Estuaries Vol. 26, No. 4A, p. 956–969 August 2003

Selenium in San Francisco Bay Zooplankton: Potential Effects of Hydrodynamics and Food Web Interactions

DAVID G. PURKERSON[1,†], MARTINA A. DOBLIN[2], STEPHEN M. BOLLENS[1,3,*], SAMUEL N. LUOMA[4], and GREGORY A. CUTTER[2]

[1] *Romberg Tiburon Center for Environmental Studies and Department of Biology, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920*
[2] *Department of Ocean, Earth, and Atmospheric Science, Old Dominion University, Norfolk, Virginia 23529*
[3] *Moss Landing Marine Laboratories, California State University, 8272 Moss Landing Road, Moss Landing, California 95039*
[4] *Water Resources Division, United States Geological Survey, 345 Middlefield Road, Menlo Park, California 94025*

ABSTRACT: The potential toxicity of elevated selenium (Se) concentrations in aquatic ecosystems has stimulated efforts to measure Se concentrations in benthos, nekton, and waterfowl in San Francisco Bay (SF Bay). In September 1998, we initiated a 14 mo field study to determine the concentration of Se in SF Bay zooplankton, which play a major role in the Bay food web, but which have not previously been studied with respect to Se. Monthly vertical plankton tows were collected at several stations throughout SF Bay, and zooplankton were separated into two operationally defined size classes for Se analyses: 73–2,000 μm, and ≥2,000 μm. Selenium values ranged 1.02–6.07 μg Se g^{-1} dry weight. No spatial differences in zooplankton Se concentrations were found. However, there were inter- and intra-annual differences. Zooplankton Se concentrations were enriched in the North Bay in Fall 1999 when compared to other seasons and locations within and outside SF Bay. The abundance and biovolume of the zooplankton community varied spatially between stations, but not seasonally within each station. Smaller herbivorous-omnivorous zooplankton had higher Se concentrations than larger omnivorous-carnivorous zooplankton. Selenium concentrations in zooplankton were negatively correlated with the proportion of total copepod biovolume comprising the large carnivorous copepod *Tortanus dextrilobatus*, but positively correlated with the proportion of copepod biovolume comprising smaller copepods of the family Oithonidae, suggesting an important role of trophic level and size in regulating zooplankton Se concentrations.

Introduction

Selenium (Se) has been an element of concern in aquatic environments for many years due to its potential toxicity. Like most other elements, Se enters aquatic environments from natural and anthropogenic sources and, at elevated concentrations, causes toxicity (Cumbie and Van Horn 1978; Garrett and Inman 1984; Ohlendorf et al. 1986; Lemly 1996). Se toxicity and bioaccumulation is complicated due to its multiple oxidation forms, each of which displays different chemical and toxicological properties (Lemly 1996). Se can also undergo transformation between inorganic and organic forms, thereby affecting bioavailability and toxicity (Besser et al. 1993; Maier et al. 1993). Selenite (SeIV, SeO_3^{2-}) and selenate (SeVI, SeO_4^{2-}), are the inorganic forms of dissolved Se, with selenite shown to be the most bioavailable form for phytoplankton uptake (Hu et al. 1997), a necessary first step in the trophic transfer of Se. Most studies addressing Se bioaccumulation have found that lower trophic levels such as phytoplankton and bacteria bioaccumulate dissolved Se, and higher trophic levels (i.e., zooplankton and fish) accumulate Se through ingestion (Luoma et al. 1992; Lemly 1993; Bowie et al. 1996; Thomas et al. 1999).

San Francisco Bay (SF Bay) is an excellent environment in which to study the trophic transfer of Se given the history of Se contamination and foodweb toxicity in the California Central Valley and Kesterson Reservoir (Ohlendorf et al. 1986; Luoma and Phillips 1988). The potential for adverse ecological effects from Se have been reported over the past 20 years in SF Bay (Luoma 1997; Thomas et al. 1999), and the impact of this element on the SF Bay-Delta foodweb-ecosystem is still under investigation. Past research showed elevated concentrations of dissolved and particulate Se and anthropogenic influences on dissolved Se speciation (Cutter 1989; Cutter and San Diego-McGlone 1990), as well as high Se exposures in benthos

* Corresponding author: e-mail: sbollens@sfsu.edu.
† Current address: Florida Department of Environmental Protection, Suite 232, 3319 Maguire Boulevard, Orlando, Florida 32803.

(Johns et al. 1988; Linville et al. 2002), some fish (White et al. 1988), and certain species of waterfowl (Urquhart and Regalado 1991). Phytoplankton readily accumulate dissolved Se (Wrench 1978; Price et al. 1987; Harrison et al. 1988; Baines and Fisher 2001), and the resultant particulate organic Se has been shown to be efficiently assimilated by the bivalves *Macoma balthica* and *Potamocorbula amurensis* (Luoma et al. 1992; Schlekat et al. 2000). Indeed, this efficient assimilation and slow loss may contribute to the especially high (10–20 $\mu g\ g^{-1}$ dry weight) Se concentrations exhibited by *P. amurensis* in SF Bay (Schlekat et al. unpublished data). These concentrations are potentially problematic to consumers of *P. amurensis* (e.g., diving ducks and sturgeon) because they exceed threshold toxicity for a food source (Skorupa 1998).

While upper and lower trophic level organisms and benthic bivalves have been the center of Se studies, little is known about the accumulation by lower level pelagic consumers such as zooplankton. Zooplankton are an integral part of estuarine and coastal food webs since they are a food source for many juvenile and adult fish (Meng and Orsi 1991), and they could also be a dietary source of Se. Most ecological studies of SF Bay zooplankton have focused on the upper estuary (e.g., Orsi and Mecum 1986; Kimmerer and Orsi 1996; Kimmerer et al. 1998), with the exception of two studies (Ambler et al. 1985; Bollens et al. 1999); much less is known about the lower, more saline reaches of the Bay. The trophic transfer of Se from phytoplankton to zooplankton to upper trophic level organisms has been addressed for freshwater systems in laboratory studies (Fisher and Reinfelder 1991; Besser et al. 1993), but the role of zooplankton in Se dynamics is poorly understood for estuarine systems such as SF Bay.

There are many factors that could influence Se concentrations in zooplankton in SF Bay, including proximity to Se sources and hydrodynamics. Se sources to SF Bay include the Sacramento and San Joaquin Rivers. The Sacramento River has low concentrations of total dissolved Se ($\sim$ 0.9 nM, Cutter 1989; Cutter and San Diego-McGlone 1990). An order of magnitude higher levels of Se are found in the San Joaquin River (Cutter and San Diego-McGlone 1990; Cutter unpublished data), which drains the naturally high seleniferous soils of the Southern Central Valley (Lemly 1993; Thomas et al. 1999). This river rarely flows into SF Bay due to municipal and agricultural withdrawals (Cutter and San Diego-McGlone 1990). Oil refineries located around Carquinez Strait are another source of Se to SF Bay (Cutter 1989; Cutter and San Diego-McGlone 1990). Interestingly, Se concentrations in clams are greatest in this region (Linville et al. 2002).

Biological factors could also influence Se concentrations in zooplankton, including body size, species, and trophic status (Liu et al. 1987; Goede et al. 1993). For example, Brugmann and Hennings (1994) found differences in Se accumulation between different zooplankton species and different life stages of the same species. Previous studies have demonstrated that zooplankton accumulate Se primarily through ingestion of particle-associated Se rather than from the dissolved state (Wang and Fisher 1998). It is also possible that the feeding habits of zooplankton (e.g., herbivores versus carnivores) could influence their Se concentrations.

The overall objective of this study was to determine the spatial (1–60 km) and temporal (seasonal and interannual) variability of Se concentrations in SF Bay zooplankton. More specifically, we studied effects of: proximity to Se sources, variation in freshwater flows, and variation in zooplankton composition, including size, structure, and trophic level.

Materials and Methods

Study Sites

SF Bay is the largest estuary in western North America with a surface area of 1,240 km^2 and an average depth of 6.1 m (Conomos 1979). It is composed of three general regions: the South, Central, and North Bays, with the latter comprised of San Pablo Bay, Carquinez Strait, and Suisun Bay (Fig. 1). The North and South Bay have distinct circulation patterns, salinity distributions, and biological communities (Ambler et al. 1985; Peterson et al. 1985; Walters et al. 1985). Two major rivers enter SF Bay through the North Bay: the Sacramento and San Joaquin Rivers. During the rainy season (Winter and Spring) freshwater discharge from the Sacramento River is high, ranging from 1,000–10,000 $m^3\ s^{-1}$, and during the dry season (late Summer and Fall) river flows range from 100–500 $m^3\ s^{-1}$ (Ambler et al. 1985). In contrast to the North Bay, the South Bay has no large direct source of freshwater and is therefore considered lagoon-like.

Field Sampling

Zooplankton were sampled on the R/V *Polaris* at 6 fixed locations throughout SF Bay (Fig. 1) during monthly cruises, September 1998–November 1999. These sites are part of the U. S. Geological Survey's long-term regional water quality monitoring program (see website: www.sfbay.wr.usgs.gov/access/wqdata). Due to time constraints, only two samples were collected at each station on each date. Zoo-

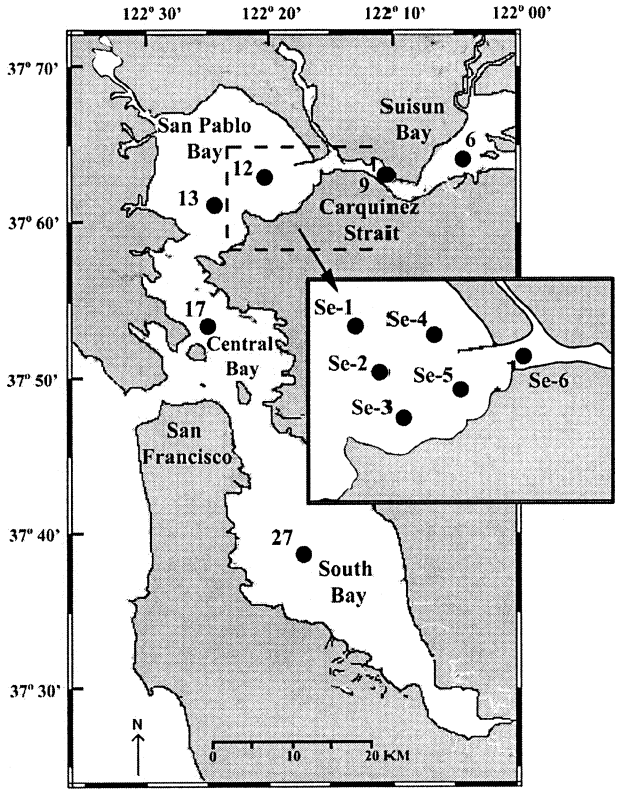

Fig. 1. Zooplankton sampling stations in San Francisco Bay and North Bay (inset).

plankton samples were taken using a 73 μm mesh, 0.5 m-diameter ring net fitted with General Oceanics flowmeter for volume calculations. Two vertical tows from within 1–2 m of the bottom to the surface were collected at each station: one for zooplankton Se determinations, and one for analysis of zooplankton species composition. In October 1999, one sample was taken outside of SF Bay in the Gulf of the Farallones, just west of the Golden Gate Bridge during peak flood tide.

Species composition samples were immediately rinsed and preserved in 5% Formalin-seawater solution. Although all zooplankton sampled <2,000 μm were combined for Se analysis, live samples for Se determinations were immediately separated into 4 operationally-defined size classes: 73–250 μm, 250–500 μm, 500–2,000 μm, and ≥2,000 μm. Each size fraction was placed in separate 1 L glass jars filled with filtered (73 μm) seawater for 2 h to allow for gut depuration and to allow detritus and phytoplankton to settle out. For samples containing high amounts of detritus or phytoplankton, zooplankton were isolated by phototaxis and were removed with a widebore pipette. Following isolation, zooplankton were rinsed with seawater (salinity = 10) and filtered over a 73 μm sieve. Low salinity seawater was used to minimize the salt content of zooplankton samples, however Se digests were also analyzed for Na^+ to correct for salt content. After rinsing, samples were stored in 5 ml glass vials at −4°C. Due to the amount of biomass required for selenium analyses (≥15 mg dry weight), zooplankton samples were combined, before freezing, into two size classes: 73–2000 μm and ≥2,000 μm. Wet weights of the 73–250, 250–500, and 500–2,000 μm size classes were measured before they were combined.

Since the size fractionated monthly zooplankton samples were combined at each station, we conducted a smaller scale study in the North Bay in February and October 1999 to address whether different sized zooplankton accumulate different amounts of Se. The area from eastern San Pablo Bay to western Carquinez Strait was chosen because of its proximity to oil refineries and potential for elevated Se concentrations. Zooplankton samples were collected on a grid of 6 stations within 2 km of United States Geological Survey Station 12 (Station Se-1 to 6; Fig. 1). Sampling and handling procedures were identical to the monthly sampling, but due to the shallow depths (3.0 ± 0.3 m) and high biomass requirement, 10-min horizontal surface tows were conducted at each station. At Station Se-2, located in the main shipping channel, an oblique tow was conducted for 10 min. Samples were collected, isolated, and sorted as described earlier.

Species Identification

Zooplankton were identified by microscopic analysis. Subsamples (approximately 1% of the total volume) were removed from each sample with a Stempel pipette and examined under a dissecting microscope (Leica MZ6). Zooplankton were identified to 16 different taxonomic groups, of which copepods were identified to the species level when possible. Zooplankton abundance (number m^{-3}) was calculated for each taxon within each sample.

Total biovolume estimates were calculated for zooplankton in each size class (73–250 μm, 250–500 μm and 500–2,000 μm), which involved calculating an average biovolume per species and size (n = 20) and multiplying by the total number of individuals. Each zooplankton taxon was assigned a 3-dimensional shape and the volume was calculated. For example, copepod volumes were calculated using the equation for oblate spheroids; where volume = $4/3\ \pi \times r^2 \times l$, where r = spheroid radius (semi-minor axis) and l = spheroid length (semi-major axis). Copepod nauplii and tintinnids were considered spheres and their volumes

TABLE 1. Summary of samples pooled for spatial (1–60 km) and temporal (seasonal and interannual) ANOVAs.

Spatial Analyses All Sampling Dates (September 1, 1998–November 10, 1999		Temporal Analyses		
		Fall 1998 (September 1–November 9)	Spring 1999 (March 9–May 7)	Fall 1999 (September 1–November 10)
Stations	n	n	n	n
6	8	2	2	3
9	9	1	3	3
12	13	3	3	3
13	13	3	3	3
17	7	0	2	3
27	11	2	3	3

were calculated accordingly. All other zooplankton were considered cylinders.

Selenium Determinations

Selenium tissue concentrations were determined using the oxidative digest and selective hydride generation atomic absorption spectroscopy (AAS) methods in Cutter (1985). Zooplankton (stored at −4°C for ≤ 6 mo) were dried at 40°C, weighed, and subsequently digested using a 3-step nitric-perchloric acid reflux procedure. After evaporation of the nitric acid, the residue was redissolved in 4M HCl and stored until final Se analysis. To determine Se concentrations, 1–2 ml aliquots of digest solution were diluted to 40 ml with distilled water in a 400 ml glass beaker to which Teflon boiling stones, 0.5 ml of 2% (w/v) persulfate solution, and 22 ml concentrated HCl were added. The beaker was covered with a watch glass, and the solution brought to a boil for 30 min, with the heat being reduced to the minimum capable of sustaining boiling. After cooling overnight, the samples were analyzed using the hydride generation procedure described by Cutter (1978). The standard additions method of calibration was used to ensure accuracy, and all determinations were made in triplicate to establish precision. In addition to the standard addition method, accuracy was verified using the digestion and determination of Se in National Institute of Standards and Technology (NIST) Oyster Tissue with each group of 10 samples. All sample weights were corrected for salt content by measuring Na concentrations using flame AAS.

Statistical Analyses

Before statistical analyses, data were checked for normality and homogeneity of variances. Having only one sample at each station on each date necessitated the pooling of data, over time and space, to allow for statistical analysis (Table 1). A one-way analysis of variance (ANOVA) was used to test spatial differences in zooplankton Se concentrations between stations, where all samples collected at a given station over the study period were pooled. One-way ANOVA was also used to test for differences between size classes, where we pooled samples from the smaller scale North Bay zooplankton sampling. A two-way ANOVA was also used to test for differences in zooplankton Se concentrations among stations and seasons. Due to the marked seasonal differences in SF Bay river flow (Walters et al. 1985), we pooled samples collected at a given station over a given season with Spring (high flow) being defined as March, April, and May, and Fall (low flow) defined as September, October, and November. In cases where ANOVA results were significant, Tukey's studentized range test was used to make multiple comparisons among means at the 95% confidence level. Arcsine transformations were applied to percent biovolume and percent wet weight data to ensure normality.

To test for similarities in zooplankton abundance and biovolume within stations, seasons, and size classes, Kendall's coefficient of concordance (W), a nonparametric multisample rank-correlation statistic was used. When concordance results were significant (i.e., samples were similar) for a given station over the period of the study, season or size class, we pooled sampling dates for that station and season. Kendall's W ranges from 0 (no association) to 1 (perfect association). Kendall's *Tau* rank correlations were used to look for differences in zooplankton abundance and biovolume between pairs of stations, seasons or size classes. In terms of either abundance or biovolume, a lack of significant correlation was interpreted as an absence of concordance indicating a substantial difference in zooplankton communities. Although alternatives to concordance and rank correlations for community analysis have been suggested (e.g., Jumars 1980; Ghent 1982), these analyses are still commonly used in community ecology (e.g., Brown-Peterson et al. 1993; Turner et al. 1995; Farnsworth and Ellison 1996; Bengtsson et al. 1997; Tolimieri et al. 1998.) Specifically, correlation analysis was considered a conservative approach for our study due to the relatively low number of taxa (n = 10) used, i.e., we avoided the problem of rare taxa leading to significant results (see Herbold 1984; Rahel et al. 1984; Grossman et

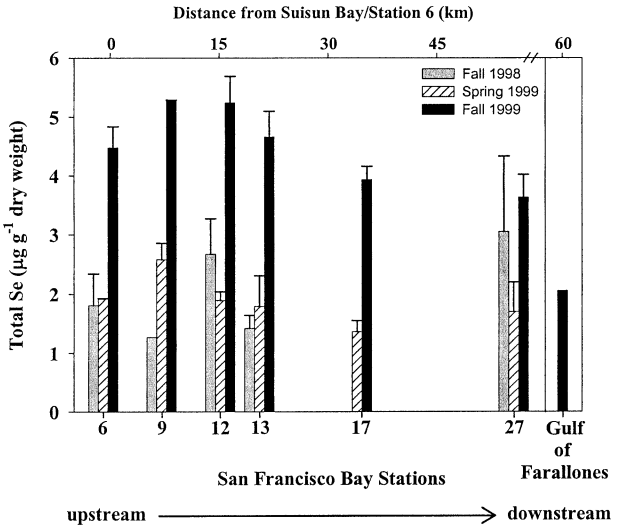

Fig. 2. Se concentrations (mean ± SE) in 73–2,000 μm size fraction of SF Bay zooplankton during Fall 1998, Spring 1999 and Fall 1999. No samples were collected from the Central Bay (Station 17) during Fall 1998.

al. 1985). All statistical analyses were completed with SPSS 9.0 (Norusis 1999). Variation of the mean is presented as standard error unless otherwise indicated.

Results

Spatial Patterns in Zooplankton Se Concentrations

Mean Se concentrations in all zooplankton size classes (73–2,000 μm) and over all collection periods ranged from 2.5 ± 1.5 μg g^{-1} at Station 6 to 3.5 ± 1.5 μg g^{-1} at Station 9 in Carquinez Strait. Se concentrations were not different among stations (ANOVA: $F_{5,55} = 0.483$, $p = 0.787$, $n = 8$ to 13). The one sample taken in the Gulf of the Farallones in October 1999 had a Se concentration of 2.1 μg g^{-1}, which was lower than Se concentrations found in SF Bay during the same period (4.5 ± 0.8 μg g^{-1}, df = 17, $p < 0.05$).

Temporal Patterns in Zooplankton Se Concentrations

Average Spring Se concentrations were 1.9 ± 0.7 μg g^{-1}, 30–60% lower than average Fall Se concentrations (3.6 ± 1.5 μg g^{-1}). There was no difference in Se concentrations between stations, but temporal differences were found between Fall 1998 and Fall 1999 and between Spring and Fall 1999 (ANOVA: $F_{2,28} = 56.311$, $p < 0.001$; Fig. 2). There was considerable interannual variability, with Se concentrations ranging from 1.0 μg g^{-1} in Fall 1998 to 6.1 μg g^{-1} in Fall 1999. Selenium concentrations in Fall 1998 and Spring 1999 were similar.

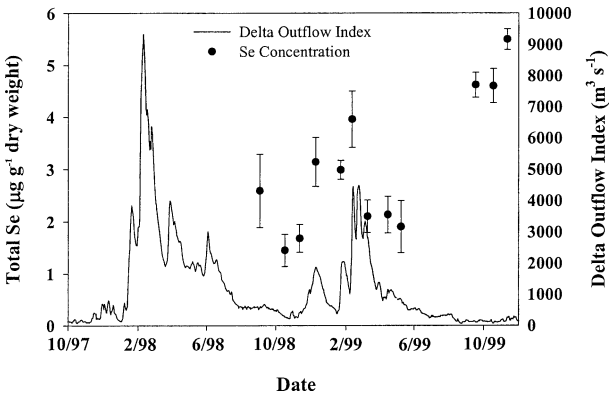

Fig. 3. Se concentration (mean ± SE) in North SF Bay zooplankton (73–2,000 μm) and Delta outflow index August 1998–December 1999.

Hydrodynamics of SF Bay versus Selenium

The high flow period of 1998–1999 was normal compared with the previous 16-yr mean. In contrast, SF Bay experienced exceptionally high river flows in 1997–1998, due to an El Niño event, when the Delta Outflow Index (DOI: the total volume of water discharged through the SF Bay watershed; http://iep.water.ca.gov/dayflow/) exceeded 9,000 $m^3\ s^{-1}$ (Fig. 3). The peak outflow also occurred in late February 1999 and tapered off during the summer and fall, a typical profile of Sacramento River discharge (Cloern and Nichols 1985).

The highest Se concentrations in zooplankton coincided with the period of lowest freshwater flow (Fall 1999). We tested whether Se concentrations in zooplankton were related to river flow (analogous to water residence time; Linville et al. 2002) by attempting to correlate DOI and zooplankton Se concentrations. Only Stations 6–13 in the North Bay were included because the Central Bay is influenced by tidal flow and its proximity to the Golden Gate, while the South Bay is mostly enclosed and has no large direct source of freshwater (Cloern and Nichols 1985; Walters et al. 1985; Cutter 1989). Zooplankton Se concentrations were quite variable during episodes of high freshwater input, resulting in a non significant correlation ($r^2 = 0.016$, $p = 0.695$, $n = 12$; Fig. 3).

Selenium in Size Fractionated Zooplankton

For samples collected during the smaller scale North Bay zooplankton sampling in February and October 1999, Se concentrations in size classes < 2,000 μm were similar (Fig. 4). Differences in Se concentrations occurred between 73–250 μm (3.5 ± 0.9 μg g^{-1}) and ≥ 2,000 μm size classes (1.7 ± 0.7 μg g^{-1}), as well as between 250–500 μm (3.1 ± 0.3 μg g^{-1}) and ≥ 2,000 μm (ANOVA: $F_{3,18} = 6.301$, $p = 0.004$; mean ± SE, $n = 4$–6). Zooplank-

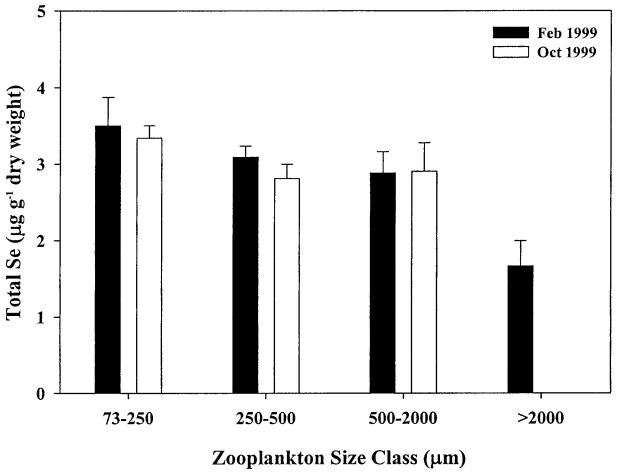

Fig. 4. Se concentrations (mean ± SE) in zooplankton from the North Bay size fractionated samples in February and October 1999. Zooplankton > 2,000 μm were not present in October 1999.

ton ≥ 2,000 μm were absent from samples collected in October 1999, and those found in February 1999 were mostly larval herring.

Occasionally, zooplankton ≥ 2,000 μm were caught in the plankton net during the monthly field sampling, and these were analyzed for Se. Mean Se concentrations in the 73–2,000 μm size class (2.6 ± 0.7 μg g^{-1}) were greater than Se concentrations in the ≥ 2,000 μm size class, (1.5 ± 0.7 μg g^{-1}) in 6 of 9 occasions (*t*-test, df = 8, $p < 0.01$). Zooplankton ≥ 2,000 μm included isopods (*Synidotea* sp.), mysids (*Acanthomysis bowmani*), and shrimp (*Crangon franciscorum*) and had Se concentrations of 1.1 ± 0.5 μg g^{-1}, 1.4 ± 0.3 μg g^{-1}, and 1.2 ± 0.3 μg g^{-1}, respectively (mean ± SE, n = 2–7). To test the relationship between zooplankton Se and size fraction, total Se was compared to the proportion of total wet weight of zooplankton in each size class, and was found to be positively correlated in the 73–250 μm size class ($r^2 = 0.09$, $p = 0.022$, n = 57; Fig. 5a) and nearly significant yet negatively correlated in the 500–2,000 μm size class ($r^2 = 0.06$, $p = 0.088$, n = 48; Fig. 5b).

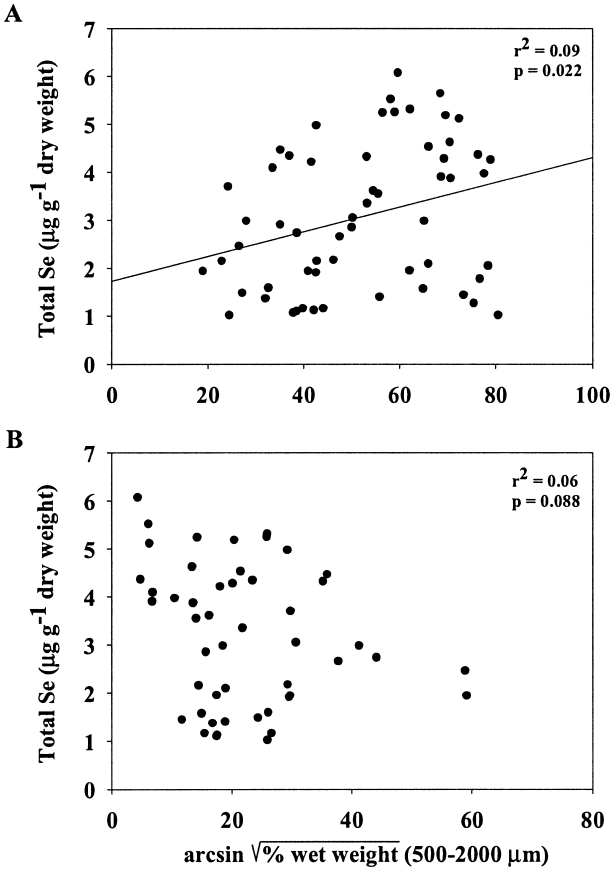

Fig. 5. Se concentrations versus wet weight of SF Bay zooplankton in two size classes, 73–250 μm (A) and 500–2,000 μm (B). The former correlation is significant ($r^2 = 0.09$, $p = 0.022$) and shows a positive relationship, whereas the latter shows a negative, but non-significant, relationship ($r^2 = 0.061$, $p = 0.088$).

Annual Zooplankton Community Composition

The 16 different taxonomic groups of zooplankton identified consisted of copepods (*Acartia* spp., *Acartiella sinensis,* Oithonidae, *Paracalanus* spp., *Pseudodiaptomus* spp., *Tortanus dextrilobatus,* Harpacticoida, copepod nauplii), protozoans (tintinnids), and other miscellaneous zooplankton (amphipods, flatworm larvae, isopods, larvaceans, larval fish, mysids, and polycheate larvae).

Smaller zooplankton (73–2,000 μm) in SF Bay were comprised mostly of calanoid and cyclopoid copepods and tintinnids (Fig. 6). Tintinnids and copepods in the family Oithonidae, which included the non-indigenous copepods *Oithona davisae* and *Limnoithona tetraspina,* were the most abundant zooplankton (30–50%). Although *O. davisae* and *L. tetraspina* are small (< 500 μm), they constituted a majority of the biovolume (10–60%) in most of our zooplankton samples, especially in the 73–250 μm size class. *Acartia* spp. occurred at every station and increased in abundance from North to South SF Bay (increasing station numbers), comprising the majority of the biovolume (50–60%) in the Central and South Bays. In contrast, the copepod *T. dextrilobatus* was more abundant in the North Bay compared to the South Bay.

On an annual scale, zooplankton communities in terms of both rank order of abundance (W = 0.64–0.79, $p < 0.001$) and biovolume (W = 0.45–0.60, $p \leq 0.001$) were concordant at a given station over the study period. On a spatial scale, when Sta-

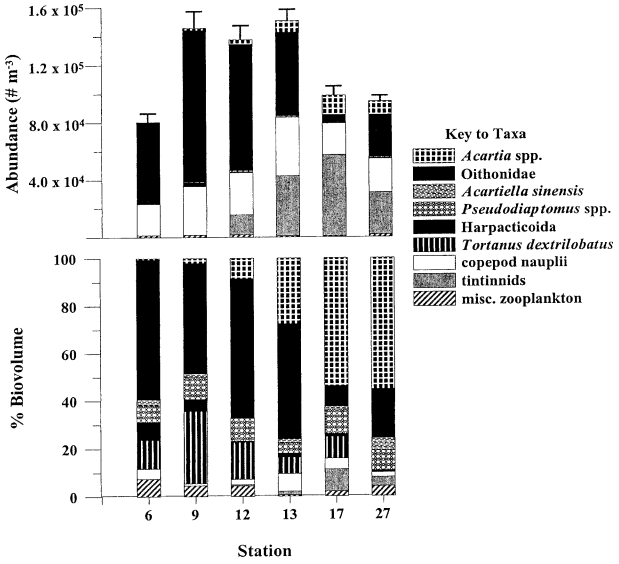

Fig. 6. Annual mean abundance (# m^{-3}) and mean % biovolume of zooplankton in San Francisco Bay November 1998–October 1999 (n = 6 to 9 at each station). Error bars represent standard error of mean for total zooplankton abundance.

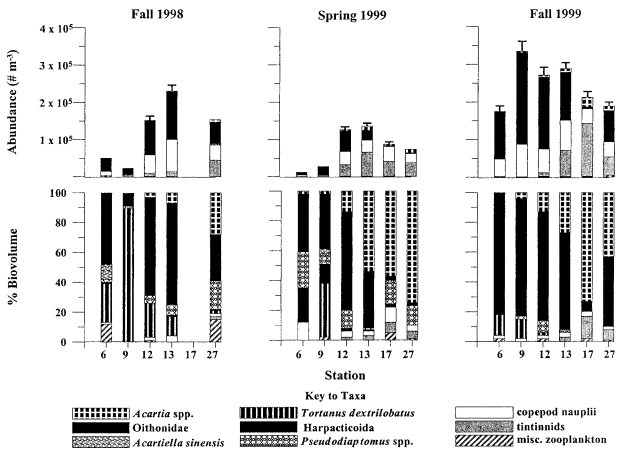

Fig. 7. Mean abundance (# m^{-3}) and mean % biovolume of zooplankton in San Francisco Bay for Fall 1998, Spring 1999, and Fall 1999 (n = 1 to 3 for each station). Error bars represent standard error of mean for total zooplankton abundance per season at each station. Due to the scale of abundance, error bars are presented when standard errors $> 5 \times 10^3$.

tions 6 and 9 were compared to all other stations, zooplankton communities (rank order of abundance and biovolume) were different (Table 2). In addition, zooplankton communities in terms of rank order of biovolume were different between Stations 12 and 27 and between Stations 13 and 17. Thus, on an annual basis, zooplankton community composition were similar within each station over time, but there were differences between stations which were not adjacent to one another.

Seasonal Zooplankton Community Composition

Seasonal comparisons showed zooplankton abundance was greater in Fall 1999 compared to Fall 1998 and Spring 1999 (Fig. 7). In addition, Oithonidae comprised a larger fraction of the biovolume in the North Bay during Fall 1999 (75%) than in either Fall 1998 (48%) or Spring 1999 (45%; Fig. 7). Zooplankton communities showed concordance, in terms of both rank order of abundance ($W = 0.67–0.99$, $p < 0.05$) and biovolume ($W = 0.64–0.99$, $p \leq 0.05$), at a given station over a given season for 12 of the 16 comparisons. Kendall's *Tau* rank correlations showed zooplankton communities were different at Station 6 between seasons (Fall 1998 versus Spring 1999 and Spring 1999 versus Fall 1999), but there was no interannual variability (i.e., no difference between Fall 1998 and Fall 1999 (Table 3). In contrast, zooplankton communities, in terms of abundance, were similar in Fall and Spring and between 1998 and 1999 at all other stations. While there was no seasonal or interannual variability in zooplankton communities in terms of rank order of abundance at different stations, there were seasonal differences in terms of rank order of biovolume at Station 6, 13, 17, and 27.

TABLE 2. Kendall's Tau rank correlation coefficients (μ, n = 10) of SF Bay zooplankton (73–2,000 μm; November 1998–October 1999) between stations for mean abundance (no. m^{-3}) and mean % biovolume. ** $p < 0.01$ and * $p < 0.05$. Bold indicates a significant difference in abundance or biovolume.

	Station	9	12	13	17	27
Abundance	6	0.864**	**0.386**	**0.341**	**0.180**	**0.270**
	9		0.523*	**0.477**	**0.315**	**0.405**
	12			0.932**	0.719**	0.854**
	13				0.719**	0.944*
	17					0.733**
% Biovolume	6	0.636*	**0.322**	**0.295**	**−0.023**	**0.135**
	9		0.598*	**0.477**	**0.159**	**0.135**
	12			0.644*	0.552**	**0.341**
	13				**0.409**	0.494*
	17					0.539*

TABLE 3. Kendall's Tau rank correlation coefficients (μ, n = 10) of SF Bay zooplankton (73–2,000 μm) of mean abundance (# m^{-3}) and mean % biovolume between Fall 1998, Spring 1999, and Fall 1999. ** $p < 0.01$ and * $p < 0.05$. nd = no data. Bold indicates a significant difference in abundance or biovolume.

	Season	6	9	12	13	17	27
Abundance	Fall 1998 versus Spring 1999	**0.110**	0.744**	0.698**	0.698**	nd	**0.744**
	Spring 1999 versus Fall 1999	**0.286**	0.605*	0.768**	0.675**	0.706**	0.756**
	Fall 1998 versus Fall 1999	0.686*	0.762**	0.614**	0.750**	nd	0.790**
% Biovolume	Fall 1998 versus Spring 1999	**0.183**	0.636*	0.542*	**0.419**	nd	0.541*
	Spring 1999 versus Fall 1999	**0.229**	0.558*	0.699**	**0.460**	**0.452**	**0.443**
	Fall 1998 versus Fall 1999	0.652*	0.843**	0.744**	0.729**	nd	0.619*

Zooplankton Community Composition of North Bay Size Fractionated Samples

During the size fractionation study, copepods in the family Oithonidae were the most abundant zooplankton comprising 64–87% of the biovolume in the 73–250 μm size class during February and October 1999 (Table 4). Oithonidae, as well as *Acartia* spp., *Eurytemora* spp., and *T. dextrilobatus,* comprised most of the biovolume in the 250–500 μm and 500–2,000 μm size classes. In both February and October 1999, concordance was high for both rank order of abundance and biovolume in a given size class over all stations (W = 0.60–0.92, $p < 0.001$). Rank correlations revealed differences in community composition between size classes in both February and October 1999 (Table 5).

Zooplankton Species-related Se Concentrations

Given the potential for zooplankton species to accumulate different amounts of Se, we examined whether the Se concentration in different size fractions was correlated with the abundance and biomass of certain taxa. Of the individual zooplankton taxa identified, only *T. dextrilobatus* and Oithonidae showed correlations between Se concentrations and the percent of the total zooplankton community (by biovolume) that they comprised (Fig. 8). *T. dextrilobatus* were mostly found in the 500–2,000 μm size class, while Oithonidae were found in the size classes <500 μm. Zooplankton Se concentrations were positively correlated with percent biovolume of Oithonidae ($r^2 = 0.11$, $p = 0.012$, n = 59; Fig. 8a), and negatively correlated with percent biovolume of *T. dextrilobatus* ($r^2 = 0.20$, $p = 0.027$, n = 25; Fig. 8b), although only a small proportion of variance was explained. However, correlations were very strong where testable within a single station (Station 9 in Carquinez Strait; i.e., Oithonidae: $r^2 = 0.91$, $p < 0.001$, n = 9; Fig. 9a; *T. dextrilobatus:* $r^2 = 0.89$, $p = 0.002$, n = 7; Fig. 9b). Station 9 was the station with the highest mean Se concentrations in zooplankton.

Discussion

To our knowledge, this study is the first to closely examine Se concentrations of zooplankton in an estuarine system. From September 1998 to November 1999, SF Bay zooplankton Se concentrations varied 1–6 μg g^{-1} dry weight. With the data collected, it is possible to address how several factors could contribute to this variability, including varying Se inputs, varying freshwater inflows, and zooplankton population characteristics (i.e., body size, community structure, and diet-trophic level).

Influence of Se Inputs on Zooplankton Se Concentrations

Average zooplankton Se concentrations from this study are similar to other systems (none of which are considered to be contaminated with Se; Table 6). Se concentrations in SF Bay zooplankton in Fall 1999 were higher than reported from elsewhere except for one sample, indicating that SF Bay zooplankton may periodically be enriched in Se. Moreover, the highest concentrations occurred in Fall 1999 at Station 9 in Carquinez Strait.

As mentioned earlier, dissolved Se levels are highest in Suisun Bay and Carquinez Strait because of their proximity to both riverine and oil refinery sources (Cutter unpublished data). However, refinery inputs have declined over the past 13 yr, with a significant decrease in the most bioavailable form of Se, selenite, with the peak in particulate Se concentrations being far less pronounced in Carquinez Strait compared to 1986 (Cutter 1989; Doblin unpublished data). But despite decreasing dissolved Se input into the SF Bay, in Fall 1999, the highest zooplankton Se concentrations coincided with elevated concentrations of particulate Se (North Bay average = 0.74 ± 0.25 μg g^{-1} [mean ± SD]) in November 1999 compared to 0.57 ± 0.23 μg g^{-1} in October 1998; Doblin unpublished data) and in bivalves (Luoma unpublished data). Several lines of data indicate that Se enrichment may still occur in this region, at least during some times of the year, and zooplankton reflect that enrichment. This suggests that samples of zooplank-

TABLE 4. Mean (SE) abundance (# m^{-3}) and mean (SE) % biovolume of zooplankton in San Pablo Bay in February and October 1999. T = trace (≤0.5%).

		February 1999			October 1999		
Size (μm)	>2,000	500–2,000	250–500	73–250	500–2,000	250–500	73–250
			Abundance				
Copepoda							
Acartia spp.	0	7 (5)	50 (20)	30 (10)	0_T	30 (10)	30 (10)
Acartiella sinensis	0	1 (0.2)	2 (1)	0	0	0	0
Eurytemora spp.	0	8 (3)	80 (60)	170 (150)	0_T	0	0
Harpacticoida	0	0	40 (10)	20 (10)	0	0_T	1 (1)
Oithonidae	0	2 (1)	330 (120)	4,070 (2,220)	0_T	200 (130)	2,060 (690)
Paracalanus spp.	0	0_T	2 (2)	0	0_T	2 (1)	1 (1)
Pseudodiaptomus spp.	0	2 (1)	10 (10)	2 (2)	0	2 (2)	0
Tortanus dextrilobatus	0	3 (2)	1 (1)	0	1 (0.4)	4 (2)	0
Copepod nauplii	0	0	20 (10)	4,364 (1,634)	0	3 (2)	800 (230)
Other							
Larval fish	0_T	0	0	0	0	0	0
Polychaete larvae	0	5 (3)	140 (50)	100 (50)	0_T	1 (0.3)	1 (1)
Tintinnids	0	0	0.0	50 (20)	0	0	20 (10)
Miscellaneous zooplankton	0	0_T	0.0	0	0_T	0	0
n	4	6	6	6	6	4	6
			% Biovolume				
Copepoda							
Acartia spp.	0	7 (3)	22 (8)	8 (4)	54 (2)	33 (6)	9 (2)
Acartiella sinensis	0	2 (1)	2 (2)	0	0	0	0
Eurytemora spp.	0	49 (15)	39 (13)	15 (8)	1 (1)	0	0
Harpacticoida	0	0	3 (1)	1 (1)	0	0_T	0_T
Oithonidae	0	1 (0.4)	16 (5)	64 (5)	1 (1)	27 (10)	87 (2)
Paracalanus spp.	0	0	0_T	0	0_T	1 (0.3)	0_T
Pseudodiaptomus spp.	0	2 (1)	5 (3)	0_T	0	2 (2)	0
Tortanus dextrilobatus	0	32 (15)	4 (4)	0	43 (6)	37 (7)	0
Copepod nauplii	0	0	0_T	8 (3)	0	0	3 (1)
Other							
Larval fish	97 (3)	0	0	0	0	0	0
Polychaete larvae	0	1 (0.4)	9 (3)	2 (1)	0	0_T	0_T
Tintinnids	0	0	0	0_T	0	0	0
Miscellaneous zooplankton	0	1 (1)	0	0	0_T	0	0
n	4	6	6	6	6	4	6

ton composited by size provide an indicator of the Se exposure to pelagic consumers, consistent with other indicators of contamination.

Influence of Freshwater Inputs on Zooplankton Se Concentration

Since Se inputs are closely linked to flow, varying freshwater inflow to the SF Bay (as measured by the DOI) could also be an important factor in explaining the variability found in zooplankton Se concentrations. Mechanistically, there are reasons to expect inflow to be important seasonally and, perhaps, among years. For instance, the difference in hydrodynamics between low flow and high flow periods within SF Bay causes definitive changes in temperature, salinity, and suspended particulate

TABLE 5. Kendall's τ rank correlation coefficients (τ, n = 13) of North Bay zooplankton between size class in February and October 1999 for mean abundance (# m^{-3}) and mean % biovolume. ** $p < 0.01$ and * $p < 0.05$. nd = no data because zooplankton ≥2,000 μm were not present in October 1999 samples. Bold indicates a significant difference in abundance or biovolume.

		February 1999			October 1999		
	Size (μm)	250–500	500–2,000	≥2,000	250–500	500–2,000	≥2,000
Abundance	73–250	0.588**	**0.114**	**−0.405**	**0.386**	**−0.016**	nd
	250–500		**0.327**	**−0.482**		**0.356**	nd
	500–2,000			**−0.246**			nd
% Biovolume	73–250	0.532*	**0.029**	**−0.405**	**0.236**	**0.070**	nd
	250–500		0.463*	**−0.482**		0.503*	nd
	500–2,000			**−0.098**			nd

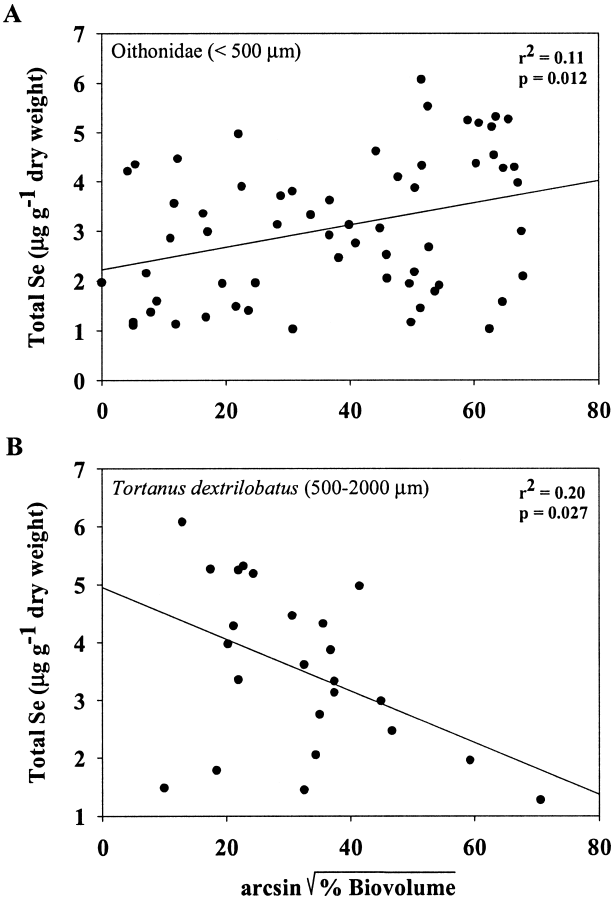

Fig. 8. Se concentration versus % biovolume of copepods from SF Bay. A. Oithonidae ($r^2 = 0.105$, $p = 0.012$). B. *Tortanus dextrilobatus* ($r^2 = 0.204$, $p = 0.027$)

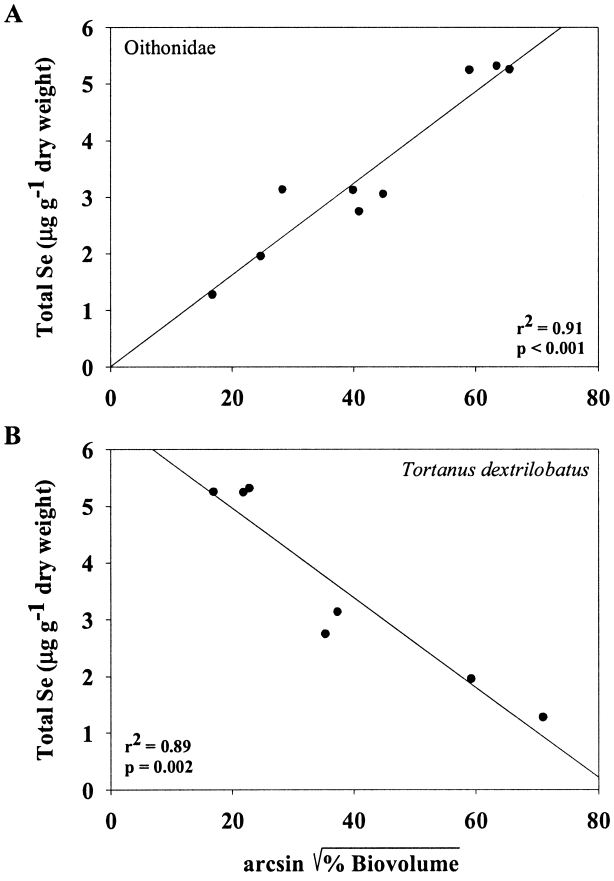

Fig. 9. Se concentration versus % biovolume of copepods in Carquinez Strait (Station 9). A. Oithonidae ($r^2 = 0.909$, $p < 0.001$). B. *Tortanus dextrilobatus* ($r^2 = 0.893$, $p < 0.001$).

TABLE 6. Published reports of Se concentrations in marine zooplankton. * = also included detritus and phytoplankton.

Sample Location	Collection Method	Zooplankton Species	[Se] µg g^{-1} (dw) (Mean ± SD)	n	Reference
Adriatic Sea	Net tow (200 µm)	Mixed	3.5 ± 1.1	45	Kosta et al. (1978)
Baltic Sea	Net tow (200 µm)	Mixed	1.4 ± 1.5	72	Brugmann and Hennings (1994)
Baltic Sea	Net tow (200 µm)	Mixed	2.8 ± 0.3	16	Brugmann and Hennings (1994)
China (Xiamen Bay)	Net tow (500 µm)	Copepods (*Labidocera euchaeta* and *Centropages tenuiremis*, dominants)	3.1	1	Liu et al. (1987)
China (Xiamen Bay)	Net tow (500 µm)	Copepods (*Tortanus derjunginii*, dominant)	3.0	1	Liu et al. (1987)
China (Xiamen Bay)	Net tow (5,000 µm)	Copepods (*Corycaeus*, *Hapracticus*, nauplii)	6.3	1	Liu et al. (1987)
Mediterranean Sea	Net tow (53 µm)	*Oithona* spp.	0.6	1	Boisson and Romeo (1996)
Mediterranean Sea	Net tow (65 µm)	Mixed*	2.7	1	Fowler and Benayoun (1976)
Mediterranean Sea	Net tow (65 µm)	Mysid (*Meganyctiphanes norvegica*)	3.5	1	Fowler and Benayoun (1976)
Gulf of the Farallones	Net tow (73 µm)	Mixed	2.1	1	This study
San Francisco Bay (Fall 1998)	Net tow (73 µm)	Mixed	**2.1 ± 1.2**	11	This study
San Francisco Bay (Spring 1999)	Net tow (73 µm)	Mixed	**1.9 ± 0.7**	16	This study
San Francisco Bay (Fall 1999)	Net tow (73 µm)	Mixed	**4.5 ± 0.8**	18	This study

matter (Cloern and Nichols 1985). As also seen in this study, intra-annual differences in hydrodynamics caused by such events as an El Niño can have an even greater influence on the physical characteristics of SF Bay's water column.

Understanding how the changes in hydrodynamics affect Se concentrations is challenging. For instance, there was no statistical correlation between inflow (i.e., DOI) and Se concentrations in zooplankton. This data set (one high flow and two low flow periods) is probably inadequate to evaluate such complex interactions, especially since the first low flow period could be called an intermediate flow period with flooding in early 1998 and prolonged high flow through the fall (see Fig. 3) caused by an El Niño event. Zooplankton Se concentrations were highest during the typical low flow period (Fall 1999; Fig. 3), when water residence time in SF Bay increases, and dissolved and particulate Se concentrations are at a maximum (Cutter and San Diego-McGlone 1990; Doblin unpublished data). Particulate Se concentrations were found to be significantly higher in Fall of 1999 than in Fall 1998 and Spring 1999, which could help explain why zooplankton Se concentrations in Fall 1999 were higher then the other sampling periods (see previous discussion; Doblin unpublished data). Se concentrations in SF Bay bivalves have also been found to be highest during low flow periods and decline during high flow periods, which has been attributed to declining Se concentrations after the seasonal peak in inflow (Linville et al. 2002). Longer water residence times might contribute to this seasonal increase in Se by providing greater opportunity for dissolved Se to be accumulated by phytoplankton and bacteria, making particulate Se available to consumer organisms (Luoma et al. 1992; Schlekat et al. 2000).

Seasonal and intra-annual changes in hydrodynamics can also effect zooplankton biomass and species composition through changes in the resident phytoplankton community and the suspended particle pool. In SF Bay, changes in phytoplankton community composition and abundance have been shown to be influenced by freshwater flow via turbidity and stratification (Cloern 1987). Furthermore, Baines and Fisher (2001) show that Se content of various phytoplankton species can vary by 2 to 4 orders of magnitude. Changes in phytoplankton community composition and abundance could profoundly influence Se bioaccumulation by zooplankton, although we have no data to support this in the SF Bay study.

Influence of Population Characteristics on Zooplankton Se Concentration

Similar to results presented here, previous studies have found higher Se concentrations in smaller compared to larger invertebrates (Liu et al. 1987; Goede et al. 1993). The differences found between the smallest and largest size classes in the smaller scale North Bay sampling coincided with differences in community composition, both in terms of rank order of abundance and biovolume. While different life stages of the same species were found in different size classes (<2,000 μm), there were no zooplankton species found in both the <2,000 μm and ≥2,000 μm size classes, indicating that differences in Se concentrations could be due to different zooplankton species and size. In this study, it is difficult to determine whether Se concentrations of smaller individuals are different than larger individuals, since monthly zooplankton samples <2,000 μm were combined before Se analysis, although we have some evidence to indicate that larger zooplankton species accumulate less Se (Fig. 4).

If there is a size effect on zooplankton Se concentration, contributing factors for the association of higher Se concentrations with smaller sized zooplankton could be size dependence of growth dilution, ingestion rate, and species composition. Selenium could have negative allometry if the Se concentration in zooplankton is proportional to ingestion rate, and the ingestion rate shows negative allometry. Weight-specific ingestion rates have been shown to decrease with increasing body mass in some zooplankton (Dam et al. 1993, 1995). There could also be differences in Se bioaccumulation between zooplankton in different size classes (see Schlekat et al unpublished data). For example, larval fish (≥2,000 μm) have been shown to assimilate Se less efficiently from their food compared to copepods (<2,000 μm; 29% compared to 70%, respectively; Reinfelder and Fisher 1994).

Over all stations sampled, and especially at Station 9 (Carquinez Strait), Se concentrations were at their highest when the biomass of copepods in the family Oithonidae was high. Conversely, Se concentrations were low when the copepod *T. dextrilobatus* biomass was high. Bioaccumulation processes, like differences in assimilation efficiencies (AEs), could combine with differences in food selection to contribute to differences in bioaccumulation of a trace element among species. However, the correlation found between zooplankton Se concentration and biovolume of family Oithonidae and *T. dextrilobatus,* especially at Station 9, could be an artifact of the increase in particulate Se between Fall 1998 and Fall 1999, in which there was an increase in the biomass of Oithonidae and decrease in *T. dextrilobatus*. While this is a possibility, there is evidence of dietary effects on zooplankton Se accumulation. For example, laboratory studies show that Oithonidae Se AEs are more than 6

times greater than juvenile *T. dextrilobatus* when fed diatoms (Schlekat et al. unpublished data). It is not known whether adult *T. dextrilobatus* have a low Se AE if fed copepods. Nevertheless, differences in Se concentrations between these two groups of copepods in the field could be due to their different Se AEs. Differences in Se concentrations between size classes of all zooplankton in SF Bay could also be related to feeding behavior or trophic level. *O. davisae* and *L. tetraspina,* which solely comprise the family Oithonidae sampled in SF Bay, are omnivorous (Paffenhofer 1993), whereas the larger copepod *T. dextrilobatus* is an obligate carnivore (Orsi 1995). Stable N isotope analyses at Station 12 in October 1999 have shown the trophic level to increase as zooplankton size class increases from 73–250 μm to 250–500 μm to 500–2,000 μm (Stewart unpublished data).

While we did not measure the distribution of Se within individuals (i.e., between tissue types) or between groups of zooplankton with different diets, it does appear likely that carnivorous zooplankton have lower levels of Se than herbivorous zooplankton. This could be partly because phytoplankton comprise a richer source of Se than crustacean prey (Reinfelder and Fisher 1994; Fisher and Reinfelder 1995). Bioaccumulation is limited in crustaceans like zooplankton and amphipods, despite high AEs, because loss rates of selenium are rapid (~15–20% per day; Schlekat et al. unpublished data). The resultant rapid loss rates in both predators and prey could yield a progressive decline of Se with trophic level. This is in contrast to the biomagnification with trophic level that occurs in bivalve food webs where bivalves have high AEs and slow loss rates of Se (Luoma et al 1992). One implication of this is that there could be less Se available to higher trophic levels (e.g., waterfowl and fishes) in the pelagic food web compared to the benthic food web (Schlekat et al. 2002).

Acknowledgments

We thank Chris Schlekat, Sean Avent, Alison Sanders, Alexander Bochdansky, and the crew of the *R/V Polaris* for their assistance in the field and the lab and for their scientific input. This study was supported by a grant from the CALFED Bay-Delta Program to S. Luoma, grant OCE-9707946 from NSF's Environmental Geochemistry and Biogeochemistry Program to G. Cutter, and a Visiting Scientist Award from Moss Landing Marine Laboratories at California State University to S. Bollens.

Literature Cited

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

Baines, S. B. and N. S. Fisher. 2001. Interspecific differences in the bioconcentration of selenite by phytoplankton and their ecological implications. *Marine Ecology Progress Series* 213:1–12.

Bengtsson, J., S. R. Baillie, and J. Lawton. 1997. Community variability increases with time. *Oikos* 78:249–256.

Besser, J. M., T. J. Canfield, and T. W. LaPoint. 1993. Bioaccumulation of organic and inorganic selenium in a laboratory food chain. *Environmental Toxicology and Chemistry* 12:57–72.

Boisson, F. and M. Romeo. 1996. Selenium in plankton from the Northwestern Mediterranean Sea. *Water Research* 30:2593–2600.

Bollens, S. M., S. Avent, J. Cordell, W. Kimmerer, and C. Penalva-Arana. 1999. San Francisco Bay zooplankton: Interannual and interdecadal variation, with special reference to non-indigenous species and ENSO effects. *EOS* 80:133.

Bowie, G. L., J. G. Sanders, G. F. Riedel, C. C. Gilmour, D. L. Breitburg, G. A. Cutter, and D. B. Porcella. 1996. Assessing selenium cycling and accumulation in aquatic ecosystems. *Water Air and Soil Pollution* 90:93–104.

Brown-Peterson, N. J., M. S. Peterson, D. A. Rydene, and R. W. Eames. 1993. Fish assemblages in natural versus well-established recolonized seagrass meadows. *Estuaries* 16:177–189.

Brugmann, L. and U. Hennings. 1994. Metals in zooplankton from the Baltic Sea, 1980–84. *Journal of Chemical Ecology* 9:87–103.

Cloern, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Continental Shelf Research* 7:1367–1381.

Cloern, J. E. and F. H. Nichols. 1985. Time scales and mechanisms of estuarine variability, a synthesis from studies of San Francisco Bay. *Hydrobiologia* 129:229–237.

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

Cumbie, P. M. and S. L. Van Horn. 1978. Selenium accumulation associated with fish mortality and reproductive failure. *Proceedings of the Annual Conference of the Southeast Association Fish and Wildlife Agencies* 32:612–624.

Cutter, G. A. 1978. Species determinations of selenium in natural waters. *Analytica Chimica Acta* 98:59–66.

Cutter, G. A. 1985. Determination of selenium speciation in biogenic particles and sediments. *Analytica Chimica Acta* 57: 2951–2955.

Cutter, G. A. 1989. The estuarine behaviour of selenium in San Francisco Bay. *Estuarine, Coastal and Shelf Science* 28:13–34.

Cutter, G. A. and M. L. C. San Diego-McGlone. 1990. Temporal variability of selenium fluxes in San Francisco Bay. *The Science of the Total Environment* 97:235–250.

Dam, H. G., C. A. Miller, and S. H. Jonasdottir. 1993. The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research, II* 40: 197–212.

Dam, H. G., X. Zhang, M. Butler, and M. R. Roman. 1995. Mesozooplankton grazing and metabolism at the equator in the central Pacific: Implications for carbon and nitrogen fluxes. *Deep-Sea Research, II* 42:735–756.

Farnsworth, E. J. and A. M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. *Ecological Monographs* 66:45–66.

Fisher, N. S. and J. R. Reinfelder. 1991. Assimilation of selenium in the marine copepod *Acartia tonsa* studied with a radiotracer ratio method. *Marine Ecology Progress Series* 70:157–164.

Fisher, N. S. and J. R. Reinfelder. 1995. The trophic transfer of metals in marine systems, p. 363–406. *In* A. Tessier and D. Turner (eds.), Metal Speciation and Bioavailability in Aquatic Systems. John Wiley and Sons, New York.

Fowler, S. W. and G. Benayoun. 1976. Selenium kinetics in marine zooplankton. *Marine Science Communications* 2:43–67.

Garrett, G. P. and C. R. Inman. 1984. Selenium-induced changes in the fish populations of a heated reservoir. *Proceedings of*

the Annual Conference of the Southeast Association Fish and Wildlife Agencies 38:291–301.

GHENT, A. W. 1982. Tau as an index of similarity in community comparisons: An approach permitting the hypothesis of unequal species abundance. *Canadian Journal of Zoology* 61:687–690.

GOEDE, A. A., H. TH. WOLTERBEEK, AND M. J. KOESE. 1993. Selenium concentrations in the marine invertebrates *Macoma balthica, Mytilus edulis,* and *Nereis diversicolor. Archives of Environmental Contamination and Toxicology* 25:85–89.

GROSSMAN, G. D., M. C. FREEMAN, P. B. MOYLE, AND J. O. WHITAKER. 1985. Stochasticity and assemblage organization in an Indiana stream fish assemblage. *American Naturalist* 126:275–285.

HARRISON, P. J., P. W. YU, P. A. THOMPSON, N. M. PRICE, AND D. J. PHILLIPS. 1988 Survey of selenium requirements in marine phytoplankton. *Marine Ecology Progress Series* 47:89–96.

HERBOLD, B. 1984. Structure of an Indiana stream fish association: Choosing an appropriate model. *American Naturalist* 124: 561–572.

HU, M. H., Y. P. YANG, J. M. MARTIN, K. YIN, AND P. J. HARRISON. 1997. Preferential uptake of Se(IV) over Se(VI) and the production of dissolved organic Se by marine phytoplankton. *Marine Environmental Research* 44:225–231.

JOHNS, C. E., S. N. LUOMA, AND V. ELROD. 1988. Selenium accumulation in benthic bivalves and fine sediments of San Francisco Bay, the Sacramento-San Joaquin Delta, and selected tributaries. *Estuarine, Coastal and Shelf Science* 27:381–396.

JUMARS, P. A. 1980. Rank correlation and concordance tests in community analyses: An inappropriate null hypothesis. *Ecology* 61:1553–1554.

KIMMERER, W. J., J. R. BURAU, AND W. A. BENNETT. 1998. Tidally-oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography* 43:1697–1709.

KIMMERER, W. J. AND J. J. ORSI. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987, p. 403–24. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The Ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.

KOSTA, L., V. RAVNIK, A. R. BYRNE, J. STIRN, M. DERMELJ, AND P. STEGNAR. 1978. Some trace elements in the waters, marine organisms and sediments of the Adriatic by neutron activation analysis. *Journal of Radioanalytical Chemistry* 44:317–332.

LEMLY, A. D. 1993. Guidelines for evaluating selenium data from aquatic monitoring and assessment studies. *Environmental Monitoring and Assessment* 28:83–100.

LEMLY, A. D. 1996. Assessing the toxic threat of selenium to fish and aquatic birds. *Ecotoxicology and Environmental Safety* 32: 280–288.

LINVILLE, R. G., S. N. LUOMA, L. CUTTER, AND G. A. CUTTER. 2002. Increased selenium threat as a result of invasion of the exotic bivalve *Potamocorbula amurensis* into the San Francisco Bay-Delta. *Aquatic Toxicology* 57:51–64.

LIU, D. L., Y. P. YANG, M. H. HU, P. J. HARRISON, AND N. M. PRICE. 1987. Selenium content of marine food chain organisms from the coast of China. *Marine Environmental Research* 22:151–165.

LUOMA, S. N. 1997. Selenium trends in North San Francisco Bay. *Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter* Spring:25–26.

LUOMA, S. N., C. JOHNS, N. S. FISHER, N. A. STEINBERG, AND R. S. OREMLAND. 1992. Determination of selenium bioavailability to a benthic bivalve from particulate and solute pathways. *Environmental Science and Technology* 26:485–491.

LUOMA, S. N. AND D. J. H. PHILLIPS. 1988. Distribution, variability, and impacts of trace elements in San Francisco Bay. *Marine Pollution Bulletin* 19:413–425.

MAIER, K. J., C. G. FOE, AND A. W. KNIGHT. 1993. Comparative toxicity of selenate, selenite, seleno-DL-methionine and seleno-DL-cystine to *Daphnia magna. Environmental Toxicology and Chemistry* 12:755–763.

MENG, L. AND J. J. ORSI. 1991. Selective predation by larval striped bass on native and introduced copepods. *Transactions of the American Fisheries Society* 120:157–192.

NORUSIS, M. J. 1999. SPSS 9.0 Guide to Data Analysis. Prentice-Hall, Inc., New York.

OHLENDORF, H. M., D. J. HOFFMAN, M. K. SAIKI, AND T. W. ALDRICH. 1986. Embryonic mortality and abnormalities of aquatic birds: Apparent impacts of selenium from irrigation drainwater. *Science of the Total Environment* 52:49–63.

ORSI, J. J. 1995. Radical changes in the estuary's zooplankton caused by introductions from ballast water. *Interagency Ecological Program Newsletter* Summer:16–17.

ORSI, J. J. AND W. L. MECUM. 1986. Zooplankton distribution and abundance in the Sacramento-San Joaquin Delta in relation to certain environmental factors. *Estuaries* 9:326–339.

PAFFENHOFER, G. A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *Journal of Plankton Research* 15:37–55.

PETERSON, D. H., R. E. SMITH, S. W. HAGER, D. D. HARMON, R. E. HERNDON, AND L. E. SCHEMEL. 1985. Interannual variability in dissolved inorganic nutrients in Northern San Francisco Bay estuary. *Hydrobiologia* 129:37–58.

PRICE, N. M., P. A. THOMPSON, AND P. J. HARRISON. 1987. Selenium: An essential element for growth of the coastal marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). *Journal of Applied Phycology* 23:1–9.

RAHEL, F. J., J. D. LYONS, AND P. A. COCHRAN. 1984. Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. *American Naturalist* 124:583–589.

REINFELDER, J. R. AND N. S. FISHER. 1994. Retention of elements absorbed by juvenile fish (*Menidia menidia, Menidia beryllina*) from zooplankton prey. *Limnology and Oceanography* 39:1783–1789.

SCHLEKAT, C. E., A. W. DECHO, AND G. T. CHANDLER. 2000. Bioavailability of particle-associated silver, cadmium, and zinc to the estuarine amphipod *Leptocheirus plumulosus* through dietary ingestion. *Limnology and Oceanography* 45:11–21.

SCHLEKAT, C. E., B.-G. LEE, AND S. N. LUOMA. 2002. Dietary metals exposure and toxicity by aquatic organisms: Implications for ecological risk assessment, p. 151–188. *In* M. Newman (ed.), Coastal and Estuarine Risk Assessment. Lewis Publishers, Boca Raton, Florida.

SCHLEKAT, C. E., B.-G. LEE, AND S. N. LUOMA. 2002. Assimilation of selenium from phytoplankton by three benthic invertebrates: Effect of phytoplankton species. *Marine Ecology Progress Series* 237:79–85.

SKORUPA, J. P. 1998. Selenium poisoning of fish and wildlife in nature: Lessons from twelve real-world examples, p. 315–354. *In* W. Frankenberger and R. A. Engberg (eds.), Environmental Chemistry of Selenium. Marcel Dekker, Inc., New York.

THOMAS, B. V., A. W. KNIGHT, AND K. J. MAIER. 1999. Selenium bioaccumulation by the water boatman *Trichocorixa reticulata* (Guerin-Meneville). *Archives of Environmental Contamination and Toxicology* 36:295–300.

TOLIMIERI, N., P. F. SALE, R. S. NEMETH, AND K. B. GESTRING. 1998. Replenishment of populations of Caribbean reef fishes: Are spatial patterns of recruitment consistent through time? *Journal of Experimental Marine Biology and Ecology* 230:55–71.

TURNER, S. J., S. F. THRUSH, R. D. PRIDMORE, J. E. HEWITT, V. J. CUMMINGS, AND M. MASKERY. 1995. Are soft-sediment communities stable? An example from a windy harbour. *Marine Ecology Progress Series* 120:219–230.

URQUHART, K. A. F. AND K. REGALADO. 1991. Selenium Verification Study: 1988–1990. Water Resources Control Report 91-

2-WQ. State Water Resources Control Board, Sacramento, California.

WALTERS, R. A., R. T. CHENG, AND T. J. CONOMOS. 1985. Time scales of circulation and mixing processes of San Francisco Bay waters. *Hydrobiologia* 129:13–36.

WANG, W.-X. AND N. S. FISHER. 1998. Accumulation of trace elements in a marine copepod. *Limnology and Oceanography* 43: 273–283.

WHITE, J. R., P. S. HOFFMAN, D. HAMMOND, AND S. BAUMGARTNER. 1988. Selenium Verification Study: 1986–1987. Water Resources Control Report. State Water Resources Control Board, Sacramento, California.

WRENCH, J. J. 1978. Selenium metabolism in the marine phytoplankters *Tetraselmis tetathele* and *Dunaliella minuta*. *Marine Biology* 49:231–236.

SOURCES OF UNPUBLISHED MATERIALS

SCHLEKAT, C. unpublished data. U.S. Borax Inc., 26877 Tourney Road, Valencia, California 91355.

STEWART, R. unpublished data. U.S. Geological Survey, 345 Middlefield Road, Menlo Park, California 94025.

Received for consideration, March 21, 2002
Revised, September 24, 2002
Accepted for publication, October 17, 2002