Predation impact of *Acartiella sinensis*, an introduced predatory copepod in the San Francisco Estuary, USA

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ABSTRACT: The San Francisco Estuary (SFE), USA, is a highly invaded ecosystem where most of the zooplankton assemblage is exotic. *Acartiella sinensis* was introduced from Asia in 1993 and has become abundant (mean adult abundance ~500 ind. m^{-3}) in brackish water during summer. The morphology of *Acartiella* species suggests a predatory habit, but predation by this genus has never been quantified. The introduction of *A. sinensis* to the upper, brackish region of the SFE coincided with several other introductions, so its predation impact could not be determined from time-series data. We determined functional responses of *A. sinensis* feeding on 2 other introduced copepod species, including several life stages of the highly abundant cyclopoid *Limnoithona tetraspina* and nauplii of *Pseudodiaptomus forbesi*, and extrapolated predation rates to the field to determine predation impact on copepod populations. Predation rates of adult female *A. sinensis* were higher on *L. tetraspina* nauplii than on adults or copepodites, and highest on *P. forbesi* nauplii, although prey selection experiments did not show a difference in consumption rate between nauplii of the 2 species. Mean clearance rates on nauplii at low density were 0.3 l d^{-1} on *L. tetraspina* and 0.6 l d^{-1} for *P. forbesi*. Predatory impact based on long-term monitoring data averaged 1% d^{-1} for adults and copepodites, and 4 and 11% d^{-1} for nauplii of *L. tetraspina* and *P. forbesi*, respectively. These predation losses are high relative to the population growth potential of these species in this unproductive region.

KEY WORDS: Functional response · Food limitation · Low-salinity zone · Food web · *Limnoithona tetraspina* · *Pseudodiaptomus forbesi*

INTRODUCTION

Copepods are key consumers in aquatic food webs, and their species composition, feeding behavior, and population dynamics can have substantial effects on the transfer of energy from microbes to higher trophic levels (Runge 1988). This key role linking trophic levels within a complex food web is controlled in part by predator–prey interactions, which can affect species and size composition, distribution, and behavior of prey (Brooks & Dodson 1965). Therefore, the introduction of a predatory organism can substantially dis-

rupt extant aquatic food webs (Grosholz et al. 2000, Gorokhova et al. 2005).

The San Francisco Estuary (SFE), USA, is a large temperate estuary with a highly invaded ecosystem (Cohen & Carlton 1998). Introductions of zooplankton have shifted the zooplankton assemblage of the upper, brackish to fresh region of the estuary to an 'east Asian fauna' dominated almost entirely by copepods introduced from high-flow estuaries in mainland Asia (Orsi & Ohtsuka 1999). Furthermore, grazing by the clam *Potamocorbula amurensis*, also introduced from east Asia, since 1987 has eliminated summer-long phytoplankton blooms and reduced abundance

of previously common zooplankton species (Alpine & Cloern 1992, Kimmerer et al. 1994, Kimmerer & Lougee 2015). Declines in abundance and evidence of food limitation of several pelagic (some endemic) fishes in the low-salinity and freshwater habitats of the SFE have prompted further investigations into food web interactions within these habitats (Kimmerer 2006, Sommer et al. 2007, York et al. 2011).

Acartiella sinensis (Calanoida, family Acartiidae) was first detected in the SFE in October 1993, and by July 1994, adult abundance had exceeded 1000 individuals (ind.) m^{-3} (Orsi & Ohtsuka 1999). Originally reported from Leizhou Peninsula at the southern tip of the Chinese mainland (Shen & Lee 1963), it has been found from Hangzhou in the north to the Mekong River Delta in the south (Xu et al. 2008, Campbell 2012), and in Thailand (cited in Orsi & Ohtsuka 1999). This tropical, stenothermal species is characteristic of warm, turbid rivers of mainland East Asia (Ohtsuka et al. 1995, Orsi & Ohtsuka 1999). *A. sinensis* has been characterized as a 'suspension-feeding omnivore' (Orsi & Ohtsuka 1999) or an omnivore-carnivore (Chen 2012).

Acartiella species are superficially similar to the much-studied genus *Acartia*, and morphological evidence places them in the same family (Bradford 1976, Barthélémy 1999). *Acartia* species are generally considered omnivorous: they can consume nauplii (Lonsdale et al. 1979) and often consume microzooplankton (Stoecker & Egloff 1987), but also consume phytoplankton, and many *Acartia* species have been cultured on diets of phytoplankton alone (Iwasaki et al. 1977, Støttrup et al. 1986, Trujillo-Ortíz 1990, Knuckey et al. 2005).

Despite their taxonomic proximity, key morphological differences, particularly in the shape of the mandible blade (Tranter & Abraham 1971), limit the ability to infer *Acartiella*'s ecology from that of *Acartia*. The jagged mandible blades of *Acartiella* species appear better suited to tearing than grinding, pointing to a more carnivorous feeding mode than that of other members of the family (Anraku & Omori 1963, Tranter & Abraham 1971).

Little is known of the ecology of *Acartiella* species, and reports from the native range of *A. sinensis* are generally limited to distribution, phylogeny, and morphology (Lian & Lin 1985, Fang et al. 2009, Zhang et al. 2012). A recent study in the St. Lucia estuary, South Africa, showed removal of chlorophyll by *A. natalensis* incubated in natural water (Carrasco et al. 2013). In contrast, *A. sinensis* consumed copepod nauplii and did not appear to consume protists in the SFE (York et al. 2014). *A. sinensis* is consumed by

hydrozoans (Wintzer et al. 2011) and juvenile fish in the SFE (e.g. delta smelt *Hypomesus transpacificus*, Slater & Baxter 2014).

Planktivores can significantly influence the distribution and composition of their zooplankton prey (e.g. Brooks & Dodson 1965, Steele & Frost 1977, Deason & Smayda 1982). Sudden changes in aquatic food webs upon introduction of predators and grazers have had clear and immediate effects, as shown for bivalves (Alpine & Cloern 1992, Strayer 2009), predatory cladocera (Gorokhova & Hansson 1997, Yan & Pawson 1997), ctenophores (Shushkina & Musaeva 1990), and fish (Zaret & Paine 1973). However, ecosystems are dynamic and ever-changing, and the effects of invasions can be either obscured or amplified by other concurrent changes (Daskalov et al. 2007).

In contrast to the examples cited above, consequences of the introduction of *A. sinensis* are shrouded in complexity. *A. sinensis* became abundant only a few years after the introduction of *Potamocorbula amurensis* (Alpine & Cloern 1992) and an omnivorous calanoid copepod, *Pseudodiaptomus forbesi*, and in the same year as the copepods *Limnoithona tetraspina* (an ambush predator on microzooplankton) and *Tortanus dextrilobatus* (a predatory copepod). These nearly concurrent introductions make it impossible to identify the effects of *A. sinensis* through analysis of change-points in abundance of potential prey or other food web attributes. Determining these effects requires process-based studies combined with data on temporal patterns of abundance of predators and potential prey.

The present study set out to determine the influence of predation by *A. sinensis* on the population dynamics of *P. forbesi* and *L. tetraspina* in brackish waters of the SFE. Samples were taken at salinities of 0.1 to 2.0 in Suisun Bay or the western Sacramento-San Joaquin Delta (see Fig. 1), where the distributions of *A. sinensis*, *L. tetraspina*, *P. forbesi*, and the endangered delta smelt *H. transpacificus* overlap. *P. forbesi* was first detected in the SFE in 1987 and became abundant in fresh to brackish waters (Orsi & Walter 1991). Declining abundance after approximately 1993 raised concern because of its importance as a food source for juvenile fish, including delta smelt, that were themselves in decline (Sommer et al. 2007, Slater & Baxter 2014). *L. tetraspina*, a much smaller cyclopoid copepod, was first detected in September 1993 (Orsi & Ohtsuka 1999) and has since been the numerically dominant copepod in brackish waters of the estuary (Bouley & Kimmerer 2006, Gould & Kimmerer 2010, see Fig. 2). All 3 species are most abundant in summer to autumn.
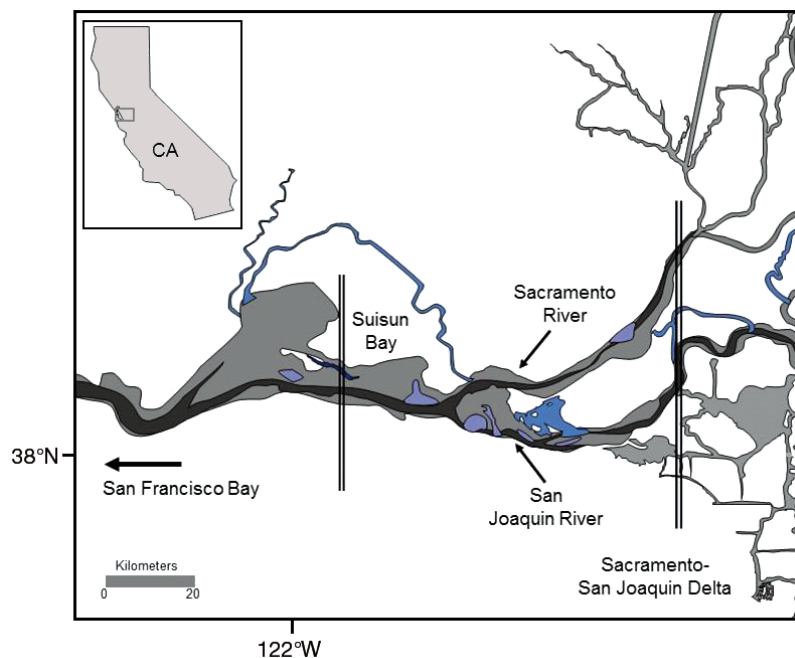
Fig. 1. Approximate range of zooplankton sampling locations in the San Francisco Estuary. Inset shows the estuary location within California, USA. Sampling was conducted based on salinity in 2006 and 2007, and on geographically fixed stations in 2008 and 2010 to 2012; all data are from stations within Suisun Bay and the western Delta. Double vertical lines indicate westernmost (left) and easternmost (right) boundaries of sampling region

We examined the functional responses and selectivity of *A. sinensis* predation on these 2 co-occurring copepods, focusing on nauplii of *P. forbesi* and all stages of *L. tetraspina* because previous results indicated predation on small copepods (York et al. 2014). The ratio of prey to predator biomass is approximately 5% for *P. forbesi* nauplii (based on *P. marinus*, Vogt et al. 2013), and approximately 0.5, 1, 3, and 5% respectively for nauplii, copepodites, and adult males and females of *L. tetraspina* (Gould & Kimmerer 2010, York et al. 2014). We then applied these predation rates to estimates of abundance in the low-salinity zone of the SFE using data from several short-term studies (2006 to 2012) and long-term monitoring (1994 to 2012) to estimate the predation impact of *A. sinensis*.

MATERIALS AND METHODS

Copepod abundance

Data on abundance of *Acartiella sinensis* and potential prey were obtained from 3 previous studies and used to estimate predation impact.

Study 1. Discrete zooplankton samples were collected every 1 or 2 wk in March to August of 2006 to 2007 (at fixed surface salinities 0.5, 2 and 5) and twice in July 2008 at geographically fixed, along-river transects (Kimmerer et al. 2014) (Fig. 1). Zooplankton was collected by vertical tow of a 53 µm mesh, 0.5 m diameter plankton net from 1 m off the bottom or at most 10 m depth to the surface. Bottom depths ranged from 2 to 21 m. Sample volumes were determined from the mouth area of the net and distance towed, using a net efficiency of 70% based on repeated tows with the same net equipped with a General Oceanics 2030R flow meter. Samples were stained with Rose Bengal and preserved in 4% formaldehyde buffered with sodium borate. A quantitative subsample was removed from a known volume by Stempel pipette from each sample to obtain at least 100, and typically 200 to 400, individuals of the numerically dominant taxa. All individuals in the subsample were counted and identified to species and gross life stage (e.g. nauplius [NI to NVI], copepodite [CI to CV], adult [CVI] male, adult [CVI] female) under an Olympus SZ16 dissecting microscope (25× to 50× magnification).

Study 2. Samples were taken during August to October of 2010 to 2012 on a total of 10 along-river transects each in the Sacramento and San Joaquin Rivers (Fig. 1). Sampling methods were the same as in the 2006 to 2008 study (Study 1), at geographically fixed sampling stations approximately 3 km apart. These stations were selected for other purposes and the salinity ranges varied with freshwater flow.

Study 3. Long-term zooplankton monitoring data (1994 to 2012) were obtained from the Interagency Ecological Program (Orsi & Mecum 1986; metadata at www.water.ca.gov/bdma/meta/zooplankton.cfm). Samples were collected monthly by oblique tow of a 154 µm mesh, 0.127 m diameter Clarke-Bumpus net equipped with a flowmeter, and with a plankton pump from which samples were size fractionated between 45 and 154 µm (Orsi & Mecum 1986). The sum of abundance (ind. m^{-3}) from the 2 sets of samples was used for this analysis. All data were reduced to samples taken during July to October, when *A. sinensis* and its prey are abundant. We converted surface electrical conductance values to salinity using the 1978 Practical Salinity Scale (UNESCO 1981).

Copepods in the monitoring data (Study 3) were identified to species (mostly adults, which were not

sexed) or genus (copepodites). *Limnoithona tetraspina* copepodites were identified starting in 1995, so we estimated copepodite abundance for 1994 as the median ratio of copepodite to adult abundance during 1995 to 2012 times adult abundance in 1994. Similar calculations were made for *A. sinensis* whose copepodites were identified starting in 2006. Total copepod nauplii were reported for every sample. *A. sinensis* and *L. tetraspina* nauplii were not identified separately, and *Pseudodiaptomus forbesi* nauplii were identified starting in 2000. We extended this record back as for copepodites, but using the ratio of *P. forbesi* nauplii to the sum of copepodite and adult abundance.

L. tetraspina adults in the monitoring data (Study 3) were distinguished from those of its very similar congener *L. sinensis* starting in 2007. First detected in 1979, *L. sinensis* is most abundant in freshwater, and total abundance of *Limnoithona* species increased by approximately 2 orders of magnitude between 1980–1992 and 1994 (Ferrari & Orsi 1984, Orsi & Ohtsuka 1999, Bouley & Kimmerer 2006). Data from the monitoring program from 2007 onwards show that *L. sinensis* comprised only 0.01% (mean) of total adult *Limnoithona* and only 20 of 300 samples had any *L. sinensis*. We therefore assumed all *Limnoithona* after 1993 to be *L. tetraspina* and refer to them as such, although it is likely that a small fraction (≪1%) of them were *L. sinensis*.

Most nauplii were not identified to species in the monitoring data (Study 3), but all were identified in the short-term studies (Studies 1 and 2). Most of the nauplii other than *P. forbesi* in samples from our short-term studies were *L. tetraspina* (i.e. median 95% of total nauplii in Study 1 and 96% in Study 2). We assumed that all unidentified nauplii in the monitoring data were *L. tetraspina*.

We used the monitoring data to determine a suitable salinity range for analysis. Salinity values were divided into 25 bins of approximately equal size, and mean abundance of adult copepods was determined for each bin. A salinity range of 0.4 to 12 encompassed all salinity bins with a mean abundance of at least 20% of the maximum for *A. sinensis* (see 'Results'). Limiting the data to this salinity range gave the following number of samples: Study 1, 3 to 12 samples per sample date; Study 2, 1 to 8 sam-

ples for each of 9 transects, with 1 transect omitted because no samples had salinity >0.4; and Study 3, 28 to 49 samples yr^{-1} beginning in 1994 (>180 yr^{-1} from 1988 to 1994).

Experiments

We conducted experiments to determine the functional responses (Expts 1 to 6) and feeding selectivity (Expts 7 to 11) of *A. sinensis* (Table 1). Copepods used in feeding experiments were collected in July 2008 and October to November 2010 to 2011 by horizontal tows of a 53 or 200 µm mesh, 0.5 m diameter plankton net. Captured plankton were diluted into 20 l insulated buckets containing surface water collected at the same time and transported to the Romberg Tiburon Center. Surface temperature and salinity were measured using a YSI 30 digital salinometer (Table 1). Feeding experiments followed methods used in previous studies with other carnivorous copepods (Ambler & Frost 1974, Mullin 1979, Hooff & Bollens 2004) except as noted below. Because we used field-collected predators and prey, processing time was kept as short as feasible (2 to 5 h) and experiments were designed with small bottles containing low total numbers of copepods (i.e. at ecologically relevant predator and prey densities). This choice limited precision of each experiment but avoided the artifacts associated with using cultured copepods.

Functional responses were determined on single prey taxa and life stages (Table 1). *Limnoithona* nau-

Table 1. *Acartiella sinensis*. Experimental conditions for functional response and selection experiments: date, prey type, number of prey and predators, container volume, and temperature and salinity. Prey are *Pseudodiaptomus forbesi* (Pf) and *Limnoithona tetraspina* (Lt) at life stage adult (A), copepodite (C), or nauplius (N)

Expt	Date	Prey	No. prey	No. predator	Vol. (ml)	Temp. (°C)	Salinity
Functional response							
1	10 Jul 2008	Lt N	6, 12, 25, 50	1	595	18	1.9
2	10 Jul 2008	Lt A	6, 12, 25, 50	2	595	18	1.9
3	14 Jul 2008	Lt N	6, 12, 25, 50	1	595	18	2.0
4	14 Jul 2008	Lt A	6, 12, 25, 50	2	595	18	2.0
5	9 Nov 2010	Lt C	6, 12, 25, 50	1	1000	15	1.5
6	26 Oct 2010	Pf N	1, 2, 4, 8, 16, 32	1	1000	19	1.6
Selection							
7	16 Nov 2010	Pf N + Lt N	25 + 25	1	1000	16	1.2
8	18 Oct 2011	Pf N + Lt N	12 + 12	1	1000	19	0.1
9	18 Oct 2011	Pf N + Lt C	12 + 12	1	1000	19	0.1
10	25 Oct 2011	Pf N + Lt N	12 + 12	1	1000	19	0.6
11	25 Oct 2011	Pf N + Lt C	12 + 12	1	1000	19	0.6

plii (mainly NII to NIV; median stages were NIV in Expt 1 and NIII in Expt 3), copepodites (CII to CIII), and adults, and *P. forbesi* nauplii (NIV to NV) were sorted from samples with glass pipets under a dissecting microscope. The range of stages in any one experiment was kept as tight as feasible (i.e. within 1 to 3 life stages) while sorting quickly. Copepods were transferred to 595 or 1000 ml polycarbonate incubation bottles containing 35 µm filtered ambient water. The 35 µm filter removed potential prey and competitors of sizes similar to our target organisms but other, smaller, organisms (e.g. 1 to 2 rotifers or copepod nauplii or eggs per bottle) were typically present. Initial prey densities were 6, 12, 25, or 50 *L. tetraspina* or 1, 2, 4, 8, 16, or 32 *P. forbesi* per container (Table 1). Adult female *A. sinensis* (1 each in nauplius and copepodite prey bottles; 2 in adult prey bottles) were placed into each incubation container to initiate the experiment. A total of 3 or 4 replicates per treatment (predator + prey) and recovery control (prey only) were prepared. Bottles were placed on a plankton wheel rotating at 1 rpm for 24 h in a temperature- and light-controlled room set to near-ambient conditions (15 to 19°C, 12 h light:12 h dark cycle). The illumination level inside the temperature-controlled room during the light phase was approximately 17 µmol m^{-2} s^{-1}, which would have provided sufficient light for phytoplankton growth within experiment containers (Kimmerer et al. 2012). At the termination of each experiment, we noted if the *Acartiella* predator was alive (active) or dead (inactive). The contents of each bottle were then filtered onto a 35 µm mesh sieve, transferred to a 20 ml glass vial, stained with vital neutral red (to confirm copepod viability) or Rose Bengal (to facilitate counting), and preserved in 4% formaldehyde buffered with sodium borate. Copepod predators and remaining prey were identified and counted under a dissecting microscope.

Selection experiments (Expts 7 to 11) were performed in which *A. sinensis* adults were offered 2 prey species, *L. tetraspina* (nauplii or copepodites) and *P. forbesi* (nauplii) (Table 1). Prey were transferred to 1 l polycarbonate containers containing 35 µm filtered ambient water. One predator was added to each treatment bottle to initiate the experiment. Three to 5 replicates per treatment (predator + prey) and recovery control (prey only) were prepared for each prey combination

or density. The experiments were run as for functional responses except that an experiment on 25 October 2011 was run for 48 h.

During Study 1, the artificial cohort method (Kimmerer & McKinnon 1987) was used to measure growth rates of numerically dominant calanoid copepods, usually *Eurytemora affinis* and *P. forbesi* (Kimmerer et al. 2014). Briefly, artificial cohorts were produced by sequential size fractionation with nylon screens of 200, 250, and 300 µm. Subsamples were incubated in 4 l Cubitainers® at ambient temperature for 0 to 3 d and then preserved in 2% glutaraldehyde. *A. sinensis* individuals in each sample were sorted out and dried, and dry weight (Sartorius SE2 Ultra Microbalance) and carbon (Costech Model 4010 Elemental Analyzer) were determined. Growth rate was determined as the slopes of the natural log of both dry weight and carbon per individual versus time.

On 2 of the sampling dates in that study, *A. sinensis* was the most abundant copepod in the sample, and its growth rate was determined but not previously reported. Incubations were made in water screened at 35 µm (Kimmerer et al. 2014), which should have removed most nauplii.

Analyses of predation rate

We assumed a Holling Type II functional response (Holling 1966) in which ingestion rate is:

$$I = CP = \frac{I_{\max}P}{k+P} \qquad (1)$$

with variables as defined in Table 2. In any disappearance-of-prey experiment, the density of prey P

Table 2. Variables with units and definitions

Variable	Units	Definition
$I(t)$	d^{-1}	Ingestion rate in prey d^{-1} per predator
$I_{\max}$	d^{-1}	Asymptotic ingestion rate as prey density→∞, prey d^{-1} per predator
N_A		Number of predators in an experimental container
$N(t)$		Number of prey in a container
$P(t)$	l^{-1}	Number of prey per unit volume (= density, $N(t)/V$)
k	l^{-1}	Half-saturation constant (prey density where $I = I_{\max}/2$)
$C(t)$	l d^{-1}	Clearance rate = I/P, i.e. slope of the functional response
C_0	l d^{-1}	Clearance rate at $P = 0$, the maximum clearance rate
V	l	Volume of experimental container
g	d^{-1}	Daily growth rate of the prey population (0 in these experiments)
m	d^{-1}	Daily mortality rate of the prey not due to predators
T	d	Duration of experiment

may change over time as prey grow and die through consumption by the predator or other causes:

$$\frac{dP}{dt} = P\left(g - m - \frac{N_A C}{V}\right) \quad (2)$$

The clearance rate C also changes as the prey density decreases during the experiment, but Marin et al. (1986) recommend ignoring that change. Simulations (not presented) showed little difference in predicted consumption rates between formulations with C assumed constant and C allowed to vary, provided the last term in Eq. (2) was less than approximately 1.

In experiments with predators, the prey can be sorted into containers, and with a good experimental setup, g in Eq. (2) is 0, m is small, and recovery of prey is high. In our experiments, we found no prey that had not taken up vital stain neutral red, so mortality was probably due entirely to predation, and recovery in controls was 93 to 100%. In that case, Eq. (2) can be integrated over the duration of the experiment to obtain the clearance rate:

$$C = \frac{V}{N_A} \ln\left(\frac{P}{P_0}\right) \quad (3)$$

where P_0 is the initial concentration of prey in bottles. Combining Eqs. (1) and (3), substituting for k in Eq. (1) (see Table 3), and rearranging gives:

$$P_f = P_0 e^{\frac{\frac{I_{max} N_A T}{I_{max} + P_0}}{C_0}} \quad (4)$$

where P_f is the density of prey at the end of the experiment.

The calculation is somewhat different for predatory animals that consume relatively large prey and therefore consume individual organisms at a low rate. It is generally a good idea to run such experiments with 1 or a few predators to minimize interference among predators (Hansson et al. 2001). Containers should be as small as possible without causing container effects to keep the total prey to be sorted at a reasonable number; however, a small container with low prey density results in low actual numbers of prey in each container, and with 1 or a few predators the total number consumed is small.

When the number of individual prey organisms consumed is small, the proportional error associated with discrete events becomes large, and precision is especially poor at the low-density end of the functional response. Ordinary curve-fitting methods will give equal weight to data points without regard to their precision, potentially resulting in a poor fit or overstated confidence in parameter values. Because consumption is a binomial process (each prey is either eaten or not), the data should be modeled by fitting the number of prey remaining with a binomial error distribution.

It is possible to fit Eq. (4) using an optimizer to obtain maximum likelihood estimates of the parameters under the assumption that the probability of a given prey being eaten has a binomial distribution. However, the underlying parameter distribution is asymmetric (both parameters must be >0), and the optimization provides only symmetrical standard errors. Furthermore, because the parameters are correlated with each other and the highest prey densities used for some prey were below densities required for saturation, the upper confidence limit of the asymptotic feeding rate I_{max} was poorly determined in those analyses.

We therefore applied a Bayesian approach, which calculates the likelihood but has the advantage that prior estimates of parameter values can help to constrain the output (Gelman et al. 2004). Analysis was run in WinBUGS v. 1.4.3 (Lunn et al. 2000) using methods described by Kimmerer & Gould (2010). Each analysis was run using triplicate Markov chains with 1000 samples to eliminate effects of random initial conditions, and 10 000 samples for output, both after thinning 10-fold. Standard testing of code and of output was conducted, including examination for autocorrelation, Gelman-Rubin statistics, and comparisons of results from the first and second 5000 samples in each chain.

Input data were initial and final counts $N(t)$ for $t = 0$ and $t = 1$ d, experimental volumes, and number of predators per container (Table 1). Prior distributions of the parameters were normal distributions with a mean of 0, truncated to be greater than 0. The standard deviation for the maximum clearance rate C_0 was 0.84 l d^{-1}, determined by estimating the volume of the predator and using the upper limit of the ratio of clearance rate to copepod volume of 10^7 (Kiørboe 2011), multiplied by 3 to further reduce the effect of the prior on the maximum likelihood estimate. The standard deviation for the maximum consumption rate I_{max} was determined from the expected maximum specific consumption rate of approximately 1.25 d^{-1} converted to numbers of prey: 25, 88, 234, and 22 for *L. tetraspina* adults, copepodites, and nauplii, and *P. forbesi* nauplii, respectively. For both parameters the observed maximum likelihood values were well below these values and posterior means were not overly sensitive to these choices, although upper confidence limits were sensitive. Model output comprised summary statistics for C_0 and I_{max}, and the individual pairs of parameter samples from the Markov chains (N = 30 000).

We calculated predation impact by combining functional responses with field abundance, assuming that *A. sinensis* consumed any nauplii and the post-naupliar stages of *L. tetraspina*. Parameters for functional responses used pooled results for adult *L. tetraspina* and the means of parameters in 2 experiments with *L. tetraspina* nauplii (see Eq. 5 below). Consumption rates were not corrected for temperature because of the narrow temperature range during the period of study: 10th and 90th percentiles of monthly means from long-term monitoring were 18 and 22°C.

Functional responses were combined as described by Rose et al. (2013):

$$I_i = \frac{\dfrac{I_{\max i}}{k_i} P_i}{1 + \sum\limits_{\text{all } i} \dfrac{P_j}{k_j}} \tag{5}$$

where the *i* values refer to the 4 prey categories: each life stage of *L. tetraspina* and nauplii of *P. forbesi*. This formulation assumes the parameters of the functional response for each prey remain fixed even when other prey are added. This assumption is necessary because functional responses were determined only on single prey.

Predation mortality was determined as the population clearance rate (d⁻¹), the daily fraction of the prey populations consumed by the entire predator population (Uye & Kayano 1994). It was calculated from per-capita ingestion rates (Eq. 5) and abundance of *A. sinensis* adults and copepodites and prey from the 3 field studies. Males are about the same size as females and their predation rate was assumed to be the same as that of females. Copepodites were assumed to feed on the same taxa at a rate equal to that of females scaled by the ratio of carbon mass of copepodites to that of females, which is approximately correct for the predatory *Tortanus* spp. (Uye & Kayano 1994). Copepodites were only identified to stage in Study 2. Ingestion rates of *A. sinensis* copepodites were assumed to be 25% of those of adults based on the mean stage in Study 2 (CIII) and the ratio of mass of that stage to adult females for *Acartia* spp. (Kimmerer & McKinnon 1987).

RESULTS

Acartiella sinensis became abundant less than a year after it was first detected and has persisted, maintaining a mean summer abundance of approximately 500 ind. m⁻³ except for a low period during
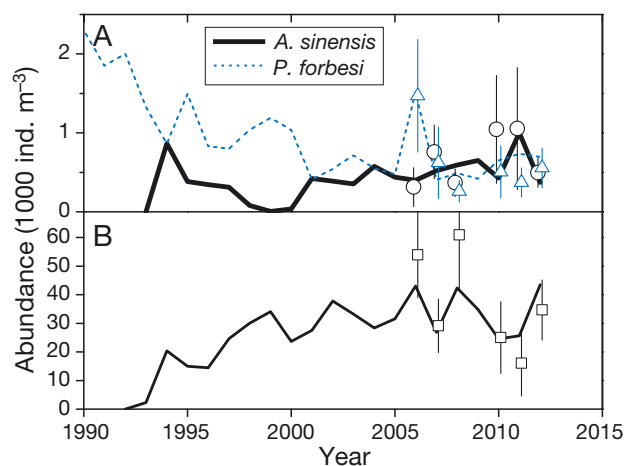

Fig. 2. Mean annual abundance of adult copepods during July through October at salinity 0.4 to 12 from the long-term monitoring program (Study 3, lines) and short-term studies (Studies 1 and 2, symbols with 95% confidence intervals). (A) *Acartiella sinensis* (black line, ○) and *Pseudodiaptomus forbesi* (dashed line, △). (B) *Limnoithona tetraspina* (□). In (B), all *Limnoithona* copepods were assumed to be *L. tetraspina* although it is possible that a small fraction (≪1%) were *L. sinensis*; values set to 0 before 1993 because only *L. sinensis* was present then

1998 to 2000 (Fig. 2). *Limnoithona tetraspina* was numerically dominant during summer. *Pseudodiaptomus forbesi* abundance declined following the introductions of *A. sinensis* and *L. tetraspina* (Fig. 2). Distributions of copepods with respect to salinity show considerable overlap between adults of *A. sinensis* and *L. tetraspina*, but *P. forbesi* was most abundant in freshwater and overlapped with *A. sinensis* over only part of its distribution (Fig. 3A). The distribution of *P. forbesi* nauplii was shifted to lower salinity than that of adults, indicating a more eastward spatial distribution, and copepodites of *L. tetraspina* were less abundant at low salinity than their adults (Fig. 3B).

Functional responses of *A. sinensis* varied among experimental dates and among life stages of *Limnoithona* prey (Fig. 4A–C). Adults and copepodites of *L. tetraspina* were consumed at a low rate (~0 to 7 ind. d⁻¹ per predator). Adults were consumed at very similar rates in 2 experiments (Fig. 4A) so the results were pooled. *L. tetraspina* nauplii were consumed at different rates in the 2 experiments (Fig. 4C), but both rates were higher (~1 to 15 ind. d⁻¹ per predator, Fig. 4C) than those for post-naupliar stages. Analysis of predatory impact on these nauplii used results from a pooled analysis since we lacked a rationale to pick either set of results for extrapolation. Nauplii of *P. forbesi* were also consumed at a high rate (~1 to
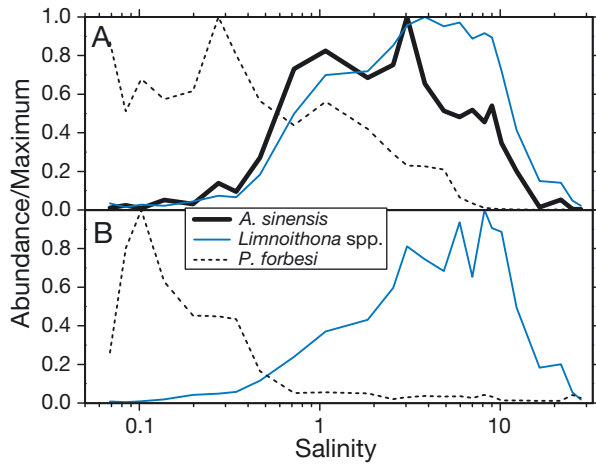
Fig. 3. Abundance of copepods as functions of surface salinity scaled to the maximum for each species and life stage. Data from long-term monitoring program for July to October 1995 to 2012. Data (N = 1220, except 845 for *Pseudodiaptomus forbesi* nauplii) were averaged in 25 salinity bins to eliminate bias due to the greater sampling effort at low salinity, then each bin mean was divided by the maximum bin mean. Salinity axis is log-transformed to focus on low salinity. (A) Adult *Acartiella sinensis*, *P. forbesi* and *Limnoithona* spp. (B) *P. forbesi* nauplii and *L. tetraspina* copepodites
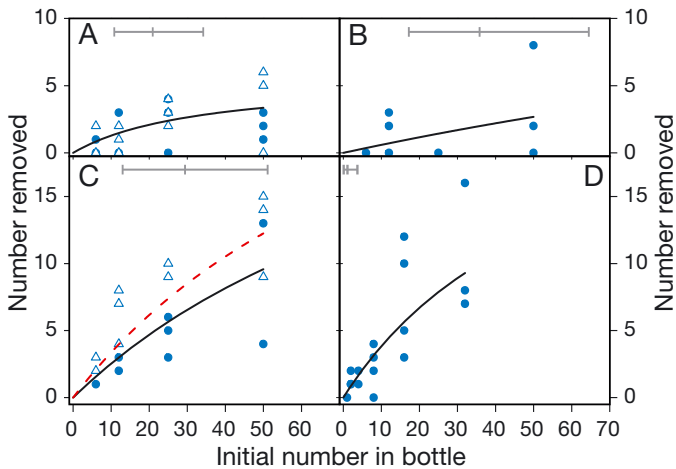
Fig. 4. Functional responses of *Acartiella sinensis* on different prey. (A–C) *Limnoithona tetraspina*, (D) *Pseudodiaptomus forbesi*. (A) adult, (B) copepodite, (C,D) nauplii. Data points from 2 experiments in (C): (○ and solid line) 10 July 2008, (△ and dashed line) 14 July 2008. Symbols in (A) as in (C), except that results were pooled to produce a single line. Horizontal lines at top of each panel give quartiles of abundance of each prey scaled to bottle volume

15 ind. d^{-1} per predator, Fig. 4D). For all prey, the functional responses had not fully saturated at the maximum prey density, and except for *P. forbesi* nauplii, the maximum experimental density was near the upper quartile of field abundance.
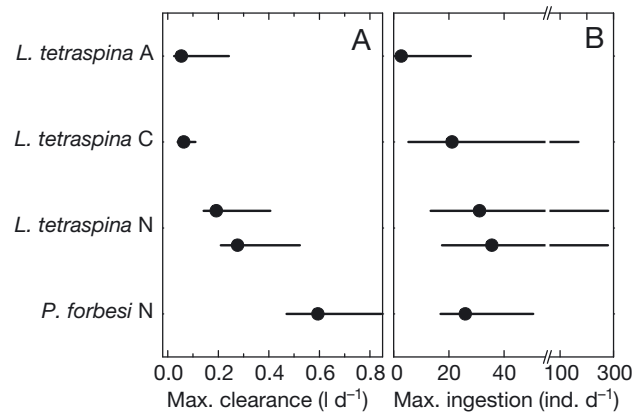

Fig. 5. *Acartiella sinensis*. (A) Maximum clearance rate C_0 and (B) maximum ingestion rate I_{max} on *Limnoithona tetraspina* stages and *Pseudodiaptomus forbesi* nauplii determined by fitting Eq. (4). Parameters of functional responses with 95% credible intervals. Data for *L. tetraspina* adults pooled between 2 experiments. A: adult, C: copepodite, N: nauplius

Parameters of the functional responses show the difference in C_0 (Eq. 4), the clearance rate at low prey density, among the life stages and between the nauplii of the 2 prey species (Fig. 5A). Clearance rates were higher for *P. forbesi* nauplii (maximum likelihood estimate, MLE ~0.6 l d^{-1}) than for *L. tetraspina* nauplii (MLE ~0.2 l d^{-1}), but confidence intervals overlapped. Clearance rates of adults and copepodites were <0.1 l d^{-1} (Fig. 5A). The maximum ingestion rates (parameter I_{max} in Eq. 4) had MLE values of 3 ind. d^{-1} for adult *L. tetraspina* and 21 to 35 ind. d^{-1} for other prey, but upper bounds of I_{max} for several prey were uncertain because the functional responses were far from saturation at these prey densities (Fig. 5B).

Eggs of *A. sinensis* were present in most containers after incubation, and were likely based at least partly on consumption of copepod prey during experiments. Four estimates of the growth rate of *A. sinensis* copepodites in the absence of nauplii were negative or 0 (Table 3).

Selection experiments showed no difference in consumption of nauplii of the 2 prey copepods. Clearance rates differed among experiments but not between species (Fig. 6A–C). A generalized linear mixed model was fitted with a binomial error distribution and prey as a fixed factor. The coefficient for the difference between *P. forbesi* and *L. tetraspina* was −0.03 ± 0.39 (±95% CI), corresponding to an odds ratio of 0.97 for the number of *P. forbesi* remaining compared to the number of *L. tetraspina* remaining. Mean clearance rates across all selection

Table 3. *Acartiella sinensis*. Results of opportunistic measurements of growth rate during summers of 2006 and 2007. Size fractions refer to the mesh sizes used to create the artificial cohort: Small (200 to 250 µm) or Large (250 to 300 µm). Data are means with 95% confidence limits based on independent measurements of carbon and dry mass (details of methods in Kimmerer et al. 2014)

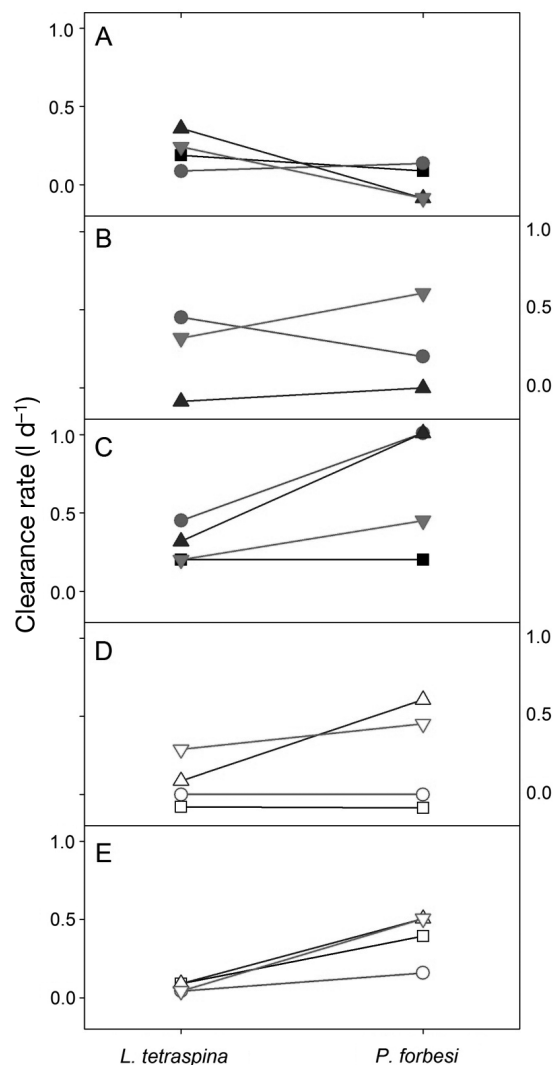| Date	Size fraction	Growth rate (d^{-1})	
		Carbon	Dry mass
8 Aug 2006	Small	−0.11 ± 0.03	−0.09 ± 0.04
8 Aug 2006	Large	−0.01 ± 0.06	−0.01 ± 0.06
23 Jul 2007	Small	−0.01 ± 0.08	−0.02 ± 0.11
23 Jul 2007	Large	0.03 ± 0.16	0.06 ± 0.16

Fig. 6. Clearance rates for *Limnoithona tetraspina* and *Pseudodiaptomus forbesi* determined in selection experiments. Each line and pair of symbols gives results for a single predator *Acartiella sinensis*. (A–C) *L. tetraspina* and *P. forbesi* nauplii, (D,E) *L. tetraspina* copepodites and *P. forbesi* nauplii

experiments (±95% CI) were 0.25 ± 0.09 l d^{-1} for *L. tetraspina* nauplii and 0.32 ± 0.15 l d^{-1} for *P. forbesi* nauplii.

Results were very different for treatments containing mixed life stages (Fig. 6D,E), in which *A. sinensis* had a lower clearance rate on *Limnoithona* copepodites (0.08 ± 0.07 l d^{-1}). The coefficient for the difference between the 2 prey types of 0.86 ± 0.53 indicated a substantially greater consumption of *P. forbesi* nauplii than *Limnoithona* copepodites, with an odds ratio of 2.4 favoring consumption of *P. forbesi* nauplii.

Predation mortality rates on *L. tetraspina* nauplii (or population clearance, the daily proportion of nauplii removed by the population of *A. sinensis*) ranged from nearly 0 in 1999 to approximately 12% d^{-1} in 2011 (Fig. 7, long-term monitoring data). Population clearance rates were generally higher in data from both of the short-term studies (Fig. 7). Approximate 95% confidence intervals around the estimates are somewhat asymmetrical owing to the skewed distributions of the parameters (Fig. 5). Means and 95% confidence limits of predation mortality on *L. tetraspina* nauplii (summarized across time from MLE in Fig. 7) were 0.07 ± 0.03, 0.07 ± 0.02, and 0.04 ± 0.01 d^{-1} for Studies 1 (2006 to 2008), 2 (2010 to 2012), and 3 (long-term, 1994 to 2012), respectively.

Predation mortality of *L. tetraspina* copepodites and adults and *P. forbesi* nauplii had similar temporal patterns (not shown) to those for *L. tetraspina* nauplii (Fig. 7), since all were influenced by the abundance of *A. sinensis* (Fig. 2). Long-term means were 0.04, 0.02, and 0.02 d^{-1} for *L. tetraspina* nauplii, copepodites, and adults, and 0.12 d^{-1} for *P. forbesi* nauplii (marks on the left in Fig. 7).

DISCUSSION

The present study provides the first quantitative estimates of predation impact by an *Acartiella* species anywhere. Although the limited range of prey densities used in experiments led to uncertainty in parameters of the functional response (Figs. 4 & 5), the predation mortality on nauplii could nevertheless be estimated because most of the abundance data were within the range of experimental data (Figs. 4 & 7). In addition, we have carried the uncertainties in the functional response through to the predation mortality (Fig. 7), and even so, it is clear that in most years this predation mortality is fairly high.

Previous studies have examined feeding by *Acartiella* species in 2 locations: the St. Lucia estuary in
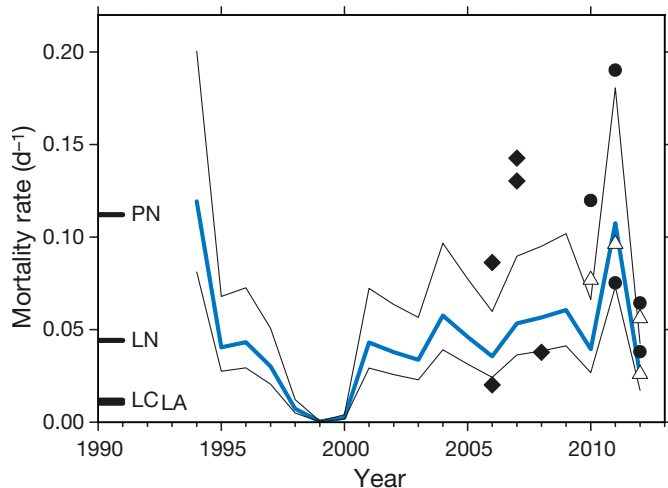
Fig. 7. Predation mortality of *Acartiella sinensis* on *Limnoithona tetraspina* life stages and *Pseudodiaptomus forbesi* nauplii during July to October. Lines give annual predation mortality of *L. tetraspina* nauplii, mean (blue line) and approximate 95% confidence limits (thin black lines) from monitoring data (Study 3). The temporal patterns of mortality of other life stages and *P. forbesi* nauplii are similar to those for *L. tetraspina* nauplii, and means of predation mortality from the monitoring data are shown as marks at left for *P. forbesi* nauplii (PN), and *L. tetraspina* nauplii (LN), copepodites (LC), and adults (LA). Symbols give predation mortality as monthly values from salinity 0.5 to 5 in 2006 to 2008 (Study 1, ◆) and from salinity 0.4 to 6 in 2010 to 2012 (Study 2) on transects in the Sacramento River (●) and the San Joaquin River (△)

South Africa (Carrasco & Perissinotto 2011, Carrasco et al. 2013) and the SFE (York et al. 2014). One of the South African studies reported a nitrogen stable-isotope ratio of *A. natalensis* close to that of *Pseudodiaptomus stuhlmanni* and consistent with suspension feeding (Carrasco & Perissinotto 2011). *A. natalensis* fed on naturally occurring phytoplankton in experiments on the effect of turbidity, but the feeding rate was very low, approximately 0.1 µg C ind.$^{-1}$ d^{-1} or 5% of body mass per day (Carrasco et al. 2013, their Fig. 3 corrected to ng pigment, N. Carrasco pers. comm.). Feeding of this species on copepods has not been studied (N. Carrasco pers. comm.).

In contrast, the study of *A. sinensis* by York et al. (2014) in the SFE showed no feeding on phytoplankton or ciliates, but some replicate experiments showed evidence of a trophic cascade, apparently through consumption of *L. tetraspina* by *A. sinensis*, which then released microplankton from grazing by *L. tetraspina*. Furthermore, copepodites of *A. sinensis* failed to grow in water screened to remove copepods (Table 3), but *P. forbesi* grew at low to moderate rates under the same conditions in experiments carried out at around the same time (Kimmerer et al. 2014). Al-

though feeding on phytoplankton by *A. sinensis* cannot be ruled out, phytoplankton is unlikely to constitute a major part of its diet. Given the contrast between findings for *A. sinensis* and *A. natalensis*, it is difficult to generalize about the diets of *Acartiella* species until additional information becomes available.

Selective feeding

The principal prey of *A. sinensis* is *L. tetraspina* because it is so abundant. This tiny cyclopoid is itself an ambush predator on microzooplankton that moves with a hop-and-sink behavior in all life stages and is therefore motionless much of the time (Bouley & Kimmerer 2006, Gifford et al. 2007).

Although adults should produce the strongest hydrodynamic signal of the 3 gross life stages of *L. tetraspina*, nauplii were consumed at a much higher rate than either adults or copepodites (Figs. 4 & 5). This may be due to a combination of better detection of a predator's impending attack in adults and copepodites than in nauplii (Fields 2010), or a stronger escape response in the larger stages (Titelman & Kiørboe 2003, Bradley et al. 2013). Clearance on copepodites was similar to that on the adults, but by the time this experiment could be conducted field temperatures were low (Table 1) and clearance rates were poorly defined (Figs. 4 & 5).

The 2 experiments in 2008 gave very similar results with adult *L. tetraspina* as prey, but rather different results for nauplii (Figs. 4A,C & 5). These experiments were conducted under the same experimental conditions only 4 d apart. We do not know why these results differed. The nauplii used in Expt 3 were about 1 life stage earlier (median) than those in Expt 1 and may have been less competent at escaping predation, although it is also possible that they were in poorer condition. This implies that single experiments at each temperature may be inadequate to determine the thermal response of predation because of variability in the size or age distribution or condition of field-collected prey (e.g. see Hooff & Bollens 2004).

Maximum clearance rates of *A. sinensis* were higher than some, but not all, rates reported for *Acartia* species feeding on nauplii. Adult female *Acartia* sp. (identified as *clausi*) feeding on their own nauplii at 10 or 20°C had maximum clearance rates of 0.01 l d^{-1} or less (Landry 1978), and *Acartia sinjiensis* fed on their own nauplii at a clearance rate of 0.001 l d^{-1} or less at 30°C (Camus & Zeng 2009, their Fig. 5). The

maximum clearance rate of *Acartia tonsa* feeding on conspecific nauplii at 20°C was approximately 0.01 l d^{-1} (Lonsdale et al. 1979, approximate slope in their Fig. 7); consumption of other species averaged 3-fold higher than on conspecific nauplii, so the clearance rate for these species would be approximately 0.03 l d^{-1}. Boersma et al. (2014) found that maximum clearance rates of *A. clausi* were similar whether feeding on conspecific nauplii or those of 2 other species: values at 10°C were 0.03−0.1 l d^{-1} (Boersma et al. 2014), which equate to 0.08−0.3 l d^{-1} at 20°C (Hansen et al. 1997). Taken together, these results suggest that *Acartia* species usually feed on nauplii of other species at generally lower clearance rates than that of *A. sinensis*, but with some overlap.

By contrast, clearance rates of *A. tonsa* feeding on microzooplankton are comparable to those for the similar-sized *A. sinensis* feeding on nauplii under similar experimental conditions. *A. tonsa* had a maximum clearance rate of 0.2 l d^{-1} when feeding on ciliates and rotifers at 20°C (Stoecker & Egloff 1987). The maximum clearance rate of *A. tonsa* on ciliates was 0.18 l d^{-1} at 18°C in calm water but up to 0.7 l d^{-1} at a turbulence dissipation rate of 0.23 cm^2 s^{-3} (Saiz & Kiørboe 1995). This is well within the range of dissipation rates in the study area (Stacey et al. 1999), suggesting that our estimates of clearance rate may be approximately 3-fold lower when extrapolated to the field.

Predation mortality

Although we estimated confidence limits on the predation mortality of all prey types (shown in Fig. 7 for *L. tetraspina*), these do not account for uncertainty in extrapolation of female predation rates to males, or the estimate of copepodite predation rate. Taking the values in Fig. 7 as calculated, our short-term studies gave estimates of predation mortality that were generally similar to those determined from the long-term monitoring data, although some short-term values were much higher because of differences in estimated abundance of prey.

What is the likely population impact of the estimated predation mortality rates? The total mortality rate of *L. tetraspina* nauplii in summer 2007 was 0.04 to 0.5 d^{-1} (median 0.25 d^{-1}) (Kimmerer 2015). The maximum likelihood estimate of mortality rate of *L. tetraspina* nauplii due to predation by *A. sinensis* was 0.04 d^{-1}, and that of copepodites and adults was 0.01 d^{-1}. The predation mortality rate of nauplii is about 20% of total mortality but other life stages

largely avoid mortality due to predation by *A. sinensis*. To place this in context requires consideration of predation by other co-occurring organisms.

The larger predatory copepod *Tortanus dextrilobatus* was introduced to the SFE around the same time as *A. sinensis* and could have had an impact on the other copepods discussed here (Hooff & Bollens 2004). However, *T. dextrilobatus* is most abundant at higher salinity than the other species, so the spatial overlap is small. Molecular evidence suggests predation by *T. dextrilobatus* on *L. tetraspina* is much lower than on the similar sized *Oithona davisae* despite the much greater abundance of *L. tetraspina* (Craig et al. 2014). All these results suggest *T. dextrilobatus* has little impact on *L. tetraspina.*

Relatively few pelagic predators are abundant enough to cause substantial mortality to *L. tetraspina*. Gelatinous plankton are uncommon in the study area (Kimmerer 2004). The planktivorous fish species in the low-salinity zone of the SFE do not consume *L. tetraspina* at high rates (Nobriga 2002, Hobbs et al. 2006, Bryant & Arnold 2007, Slater & Baxter 2014).

Ingestion of copepod nauplii by the introduced clam *Potamocorbula amurensis* exerts substantial mortality on nauplii of *Eurytemora affinis* (Kimmerer et al. 1994) and probably other copepod species (Kimmerer & Lougee 2015). Population clearance rates of phytoplankton by these clams averaged approximately 0.4 d^{-1} during July to October 1994 to 2008 (Kimmerer & Thompson 2014). Based on estimates of escape probability, the mean population clearance rate on *E. affinis* nauplii would have been approximately 0.15 d^{-1}. Preliminary observations made in our laboratory show that all stages of *L. tetraspina* are vulnerable to entrainment in siphon currents and have weaker escape responses than *E. affinis* nauplii. Thus, clam predation may comprise a substantial part of the total mortality of this copepod, and would be additive to predation by *A. sinensis*.

The predation impact of *A. sinensis* on *P. forbesi* nauplii is apparently higher than that on *L. tetraspina* (Fig. 7), despite the low overlap of these species (Fig. 3). In addition, clam grazing likely has a similar effect on *P. forbesi* as it does on *E. affinis*, for which predation mortality is around 0.15 d^{-1} in the low-salinity zone during late summer (Kimmerer & Lougee 2015). Reproductive and growth rates of *P. forbesi* are low (Kimmerer et al. 2014), and a mortality rate of nauplii due to both clams and *A. sinensis* would be approximately 0.25 d^{-1}, which is probably unsustainable. However, *P. forbesi* is most abundant in a freshwater refuge where neither *P. amurensis*

nor *A. sinensis* are abundant (Fig. 3). Thus, the high loss rate of *P. forbesi* nauplii in the low-salinity zone is likely supported by transport from the freshwater region of high abundance.

The abundant copepod *L. tetraspina* feeds principally on microzooplankton (Bouley & Kimmerer 2006, Gifford et al. 2007), which themselves exist in a region of low primary productivity (Kimmerer et al. 2012), are subject to consumption by clams (Greene et al. 2011), and are key prey of *A. sinensis*. Thus, the predatory habit of *A. sinensis* and its moderate to high summer abundance make it an important link in the food web supporting delta smelt and other declining fish species (Mac Nally et al. 2010, Slater & Baxter 2014). The present study highlights a shift in the low-salinity zone of the SFE not only toward low primary productivity but also toward additional trophic links that limit productivity of consumers such as copepods that are large enough to be consumed by fish. These changes together are no doubt important in the continued low abundance of fishes in this part of the estuary.

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