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Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in the upper San Francisco Estuary

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ABSTRACT: *Limnoithona tetraspina* is a small cyclopoid copepod that was introduced to the San Francisco Estuary (SFE), USA, in 1993 and became the most abundant copepod species in the low-salinity zone (LSZ). Two previous studies have shown that it feeds only on motile prey, predominantly ciliates. Little is otherwise known of its biology or its role in the estuarine foodweb. We determined development times, growth rates, and fecundity of *L. tetraspina* from March to August of 2006 and 2007. The mean growth rate of copepodites in both years was 0.03 d^{-1}, which is low relative to values reported for related *Oithona* spp. Development times were longer in the field than in the laboratory at food saturation, indicating food limitation in the SFE. Mean weight-specific fecundity rate in 2007 was 0.10 d^{-1}, which is twice that of 2006, but within the range of reported values for *Oithona* spp. Low growth and fecundity rates indicate that the population success of *L. tetraspina* is due to low mortality. *L. tetraspina* may avoid certain mortality agents (e.g. visual predation) to which larger copepods are susceptible.

KEY WORDS: Egg production · Estuary · Low-Salinity Zone · Bayesian methods · *Limnoithona tetraspina*

INTRODUCTION

Copepods are the most abundant group of zooplankton in the world and they play an important role in linking primary carbon production to higher trophic levels (Banse 1995, Hirst et al. 2005). Studies on the population dynamics and production of many copepod species in both marine and freshwater systems throughout the world have been synthesized (Hirst & Bunker 2003, Bunker & Hirst 2004). However, the majority of these studies have focused on calanoid copepods, leaving cyclopoid species being significantly underrepresented in the scientific literature (Paffenhöfer 1993, Peterson 2001). This is likely due to the smaller size of most cyclopoids relative to calanoids and the traditional use of medium sized (200 to 330 µm) zooplankton nets (Gallienne & Robins 2001). Despite their small size, cyclopoids can sometimes dominate plankton communities both in abundance and in biomass (Gallienne & Robins 2001). More attention should therefore be focused on understanding the role of cyclopoid copepods in waters around the world.

Of the studies that have been conducted on cyclopoids in marine and estuarine waters, most have focused on members of the genus *Oithona,* which is the most abundant genus of copepods worldwide (Paffenhöfer 1993, Gallienne & Robins 2001, Turner 2004). *Oithona* species can be abundant in estuaries, but generally not at low salinity (Uye & Sano 1995, Johnson & Allen 2005, Williams & Muxagata 2006). The genus *Limnoithona* consists of 2 estuarine species that are native to China, both of which have been introduced to the San Francisco Estuary (SFE), USA (Orsi & Ohtsuka 1999). It is currently the most abundant copepod genus

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in the brackish region of the SFE (Bouley & Kimmerer 2006). Abiahy et al. (2006) removed *Limnoithona* from the Oithonidae based on several morphological features, but molecular evidence places *Limnoithona* within the Oithonidae (G. Wyngaard pers. comm.). The feeding ecology (Bouley & Kimmerer 2006) and small size of *Limnoithona* species suggest that they may play an ecological role similar to that of *Oithona* species.

Of the 2 *Limnothona* species that were introduced to the SFE, only *L. tetraspina* has had a major impact. *L. sinensis* was first found in the SFE in 1979 (Orsi & Ohtsuka 1999) where it inhabits fresh to brackish water at low abundance. *L. tetraspina,* which was originally described from the brackish region of the Yangtze River in China, was introduced to the SFE in 1993 (Orsi & Ohtsuka 1999). Peak abundance of *L. tetraspina* occurs within a salinity range of 0.5 to 10 and exceeds 20 000 ind. m^{-3} in late summer (Bouley & Kimmerer 2006). Although individual carbon biomass is ~1/10 that of larger calanoids in the region, total adult biomass in the region is roughly equal to the combined biomass of the 2 most common calanoids *Eurytemora affinis* and *Pseudodiaptomus forbesi* (Bouley & Kimmerer 2006, their Fig. 4).

Limnoithona tetraspina are sac-spawners that carry their eggs until hatching. To date, the only studies on *L. tetraspina* have focused on their feeding ecology within the SFE (Bouley & Kimmerer 2006, Gifford et al. 2007). These studies have shown *L. tetraspina* to be ambush predators of motile prey such as ciliates and flagellates, with a clearance rate of <1.0 ml $predator^{-1}$ h^{-1} (Bouley & Kimmerer 2006, Gifford et al. 2007). All of these characteristics indicate similarity between *L. tetraspina* and small species of *Oithona* (Paffenhöfer 1993, Johnson & Allen 2005). *L. tetraspina* is unlikely to consume nauplii of other species since nauplii of co-occurring species are >130 µm long, or ~30% of the length of an adult female *L. tetraspina*, although we cannot rule out this possibility. *Oithona* species are generally reported to consume ciliates and other protozooplankton but can also consume nauplii (Nakamura & Turner 1997).

The SFE is one of the most highly invaded estuaries in the world (Cohen & Carlton 1998). In addition to *Limnoithona* spp., most of the other copepod species in the low-salinity zone (LSZ, salinity of ~0.5 to 5) are introduced (Kimmerer & Orsi 1996, Orsi & Ohtsuka 1999), and some have had significant impacts on the foodweb. The introduction of the overbite clam *Corbula amurensis* to the SFE in 1986 led to reductions in primary production (Alpine & Cloern 1992, Kimmerer et al. 1994) and in the abundance of common calanoid copepod species in the northern estuary (*Eurytemora affinis, Sinocalanus doerrii,* and *Acartia* spp.; Kimmerer et al. 1994, Kimmerer & Orsi 1996). This reduction in phytoplankton and calanoid copepod abundance has resulted in the northern anchovy *Engraulis mordax* moving out of the LSZ into higher salinities, virtually eliminating filter-feeding fish from the LSZ (Kimmerer 2006). Despite the decrease in the abundance of calanoid copepods in the LSZ, total copepod biomass in the region has remained nearly unchanged because of the recent increase in the abundance of *L. tetraspina* (Bouley & Kimmerer 2006). How did *L. tetraspina* become the most abundant copepod in the region? With relatively low feeding rates (Bouley & Kimmerer 2006, Gifford et al. 2007) in an environment of low primary productivity (Alpine & Cloern 1992), one would not expect the population to thrive. To understand the demographic characteristics leading to population success, we examined the development, growth, and reproductive rates of *L. tetraspina* throughout spring and summer in the LSZ during 2006 and 2007.

MATERIALS AND METHODS

Study site. The SFE has a Mediterranean climate with the highest freshwater runoff from the Sacramento and San Joaquin Rivers in winter. Freshwater flow in spring and summer is largely controlled for agricultural water supply and human consumption. Turbidity and grazing by *Corbula amurensis* limit primary production to low levels in the brackish regions of the upper estuary (Jassby et al. 2002).

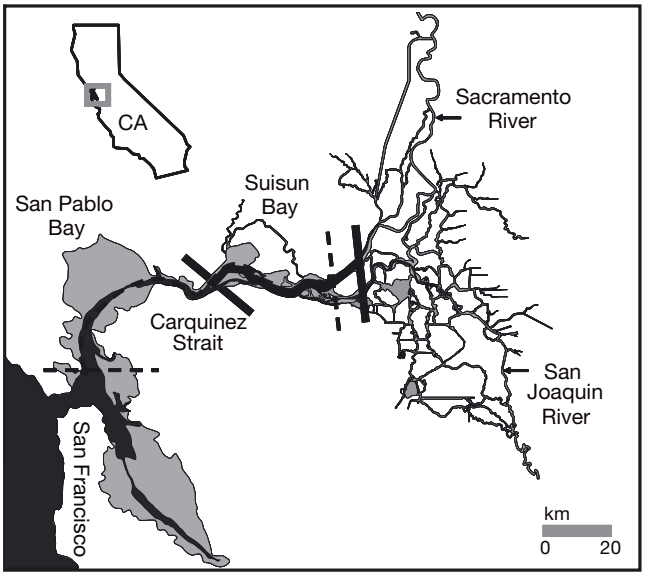

Fig. 1. Sampling region in the San Francisco Estuary. Dashed line: limits of sampling in the low-salinity zone (salinity range: 0.5 – 5) for 2006; and solid line: for 2007. CA: California

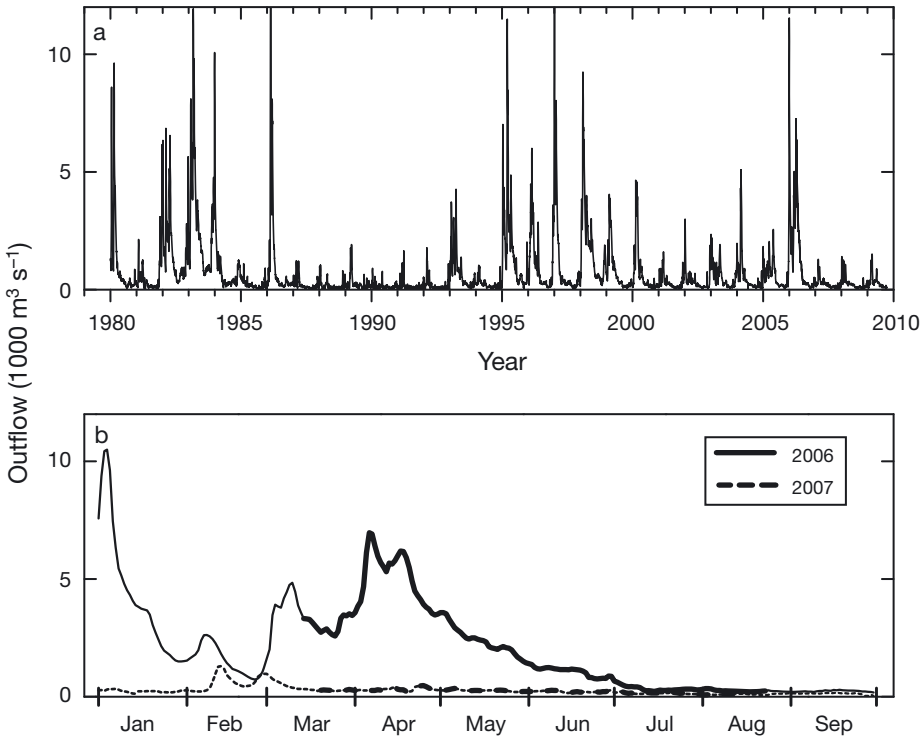

Fig. 2. (a) Historical net delta outflow into the San Francisco Estuary since 1980, and (b) throughout 2006 and 2007. Heavy line: sampling period. All data obtained from www.iep.ca.gov/dayflow/

The present study was part of a larger project that was designed to understand the foodweb of the upper SFE. Sampling in the LSZ was determined by salinity: target surface salinities were 0.5, 2, and 5 (LSZ sampling areas shown in Fig. 1), and included most of the distribution range of *Limnoithona tetraspina* (Fig. 2 in Bouley & Kimmerer 2006). Sampling was done in different geographic locations in the 2 yr because of differences in hydrological conditions: 2006 was very wet and 2007 was dry (our Fig. 2). Sampling moved progressively inland with salinity throughout each season.

Sampling was conducted weekly in 2006 and biweekly in 2007 from March to August onboard the RV 'Questuary'. Temperature and salinity data were collected at each sampling station with a CTD (Seabird SBE-19). Samples of *Limnoithona tetraspina* were collected with a 0.5 m diameter, 53 µm mesh zooplankton net that was pulled vertically through the water column. Additional water samples (8 l) were collected 1 m below the surface throughout the sampling period in 2007 using a horizontal water sampler (WildCo Alpha), and filtered with a 35 µm mesh to collect all copepods. All samples were immediately stained with Rose Bengal and preserved in a buffered 5% formaldehyde solution.

Live copepods were collected at a salinity of 2 using a 53 µm zooplankton net that was attached to a 1 l cod end and towed gently for several minutes just below the surface. Copepods were brought to the laboratory in insulated 20 l containers filled with surface water from the same station to minimize disturbance. Surface water was also collected and transported in 20 l buckets for use in experiments for these stations. All experimental setups were completed within 5 h of collection at San Francisco State University's Romberg Tiburon Center for Environmental Studies in Tiburon, California.

Development and growth experiments. The development of *Limnoithona tetraspina* was examined by following cohorts under controlled temperature and food-saturated conditions. Development data for the naupliar (N1 to N6) and copepodite (C1 to Adult) stages were collected from 2 independent experiments, in April and November of 2008, respectively. April cohorts were not dense enough and there were no copepods left to sample during the later copepodite stages. A second set of cohorts was, therefore, set up in November and sampled from the late naupliar stages until adulthood. Development times of each stage were determined from the 2 sets of cohorts.

Approximately 6000 gravid *Limnoithona tetraspina* females from live surface tows were size fractionated between 125 and 150 µm and acclimated for 24 h at 18°C on a 12 h light:12 h dark cycle. Two sets of ~3000 females were then suspended in 80 µm mesh filters in 20 l buckets that were filled with ~18 l of surface water (filtered through a 35 µm mesh to remove larger particles and zooplankton). After 12 h, females were removed with the 80 µm filters, leaving the nauplii produced during incubation in the buckets. Filters were resuspended in 2 additional buckets and more nauplii were collected, producing a total of 4 cohorts of *L. tetraspina*. The 4 cohorts were fed daily an optimal diet determined in prior experiments. Cultures were maintained at 18°C on the same light cycle. Some culture water (4 l) was removed weekly by reverse filtration through a 35 µm mesh sieve and replaced with freshly collected, 35 µm filtered surface water from the same salinity. Subsamples of at least 30 ind. were removed every 12 h, stained with Rose Bengal, and preserved in a buffered 5% formaldehyde solution. All copepods in each subsample were counted and identified as to developmental stage.

Preliminary experiments were conducted to determine the optimal conditions at which *Limnoithona tetraspina* should be maintained and cultured prior to the determination of development times. The diet that produced the fastest growth was used for culturing *L. tetraspina* for all subsequent experiments. This diet consisted of a combination of the unicellular microalga *Nannochloropsis oculata*, a concentrated natural assemblage of microzooplankton (<35 µm) reared on *N. oculata*, and a dilution of Instant Algae Shellfish Diet 1800 (a mixture of *Isochrysis* spp., *Pavlova* spp., *Tetraselmis* spp. and *Thalassiosira weissflogii*). We did not determine prey biomass in the culture containers; the potential for food limitation in the cultures is low and addressed in the 'Discussion'.

Twenty *Limnoithona tetraspina* of each copepodite stage from the November cohorts were preserved in 5% glutaraldehyde (Kimmerer & McKinnon 1986) and their prosome lengths were measured to the nearest 5 µm with an inverted microscope at 200×. Approximately 100 ind. of each stage (C1 to Adult, male and female) from the same cohorts were rinsed in milli-Q water and placed into pre-weighed tin capsules (8 × 5 mm). The copepods were dried at 50°C for at least 24 h, weighed, and combusted in an elemental analyzer (Costech, Model 4010). The carbon content of each copepodite stage was determined following the manufacturer's procedures and calibrated with a cystine standard. The carbon weights of successive copepodite stages were used to calculate growth rates.

Development time and growth of *Limnoithona tetraspina* in the field were determined from molt rate experiments (Twombly & Burns 1996, Hirst et al. 2005), using copepods that were collected by live surface tows from the sampling stations at a salinity of 2. Copepodites (C2 to C4) were removed from the samples under a dissecting microscope. The life stages could not be confirmed until after incubation because individuals were so small; thus, the number of individuals at each stage varied among experiments. Copepods were placed individually in 20 or 40 ml scintillation vials that were filled with 35 µm filtered baywater, and incubated on a plankton wheel at 1 rpm to ensure food suspension. Incubations were conducted at 18°C, and the relationship between egg development and temperature (determined from egg hatching experiments) was used to adjust growth rates for differences in values between 18°C and the field temperature at collection. In 2006, individuals were incubated in 20 ml glass scintillation vials for 24, 48, and 72 h (n = 20 each), but there was evidence of slowing of development probably due to food limitation. Based on these results, individuals in the 2007 experiments were incubated for 48 h in 40 ml vials (n = 60). A 48 h incubation time allowed a larger proportion of individuals to molt so that we could confidently estimate growth, and the 40 ml vials minimized food limitation. After incubation, the contents of each vial were stained with Chlorazol Black E and preserved in a buffered 5% formaldehyde solution. Each sample was examined for an exuvium, and copepodites were identified as to development stage. To determine the accuracy of molt recovery, a known random number of molts was placed into 3 additional scintillation vials on 2 dates in 2007 and treated as previously described. The number of molts in each vial was counted at a later date to determine the recovery fraction (f_r, 47/51), which was then used to scale the total number of molts recovered from each set of experiments.

Modeling of development and growth. Development times and growth rates in the laboratory and in the field were determined using Bayesian hierarchical models (Gelman et al. 2004, Kimmerer & Gould 2010). The Bayesian approach allowed the use of all data, carried through error terms from each component variable in the calculations, and provided full posterior probability distributions of parameters from which confidence limits could be determined. We used the empirically derived laboratory development times as priors in the Bayesian determination of field development times of *Limnoithona tetraspina*, making the field estimates more robust. Details of the method used to estimate laboratory development times are presented separately (Kimmerer & Gould 2010) and are described only briefly here.

The Bayesian models were fit using WinBUGS 1.4.3 (Lunn et al. 2000) with triplicate Markov chains and 10-fold thinning to reduce autocorrelation. The first

1000 iterations (after thinning) were discarded to remove effects of initial values; the subsequent 10 000 iterations were used to calculate statistics. Results from the first and second half of these iterations were nearly identical, indicating that both the initial 1000 iterations that were discarded and the iteration length were adequate. Gelman-Rubin statistics (Gelman et al. 2004) and plots of autocorrelation and time series of iterations (history plots) were used as checks on model convergence. Uninformative prior probability distributions (either uniform or normal with large SDs) were used for all parameters except as noted below, and alternative priors were used to confirm the lack of influence on posterior distributions.

Analyses of copepod development have previously used ad hoc probability distribution functions of stage durations to estimate median development times but often leave out data points or make unsupported assumptions (e.g. that stage development time is uniformly distributed) (Klein Breteler et al. 1994). Although these methods have been refined through the use of maximum-likelihood methods (Klein Breteler et al. 1994), only Bayesian methods allow for accurate calculation of confidence limits around stage durations. Our model for laboratory development time comprised a series of skewed logistic curves that were fitted to the proportion of copepods at and below each stage over time, with the spread of each curve (for each stage) being allowed to vary to account for the increasing spread in development time of individuals with life stage (Kimmerer & Gould 2010). A multinomial distribution was used to account for variability in the count data. Data from all replicates were analyzed simultaneously using a model analogous to ANOVA, in which replicates were treated as blocking factors; the deviations of individual replicates from the overall mean were small (~0.3 d). The development times of late nauplii and copepodites from the April experiment were used as priors for the November experiment. Data presented here are mean development times with 95% Bayesian credible intervals, which are roughly equivalent to confidence intervals (Gelman et al. 2004).

Field molt rate data were analyzed using the lab-based development times as priors to calculate expected molt rates at 18°C. We fitted the observed number of individuals that were molting in each experiment to a binomial frequency distribution to achieve the following 2 outputs: the ratio of the observed to the expected molt rate and the realized stage durations. Our assumptions were that (1) the age distribution within a given life stage was stable (Hirst et al. 2005), and (2) deviations of field-derived molt rates from those calculated from laboratory development times can be modeled as the product of corrections for the experiment (i.e. the degree to which development is food limited), the life stage, and the duration of the incubation. The latter 2 corrections were assumed to be the same across all experiments, and were applied to allow all data to be used in the calculations. The development rate model is:

$$r_{i,s,d} = \min\left(1, \frac{d\,\Phi_i \Phi_s \Phi_d}{f_r D_s}\right) M_{i,s,d} \sim \text{binomial}(r_{i,s,d}, N_{i,s,d})$$

$$D_{i,s} = \frac{D_s}{\Phi_i \Phi_s} \quad (1)$$

where the subscript i is the experiment number, s is the initial life stage, and d is the duration of incubation. Inputs include f_r, the fractional recovery (47/51) in the molt recovery experiment; D_s, the duration of life stage s from the laboratory; and $M_{i,s,d}$ and $N_{i,s,d}$, the number that molted and the total number by experiment, stage, and incubation duration. Values of D_s were entered as normal variates, with means and SDs being obtained from the laboratory development experiments. Calculated parameters include r, the proportion of individuals that were molting; Φ_i, the ratio of realized molt rate for stage 1 with $d = 1$ in experiment i, to that expected from laboratory measurements; Φ_s, the ratio of molt rate for stage s to that at stage 1; and Φ_d, the ratio of molt rate for duration of incubation d to that for 1 d of incubation. Outputs include these parameters and $D_{i,s}$, the realized development time of each stage during each measurement.

Growth rates were calculated from the stage durations that were determined from each molt rate experiment and the carbon content of each life stage. These calculations were complicated by the fact that carbon content was measured (with error) within a stage and was assumed to be the within-stage mean, whereas development time was the duration of each stage, i.e. the time between successive molts (Hirst et al. 2005). Growth rate that is based on development times and mean weights of a series of stages is indeterminate, and requires an additional assumption (e.g. Hirst et al. 2005 assumed constant growth between midpoints of stages). As an alternative, we initially assumed that growth rate could vary linearly with life stage but was constant within each life stage. The following model was first fitted to the laboratory development times and then to the field development times. Under the above assumption about growth rate, the mean carbon weight in a life stage can be calculated by integrating an exponential growth curve over each life stage. This relationship is:

$$g_s = \alpha - \beta s$$

$$\overline{W}_{i,s} = \frac{1}{D_s}\int_0^{D_s} W_{i,0}\, e^{g_s a}\, da = \frac{W_{i,0}\, e^{\sum_{k<s} g_k D_k}\,(e^{g_s D_s} - 1)}{g_s D_s}$$

$$W_{i,j,s} \sim \text{Normal}(\overline{W}_{i,s}, \sigma) \quad (2)$$

where the subscript *i* is the experiment number, *s* is the life stage, *a* is the age within a stage, and *j* is the sample for carbon weight $W_{i,j,s}$ (n = 12 for C1 to C4). $W_{i,0}$ is the (unknown) initial carbon weight of the first stage, α and β define the relationship of specific growth rate g_s to stage *s*, and D_s is the duration of stage *s*. Priors were: normal, with means and SDs that were calculated from development time (for laboratory growth rate) or molt rate experiments for D_s; uniform (0.01, 10) for the SD of weight σ; normal (0, 10) for α and β; normal (25, 30), truncated to >0 for W_0 in the laboratory experiments; and normal (28.1, 2.3) for W_0 in the field experiments that were based on the results of the laboratory experiments, since the weights were based on the same data. The model that was run with the laboratory data showed that the parameter β was 0.016 ± 0.05, and that variation in β inflated the variation in α; hence, the model was rerun with β set to 0 and only α estimated from the laboratory and field data, i.e. specific growth rate did not vary with stage of copepods. This is consistent with limited data on *Oithona* spp. (e.g. Uye & Sano 1998) and cross-taxon comparisons among egg-carrying copepods (Hirst & Bunker 2003).

Fecundity. Egg production was determined by the egg ratio method (Edmondson 1971) based on egg ratios from field samples and egg development time determined in the laboratory. Egg development time was determined as described by Nielsen et al. (2002) at 13, 15, 18, 21, and 24°C. Cultures of *Limnoithona tetraspina* were maintained under the same conditions as for the development experiments, and held at each experimental temperature for an acclimation period of 1 wk prior to the experiments. After acclimation, ~96 gravid females were removed from the culture and individually incubated in 5 ml wells. Each well was monitored for egg hatching every 4 to 12 h, depending on the incubation temperature. After eggs hatched, females were removed from the wells. Egg development time D_E was determined as the 100% intercept of a regression of percent eggs hatched vs. time (Nielsen et al. 2002). This method was preferable to methods requiring longer incubations (e.g. Uye & Sano 1995) because feeding in small containers (as inferred from development, see below) apparently declined with duration of incubation. Egg development times were related to temperature and modeled with an exponential function, which provided a better fit than the Bělehrádek function recommended by McLaren (1995) within this temperature range. The temperature dependence of egg development was also used to correct estimates of field growth rates for differences in values between incubation and ambient temperatures (Corkett & McLaren 1970).

Preserved net samples taken in March through August in 2006 and 2007, and the samples collected with the bottle sampler in 2007, were analyzed to determine the egg production rate of *Limnoithona tetraspina*. Males, females, and gravid females were counted from a subsample of each preserved sample. Additionally, the number of egg sacs on each gravid female and the number of eggs within each egg sac were counted. Loose eggs and egg sacs that were identified by their small size were also counted. The egg production rate (EPR) was calculated as:

$$\mathrm{EPR} = \frac{\left(\frac{e}{f}\right)}{D_E} \quad (3)$$

where *f* is the total number of females, *e* is the total number of eggs, and D_E is the egg development time at the surface temperature upon collection. Egg production rates were also converted into specific production rates using the mean adult female body carbon mass and the estimated egg carbon mass (C_E) of 0.0078 µg C as determined from Fig. 9 in Uye & Sano (1995) using the measured *L. tetraspina* egg diameter of 50 µm.

RESULTS

Development and growth

The average prosome lengths of copepodite stages C1 to C4 ranged from 173 to 239 µm with corresponding average carbon weights of 0.032 to 0.053 µg (Fig. 3). Male C5 and adult stages were smaller than females of the same stage. Adult female prosome length was 286 µm and carbon mass was 0.100 µg.

The individual life stages of *Limnoithona tetraspina* varied in duration, and these durations were highly

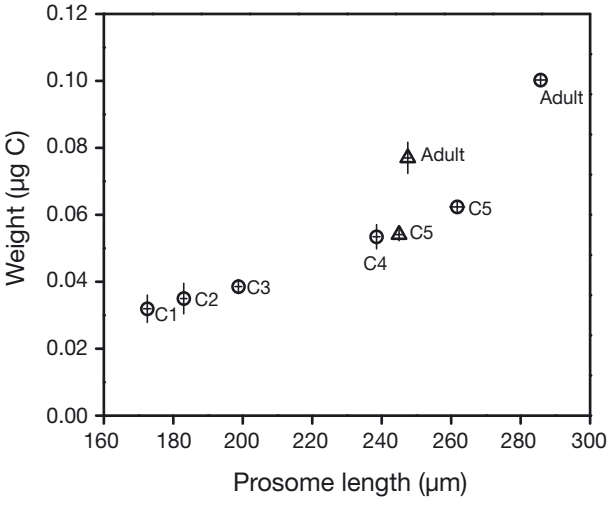

Fig. 3. *Limnoithona tetraspina.* Carbon weights and prosome lengths of copepodite stages. Identification of sex only possible for C5 and adult stages. (Δ) Males. Error bars are 95% CIs

consistent among replicates (Fig. 4). The duration of the naupliar stages ranged from 1.4 to 2.8 d. The first and second naupliar stages had the longest duration whereas the fourth and fifth naupliar stages were the shortest. The copepodite stage durations ranged from 1.7 to 4.4 d, with C5 females having the longest duration.

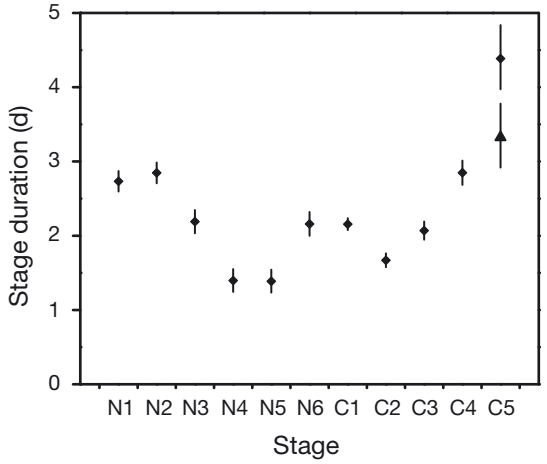

Fig. 4. *Limnoithona tetraspina*. Individual stage durations at 18°C. Identification of sex only possible for C5 stage. (▲) Males. Error bars are Bayesian 95% credible intervals

Bayesian analysis of field molt rate experiments indicated that the estimated development times increased with incubation time in 2006. The ratio of molt rates for incubation times of 48 and 72 h to those for 24 h (Φ_d) were 0.52 and 0.58, respectively.

The *in situ* development times of copepodite stages C1 to C4 at 18°C were much longer than the development times determined in the food-saturated laboratory experiments (Fig. 5). In particular, the C2 and C3 stages were consistently longer in the field than in the laboratory. The ratio of the observed number of individual copepodites (C1 to C4) that molted to the number that would molt under food-saturated conditions during each experiment as expected from laboratory development times (Φ_i, Fig. 6) was always <1 during both years, with a mean of 0.33 ± 0.15. The maximum ratio of the observed to the expected number of copepodites that molted was 0.7 in May 2006.

The growth rate of copepodites based on the laboratory development experiment was 0.06 ± 0.02 d^{-1}. The mean *in situ* growth rate of *Limnoithona tetraspina* as

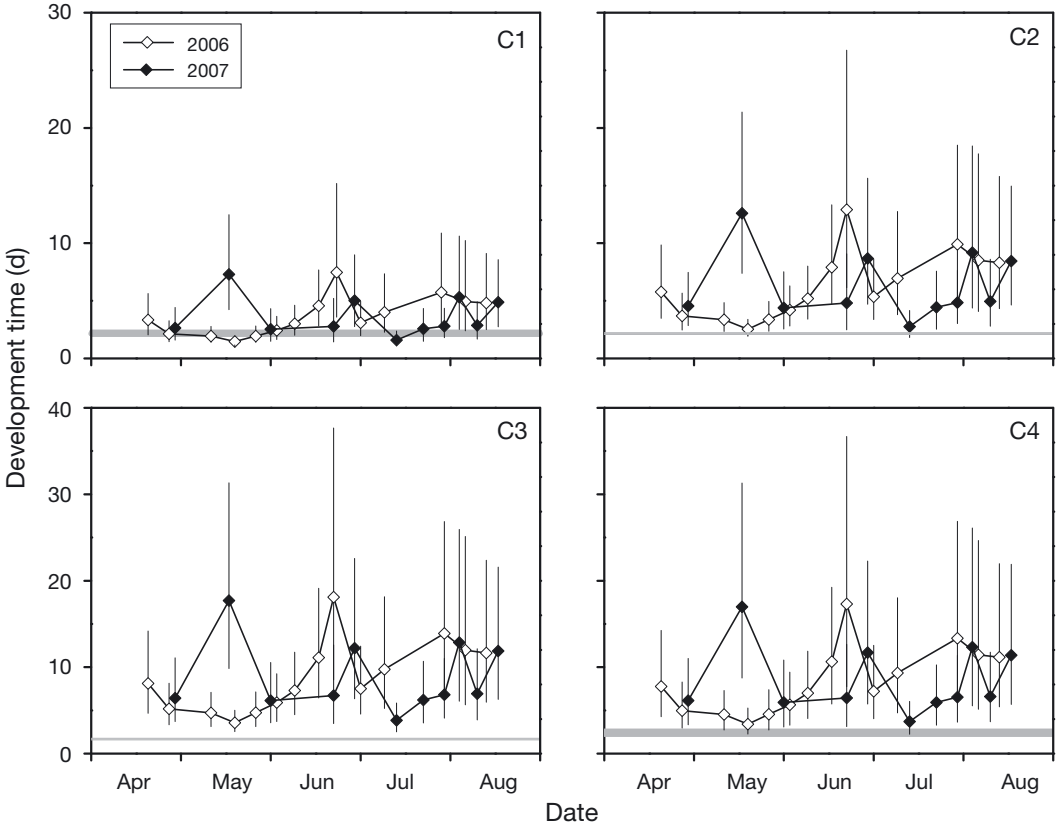

Fig. 5. *Limnoithona tetraspina*. Durations of copepodite stages (C1–C4) at 18°C as determined from molt rate experiments in 2006 and 2007. Shaded areas represent mean laboratory stage durations with 95% credible intervals at 18°C under food-saturated conditions. Note change in *y*-axis scale between top and bottom rows. Error bars are 95% CIs

determined from the molt rate experiments and adjusted for temperature during the entire study was 0.027 ± 0.015 d^{-1} and varied within each sampling year (Fig. 7). Yearly means were similar, whereas seasonal means varied greatly in 2006 and only slightly in 2007 (Table 1). The maximum and minimum growth rates observed were 0.061 and 0.0084 d^{-1} in April of 2006 and May of 2007, respectively.

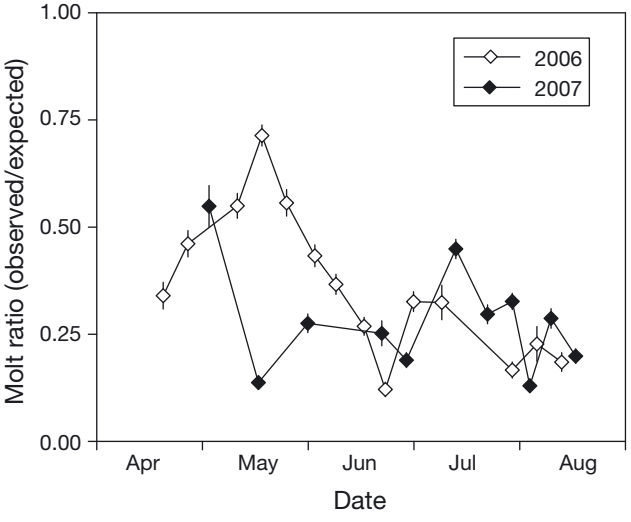

Fig. 6. *Limnoithona tetraspina.* Ratio of the observed number of individual copepodites that molted in molt rate experiments to the expected number under food-saturated conditions (Φ_i) in 2006 and 2007. Error bars are 95% CIs

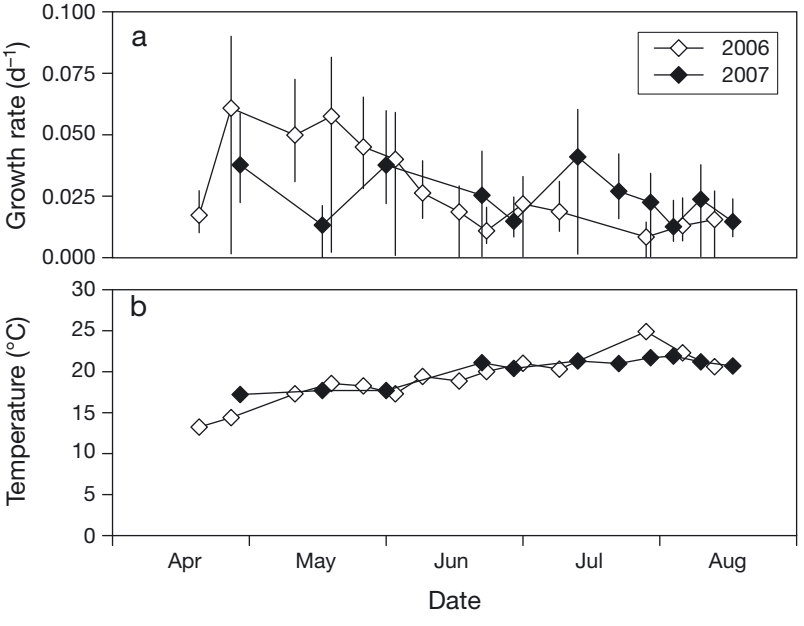

Fig. 7. *Limnoithona tetraspina.* Copepodite (C1–C4) growth rates throughout the spring and summer of 2006 and 2007 as determined from (a) molt rate experiments and corrected for (b) field temperatures. Error bars represent 95% CIs

Table 1. *Limnoithona tetraspina.* Yearly and seasonal mean growth rates and SDs among dates in the low-salinity zone

Date	Mean growth rate (d^{-1})	SD	n
2006 (Apr–Aug)	0.029	0.018	14
Spring (Apr–May)	0.046	0.017	5
Summer (Jun–Aug)	0.019	0.019	9
2007 (Apr–Aug)	0.025	0.010	11
Spring (Apr–May)	0.030	0.014	3
Summer (Jun–Aug)	0.023	0.009	8
2006 and 2007	0.027	0.015	25

Fecundity

Egg development times varied inversely with temperature, ranging from 5.7 to 1.9 d at 13 to 24°C (Fig. 8, Table 2). The effect of temperature (T) on the egg development time (D_E) of *Limnoithona tetraspina* (Fig. 9) was:

$$D_E = 22.6\ e^{(-0.103 \pm 0.004)T} \quad (r^2 = 0.99, n = 5) \quad (4)$$

The egg production rate of *Limnoithona tetraspina* varied throughout the sampling periods in 2006 and 2007 (Fig. 10). The average egg production rate as determined from the vertical tow samples at a salinity of 2 in 2007 was twice that of 2006 (Table 3). The average rate from the vertical tow samples was consistently lower than that from the bottle samples in 2007 (Fig. 10). The average egg production from the bottle samples in 2007 was 2.0 ± 0.6 eggs $female^{-1}$ d^{-1}, or a specific production rate of 0.16 ± 0.05 eggs $female^{-1}$ d^{-1}, across all salinities. Differences in egg production between the 2 sampling methods ranged from 0.069 to 1.56 eggs $female^{-1}$ d^{-1}.

DISCUSSION

In general, copepods gain about the same proportional weight at each molt; thus, an isochronal development pattern might be expected (Miller et al. 1977). Actual stage durations reflect selective pressure resulting from physiological constraints and external factors (Peterson 2001), principally predation. Therefore, stages that are consistently exposed to the highest risk of predation mortality are expected to be the shortest (Miller et al. 1977, Peterson 2001). One consequence of isochronal develop-

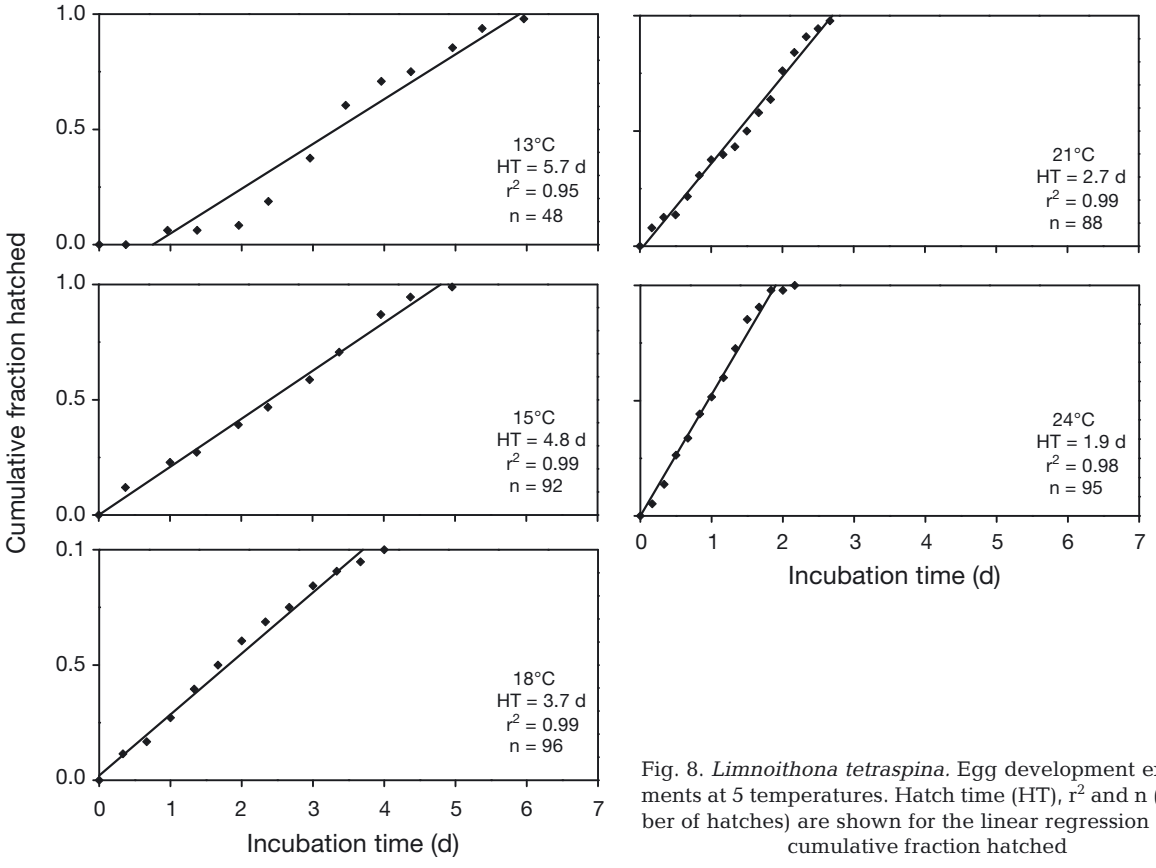

Fig. 8. *Limnoithona tetraspina.* Egg development experiments at 5 temperatures. Hatch time (HT), r^2 and n (number of hatches) are shown for the linear regression of the cumulative fraction hatched

ment, as has been seen in *Acartia* spp., is less time spent in the 5 older copepodite stages (Miller et al. 1977). This pattern may be advantageous for copepods in estuaries where the risk of predation on older stages is higher (Miller et al. 1977).

Few copepod species develop strictly isochronally (Landry 1983, Hart 1990, Peterson 2001). Common development patterns include shorter duration of the non-feeding N1 stage (Landry 1983, Peterson 2001), prolonged duration of the first-feeding stages, N2 and N3, to recover from weight loss (Landry 1983, Peterson 2001), extended duration of the N3 stage when differentiation between cells and organs occurs and the gut fully develops (Peterson 2001), and longer duration of the 5th copepodite stage which undergoes the final physical changes before sexual maturity (Landry 1983, Hart 1990, Peterson 2001). Major physiological changes occur between naupliar and copepodite stages, such as the unfolding of new mouthparts and 2 new pairs of swimming legs. The N6 stage, therefore, would be expected to be of longer duration, but is often short (Peterson 2001).

Information on the development of small cyclopoid copepod species is sparse. The development of *Oithona similis* is nearly isochronal, averaging 1.67 d stage^{-1} at 15°C (Sabatini & Kiørboe 1994). However, the development of *O. brevicornis* is not isochronal and this species has prolonged N1 and C5 stages (Uchima 1979). In contrast to many calanoids, *Oithona* spp. commence feeding at the 1st naupliar stage (Eaton 1971, Uchima & Hirano 1986, Sabatini & Kiørboe 1994) and may remain in this stage longer than in later stages.

Tight credible intervals around the development time estimates (Fig. 4) clarify that the development of *Limnoithona tetraspina* was far from isochronal. The

Table 2. *Limnoithona tetraspina.* Linear regressions from egg development time D_E experiments: $y' = 1 - y$ (y = cumulative fraction of eggs hatched) and $x = a + by'$ (x = time, in days)

Temp. (°C)	D_E (d ± 95% CI)	Total no. of hatches	No. of samples (n)	r^2	a	b
13	5.73 ± 0.52	48	13	0.95	−0.133	0.193
15	4.81 ± 0.19	92	11	0.99	0.008	0.206
18	3.70 ± 0.16	96	12	0.99	0.034	0.259
21	2.68 ± 0.088	88	17	0.99	−0.022	0.379
24	1.94 ± 0.092	95	14	0.99	0.002	0.511

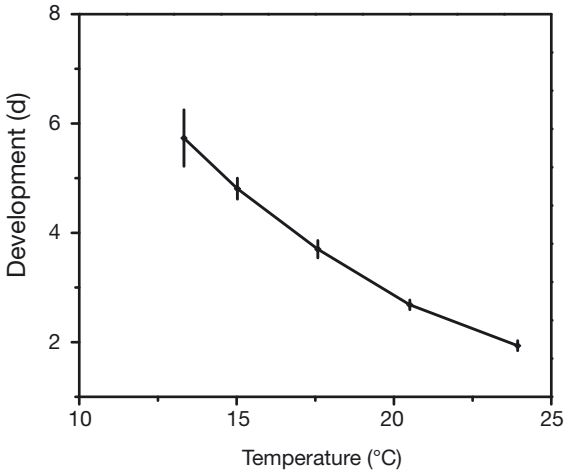

Fig. 9. *Limnoithona tetraspina.* Egg development time as a function of temperature, with fitted exponential function. Error bars are 95% CIs

N1 and N2 stages were prolonged, suggesting that feeding commences immediately after hatching. The N4 and N5 stages were the shortest, which may imply increased predation pressure on these stages. The final naupliar stage and the early copepodite stages had similar durations of ~2 d. The final copepodite stages were prolonged, but the C5 stage had the longest duration, suggesting that major morphological changes, such as sexual differentiation, may be occurring during this stage. The increased weight of adults relative to C5s was a result of having reached full sexual maturity and in the case of females, producing an egg mass internally. A larger proportion of time was spent in each copepodite stage than in later naupliar stages. This implies that selective pressures on later stages, on which the risk of visual predation in shallow waters should be highest (Kimmerer 1991, 2006), may be relatively weak.

The methods used here to determine development times produced very small errors (Fig. 4). This is a result of frequent sampling (every 12 h) from the cohorts, high replication (n = 4) compared to most studies (e.g. Klein Breteler et al. 1994, n = 2), and the use of a Bayesian model to calculate the confidence limits directly from the data. Our assumption that food was not limiting in the containers during the cohort development experiments was supported by the extremely tight confidence limits in mean development times across replicates, and by the longer development times relative to all field measurements.

Limnoithona tetraspina has been reported only in the turbid, brackish regions of the river-dominated SFE and the Yangtze River estuary in China. There have been no reported studies on the development of *L. tetraspina* in its native range. In the 16 yr that *L. tetraspina* has been in the SFE, it is possible that its development patterns have changed from those of its native range. SFE is different from typical turbid estuaries in several ways: primary production is relatively low in the LSZ, the abundance of several copepod species has declined (Kimmerer & Orsi 1996), and few filter-feeding planktivorous fish remain (Kimmerer 2006).

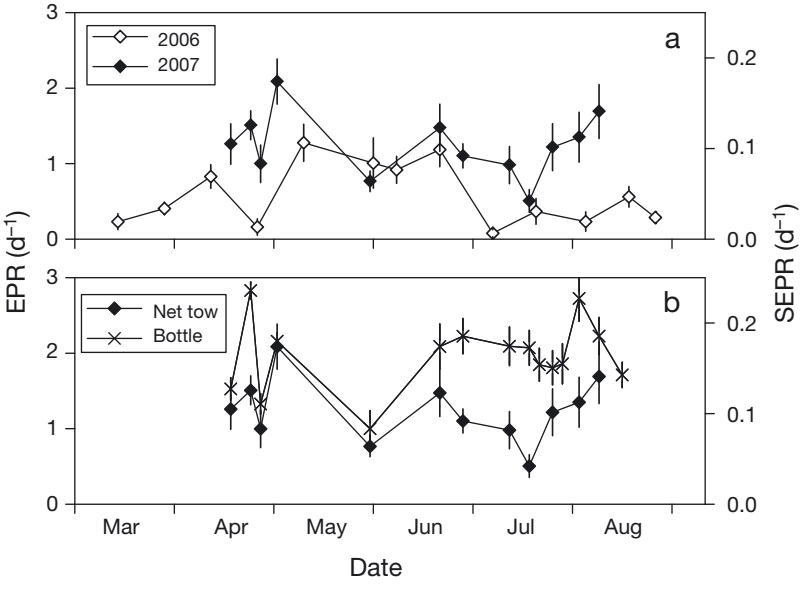

Fig. 10. *Limnoithona tetraspina.* Seasonal variation in average egg production rate (EPR) and specific egg production rate (SEPR) at a salinity of 2. (a) Rates from vertical net tows in 2006 and 2007, and (b) rates from vertical net tows and bottle samples in 2007. Error bars are 95% CIs

Development and growth rates of *Limnoithona tetraspina* were consistently lower in the field than under food-saturated laboratory conditions throughout the 2 yr study. This implies food limitation or some effect of toxins in the field. Although toxic events mostly from heavy metals associated with sediments are common in the estuary, they are usually sporadic rather than continuous (Lu et al. 2005). Therefore, low growth and development rates were probably a result of food limitation in the LSZ, which possibly drove selective pressure for stage durations of *L. tetraspina.*

Evidence from other studies of zooplankton in the upper SFE suggests that food-limited growth is chronic in the region (Müller-Solger et al. 2002, Kimmerer et al. 2005). SFE is notorious for having low primary production compared with other temperate estuaries. Mean annual phytoplankton production in the LSZ is limited by light availability

Table 3. *Limnoithona tetraspina*. Yearly and seasonal mean egg production rates (EPR) and specific production grouped by salinity and sampling method. –: no data available

Date	Salinity	n	EPR ± SD (eggs female^{-1} d^{-1})		Specific production ± SD (d^{-1})	
			Vertical tow	Bottle sample	Vertical tow	Bottle sample
2006 (Mar–Aug)	2	13	0.58 ± 0.41	–	0.045 ± 0.032	–
Spring (Mar–May)	2	6	0.65 ± 0.45	–	0.051 ± 0.035	–
Summer (Jun–Aug)	2	7	0.52 ± 0.40	–	0.040 ± 0.031	–
2007 (Mar–Aug)	2	12, 15	1.3 ± 0.42	2.0 ± 0.48	0.097 ± 0.033	0.15 ± 0.037
	0.5	9	–	1.9 ± 1.0	–	0.15 ± 0.081
	5	10	–	2.0 ± 0.51	–	0.15 ± 0.040
	0.5–5	34	–	2.0 ± 0.59	–	0.16 ± 0.046
Spring (Mar–May)	2	5, 5	1.3 ± 0.51	1.8 ± 0.73	0.10 ± 0.040	0.14 ± 0.057
	0.5–5	10	–	1.6 ± 0.67	–	0.13 ± 0.052
Summer (Jun–Aug)	2	7, 10	1.2 ± 0.38	2.1 ± 0.30	0.093 ± 0.030	0.16 ± 0.023
	0.5–5	24	–	2.2 ± 0.48	–	0.17 ± 0.038

Table 4. Weight-specific growth rate of *Limnoithona tetraspina* compared with data for oithonids. –: no data available

Copepod	Temperature (°C)	Food conditions	Growth rate (d^{-1})	Source
Oithona similis (N2–C4)	15	>5 ppm	0.200	Sabatini & Kiørboe (1994)
Oithona adults	15	10.24–0.069 µg chl *a* l^{-1}	0.071–0.204[a]	Hirst & Bunker (2003)
Oithona davisae				Uye & Sano (1998)
Nauplii	18	Food-satiated	0.183	
Copepodites	18	Food-satiated	0.170	
Juvenile sac-spawner	18	–	0.200[b]	Hirst & Bunker (2003)
Limnoithona tetraspina				Present study
Adults	18	*In situ*	0.160[c]	
Copepodites	18	*In situ*	0.024	
Copepodites	18	Food-satiated	0.060	

[a]Based on estimates of weight-specific fecundities and growth
[b]Growth rate estimated using mean *L. tetraspina* copepodite body weight (0.05 µg C ind.$^{-1}$)
[c]Weight-specific egg production rate

due to high turbidity (Cloern 1999, Jassby et al. 2002), and phytoplankton biomass is kept low by grazing by the invasive overbite clam *Corbula amurensis* (Alpine & Cloern 1992, Jassby et al. 2002). Total phytoplankton biomass at a salinity of 2 averaged only 4.3 and 2.5 mg chl *a* l^{-1} in 2006 and 2007, respectively (Lidström 2009).

Limnoithona tetraspina feeds primarily on motile prey; hence, total chl *a* biomass may not be the best indicator of food availability. Aloricate ciliates, which are a common prey item for *L. tetraspina* (Bouley & Kimmerer 2006, Gifford et al. 2007), comprised over half of the biomass of the microzooplankton collected during the present study, averaging ~4.1 mg C l^{-1}, or an average abundance of 2.7 cells ml^{-1} (J. K. York pers. comm.). This average abundance is at the lower end of the food-saturated range of *L. tetraspina* (Fig. 6 in Bouley & Kimmerer 2006), which also suggests that food limitation may be frequent in the LSZ.

Food limitation in copepods can manifest as reduced growth or development rate and reduced egg production rate. Growth and development rates appeared to be food limited in the upper SFE. Even under food-saturated conditions, *Limnoithona tetraspina* had a lower growth rate than other closely related cyclopoids (Table 4). For example, the growth rate of *Oithona similis* was 0.2 d^{-1} (Sabatini & Kiørboe 1994), which is roughly the same as that predicted for *O. davisae* at 15°C (Uye & Sano, 1998). The mean copepodite growth rate of *L. tetraspina* in the laboratory under food-saturated conditions and the maximum growth rate from field samples were both only 0.06 d^{-1}. However, the mean growth rate in the field was ~1/10 of the estimated values for other cyclopoids, averaging only 0.024 d^{-1} at 18°C (Table 4).

The low field growth rates that were observed from the molt rate experiments could also be an artifact of the experimental design. Kimmerer et al. (2007) suggested that when designing molt rate experiments to determine growth rates, the incubation time should be ~80% of the anticipated stage duration of target

stages. In food-limited systems, development times are extended, and suggested incubation times (e.g. 48 h) are too short. As seen in the present study, even incubation times greater than the target stage durations (72 h) were not long enough to observe molting. There was evidence from the 2006 data that development was slowing as incubations progressed beyond 24 h; hence, the values of Φ_d were <1 at incubation times of 2 or 3 d. This is likely due to depletion of the food supply within the container with increasing incubation time. In 2007, individuals were incubated in larger volumes (40 ml) to minimize the effect of food depletion. The low fraction of individuals that molted in each experiment contributed to the rather large uncertainties surrounding the resulting stage durations (Fig. 5). We therefore suggest that the best incubation time for molt rate experiments should be determined in pilot studies to ensure adequate food supply throughout the experiment, thereby minimizing delayed development and allowing most individuals to molt.

An advantage of using the Bayesian approach for calculating growth rates from the molt rate method is the ability to carry errors forward, including errors from the experimental design and sampling as well as errors associated with calculating each variable in the growth model (Eq. 2). The large error of the growth rates compared to those for the development times is associated with the large errors in copepodite stage weights, particularly in stages C1 and C2. The weight gain from the 1st to the 2nd copepodite stage was small and the confidence limits on the mean weight estimates of these stages overlapped, although the prosome lengths were clearly greater in C2 than in C1 (Fig. 3). Coupled with the small actual weight gain observed is the lower precision in measurements of such small weights.

The egg production rate of *Limnoithona tetraspina* was also lower than those reported for other cyclopoid copepods (Table 5). The average egg production rate for *Oithona* spp. was reported to be between 2.0 and 4.5 eggs female^{-1} d^{-1} at temperatures of 15 to 20°C (Table 5). The average egg production rate of *L. tetraspina* from the bottle samples was 2 eggs female^{-1} d^{-1}. Bunker & Hirst (2004) predicted the egg production rate of sac-spawners at the mean body weight of adult female *L. tetraspina* to be 1.7 eggs female^{-1} d^{-1}. This value falls within the range of the observed egg production rate of *L. tetraspina* in the present study. Therefore, the low egg production rate of *L. tetraspina* may be a function of their lower body weight compared to other copepods. Egg production rates of sac-spawners in general, and *Oithona* species in particular, are insensitive to food as indexed by chlorophyll concentration (Bunker & Hirst 2004).

The egg production rates from the net tows were consistently lower than those from the bottle samples. This suggests that the vertical net tows yielded an underestimate of egg production for these sac-carrying cyclopoids, likely due to loss of egg sacs from net abrasion and turbulence, as has been previously reported for cyclopoids (e.g. Hopcroft & Roff 1998). We do not know why this effect appeared greater in summer than in spring. In any case, bottle sampling is preferable to net sampling for accurately determining egg production rates of small, sac-carrying copepods.

Food limitation of copepods usually affects older stages more than the earlier stages, and egg production is usually the most affected rate (Richardson & Verheye 1998, Finlay & Roff 2006, Leandro et al. 2006). This was not the case with *Limnoithona tetraspina*. The somatic growth rate of copepodites was usually below maximum, whereas egg production as specific growth rate was higher than somatic growth and close to literature values reported for *Oithona* spp. (Table 5). *L. tetraspina* adults appear to be less food limited than copepodites, suggesting different dietary requirements for egg production and

Table 5. Egg and weight-specific production rates of *Limnoithona tetraspina* compared with data for oithonids. –: data not available

Copepod	Temperature (°C)	Egg production rate (eggs female^{-1} d^{-1} ± SD)	Specific production rate (d^{-1} ± SD)	Source
Oithona davisae	18	–	0.214	Uye & Sano (1998)
Oithona similis	11	1.6 ± 0.30	–	Castellani et al. (2005)
	15	4.5 ± 0.090	0.100 ± 0.004	Sabatini & Kiørboe (1994)
Oithona colcarva	15	2	–	Lonsdale (1981a,b)
	20	3.6	–	
Oithona plumifera	20	3.8	–	Paffenhöfer (1993)
Oithona spp.	15	2.6–4.6	–	Bunker & Hirst (2004)
Sac-spawners	18	1.7[a]	–	Bunker & Hirst (2004)
Limnoithona tetraspina	18	2.0 ± 0.59[b]	0.16 ± 0.046	Present study

[a]Based on calculations using mean female body weight of *L. tetraspina* (0.10 µg C)
[b]Mean egg production rate estimated from bottle samples only

somatic growth. This reversal of the expected pattern of food limitation by life stage remains unexplained. The present study did not examine the field growth rate of *L. tetraspina* nauplii, so their response to food limitation is unknown.

The mean growth rates of *Limnoithona tetraspina* did not differ between the 2 yr, but the mean egg production rate of *L. tetraspina* from the vertical tow samples was 2-fold higher in 2007 than in 2006 (Table 3). Some of the differences in egg production rates between the 2006 and 2007 net tows may have been a result of the loss of eggs due to the sampling method. The fecundity of *L. tetraspina* may have also been more food limited in 2006, when high runoff increased freshwater flow into the LSZ (Fig. 2) and moved the LSZ far seaward. Copepod egg production varies with food quality and quantity (Durbin et al. 1983, Kleppel et al. 1998). For example, the egg production rate of *Oithona similis* increased with both food concentration and the addition of a heterotrophic dinoflagellate to the diet (Sabatini & Kiørboe 1994). The difference in egg production of *L. tetraspina* between 2006 and 2007 may have been a result of unobserved changes in the microzooplankton community that was available as prey.

Despite low growth and fecundity rates in the SFE, the population of *Limnoithona tetraspina* is thriving. Therefore, the mortality rates of *L. tetraspina* must also be low. We estimated approximate life-cycle mortality using Eq. (1) in Hirst & Kiørboe (2002). Inputs included egg production rates and development times for nauplii from the laboratory and for copepodites from the field. The sex ratio of adults was ~1:1 in our samples. This gave a mortality rate for all life stages of 0.05 d^{-1}, which is well below the lower error limits for predictions of the global model of Hirst & Kiørboe (2002), this global model predicting a mean mortality of 0.18 d^{-1} for sac-spawners at 20°C.

The low mortality of *Limnoithona tetraspina* is consistent with the theory that copepod populations are generally less sensitive to variation in fecundity than to variation in mortality (Kiørboe 1998). In the upper SFE, predation is dominated by visual fish predators and the benthic grazer *Corbula amurensis*. The effect of *C. amurensis* on the mortality rates of *L. tetraspina* is unknown. Visual fish predation can cause high mortality of larger copepods, favoring smaller copepods (Kimmerer 1991). An individual *L. tetraspina* has a biomass that is 1/10 that of larger calanoid copepods in the region and may not be energetically cost-effective for visual predators to consume (Brooks & Dodson 1965). The behavior of *L. tetraspina* may also lower their mortality risks. Like many cyclopoids, *L. tetraspina* behaves as an ambush predator, minimizing its movement, and therefore also its detectability, in the water column (Paffenhöfer 1993, Bouley & Kimmerer 2006). In addition, the low mortality of copepods could be a result of the recent collapse of several fish populations in the upper SFE (Kimmerer 2006, Sommer et al. 2007), and the relatively low abundance of gelatinous zooplankton predators (Orsi & Mecum 1986, Kimmerer 2006).

The low mortality implies that *Limnoithona tetraspina* is not contributing much to higher trophic levels, and is acting as somewhat of a dead-end in the food-web of the LSZ. At such high abundances, *L. tetraspina* may have a significant impact on similar microzooplankton that are preyed upon by other omnivorous copepods in the region. *L. tetraspina* may be competing for prey with such copepods as the calanoid *Pseudodiaptomus forbesi* that are important prey for fish such as the endangered delta smelt *Hypomesus transpacificus* (Sommer et al. 2007). These calanoid copepod populations also appear to be food limited (W. J. Kimmerer unpubl.) and the populations of delta smelt and several other fish species are declining (Sommer et al. 2007). It, therefore, seems possible that the characteristics of *L. tetraspina*, which are unusual in a temperate estuarine copepod, could be contributing to the decline in fish abundances in the LSZ.

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LITERATURE CITED

Abiahy BB, da Rocha CEF, Ferrari FD (2006) Redescription of *Limnoithona tetraspina* Zhang et Li, 1976 (Copepoda, Cyclopoida) with a discussion of character states shared with the Oithonidae and older cyclopoids. Invertebr Zool 3: 115–135

Alpine AE, Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946–955

Banse K (1995) Zooplankton: pivotal role in the control of ocean production. ICES J Mar Sci 52:265–277

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

Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. Science 150:28–35

Bunker AJ, Hirst AG (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

Castellani C, Irigoien X, Harris RP, Lampitt RS (2005) Feeding and egg production of *Oithona similis* in the North Atlantic. Mar Ecol Prog Ser 288:173–182

Cloern JE (1999) The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment. Aquat Ecol 33:3–15

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Corkett CJ, McLaren IA (1970) Relationships between development of eggs and older stages of copepods. J Mar Biol Assoc UK 50:161–168

Durbin EG, Durbin AG, Smayda TJ, Verity PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol Oceanogr 28: 1199–1213

Eaton JM (1971) Studies on the feeding and reproductive biology of the marine cyclopoid copepod *Oithona similis* Claus. PhD thesis, Dalhousie University, Halifax

Edmondson WT (1971) Reproductive rates determined directly from egg ratios. In: Edmondson WT, Winberg GG (eds) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific, Oxford, p 165–169

Finlay K, Roff JC (2006) Ontogenetic growth rate responses of temperate marine copepods to chlorophyll concentration and light. Mar Ecol Prog Ser 313:145–156

Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? J Plankton Res 23: 1421–1432

Gelman A, Carlin JB, Stern HS, Rubin DB (2004) Bayesian data analysis. CRC Press, Boca Raton, FL

Gifford SM, Rollwagen Bollens GC, Bollens SM (2007) Mesoplankton omnivory in the upper San Francisco Estuary. Mar Ecol Prog Ser 348:33–46

Hart RC (1990) Copepod post-embryonic durations: pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodid-naupliar duration. Hydrobiology 206:175–206

Hirst AG, Bunker AJ (2003) Growth in marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature and body weight. Limnol Oceanogr 48:195–209

Hirst AG, Peterson WT, Rothery P (2005) Errors in juvenile copepod growth rate estimates are widespread: problems with the Moult Rate method. Mar Ecol Prog Ser 296:263–297

Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. Mar Ecol Prog Ser 230:195–209

Hopcroft RR, Roff JC (1998) Zooplankton growth rates: the influence of size in nauplii of tropical marine copepods. Mar Biol 132:87–96

Jassby AD, Cloern JE, Cole BE (2002) Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnol Oceanogr 47:698–712

Johnson WS, Allen DM (2005) Zooplankton of the Atlantic and Gulf Coasts. JHU Press, Baltimore, MD

Kimmerer WJ (1991) Predatory influences on copepod distributions in coastal waters. Proc 4th Int Conf on Copepoda: Bull Plankton Soc Jpn, p 161–174

Kimmerer WJ (2006) Response of anchovies dampens food-web responses to an invasive bivalve (*Corbula amurensis*) in the San Francisco Estuary. Mar Ecol Prog Ser 324: 207–218

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

Kimmerer WJ, McKinnon AD (1986) Glutaraldehyde fixation to maintain biomass of preserved plankton. J Plankton Res 8:1003–1008

Kimmerer WJ, Orsi JJ (1996) Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In: Hollibaugh JT (ed) San Francisco Bay: the ecosystem. AAAS, San Francisco, CA, p 403–424

Kimmerer WJ, Gartside E, Orsi JJ (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 WJ, Nicolini MH, Ferm N, Peñalva C (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 WJ, Hirst AG, Hopcroft RR, McKinnon AD (2007) Estimating juvenile copepod growth rates: corrections, inter-comparisons and recommendations. Mar Ecol Prog Ser 336:187–202

Kiørboe T (1998) Population regulation and role of mesozooplankton in shaping marine pelagic food webs. Hydrobiology 363:13–27

Klein Breteler WCM, Schogt N, van der Meer J (1994) The duration of copepod life stages estimated from stage-frequency data. J Plankton Res 16:1039–1057

Kleppel GS, Burkart CA, Houchin L (1998) Nutrition and regulation of egg production in the calanoid copepod *Acartia tonsa*. Limnol Oceanogr 43:1000–1007

Landry MR (1983) The development of marine calanoid copepods with comment on the isochronal rule. Limnol Oceanogr 28:614–624

Leandro SM, Tiselius P, Queiroga H (2006) Growth and development of nauplii and copepodites of the estuarine copepod *Acartia tonsa* from southern Europe (Ria de Aveiro, Portugal) under saturating food conditions. Mar Biol 150:121–129

Lidström UE (2009) Primary production, biomass and species compositions of phytoplankton in the low salinity zone of the northern San Francisco Estuary. MSc thesis, San Francisco State University, San Francisco, CA

Lonsdale DJ (1981a) Influence of age-specific mortality on the life history of two estuarine copepods. Mar Ecol Prog Ser 5:333–340

Lonsdale DJ (1981b) Regulatory role of physical factors and predation for two Chesapeake Bay copepod species. Mar Ecol Prog Ser 5:341–351

Lu XQ, Werner I, Young TM (2005) Geochemistry and bioavailability of metals in sediments from northern San Francisco Bay. Environ Int 31:593–602

Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Stat Comput 10:325–337

McLaren IA (1995) Temperature-dependent development in marine copepods: comments on choices of models. J Plankton Res 17:1385–1390

Miller CB, Johnson JK, Heinle DR (1977) Growth rules in the marine copepod genus *Acartia*. Limnol Oceanogr 22: 326–335

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

Nakamura Y, Turner JT (1997) Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? J Plankton Res 19:1275–1288

Nielsen TG, Møller EF, Satapoomin S, Ringuette M, Hopcroft RR (2002) Egg hatching rate of the cyclopoid copepod *Oithona similis* in Arctic and temperate waters. Mar Ecol Prog Ser 236:301–306

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

Orsi JJ, 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

Paffenhöfer GA (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). J Plankton Res 15: 37–55

Peterson WT (2001) Patterns in stage duration and development among marine and freshwater calanoid and cyclopoid copepods: a review of rules, physiological constraints, and evolutionary significance. Hydrobiologia 453–454:91–105

Richardson AJ, Verheye HM (1998) Growth rates of copepods in the southern Benguela upwelling system: the interplay between body size and food. Limnol Oceanogr 44: 382–392

Sabatini M, Kiørboe T (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis.* J Plankton Res 16:1329–1351

Sommer T, Armor C, Baxter R, Breuer R and others (2007) The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries (Bethesda) 32:270–277

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine foodwebs. Zool Stud 43:255–266

Twombly S, Burns CW (1996) Exuvium analysis: a nondestructive method of analyzing copepod growth and development. Limnol Oceanogr 41:1324–1329

Uchima M (1979) Morphological observation of developmental stages in *Oithona brevicornis* (Copepoda, Cyclopoida). Bull Plankton Soc Jpn 26:59–76

Uchima M, Hirano R (1986) Food of *Oithona davisae* (Copepoda, Cyclopoida) and the effect of food concentration at first feeding on the larval growth. Bull Plankton Soc Japan 33:21–28

Uye S, 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, 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

Williams JA, Muxagata E (2006) The seasonal production and abundance of *Oithona nana* (Copepoda: Cyclopoida) in Southampton Water. J Plankton Res 28:1055–1065

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