	2006		3.6 ± 1.3	1.1 ± 0.5	1.0 ± 0.6	0.7 ± 0.5
	2007		3.1 ± 1.0	1.6 ± 0.8	1.7 ± 0.9	2.0 ± 0.2
Specific egg production (day^{-1})	2006		0.05 ± 0.02	0.02 ± 0.01	0.04 ± 0.03	0.03 ± 0.02
	2007		0.04 ± 0.01	0.03 ± 0.02	0.08 ± 0.04	0.09 ± 0.01
EPR as percent of maximum	2006		12 (11)	5 (12)		
	2007		10 (8)	10 (22)		
Specific growth rate (day^{-1})	2006	S	0.17 ± 0.14	0.13 ± 0.07	0.04 ± 0.02	0.029 ± 0.006
		L	0.07 ± 0.07	0.01 ± 0.09		
	2007	S	0.30 ± 0.06	0.17 ± 0.04	0.028 ± 0.034	0.043 ± 0.015
		L	0.23 ± 0.19	0.052 ± 0.046		
Specific growth rate as percent of maximum	2006	S	51	24	82	27
		L	22	6		
	2007	S	78	42	48	38
		L	63	18		

Egg production rate from 1996 to 2007 from re-examination of archived samples (see section Method). Egg production data for *L. tetraspina* only during 2007 from bottle samples which produced higher egg ratios than did net samples; data for 2006 from net samples only, increased by the mean ratio of eggs per female in bottle to net samples in 2007 (Gould and Kimmerer, 2010). All data are given as means with 95% confidence intervals. "EPR as percent of maximum" includes maximum values from growth rate of copepodites and from literature (in parentheses; see section Method).

Bias could arise if copepods grow at a variable rate, such as by an early growth spurt followed by a period of consolidation (Miller, 2008). This would be difficult to resolve with small copepods because, using available technology, tens to hundreds of copepods must be aggregated to determine dry weight and carbon content. This could be resolved through measurements on individual organisms (Salonen, 1979) if the apparatus were widely available.

Egg ratios of naturally spawning copepod populations depend on a variety of factors besides the underlying individual reproductive rates, most notably the age structure of the population of females and therefore their mortality rate (Ohman *et al.*, 1996). However, determining the mortality rate is far more difficult and laborious than determining egg ratios and egg development times. Mortality estimates can be variable (e.g. Hirst and Ward, 2008) especially if the life-stage structure is unstable, e.g. because of pulses of reproduction, and the key assumption of a closed population is unlikely to be met in an estuary. Thus, we are faced with having to correct an easily measured variable (egg production rate) using a much less well-constrained parameter (mortality). It would be better to present the egg production estimates in the context of general estimates of mortality: mortality rate of female copepods in the study area is likely to be low because of low rates of planktivory (Kimmerer, 2006; Gould and Kimmerer, 2010) such that reproductive rate estimates were only weakly biased by ignoring mortality.

Influence of environment

One of the key forcing functions in estuaries is variability in freshwater flow. In the SFE, freshwater flow is positively related to abundance of several species of fish and shrimp, but responses of abundance or biomass at lower trophic levels are mixed (Jassby *et al.*, 1995; Kimmerer, 2002; Kimmerer *et al.*, 2009). Here we have shown that growth and reproductive rates of copepods in the LSZ are also unresponsive to flow. Therefore, the earlier conclusion (Kimmerer, 2002) remains valid: the response of some fish species to flow is not driven by a flow signal propagating up the foodweb through copepods.

Although abundance was higher in 2006 than in 2007, vital rates were either similar or higher in 2007 than in 2006 (egg production of *E. affinis* and *L. tetraspina*, Table III) despite the much higher freshwater flow in 2006. The small interannual differences in copepod vital rates are consistent with rather small differences in several measures of food supply in the LSZ (Kimmerer *et al.*, 2012). Only total chlorophyll concentration was greater in 2006 than in 2007, particularly in spring. Chlorophyll concentration in the >5-μm size fraction was about the same in both years, as were both size fractions of phytoplankton carbon based on cell counts and primary production (Kimmerer *et al.*, 2012).

Our data on egg production rates of *P. forbesi* from recounts of samples from the monitoring program likewise did not show a relationship between egg production rate and freshwater flow over several alternative averaging periods. This is consistent with a lack of response of primary production to freshwater flow in the long-term data (Kimmerer *et al.*, 2012).

Salinity is a key determinant of spatial distributions of planktonic species (Fig. 3), but osmotic stress may not be a key influence on physiology of zooplankton because they move with water (Laprise and Dodson, 1993). The distribution of *E. affinis* in salinity is much narrower than indicated by its broad salinity tolerance, suggesting a behavioral mechanism for its distribution (Kimmerer *et al.*, 1998). For all three species we observed consistent differences in abundance (Fig. 3) but not growth (Fig. 6, a few occasions in 2006) or reproductive rate (Fig. 7) among salinity stations.

Food limitation

All three copepod species generally grew and reproduced at rates below their maxima estimated by correcting laboratory rates for temperature (Figs 6, 7 and 9, Table III). The upper 95% confidence limit of somatic growth of *E. affinis* included the maxima on two occasions in 2006 and growth rate on average was about two-thirds of the maximum in 2007. Overall, growth rate was significantly below the maximum for this species, particularly for the large fraction (Fig. 6, Table III). Seasonal average growth rates of *P. forbesi* and egg production rate of both calanoid species were well below their respective maxima. Growth but not egg production rates of *L. tetraspina* were always below those of the calanoid copepods (Fig. 9).

The low rates for all species are likely to be the result of food limitation, which is commonly inferred when growth and reproductive rates are below their maxima for the same temperatures. Food limitation was also reported from the SFE for growth of *Daphnia magna* in bioassays using water from various sites in the freshwater reaches of the estuary (Müller-Solger *et al.*, 2002) and for egg production rate of *Acartia* spp. (Kimmerer *et al.*, 2005). Feeding rate of *L. tetraspina* also appeared to be generally below saturating rates during 2003–2004 (Bouley and Kimmerer, 2006).

The lack of a relationship between any of the growth measures and any measure of phytoplankton availability is puzzling (Fig. 8, Table II). At the low levels of food availability found in this estuary, feeding and growth

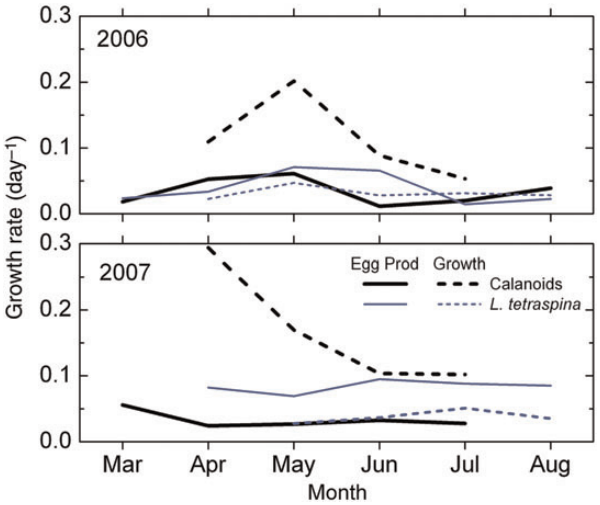

Fig. 9. Monthly means of specific egg production and growth rates for calanoid copepods (*Eurytemora affinis* and *Pseudodiaptomus forbesi* are combined) and for *Limnoithona tetraspina*. Values were averaged first across size classes (calanoid growth only), then across stations and then dates within months.

should have been approximately proportional to food supply. This lack of a relationship is not an artifact of these kinds of measurements. For example, egg production of copepods is often positively related to measures of food such as chlorophyll (Checkley, 1980; Kimmerer *et al.*, 2005), and somatic growth rates of especially the later life stages also generally respond to food quantity in artificial-cohort experiments (Kimmerer and McKinnon, 1987). However, sac-spawning copepods generally are less responsive to changes in phytoplankton biomass than broadcast-spawning copepods, both in reproductive rates and development rates (Hirst and Bunker, 2003). It seems likely that measures of food concentration in our study were not variable enough to provide an adequate signal, and also that chlorophyll concentration did not represent the food of the copepods, either because of variable food quality or because of consumption of microzooplankton.

If microzooplankton made up a large part of the copepods' diet and the biomass of microzooplankton were uncoupled from that of phytoplankton, then copepod growth and reproduction would not be solely determined by phytoplankton biomass and production. The copepod species in our study are all omnivorous and capable of feeding on microzooplankton such as ciliates, and *L. tetraspina* feeds only on motile prey (Merrell and Stoecker, 1998; Bouley and Kimmerer, 2006; Gifford *et al.*, 2007; York *et al.*, 2013). The abundance and biomass of microzooplankton was measured during several periods of our study (York *et al.*, 2011) but not frequently enough to provide correlative evidence for variability in copepod vital rates with microzooplankton biomass. Microzooplankton grew at rates that were saturated with respect to food in 6 of 8 dilution experiments in which grazing was different from zero (York *et al.*, 2011). Furthermore, grazing by clams may be a substantial control on the biomass of both phytoplankton and microzooplankton (Greene *et al.*, 2011). Thus, microzooplankton biomass may be uncoupled from that of phytoplankton.

This situation contrasts with that for egg production of *Acartia* spp. in the more saline parts of the estuary, which varied strongly with chlorophyll concentration (Kimmerer *et al.*, 2005). Chlorophyll in that study was as high as 16 mg m^{-3} during spring blooms, providing a wider range of values and therefore greater statistical power to detect responses of copepods. In addition, egg production in *Acartia* spp. responds rapidly and strongly to changes in food concentration (Dagg, 1977). However, *Acartia* species in the San Francisco Estuary often consume mainly ciliates (Rollwagen Bollens and Penry, 2003), and the response of egg production to chlorophyll concentration may have occurred through the response of ciliates to the spring blooms.

Indirect evidence for food limitation includes the consistently lower growth rates of the late copepodite stages than the early stages of the two calanoids in relation to their laboratory-determined growth rates (Fig. 6). In addition, the generally higher growth rates of early copepodites of *E. affinis* in spring compared with those of *P. forbesi* in summer may reflect the higher biomass in spring of phytoplankton determined from cell counts and measurements (Lidström, 2009) and from chlorophyll (Kimmerer *et al.*, 2012), despite the lack of correlations between these measures of food and growth. Furthermore, egg production rates of *E. affinis* from other estuaries are typically higher; notably rates from the Chesapeake Bay were much higher than rates presented here, and unrelated to food availability, which was attributed to food saturation (Lloyd *et al.*, 2013).

Copepod vital rates in context

The literature on the degree of food limitation of sac-spawning copepods is equivocal. Reviews of global reproductive and growth rates indicate that sac spawners have overall lower growth and reproductive rates than broadcast spawners of equivalent size at similar temperatures (Hirst and Bunker, 2003; Bunker and Hirst, 2004). One implication of this work was that food limitation should be much more frequent for broadcast spawners than for sac spawners (Fig. 10 in Bunker and Hirst, 2004). The overall food-saturated value of specific egg production rate of sac-spawning copepods corrected to 15°C was 0.17 day^{-1}, but the value for seven species of *Oithona* was 0.071 day^{-1} and 13 species not including *Oithona* had food-saturated specific egg production rates of 0.21 day^{-1} (Table 5 in

Hirst and Bunker, 2003). These rates are well below typical rates for broadcast spawners at this temperature.

There is some evidence that food-saturated specific egg production rates may be higher than indicated by Hirst and Bunker (Hirst and Bunker, 2003). For example, the specific egg production rate of *O. davisae* in Fukuyama Harbor was 0.14 day^{-1} at 15°C and 0.37 day^{-1} at 21°C (Uye and Sano, 1998). Much of the literature on dynamics of *Oithona* spp. is from high latitudes, and extrapolation to higher temperature may introduce inaccuracies. Specific egg production rates of sac-spawning calanoids appear to be similar to those of *Oithona* spp. For example, the specific egg production of *P. marinus* in Fukuyama Harbor was 0.10 day^{-1} at 15°C and 0.17 day^{-1} at 21°C, which the authors assumed were saturated rates (Liang and Uye, 1997). The egg production rate of *E. affinis* in the laboratory at high food concentration was 34 eggs $female^{-1}$ day^{-1} at 15 or 20°C (Ban, 1994), corresponding to a specific growth rate of 0.43 day^{-1} (thin lines for spring, Fig. 7). Note, however, that *E. affinis* is a species complex and that some life-history traits differ among populations (Lee, 2000; Beyrend-Dur, *et al.*, 2009), so that the actual maximum fecundity of *E. affinis* from the SFE is likely to differ from the above value.

Our estimates of maximum egg production rates were based alternatively on literature values and on growth of late copepodites, under the assumption that this growth continues in the females but is manifested as egg production. These values agreed well for *E. affinis* but the literature estimate for a congener of *P. forbesi* was about half of the rate estimated from copepodite growth (Fig. 7). The global estimate for sac spawners at this body mass and temperature range (Bunker and Hirst, 2004) was between these two estimates (not shown). Despite this uncertainty in the maximum egg production rate, the observed rates were always lower than the lowest estimate of maximum reproductive rate.

Somatic growth rates of sac-spawning copepods generally are considered to be much lower than those of broadcast spawners (Hirst and Bunker, 2003). Based on the global estimates of Hirst and Bunker (Hirst and Bunker, 2003), the food-saturated growth rate of copepodites of sac-spawning species averages 0.17 day^{-1} for a 10 μgC copepod at 15°C. The variation with body mass is small, such that the global mean somatic growth rate is 0.18 day^{-1} for a copepod of 0.1 μgC body mass (Tables 3–5 in Hirst and Bunker, 2003). However, somatic growth rates of both *E. affinis* and *P. forbesi*, determined in the laboratory and corrected to 15°C (T. Ignoffo, unpublished data), were considerably higher than this value and closer to the values presented by Hirst and Bunker (Hirst and Bunker, 2003) for broadcast spawners. In contrast, the maximum growth rate of *L. tetraspina* at 15°C in the laboratory was only one-third of the global value for a copepod of this size (Table III).

None of this is meant to question the value of global syntheses such as that of Hirst and Bunker (Hirst and Bunker, 2003). Rather it is to point out that the maximum reproductive and growth rates of individual species may differ considerably from global means, partly because of the sampling bias inherent in those means, but also merely because each species is different. To understand food limitation in field populations, it is necessary to determine the maximum growth rates of each population of each species and to assess field growth rates against those maxima. In our own study we suggest that the maxima for specific egg production rates are only rough estimates that need to be updated with laboratory-based maxima.

Seasonal patterns

The seasonal patterns of abundance of the three species have persisted since *L. tetraspina* became abundant in 1993 (Fig. 3). These patterns are apparent both in our data from 2006 to 2007 and in the record from the long-term monitoring program, although with some interannual variability. Each spring, *E. affinis*, formerly the numerically dominant copepod through summer (Orsi and Mecum, 1986), declines to a level at which it is seldom detected in plankton samples. At around the same time, *P. forbesi* increases in abundance to about the level maintained by *E. affinis* before 1987. The initial spring decline of *E. affinis* was related to inadvertent predation and competition for food by the clam *Potamocorbula amurensis* (Kimmerer *et al.*, 1994). The mechanism behind the rise of *P. forbesi* each spring is likely simply temperature, since the native range of this species is subtropical to tropical, roughly from Shanghai to the southern end of Vietnam (Razouls *et al.*, 2007). However, the consistency in the timing of these seasonal shifts remains a puzzle.

Neither differences in the growth rate nor reproductive rate are useful in explaining the inverse seasonal patterns of these two species. *Eurytemora affinis* had a higher growth rate that was closer to saturation in spring than was the case for *P. forbesi* in summer, despite the temperature difference. Egg production of *E. affinis* declined somewhat through spring (Fig. 7) but when the two species overlapped, the egg production rates were similar. Thus, the annual decline in *E. affinis* is not explained by poor growth alone, and patterns of mortality including losses to advection and dispersion must be determined to fill in this gap in our understanding.

ACKNOWLEDGEMENTS

We thank V. Greene, U. Lidström, A. Parker, J. Tirindelli and J.York for help in the field, A. Hennessy for long-term data, D. Bell and D. Morgan for vessel and logistic

support, and M. Weaver for helpful comments on the manuscript.

FUNDING

Funding was provided by the CALFED Bay-Delta Science Program under grant SCI-05-C107, and the Interagency Ecological Program under Department of Water Resources Contract 4600007494 and Agreement R10AC20074 between the US Bureau of Reclamation and San Francisco State University.

REFERENCES

Alpine, A. E. and Cloern, J. E. (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol. Oceanogr.*, **37**, 946–955.

Ban, S. (1994) Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. *J. Plankton Res.*, **16**, 721–735.

Bartram, W. C. (1981) Experimental development of a model for the feeding of neritic copepods on phytoplankton. *J. Plankton Res.*, **3**, 25–52.

Bennett, W. A. (2005) Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary Watershed Sci.*, **3**, Issue 2 Article 1.

Beyrend-Dur, D., Souissi, S. and Devreker, D. *et al.* (2009) Life cycle traits of two transatlantic populations of *Eurytemora affinis* (Copepoda: Calanoida): salinity effects. *J. Plankton Res.*, **31**, 713–728.

Bouley, P. and Kimmerer, W. J. (2006) Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. *Mar. Ecol. Prog Ser.*, **324**, 219–228.

Bryant, M. E. and Arnold, J. D. (2007) Diets of age-0 striped bass in the San Francisco Estuary, 1973–2002. *Calif. Fish Game*, **93**, 1–22.

Bunker, A. J. and Hirst, A. G. (2004) Fecundity of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature and body weight. *Mar. Ecol. Prog Ser.*, **279**, 161–181.

Checkley, D. M. (1980) Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. *Limnol. Oceanogr.*, **25**, 991–998.

Cloern, J. E. and Jassby, A. D. (2008) Complex seasonal patterns of primary producers at the land-sea interface. *Ecol. Lett.*, **11**, 1294–1303.

Dagg, M. (1977) Some effects of patchy food environments in copepods. *Limnol. Oceanogr.*, **22**, 99–107.

Durbin, E. G. and Durbin, A. G. (1978) Length and weight relationships of *Acartia clausi* from Narragansett Bay, Rhode Island. *Limnol. Oceanogr.*, **23**, 958–969.

Edmondson, W. T., Anderson, G. C. and Comita, G. W. (1962) Reproductive rate of copepods in nature and its relation to phytoplankton population. *Ecology*, **43**, 625–634.

Gifford, S. M., Rollwagen Bollens, G. C. and Bollens, S. M. (2007) Mesozooplankton omnivory in the upper San Francisco Estuary. *Mar. Ecol. Prog. Ser.*, **348**, 33–46.

Gould, A. L. and Kimmerer, W. J. (2010) Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in the upper San Francisco Estuary. *Mar. Ecol. Prog. Ser.*, **412**, 163–177.

Greene, V. E., Sullivan, L. J., Thompson, J. K. *et al.* (2011) Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. *Mar. Ecol. Prog. Ser.*, **431**, 183–193.

Hirst, A. G. and Bunker, A. J. (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol. Oceanogr.*, **48**, 1988–2010.

Hirst, A. G. and Ward, P. (2008) Spring mortality of the cyclopoid copepod *Oithona similis* in polar waters. *Mar. Ecol. Prog Ser.*, **372**, 169–180.

Jassby, A. D. (2008) Phytoplankton in the upper San Francisco Estuary: recent biomass trends, their causes and their trophic significance. *San Francisco Estuary Watershed Sci.*, **6**, Issue 1 Article 2.

Jassby, A. D., Cloern, J. E. and Cole, B. E. (2002) Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal estuary. *Limnol. Oceanogr.*, **47**, 698–712.

Jassby, A. D., Kimmerer, W. J. and Monismith, S. G. *et al.* (1995) Isohaline position as a habitat indicator for estuarine populations. *Ecol. Appl.*, **5**, 272–289.

Ketchum, B. H. (1954) Relation between circulation and planktonic populations in estuaries. *Ecology*, **35**, 191–200.

Kimmerer, W. J. (2002) Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. *Estuaries*, **25**, 1275–1290.

Kimmerer, W. J. (2006) Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. *Mar. Ecol. Prog Ser.*, **324**, 207–218.

Kimmerer, W. J., Bennett, W. A. and Burau, J. R. (2002) Persistence of tidally-oriented vertical migration by zooplankton in a temperate estuary. *Estuaries*, **25**, 359–371.

Kimmerer, W. J., Burau, J. R. and Bennett, W. A. (1998) Tidally-oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnol. Oceanogr.*, **43**, 1697–1709.

Kimmerer, W. J., Gartside, E. and Orsi, J. J. (1994) Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. *Mar. Ecol. Prog. Ser.*, **113**, 81–93.

Kimmerer, W. and Gould, A. (2010) A Bayesian approach to estimating copepod development times from stage frequency data. *Limnol. Oceanogr. Methods*, **8**, 118–126.

Kimmerer, W. J., Gross, E. S. and MacWilliams, M. (2009) Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? *Estuaries Coast*, **32**, 375–389.

Kimmerer, W. J., Hirst, A. G., Hopcroft, R. R. *et al.* (2007) Estimating juvenile copepod growth rates: corrections, inter-comparisons and recommendations. *Mar. Ecol. Prog. Ser.*, **336**, 187–202.

Kimmerer, W. J. and McKinnon, A. D. (1986) Glutaraldehyde fixation to maintain biomass of preserved plankton. *J. Plankton Res.*, **5**, 1003–1008.

Kimmerer, W. J. and McKinnon, A. D. (1987) Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnol. Oceanogr.*, **32**, 14–28.

Kimmerer, W. J., Nicolini, M. H., Ferm, N. *et al.* (2005) Chronic food limitation of egg production in populations of copepods of the genus *Acartia* in the San Francisco Estuary. *Estuaries*, **28**, 541–550.

Kimmerer, W. J., Parker, A. E., Lidström, U. *et al.* (2012) Short-term and interannual variability in primary production in the low-salinity zone of the San Francisco Estuary. *Estuaries Coast*, **35**, 913–929.

Kiørboe, T. and Sabatini, M. (1995) Scaling of fecundity, growth and development in marine planktonic copepods. *Mar. Ecol. Prog. Ser.*, **120**, 285–298.

Laprise, R. and Dodson, J. J. (1993) Nature of environmental variability experienced by benthic and pelagic animals in the St. Lawrence Estuary, Canada. *Mar. Ecol. Prog. Ser.*, **94**, 129–139.

Lee, C. E. (2000) Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate "populations". *Evolution*, **54**, 2014–2027.

Liang, D. and Uye, S. (1997) Seasonal reproductive biology of the egg-carrying calanoid copepod *Pseudodiaptomus marinus* in a eutrophic inlet of the Inland Sea of Japan. *Mar. Biol.*, **128**, 409–414.

Lidström, U. E. (2009) Primary production, biomass and species composition of phytoplankton in the low salinity zone of the northern San Francisco Estuary. MS Thesis. San Francisco State University.

Lloyd, S. S., Elliott, D. T. and Roman, M. R. (2013) Egg production by the copepod, *Eurytemora affinis*, in Chesapeake Bay turbidity maximum regions. *J. Plankton Res.*, **35**, 299–308.

Merrell, J. R. and Stoecker, D. K. (1998) Differential grazing on protozoan microplankton by developmental stages of the calanoid copepod *Eurytemora affinis* Poppe. *J. Plankton Res.*, **20**, 289–304.

Miller, C. B. (2008) Copepod growth in detail: pattern similarity to decapod larvae. *ICES J. Mar. Sci.*, **65**, 332–338.

Müller-Solger, A. B., Jassby, A. D. and Müller-Navarra, D. (2002) Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). *Limnol. Oceanogr.*, **47**, 1468–1476.

Nixon, S. W. (1988) Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnol. Oceanogr.*, **33**, 1005–1025.

Nobriga, M. L. (2002) Larval delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. *Calif. Fish Game*, **88**, 149–164.

Ohman, M. D., Aksnes, D. L. and Runge, J. A. (1996) The interrelationship of copepod fecundity and mortality. *Limnol. Oceanogr.*, **41**, 1470–1477.

Orsi, J. and Mecum, W. (1986) Zooplankton distribution and abundance in the Sacramento-San Joaquin Delta in relation to certain environmental factors. *Estuaries*, **9**, 326–339.

Orsi, J. J. and Ohtsuka, S. (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 Biol. Ecol.*, **46**, 128–131.

Orsi, J. J. and Walter, T. E. (1991) *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin Estuary. In Uye, S.-I., Nishida, S. and Ho, J.-S. (eds), *Proceedings of the Fourth International Conference on Copepoda*. Bull. Plankton Soc. Japan, Spec. Vol., Hiroshima, pp. 553–562.

Razouls, C., De Bovée, F. and Kouwenberg, J. (2007) *Diversity and Geographic Distribution of Marine Planktonic Copepods*. Observatoire Océanologique de Banyuls, Université Pierre et Marie Curie (Paris VI), Banyuls/Mer Cedex, France.

Rollwagen Bollens, G. C. and Penry, D. L. (2003) Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). *Mar. Ecol. Prog. Ser.*, **257**, 139–158.

Runge, J. A. (1988) Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. *Hydrobiologia*, **167/168**, 61–71.

Saiz, E. and Calbet, A. (2011) Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. *Hydrobiologia*, **666**, 181–196.

Salonen, K. (1979) Versatile method for the rapid and accurate determination of carbon by high-temperature combustion. *Limnol. Oceanogr.*, **24**, 177–183.

Sommer, T., Armor, C., Baxter, R. *et al*. (2007) The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries*, **32**, 270–277.

Sullivan, L. J. and Kimmerer, W. J. (2013) Egg development time of *Eurytemora affinis* and *Pseudodiaptomus forbesi* (Copepoda, Calanoida) from the upper San Francisco Estuary with notes on methods. *J. Plankton Res.*, **35**, 1331–1338.

Uye, S. and Sano, K. (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Mar. Ecol. Prog. Ser.*, **118**, 121–128.

Uye, S. and Sano, K. (1998) Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Mar. Ecol. Prog. Ser.*, **163**, 37–44.

Venables, W. N. and Ripley, B. N. (2003) *Modern Applied Statistics with S.*, Vol. Springer-Verlag, New York.

Winder, M. and Jassby, A. D. (2011) Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. *Estuaries Coast*, **34**, 675–690.

York, J. L., Costas, B. A. and McManus, G. B. (2011) Microzooplankton grazing in green water—results from two contrasting estuaries. *Estuaries Coast*, **34**, 373–385.

York, J. K., McManus, G. B. and Kimmerer, W. J. *et al*. (2013) Trophic links in the plankton in the low salinity zone of a large temperate estuary: top-down effects of introduced copepods. *Estuaries Coast*, in press. doi 10.1007/s12237-013-9698-9