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Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary

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ABSTRACT: Despite a dramatic increase in the introduction of non-indigenous estuarine zooplankton in recent decades, the trophic implications of such introductions have rarely been quantified. Here we investigate predation rates of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary that achieves peak abundances in excess of 1000 ind. m^{-3}. The functional response of *T. dextrilobatus* feeding upon 2 copepod prey types — the non-indigenous cyclopoid *Oithona davisae*, and the 'native' calanoid *Acartia* (*Acartiura*) sp. — was described by a type II functional response (Ivlev function) at 2 experimental temperatures. In 3 of these 4 treatments, 90% I_{max} was achieved within a naturally occurring range of prey densities. Taxon-specific seasonal size variation was identified, and carbon-based consumption values were used to determine temperature-dependent rates of predation on both prey types. These empirically derived consumption rates and temperature dependence values were then applied to broadscale surveys (1997 to 1999) of zooplankton community composition in order to estimate the predatory impact of *T. dextrilobatus* upon prey populations in the San Francisco Estuary. Predatory impact estimates (% population consumed d^{-1}) greater than 1% occurred on a regular basis when *T. dextrilobatus* was abundant, with maxima exceeding 20, 65, and 25% for *O. davisae*, *Acartia* (*Acartiiura*) sp. and all Copepoda, respectively. These observations support the hypothesis that non-indigenous invertebrate zooplanktivores can play a significant role, at least seasonally or episodically, in the secondary production dynamics of aquatic ecosystems.

KEY WORDS: Zooplankton ecology · Feeding · Predation · Copepods · *Tortanus dextrilobatus* · Non-indigenous · Invasion · San Francisco Estuary

INTRODUCTION

Planktonic invertebrate predators can significantly influence size, distribution, composition, and population dynamics of their zooplankton prey (Neill 1981, 1990, Ohman et al. 1986, Frost & Bollens 1992, Wahlstrom & Westman 1999), and therefore may play an important role in regulating community structure (Verity & Smetacek 1996, Pace et al. 1999). Empirical investigations of feeding selectivity and functional responses have proven useful for estimating the feeding rates of secondary consumers in zooplankton communities (e.g. Ambler & Frost 1974, Yen 1983, Landry & Fagerness 1988), but the application of such data to modeling impacts on natural prey assemblages has been more limited, particularly in marine systems (Bollens 1988, Uye & Kayano 1994a, Sell et al. 2001).

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A rapid increase in biological invasions of estuarine habitats in recent decades has increased the prospect of potential deleterious effects on community and ecosystem level dynamics (Carlton & Geller 1991, 1993, Ruiz et al. 1997, Parker et al. 1999). Yet, a recent literature review by Bollens et al. (2002) revealed a scarcity of studies exploring such impacts in zooplankton communities, despite widespread documentation of invasion occurrence and mechanisms. Determining the impacts of human mediated introductions has been a challenge for natural resource managers and ecologists alike, and while they may represent unfortunate cases of often inadvertent biomanipulation, they provide a unique opportunity for investigating fundamental questions in plankton community ecology and invasion biology. One such question is the degree to which predation pressures may be important in regulating population dynamics of secondary producers.

The San Francisco Estuary has been identified as one of the most highly invaded aquatic ecosystems (Cohen & Carlton 1998), and the zooplankton community has proven particularly vulnerable to introductions. Ballast water transfer (attributed to increased and more efficient commercial shipping traffic) has been a likely source for the introduction of at least 7 copepod species into the system in the last 20 yr (Ferrari & Orsi 1984, Ambler et al. 1985, Orsi & Ohtsuka 1999, Bollens et al. 2002). This includes *Tortanus dextrilobatus* Chen and Zhang (Copepoda: Calanoida), a carnivorous copepod that has become a prominent member of the zooplankton community since its introduction in the early 1990s (Orsi & Ohtsuka 1999).

Predatory feeding by the genus *Tortanus* has been documented in various regions (Ambler & Frost 1974, Goswami 1977, Mullin 1979, Uye & Kayano 1994a,b), but previous studies have exclusively focused on 2 of 5 subgenera; *Boreotortanus* (*T. discaudatus*) and *Tortanus* (*T. forcipatus* and *T. gracilis*). *Tortanus* demonstrate feeding behavior that involves random darting motions in order to sense potential prey items, apparently via tactile stimuli detection (Ambler & Frost 1974). A wide variety of prey items have been noted for this genus of carnivorous copepods, ranging from non-motile fish eggs to juvenile chaetognaths and fish larvae. Most commonly, however, dietary selection has been demonstrated on copepod prey, where adult female predators capture and ingest prey that are 1.6 to 70.9% of their own body weight (Ambler & Frost 1974, Mullin 1979, Uye & Kayano 1994b). The subgenus of *T. dextrilobatus*, *Eutortanus*, has only been described with regard to distribution and phylogeny (Ohtsuka & Yoon 1992, Ohtsuka & Reid 1998).

In this study, we examine the functional response of *Tortanus dextrilobatus* feeding on 2 potential prey types that are abundant throughout the San Francisco Estuary: the 'native' calanoid copepod *Acartia* (*Acartiura*) sp., and the introduced cyclopoid copepod *Oithona davisae*, a probable prey item of *Tortanus* sp. in their native range (Uye & Kayano 1994a). We then apply these predation rates (empirically derived at 2 experimental temperatures) to broadscale field surveys (1997 to 1999) of the San Francisco Estuary zooplankton community to estimate the potential predatory impact of this recently introduced invertebrate predator.

MATERIALS AND METHODS

Study site. The San Francisco Estuary is a shallow coastal ecosystem characterized by 2 distinct estuarine systems that meet at the outlet to the Pacific Ocean (Fig. 1). The North Bay, composed of San Pablo and Suisun Bays and the Sacramento-San Joaquin Delta,

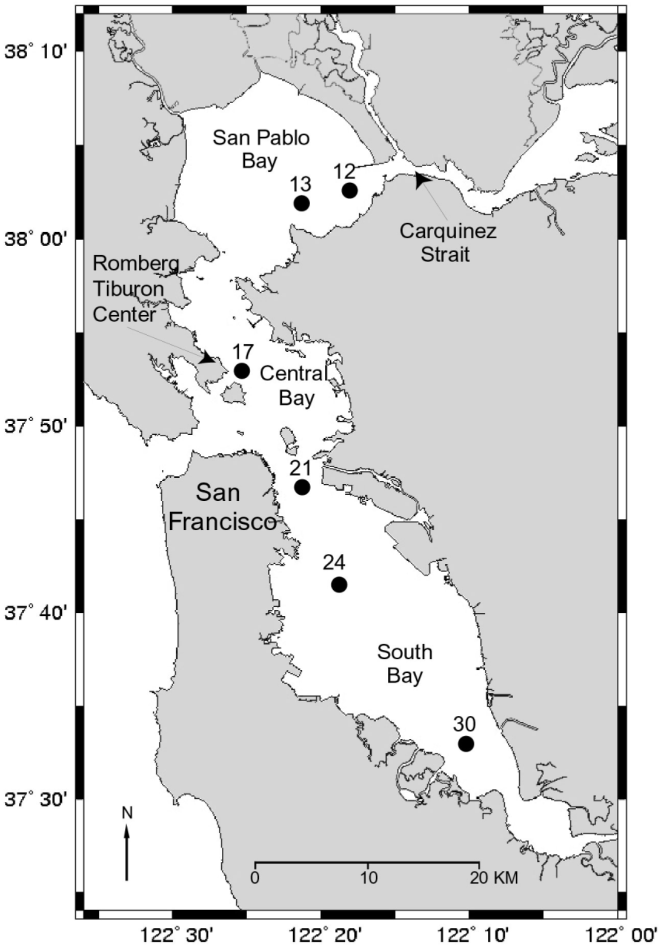

Fig. 1. Map of San Francisco Estuary, including South Bay, Central Bay, and San Pablo Bay. Numbers refer to the US Geological Survey historical stations sampled for zooplankton abundance and composition

is a partially mixed drowned river estuary wherein prominent hydrographic gradients are observed between central bay and upriver beyond the confluence of the Sacramento and San Joaquin Rivers (Cloern & Nichols 1985). Considerable seasonal and inter-annual variation in freshwater input from these drainages results in a wide range of observed temperature and salinity values (see Fig. 2B,C). In contrast, the South Bay is a well mixed coastal embayment which receives substantially less riverine input and is typically less turbid than the northern bay region. However, physical forcing (e.g. tidal, wind, river runoff) can promote water column stratification in South Bay resulting in both seasonal and episodic events of high primary productivity (Cloern 1996).

Functional response experiments. Predation by adult female *Tortanus dextrilobatus* upon 2 potential prey items *Acartia* (*Acartiura*) sp. and *Oithona davisae* in the San Francisco Estuary was determined experimentally during 2 seasons (2 temperatures). The choice of prey items was based on 3 criteria: (1) co-occurrence (temporally and spatially) with *T. dextrilobatus* in the San Francisco Estuary; (2) results from preliminary dietary selectivity experiments (Bollens et al. 2002, S. M. Bollens & R. C. Hooff unpubl. data); and (3) results from previous feeding studies involving copepods of the genus *Tortanus* (Mullin 1979, Uye & Kayano 1994a,b).

Tortanus dextrilobatus and its prey were collected in San Pablo Bay and Carquinez Strait (Fig. 1) by oblique hauls of 73 µm mesh, 0.5 m diameter and 153 µm mesh, 0.5 m diameter plankton nets. Collections were diluted into 5 gallon (18.9 l) buckets, filled to the rim with water approximately equal to water column average salinity and temperature, and sealed for transport to laboratory facilities at the Romberg Tiburon Center (Fig. 1). Experimental predator and prey subjects were field captured no more than 10 h prior to initiation of the experiments.

Experimental methods were based on previous work with other carnivorous copepods (Ambler & Frost 1974, Mullin 1979, Yen 1983, Uye & Kayano 1994a). Upon return to the laboratory, collections were stored in a temperature controlled room set to the ambient conditions (±1°C) of the collection site. *Tortanus dextrilobatus* and prey items were sorted using dissecting microscopes and a minimum of pipette transfers. Adult female *T. dextrilobatus* were isolated and starved for approximately 4 h prior to initiating the experiments. Prey items (CV–CVI females of specified taxa) were isolated and stored in 1 l jars at prescribed initial densities (for *Acartia* [*Acartiura*] sp.: 3, 6, 10, 20, 30, 40, 55, and 70 ind. l^{-1}; for *Oithona davisae*: 15, 30, 50, 100, 135, 175, 250, 300 ind. l^{-1}). A single *T. dextrilobatus* was then placed into each experimental jar to initiate the experiment. Jars were attached to a plankton wheel (1 rpm) in a temperature controlled room under dark conditions.

After 24 h, contents of the jars were poured over a 5 µm mesh sieve, transferred to scintillation vials, and preserved in 5 to 10% formaldehyde seawater solution. The remaining prey were later counted and measured for prosome length (PL) (all predators and 50 prey individuals per treatment were measured). Three replicates were run at each initial prey density; however, in 1 treatment of 1 experiment (*Acartia* sp. prey at 19°C), metadata and statistical analyses (i.e. failed constant variance test; $p < 0.01$) supported the removal of 1 replicate in order to achieve normality and variance assumptions of the curvilinear model fit.

Chemical composition of individual predators and prey (3 replicates of n = 3 *Tortanus dextrilobatus*, 10 *Acartia* (*Acartiura*) sp., or 15 *Oithona davisae*) from each temperature regime was determined post hoc with a CHN analyzer (Perkin Elmer 2400-II).

A set of controls was run for each prey item treatment to test for recovery efficiency of the experimental protocol. Prey items, but no *Tortanus dextrilobatus*, were counted and placed into jars at each initial density as described above and the experiment run for 24 h. Mean percent loss values (for each prey item) were calculated and applied to experimental results, such that:

$$I = (c_i)x - c_t \tag{1}$$

where I is prey ingestion, c_i is the initial prey density, x is the proportion of prey recovered from control jars, and c_t is the number of prey items remaining at the conclusion of a 24 h incubation. Prey recovery (x) from control vessels was 98.2 and 99.75% for *Oithona davisae* and *Acartia* (*Acartiura*) sp., respectively.

Functional response was estimated in SigmaPlot™ by fitting non-weighted daily ingestion rates to the Ivlev equation:

$$I = I_{max}(1 - e^{-ac}) \tag{2}$$

where ingestion maximum (I_{max}) and the proportionality constant (a) are estimated parameters fitting the curvilinear regression of ingestion (I) as a function of initial prey density (c). Marin et al. (1986) discuss statistical complications that may arise from presenting ingestion as a function of mean prey density (vs initial prey density); a dependent variable choice which may more accurately reflect a decreased prey density during incubation time, but which also tends to result in comparably higher ingestion rate estimates. Therefore, in order to provide more conservative estimates of predatory impact, we have opted to present our ingestion rates as a function of initial prey density.

San Francisco Estuary zooplankton surveys (1997 to 1999). Ingestion rates derived from the functional response experiments were applied to broadscale surveys of zooplankton for San Francisco Estuary from 1997 to 1999. These data were gathered in cooperation with the San Francisco Bay Water Resources Division of the US Geological Survey aboard the R/V 'Polaris', with some preliminary analyses described by Bollens et al. (2002). Vertical haul collections were obtained at 12 stations on a monthly basis using a 73 µm mesh, 0.5 m diameter plankton net. Samples were concentrated and preserved at 5 to 10% formaldehyde seawater solution. Sample volume was calculated using a calibrated low-speed flow meter. Hydrographic data were collected simultaneously using a Sea-bird Electronics™ Conductivity-Temperature-Depth (CTD) instrument.

Samples from every other month (6 yr^{-1}), and approximately every other station (2 North Bay stations, 2 Central Bay stations, and 2 South Bay stations) were analyzed to the lowest possible taxon using standard microscopy. For the purposes of this study, abundances of all copepodid stages, including adults, have been summed for any given taxon within a sample.

Modeling predatory impact. Daily predation rates, estimated from the functional response experiments, were applied to the prey distributions (San Francisco Esuary Zooplankton Surveys: 1997 to 1999) to estimate the potential predatory impact (% of prey population removed d^{-1}) of *Tortanus dextrilobatus*. Results are reported using 2 modeling approaches. First, using a strict interpretation of our experimental observations, we estimate the impact of adult-stage predators feeding upon adult-stage prey. Then, in order to develop estimates of predation impact by *T. dextrilobatus* populations in the San Francisco Estuary, we assume predation rates (individuals consumed predator^{-1} d^{-1}) by juvenile stages of the predator (e.g. early copepodids) feeding upon juvenile life stages of prey (e.g. early copepodids) to be equal to that of the observed predation rate of adult predators feeding upon adult prey. Making a rough and conservative estimate of the population feeding rate based on the latter approach is supported by copepod investigations demonstrating a linear or allometric relationship of consumption through development (Berggreen et al. 1988, Uye & Kayano 1994a). Specifically, Uye & Kayano (1994a) showed that CI–CIII *Tortanus* spp. typically ate at rates comparable to or higher than adult females, suggesting that our modeling results may be a conservative estimate of *T. dextrilobatus* population feeding rates.

Change in predation intensity as a function of spatial and temporal variation in ambient temperature was estimated based on the van't Hoff rule approximation of Q_{10} (Bamstedt et al. 2000):

$$Q_{10} = (M_1/M_2)^{10}/(T_1 - T_2) \qquad (3)$$

where M_1 and M_2 are the maximum daily ration estimates of *Tortanus dextrilobatus* feeding upon prey items at 14°C (T_1) and 19°C (T_2), respectively.

A population feeding rate for *Tortanus dextrilobatus* at each sampling date (1997 to 1999) and location was generated based on the predator density (ind. m^{-3}) and the temperature adjusted ingestion rate as a function of prey density (using the Ivlev formula) such that: predator population feeding rate (prey individuals consumed m^{-3} d^{-1}) = predator density × predator ingestion rate (I_c) × (temperature correction from Eq. (3). Potential predatory impact (% prey population consumed d^{-1}) was then calculated as predator population feeding rate/prey abundance. Contour plots of potential predatory impact by all life stages of predators (copepodids and adults) feeding upon all life stages of prey, calculated over a grid of 107 sample date-locations (the sample from Stn 21 in May 1999 was lost), were generated using triangulation with linear interpolation in Surfer 7.0 (Golden Software™).

RESULTS

Since first detected in 1993 (Orsi & Ohtsuka 1999), *Tortanus dextrilobatus* has become a prominent member of the San Francisco Estuary zooplankton community, at times achieving peak densities in excess of 10^3 m^{-3} (Fig. 2). Our broad-scale surveys revealed this invertebrate predator to have a widespread distribution pattern thoughout the estuary, although it tends to be more abundant in San Pablo and South Bays than in Central Bay. Due to El Niño, the San Francisco Estuary experienced significant flooding during the winter–spring of 1998, a consequence of which included increased zooplankton abundance for most taxa, including *T. dextrilobatus.*

Functional response

Predation by *Tortanus dextrilobatus* on *Oithona davisae* and *Acartia* (*Acartiura*) sp. at 2 experimental temperatures exhibited a type II functional response (Holling 1966; Figs. 3 & 4). As prey density increased, consumption rates increased and approached asymptotic values demonstrating saturation in all treatments, except *O. davisae* at 19°C (Fig. 3B,D). The Ivlev formula (Eq. 2) describes this relationship and predicts ingestion values (I) at given prey density (c) and the maximum ingestion rate parameter ($I_{\max}$). At 14 and 19°C, *T. dextrilobatus* feeding on the cyclopoid copepod *O. davisae* exhibited an $I_{\max}$ of 14.0 and 21.7 ind. d^{-1}, respectively

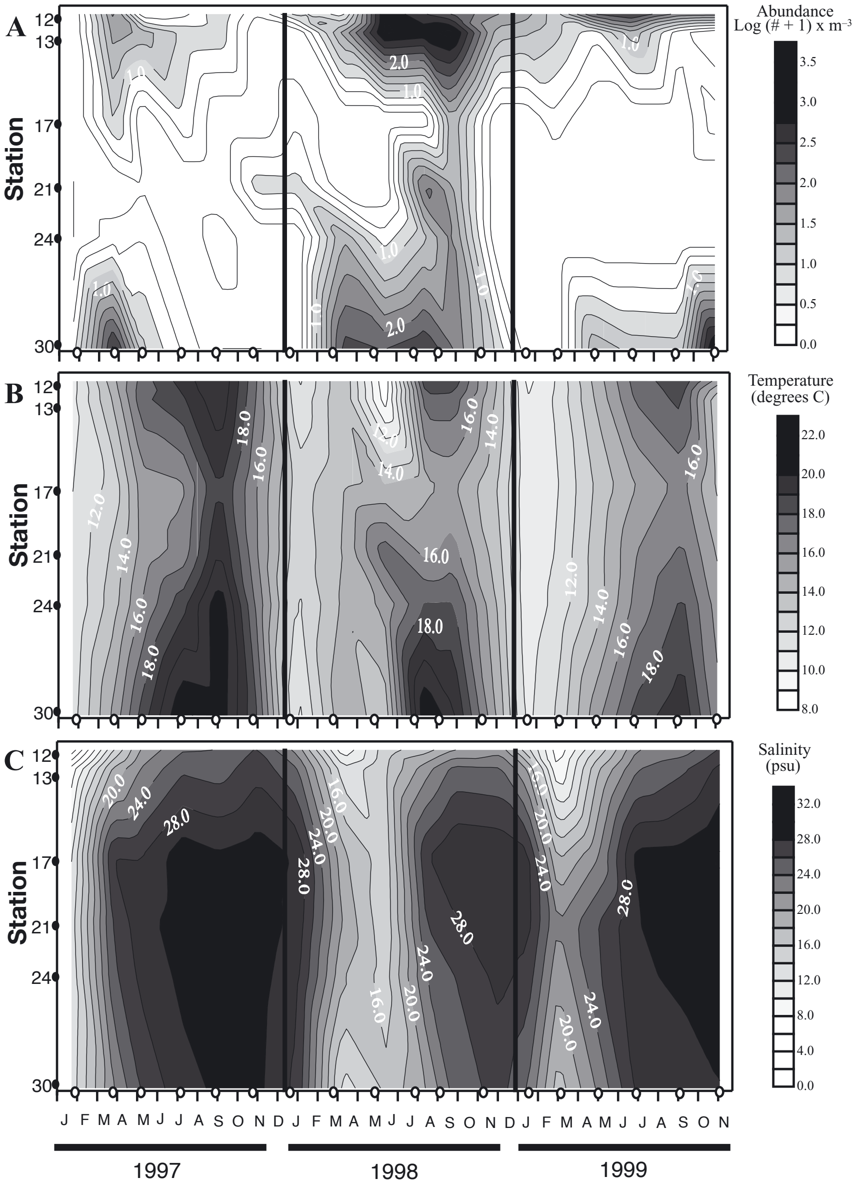

Fig. 2. (A) Abundance of *Tortanus dextrilobatus* (Log [individuals + 1] m^{-3}); all copepodid stages combined. (B) Water column average values of temperature, and (C) salinity obtained simultaneously with zooplankton collections in the San Francisco Estuary, 1997 to 1999. Open circles on *x*-axis represent sampling dates; dark circles on *y*-axis are sampling locations (plotted as distance) as represented in Fig. 1

(Fig. 3A,B). At the same experimental temperatures, the I_{max} values of *T. dextrilobatus* feeding on *Acartia* (*Acartiura*) sp. were 14.1 and 14.8 ind. d^{-1} (Fig. 4A,B). For all treatments in this study (except *O. davisae* at 19°C), 90% I_{max} occurred within the range of prey densities observed to occur naturally in the San Francisco Estuary (Table 1; Figs. 5A & 6A).

The chemical content of predator and prey from the different experimental treatments revealed interesting and taxon-specific seasonal variation (Table 2). For instance, adult female *Tortanus dextrilobatus* showed a carbon content increase of 30.7% between 19 and 14°C (summer and autumn, respectively), and *Acartia* (*Acartiura*) sp. revealed a similar increase of 25.6%. For *Oithona davisae*, however, the number of individuals pooled per sample (n = 15) was insufficient to obtain reliable C/N values. Instead, prosome lengths from 19°C (289.6 ± 2.1 µm) and 14°C (299.4 ± 1.9 µm) were applied to a length–carbon weight regression for *O. davisae* (Uye & Sano 1998), which yielded a more modest 20% increase (Table 2).

Carbon-based consumption estimates were calculated from individual-based ingestion rates described above and the carbon content values of adult female *Tortanus dextrilobatus*, *Oithona davisae* and *Acartia* (*Acartiura*) sp. at 14 and 19°C (Table 2). Maximum daily ration of *T. dextrilobatus* (I_{max}) was substantially less with *O. davisae* as prey (13 to 24% body C predator^{-1} d^{-1}; Fig. 3C,D) than for the larger *Acartia* (*Acartiura*) sp. as prey (173 to 189% body C predator^{-1} d^{-1}; Fig. 4C,D).

The influence of temperature on *Tortanus dextrilobatus* ingestion rates differed between the 2 prey types. For *T. dextrilobatus* feeding on *Oithona davisae*, maximum daily rations at 14 and 19°C yielded a Q_{10} value of 3.45 (Table 2; Fig. 3C,D). Consumption rates on *Acartia* (*Acartiura*) sp., however, yielded a much lower Q_{10} of 1.2 (Table 2; Fig. 4C,D). The Q_{10} rates calculated in this study are not only a function of metabolic and attack rates of the predator, but may also be influenced by variability in prey escape response.

Potential predatory impact

Two of the more abundant copepods in the San Francisco Estuary, the introduced cyclopoid *Oithona davisae* (Fig. 5A) and the 'native' calanoid *Acartia* (*Acartiura*) sp. (Fig. 6A), were chosen as representative prey items from the zooplankton community for modeling the potential predatory impact of *Tortanus dextrilobatus.* These 2 copepods rank as the first and third most abundant copepods from our surveys (>73 µm size class), together comprising 36.8% of total copepod

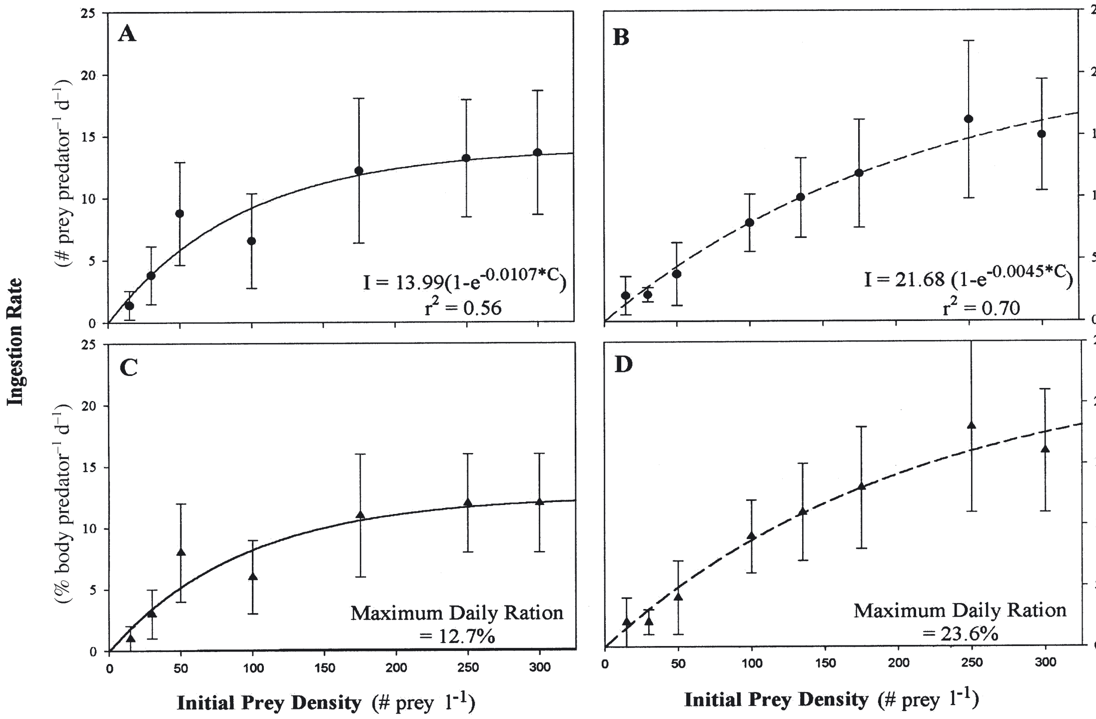

Fig. 3. *Tortanus dextrilobatus.* Functional response of adult females feeding on *Oithona davisae* (CV–CVI) at (A,C) 14°C (solid line) and at (B,D) 19°C (dashed line). Values expressed as (A,B) mean number individuals consumed predator^{-1} d^{-1} (●) and (C,D) % body carbon consumed predator^{-1} d^{-1} (▲). Error bars represent ±1 SD

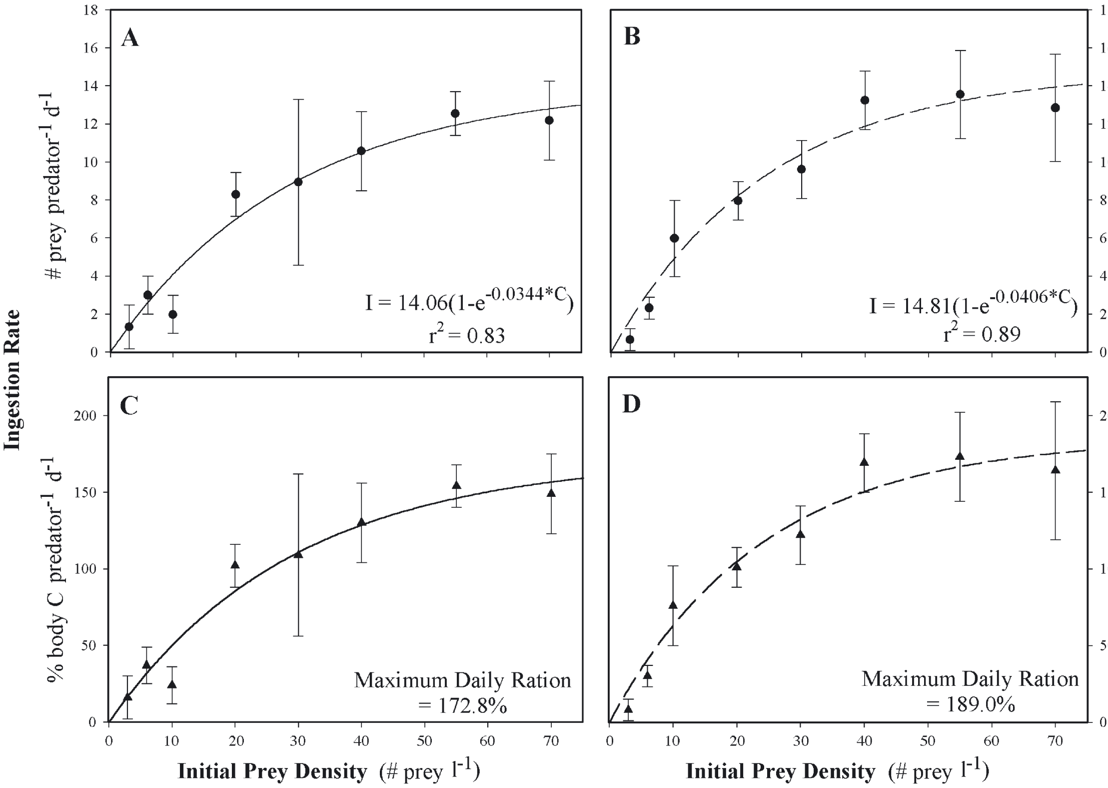

Fig. 4. *Tortanus dextrilobatus.* Functional response of adult females feeding on *Acartia* (*Acartiura*) sp. (CV–CVI) at (A,C) 14°C (solid line) and at (B,D) 19°C (dashed line). Values expressed as (A,B) mean number individuals consumed predator^{-1} d^{-1} (●) and (C,D) % body carbon consumed predator^{-1} d^{-1} (▲). Error bars represent ±1 SD

Table 1. *Tortanus dextrilobatus.* Functional response parameters (based on Eq. 2) of adult females feeding on adult female copepodids of 2 prey items at 2 temperatures (Temp.)

Treatment	Temp. °C	I_{max}	C (I_{max})	90% I_{max}	C (90% I_{max})	*a*	Q_{10}
# prey predator^{-1} d^{-1}							
O. davisae prey	14	14.0	1076	12.6	215	0.017	
	19	21.7	2558	19.5	512	0.005	2.4
Acartia sp. prey	14	14.1	335	12.7	67	0.034	
	19	14.8	284	13.3	57	0.041	1.1
% body C predator^{-1} d^{-1}							
O. davisae prey	14	0.13	1107	0.1	221	0.01	
	19	0.24	2503	0.2	501	0.034	3.5
Acartia sp. prey	14	1.73	337	1.6	67	0.005	
	19	1.89	284	1.7	57	0.04	1.2

numerical abundance (S. M. Bollens unpubl. data). Based on 2 modeling approaches, results suggest that in South and San Pablo Bays, where *T. dextrilobatus* is seasonally abundant (Fig. 2), predatory impact on either *O. davisae* or *Acartia* (*Acartiura*) sp. can be significant. Specifically, the most substantial impacts (based on all modeling scenarios) were estimated at Stns 12 and 13 in San Pablo Bay, and at Stn 30 in South Bay (Table 3; Figs. 5C & 6C).

When assuming that copepodid *Tortanus dextrilobatus* feed on copepodid prey at rates (individuals consumed predator^{-1} d^{-1}) comparable to adults feeding upon adults, maximum potential predatory impact was observed at Stn 30 during November 1999 (22.7 and 67.3% of *Oithona davisae* and *Acartia* sp. consumed d^{-1}, respectively). Similar levels of predatory impact were also determined for stations in San Pablo Bay during the summer months of 1998. Mean potential predatory impact by *T. dextrilobatus* upon *O. davisae* and *Acartia* (*Acartiura*) sp. over all sample dates and locations (n = 107) in the San Francisco Estuary (1997 to 1999) were 1.03 and 3.99% d^{-1}, respectively (Table 3), while the median values were 0.02% and 0.09% d^{-1}, respectively.

We also examined the effect of *Tortanus dextrilobatus* predation upon all Copepoda (copepodids and adults of all cyclopoid and calanoid species combined) (Fig. 7). The mean value of our experimentally derived parameter estimates for *T. dextrilobatus* feeding on *Oithona davisae* and *Acartia* (*Acartiura*) sp. (Table 3) were employed for modeling the potential predatory impact on this broader taxonomic assemblage of prey (i.e. mean parameter values applied to total abundance of all copepodids combined). These values resulted in a mean potential predatory impact of *T. dextrilobatus* on all Copepoda of 0.9% d^{-1}, and maxima of 8% d^{-1} in San Pablo Bay (Stn 13, August 1998) and 29% d^{-1} in South Bay (Stn 30, November 1999) (Fig. 7C). While these maximum predatory impact rates are rare events, potential impacts of >1% d^{-1} may occur regularly from March to November in both north bay and south bay regions of the San Francisco Estuary (Figs. 5C, 6C & 7C).

DISCUSSION

Consumption rates by carnivorous and omnivorous copepods have been determined using experimental incubations in a variety of studies (Ambler & Frost 1974, Mullin 1979, Atkinson & Snyder 1997, Sell et al. 2001). While numerous authors have explored problems associated with this experimental approach (e.g. Roman & Rublee 1980), food removal incubation studies remain the most accurate and informative method currently available for investigating predation on non-phytoplankton taxa (Bamstedt et al. 2000). Few studies of marine invertebrate predators, however, have used the same experimental system to compare temperature-dependent consumption on multiple prey types, using freshly field-captured predators and prey at naturally occurring temperatures and densities. These efforts are important for minimizing behavioral modifications and generating parameter estimates most useful to modeling predatory impacts (Yen 1983, Landry & Fagerness 1988).

Table 2. Length and chemical composition values for the predator, adult female *Tortanus dextrilobatus*, and 2 prey items (adult female *Oithona davisae* and adult female *Acartia* sp.) obtained from specimens collected from the field for 2 experimental temperature treatments. *C:N analyses for *Oithona davisae* were not available (n.a.), therefore a length-carbon weight regression (Uye & Sano 1998) was used to estimate carbon content

Taxa (CV–CVI)	Expt./collection temperature (±1°C)	Length (µm) mean (±SE)	Carbon (µg) mean (±SE)	Nitrogen (µg) mean (±SE)	C:N
T. dextrilobatus	19	1575.4 (9.2)	18.69 (1.39)	5.51 (0.98)	3.4
	14	1607.5 (12.8)	24.42 (2.60)	8.13 (0.37)	3.0
O. davisae	19	289.6 (2.1)	0.20*	n.a.	n.a.
	14	299.4 (1.9)	0.24*	n.a.	n.a.
Acartia sp.	19	820.8 (9.7)	2.38 (0.28)	0.52 (0.03)	4.6
	14	754.0 (5.0)	2.99 (0.24)	0.60 (0.01)	5.0

The functional response in 2 of our 4 experimental treatments (Figs. 3B,D & 4A,C) suggests a potential sigmoidal pattern. A type III functional response (Holling 1966) has been suggested to incorporate suppressed feeding or searching by predators when encountering low prey densities. While this may be appealing based on theoretical bioenergetic strategies, few empirical studies of zooplankton feeding have provided evidence to support this hypothesis (Bamstedt et al. 2000). Our functional response data, fitted with the 2-parameter Ivlev equation (r^2 = 0.56, 0.70, 0.83, 0.89; Figs. 3A,B & 4A,B, respectively), suggest no significant difference compared with an alternate type III model (r^2 = 0.54, 0.71, 0.83, 0.89; Figs. 3A,B & 4A,B, respectively); therefore, the less complex Ivlev function was chosen as a preferred model to represent our results.

To assess the potential significance of marine planktonic predators on prey populations, Ambler & Frost (1974) compared maximum ingestion rates from a variety of functional response studies, and found them to range from 64 to 192 % predator body weight d^{-1}. Ambler & Frost (1974) reported maximum ingestion rates of 68 and 96 % body weight d^{-1} for adult female *Tortanus discaudatus* feeding on NIII and NIV *Calanus pacificus*, respectively. When fed mixed-stage *Acartia clausii*, however, adult female *T. discaudatus* demonstrated maximum daily rations of 120 % body weight d^{-1} (Mullin 1979). In another study, Uye & Kayano (1994b) showed that adult female *Tortanus* spp. (*T. forcipatus* and *T. gracilus*) feeding on adult *Oithona davisae* and *Artemia* nauplii showed maximum daily rations of 63 and 251 % body weight d^{-1}, respectively (note, however, that *Artemia* nauplii are not a naturally occurring potential prey item). All of these values are comparable to the values determined in this study (Figs. 3D & 4D).

There are several assumptions and limitations to our study, including both experimental design and data analysis. For instance, in order to minimize 'bottle effects', Roman & Rublee (1980) promote the use of shorter incubation times and larger vessel sizes. We chose to run 24 h incubations in order to compensate for potential diel feeding periodicity (Peterson et al. 1990). Experimental vessels (1 l) were selected in order to (1) accommodate *in situ* densities of both predator and prey, and (2) minimize the sorting time required between field collection and initiation of incubations. One predator was used per experimental vessel (1 l), and therefore the experimental design does not address potential devia-

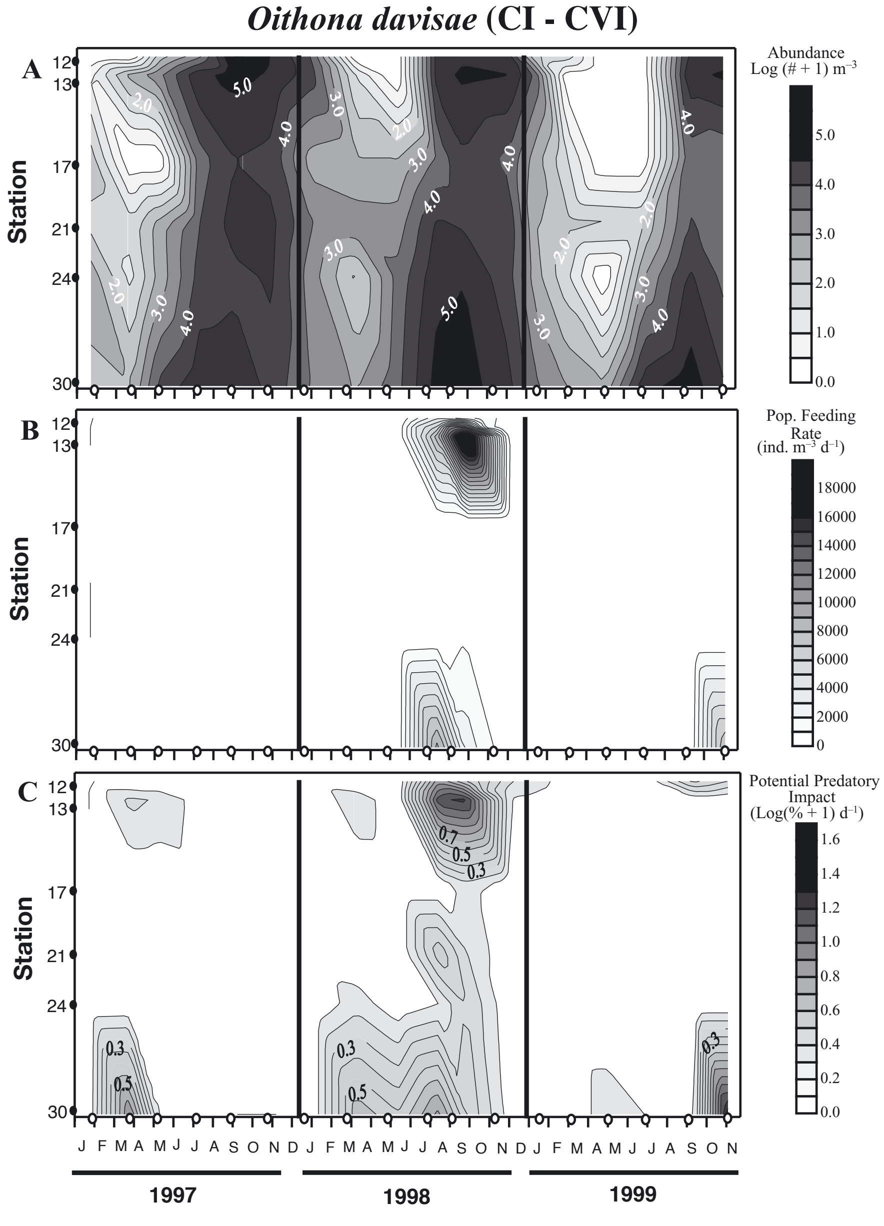

Fig. 5. *Oithona davisae*. (A) Abundance [Log (individuals + 1) m^{-3}] and distribution of *O. davisae* (all copepodid stages combined), (B) estimated population (Pop.) feeding rate (prey individuals consumed m^{-3} d^{-1}) of *Tortanus dextrilobatus* preying upon *O. davisae*, and (C) potential predatory impact of *T. dextrilobatus* feeding upon *O. davisae* prey (% prey population consumed d^{-1}) over a 3 yr period in the San Francisco Estuary (open circles on x-axis represent sampling dates; dark circles on y-axis are locations of sampling). Data between sampling dates and locations have been estimated using triangulation with linear interpolation

tions from a type II functional response due to predator interference (Skalski & Gilliam 2001). However, because *in situ* predator abundance rarely exceeded the density used in our functional response experiments (Fig. 2A), our results should be robust with respect to such concerns.

We analyzed our functional response data using initial prey density, rather than mean density, as the dependent variable; a problem that has been discussed regarding similar experimental approaches (Marin et al. 1986). Had we used mean density as the dependent variable when fitting the Ivlev function to our data, the resulting average predatory impact estimates upon *Oithona davisae* and *Acartia* sp. populations, for example, would be 1.08 and 4.81 % consumed d^{-1}, respectively (an increase of 0.05 and 0.82 compared to our values based on initial prey densities). Thus, our decision to use initial rather than mean prey density results in estimates of ingestion rates and potential predatory impacts that are slightly more conservative.

Prey size selectivity for all developmental stages of *Tortanus dextrilobatus* remains largely unknown. Additionally, more thorough understanding of species-specific escape responses and vertical distributions of smaller copepods (such as the seasonally abundant, introduced cyclopoid *Limnoithona tetraspina* [S. M. Bollens unpubl. data]) and larger potential prey items (>850 µm PL), will be important aspects for clarifying prey selection behavior by this predator. In preliminary studies, Bollens et al. (2002) suggested that prey size may be a strong discriminating factor in *T. dextrilobatus* feeding selectivity; however, subsequent investigations have provided contradictory results that indicate the importance of predator pre-conditioning (i.e. prey field) prior to incubations (S. M. Bollens & R. C. Hooff unpubl. data). The relative magnitude and plasticity of *T. dextrilobatus* interactions with different prey populations will greatly determine the magnitude of impacts on the overall community, and hence requires further investigation. Clearly, by applying our single taxon functional response data to all copepods in the San Francisco Estuary, our study provides only a rough estimate of *T. dextrilobatus* predatory impact. Nevertheless, the 2 prey items used in our study share a wide distribution range with the predator, are numerically abundant, represent a size and weight range relevant to this predator, and therefore provide a reasonable basis for estimating predation rate parameters on other copepods in the zooplankton community (Fig. 7).

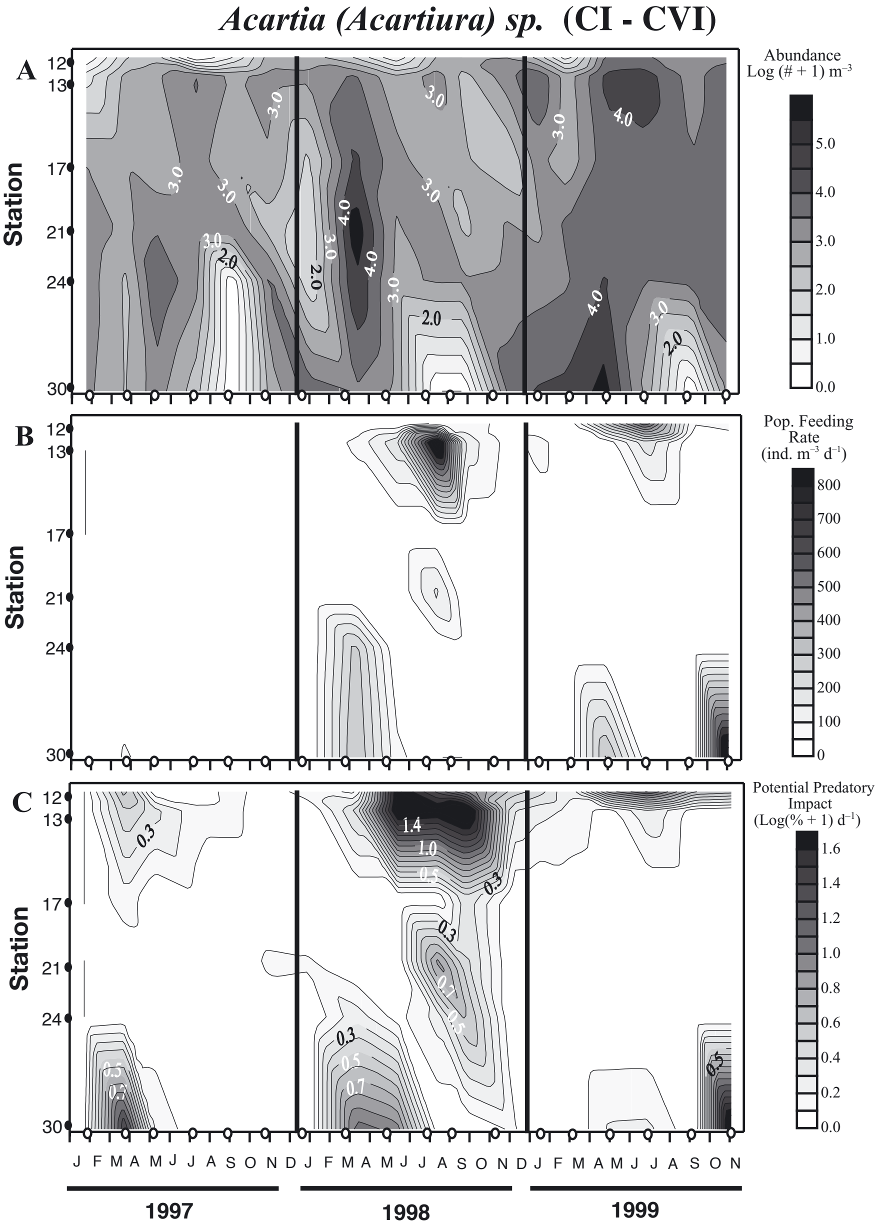

Fig. 6. *Acartia* (*Acartiura*) sp. (A) Abundance (Log [individuals + 1] m^{-3}) and distribution of *Acartia* (*Acartiura*) sp. (all copepodid stages combined), (B) estimated population feeding rate (prey individuals consumed m^{-3} d^{-1}) of *Tortanus dextrilobatus* preying upon *Acartia* (*Acartiura*) sp., and (C) potential predatory impact of *T. dextrilobatus* feeding upon *Acartia* (*Acartiura*) sp. prey (% prey population consumed d^{-1}) over a 3 yr period in the San Francisco Estuary (open circles on *x*-axis represent sampling dates; dark circles on *y*-axis are locations of sampling). Data between sampling dates and locations have been estimated using triangulation with linear interpolation

Table 3. Model parameters and results. Functional response parameters (based on Ivlev function) of adult female *Tortanus dextrilobatus* feeding on adult female copepodids of 2 prey items at 14°C. Differences in carbon-based maximum ingestion rate were used to determine Q_{10} values for each of the 2 prey items. Functional response and Q_{10} parameters for 'All Copepoda' are the mean of the empirically derived values for the other 2 taxa. Predatory impact estimates were calculated based on 2 predator-prey interaction scenarios; first, 'adults-only' (adult stage predators feeding upon adult prey), and alternatively, calculations assuming all copepodid and adult stage predators feeding upon an assemblage made up of all copepodid and adult stage prey

Prey taxa		Functional response parameters		Q_{10}	Potential predatory impact (% × d^{-1})					
					Adults only			All stages		
		I_{max}	a		Max	Median	Mean	Max	Median	Mean
O. davisae		14.0	0.011	3.5	5.4	0.00	0.2	22.7	0.02	1.0
	+SE	16.3	0.016		8.8	0.00	0.3	35.4	0.04	1.5
	−SE	11.7	0.006		2.6	0.00	0.1	11.4	0.01	0.5
Acartia sp.		14.1	0.034	1.2	45.6	0.00	1.5	67.3	0.09	4.0
	+SE	15.8	0.044		65.6	0.00	2.2	96.4	0.13	5.7
	−SE	12.3	0.025		28.7	0.00	1.0	42.7	0.06	2.5
All Copepoda		14.0	0.023	2.3	7.3	0.00	0.4	29.2	0.04	0.9
	+SE	16.1	0.03		9.9	0.00	0.4	37.7	0.05	1.1
	−SE	12.0	0.015		4.8	0.00	0.3	20.2	0.03	0.7

To estimate the potential predatory impact of *Tortanus dextrilobatus* upon prey populations in the San Francisco Estuary, we applied our laboratory derived consumption rates (adult female *T. dextrilobatus* feeding upon adult female prey) to other copepodid life-history stages assuming a linear relationship across developmental stages (i.e. immature copepodite predators feed on immature copepodite prey at the same rate as adult female predators feed upon adult female prey). This assumption is supported by Uye & Kayano (1994a), wherein they reported CI-CV *Tortanus* spp. (*T. forcipatus* and *T. gracilis*) preying upon a variety of copepod taxa and stages that were 54 to 115% of their body length, and that maximum daily ration (% body weight predator^{-1} d^{-1}) was comparable to or higher than that of CVI adults.

Another important assumption of our model is of an over-simplified homogenous vertical distribution of predators and prey. Results from Lougee et al. (2002) suggest considerable overlap between *Tortanus dextrilobatus* and the 2 prey items used in our feeding studies, though the degree of overlap may be reduced when strong water column stratification is present. This warrants further investigation in the field.

Our results suggest that weight (body carbon) may be more seasonally variable for adult females of *Tortanus dextrilobatus* and *Acartia* (*Acartiura*) sp. than for *Oithona davisae* (Table 1). Recalculating *T. dextrilobatus* consumption rates as a function of individual-based *O. davisae* carbon content (Figs. 3C,D & 4C,D) results in a more pronounced Q_{10} (3.45) compared to calculations based on # individuals consumed predator^{-1} d^{-1} (Q_{10} = 2.40). This has important implications for estimating potential predatory impact in the field. The Q_{10} generated for *T. dextrilobatus* consumption of *Acartia* (*Acartiura*) sp. based on prey weight, however, was only slightly different than that based on prey number (1.2 vs 1.1). Although Q_{10} values for most zooplankton metabolic processes are generally considered to be in the range of 2.0 to 3.0 (Vidal 1980, Bamstedt et al. 2000), values obtained in this study (Table 1) are within the range of values reported for other predatory zooplankton. For example, between 15 and 25°C, Uye & Kayano (1994a) obtained a Q_{10} for adult *Tortanus* spp. (*T. gracilis* and *T. forcipatus*) feeding on *O. davisae* prey of 2.3 and 4.3 (females and males, respectively). In contrast, Sell et al. (2001) found no significant difference in predation by the omnivorous *Centropages typicus* on *Calanus* nauplii at 6 and 11°C.

While it would have been preferable to base a Q_{10} calculation from a temperature range greater than 5°C, the need for sufficient numbers of field captured predators and prey for efficient pre-experimental sorting limited our investigations to 14 and 19°C. However, there were few instances when abundance of *Tortanus dextrilobatus* in the San Francisco Estuary occurred outside a range of 12 to 21°C (Fig. 2A,B). Therefore, we expect application of temperature-dependent rates to our field surveys (even if slightly beyond the range of our empirically derived values) to be valid in predicting predatory impacts.

To examine the sensitivity of our modeling results to seasonal variation in prey size and resulting Q_{10} values, we recalculated our *Acartia* (*Acartiura*) sp. functional response data using a length–carbon content regression for adult female *A. clausii* (Ayukai 1987). The resulting Q_{10} (3.03) was substantially higher than that achieved using our carbon-based results (Q_{10} = 1.2). Modeling predatory impact with this alternate Q_{10} estimate (i.e. 3.03) had the effect of altering some station-specific values by as much as ±20% d^{-1}, yet the average impact value over our 1997–1999 broadscale survey increased only slightly, from 3.99 to 4.53% d^{-1}. As an additional test of our model's sensitivity to variability in our empirical data, we re-calculated potential predatory impact using error estimates (±1 SE) of the functional response parameters (Table 3). The estimated predatory impact values presented in this study (as applied to the 2 copepod populations or the assemblage of all copepods) are in all cases substantially higher than those observed for invertebrate predators in other systems (Turner et al. 1984, Ohman 1986, Uye & Kayano 1994a).

Numerous studies have reported consumption rates by marine zooplanktivores, but only a limited number have extended their results to estimate potential prey mortality in nature (Ohman 1986, Bollens 1988, Uye & Kayano 1994b, Atkinson & Snyder 1997, Sell et al. 2001). Of course, the potential for compounding errors is reason to exercise caution in applying any simplified modeling approach. However, provided that assumptions can be reasonably justified, we believe that this is an important application of empirical results, particularly in light of rising concerns over the potential impacts of non-indigenous species (Carlton & Geller 1991, 1993, Ruiz et al. 1997, Bollens et al. 2002).

To estimate predation impacts by the omnivore *Euphausia superba*, Atkinson & Snyder (1997) used a similar experimental design; extrapolating feeding rates from bottle incubations and then applying the rates to acoustic surveys. They found that *E. superba* was capable of removing 1.6% of small calanoid copepods d^{-1}. Similarly, Ohman (1986) reported daily impact values of 3 dominant predators affecting population dynamics of *Pseudocalanus* sp. to be 3.5% (the carnivorous copepod *Eucheta elongata*), 1.0% (the euphausiid *Euphausia pacifica*), and 0.5% (the chaetognath *Sagitta elegans*). Uye & Kayano (1994a) found maximum impacts of *Tortanus* spp. (the smaller Tortanidae species *T. gracilis* and *T. forcipatus*) predation on small planktonic crustaceans (primarily *Oithona davisae*) to be 2% d^{-1}, and the mean impact over a 2 mo period to be 0.8% d^{-1}. Although our mean estimated impacts based on broadscale surveys (multiple sampling stations over a 3 yr period) are consistent with the above values from the literature (1 to 4% d^{-1}), our results reveal episodic and perhaps seasonal events in which *T. dextrilobatus* predation upon copepod populations may be much higher (22 to 67% consumed d^{-1}). These events can be attributed to high population densities achieved by *T. dextrilobatus* in its recently invaded habitat compared to carnivorous copepods in other systems.

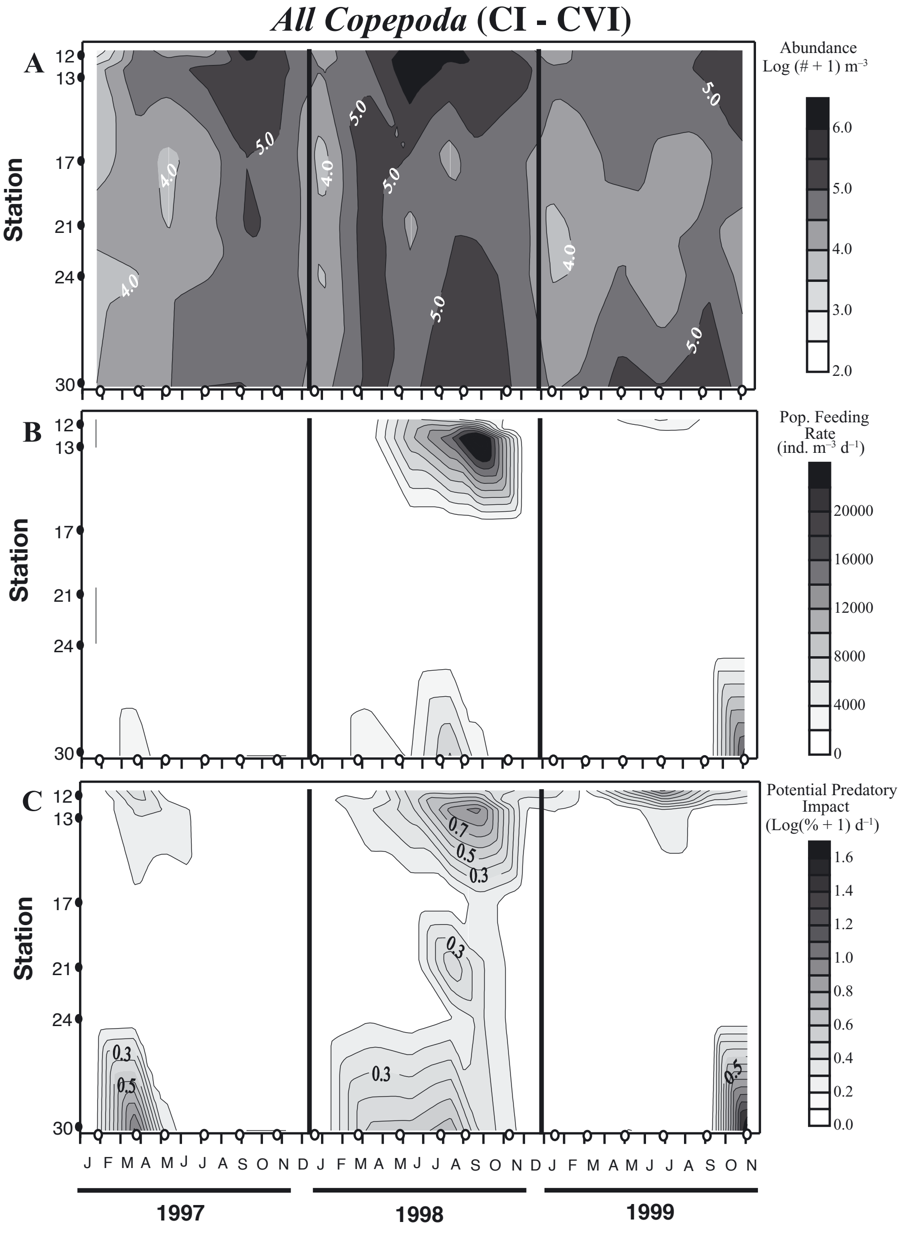

Fig. 7. All Copepoda (A) Abundance (Log [individuals + 1] m^{-3}) and distribution of all Copepoda (all copepodid stages combined), (B) estimated population feeding rate (prey individuals consumed m^{-3} d^{-1}) of *Tortanus dextrilobatus* preying all Copepoda, and (C) potential predatory impact of *T. dextrilobatus* feeding upon all Copepoda prey (% prey population consumed d^{-1}) over a 3 yr period in the San Francisco Estuary (open circles on *x*-axis represent sampling dates; dark circles on *y*-axis are locations of sampling). Data between sampling dates and locations have been estimated using triangulation with linear interpolation

Determining the impact of *Bythotrephes* sp., a nonindigenous freshwater zooplanktivore introduced to North American lakes, has benefited from mesocosm enclosure studies (Vanderploeg et al. 1993) and long-term records revealing pre- and post-invasion impacts in an undisturbed system (Yan & Pawson 1997). Such experimental approaches are difficult to apply to a physically dynamic and highly urbanized estuarine system where a variety of concurrent stressors (biotic and abiotic) may be responsible for altering trophic linkages. While large-scale enclosure studies would be another important approach in exploring *in situ* multi-trophic level consequences of the *Tortanus dextrilobatus* invasion, long-term monitoring of zooplankton community abundance and distribution can offer important clues in determining the system response to invasion disturbance. Relative to the 1993 introduction of *T. dextrilobatus*, it may be important to interpret our 1997–1999 broadscale surveys with respect to a potential lag-time in response of prey defense or escape mechanisms to the introduction of a new predatory pressure (Shea & Chesson 2002). Similarly, natural mortality of *T. dextrilobatus* may have been suppressed following its initial invasion until its potential predators (e.g. planktivorous fishes) adapt to this new food source (Keane & Crawley 2002). A better understanding of these processes (via long-term records and additional experimental studies) may help explain the extraordinarily high seasonal densities of this carnivorous copepod and its substantial predatory impact on other copepods in the San Francisco Estuary.

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