

# Mesozooplankton of the lower San Francisco Estuary: spatio-temporal patterns, ENSO effects and the prevalence of non-indigenous species

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The San Francisco Estuary (SFE) is a large, highly dynamic and ecologically important estuary on the west coast of the USA. We collected zooplankton and hydrographic data over a 3-year period (1997–1999) at six stations spanning the lower SFE to investigate long-term changes through comparison with a 1980–1981 survey of the area, El Niño-Southern Oscillation (ENSO) effects and the prevalence of non-indigenous species. Spatio-temporal patterns in the zooplankton were primarily regulated by seasonal and inter-annual fluctuations in marine and riverine forcings. Non-metric multidimensional scaling accounted for 82.7% of the variation in zooplankton composition. The strongest correlates of the three axes were salinity ( $r^2 = 0.692$ ), distance to marine influence and temperature ( $r^2 = 0.492$  and  $0.309$ , respectively) and a lagged multivariate ENSO index ( $r^2 = 0.299$ ). Five zooplankton communities were identified, which showed predictable spatio-temporal progressions through the lower estuary. Inter-annual differences between El Niño and La Niña periods were substantial and appeared to be related to variable strengths of riverine and oceanic forcing. Between 1980–1981 and 1997–1999, a dramatic change occurred in the zooplankton of the lower SFE, such that dominance has shifted from native calanoid copepods to non-indigenous (Asian) cyclopoids. These changes in the zooplankton are expected to have significant but as yet unknown impacts on higher trophic levels and food web dynamics in the lower SFE.

**KEYWORDS:** plankton ecology; species diversity; non-indigenous species; San Francisco Bay; estuaries

## INTRODUCTION

Estuaries are dynamic environments subject to both oceanic and riverine forcings on a wide range of spatial and temporal scales. The generally high nutrient input received by estuaries makes them home to an abundant, diverse and variable biota (Day *et al.*, 1989; Mallin and Paerl, 1994). The San Francisco Estuary (SFE) is the largest estuary on the west coast of the USA and provides critical habitat for invertebrates, fish, migrating birds and marine mammals (Emmett *et al.*, 2000; Gewant and Bollens, 2005). Microzooplankton and mesozooplankton are important intermediaries in the flow of material and energy from phytoplankton to higher trophic levels (Runge, 1988; Rollwagen-Bollens and Penry, 2003; Rollwagen-Bollens *et al.* 2011).

The distribution and abundance of estuarine zooplankton are often related to temperature and salinity (Soetaert and Van Rijswijk, 1993; Lawrence *et al.*, 2004; Graham and Bollens, 2010). Horizontal gradients of these variables affect the spatial partitioning of zooplankton in estuaries, with species segregated according to respective salinity and temperature tolerances (Soetaert and Van Rijswijk, 1993; Lawrence *et al.*, 2004). In temperate estuaries, there are also seasonal changes in temperature and salinity (Soetaert and Van Rijswijk, 1993) and these influence zooplankton dynamics, particularly with respect to the relative abundance of dominant copepod species (Lawrence *et al.*, 2004).

Annual timing and magnitude of climate-driven freshwater and marine inputs play a large role in the structuring of estuarine communities (Kimmel and Roman, 2004; Kimmel *et al.*, 2009). In the SFE, the strongest recorded El Niño event occurred in 1997–1998 (McPhaden, 1999), followed by a strong La Niña (Behrenfeld *et al.*, 2001; Cloern *et al.*, 2007). El Niño events have been shown to decrease zooplankton biomass in the California Current System (McGowan *et al.*, 1998; Schwing *et al.*, 2002) and to affect zooplankton species composition in the eastern Pacific (Hooff and Peterson, 2006). In addition to changes in sea surface temperature, El Niño events influence basin-wide and near-shore ocean circulation, precipitation patterns and sea level height (Ryan and Noble, 2007) which directly impact the strength of the two major forcings (riverine and marine) acting on estuaries. The response of estuaries to El Niño events, therefore, might be expected to differ from that of the neighboring coastal ocean.

The SFE is in some regards a well-studied system (Cloern and Nichols, 1985; Cloern, 1996; Hollibaugh, 1996; Bollens *et al.*, 2002; Kimmerer, 2002; Lehman, 2004), yet our understanding of some aspects of the SFE

ecosystem remains elusive, especially those associated with anthropogenic impacts and the associated substantial changes in the system. For instance, one of the largest contributors to changes in the SFE ecosystem is the introduction of non-native species. Indeed, the SFE is an extraordinary example of susceptibility to biological introductions and has been identified as the most highly invaded estuary in the world (Cohen and Carlton, 1998). More than 200 non-indigenous species have been identified, some of which have dramatically altered defining properties of ecosystem function (Kimmerer *et al.*, 1994; Cloern, 1996; Cohen and Carlton, 1998; Hooff and Bollens, 2004). Accompanying these changes in species assemblages, the SFE has experienced large population declines in both phytoplankton (Cloern, 1996) and fish (Sommer *et al.*, 2007). Phytoplankton populations rebounded beginning in 2000 after populations of suspension feeding bivalves decreased (Cloern *et al.*, 2007; Cloern *et al.*, 2010).

With respect to zooplankton, the SFE is home to nine non-indigenous copepods, *Oithona davisae*, *Limnoithona tetraspina*, *Limnoithona sinensis*, *Pseudodiaptomus marinus*, *Pseudodiaptomus forbesi*, *Tortanus dextrilobatus*, *Eurytemora affinis*, *Sinocalanus doerrii*, and *Acartiella sinensis* (Orsi *et al.*, 1983; Ferrari and Orsi, 1984; Orsi and Ohtsuka, 1999; Bollens *et al.*, 2002; Cordell *et al.*, 2008), several of which now numerically dominate the mesozooplankton community (Orsi and Ohtsuka, 1999; Bollens *et al.*, 2002). Zooplankton monitoring studies have concentrated in the Sacramento–San Joaquin delta and Suisun Bay (e.g. Ferrari and Orsi, 1984; Kimmerer and Orsi, 1996; Orsi and Ohtsuka, 1999; Kimmerer, 2002; Lehman, 2004), both of which are highly modified and invaded regions. Zooplankton communities of the lower SFE, however, have received much less attention, with only one published account of detailed broad-scale surveys that occurred in 1980 (Ambler *et al.*, 1985).

Here we describe the mesozooplankton (>73 µm) community of the lower SFE sampled during bi-monthly cruises from January 1997 to November 1999, and we investigate environmental forcings related to community level variation using ordination analysis. Specifically, we address three main questions: First, how do spatio-temporal patterns of key SFE mesozooplankton taxa compare between our sampling period (1997–1999) and the historical data (1980–1981) reported by Ambler *et al.* (Ambler *et al.*, 1985)? Second, what is the importance of non-indigenous species to changes in mesozooplankton community composition in the SFE? And third, how did the ENSO event of 1997–1998 affect variation in environmental forcings and mesozooplankton community composition?

## METHOD

### Study site description

The SFE has a Mediterranean climate, with most of the annual rainfall occurring between November and April, and minimal precipitation between May and October. The SFE is characterized by two distinct estuarine systems that meet at Central Bay, the outlet to the Pacific Ocean (Fig. 1). San Pablo Bay, to the north, is a partially mixed drowned river estuary which drains the Sacramento and San Joaquin river systems (150 000 km<sup>2</sup> watershed) (Cloern, 1996). San Pablo Bay experiences prominent hydrographic gradients extending between Central Bay to upriver beyond the confluence of the Sacramento and San Joaquin Rivers (Cloern and Nichols, 1985). Considerable seasonal and inter-annual variation in freshwater input through the delta results in wide temperature and salinity ranges as well as variable retention times. In contrast, the South Bay is a well-mixed coastal embayment that receives substantially less riverine input and is typically less turbid than the northern bay region. 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 production (Cloern, 1996).

### Data collection and analysis

Zooplankton and hydrographic data were collected aboard the United States Geological Survey (USGS) *R/V Polaris*, with some preliminary analyses described by Bollens *et al.* (Bollens *et al.*, 2002). For a 3-year period (January 1997 through November 1999), bi-monthly zooplankton collections were obtained over 2–3 days at six standard stations spanning the lower SFE (San Pablo Bay—stations 12 and 13, Central Bay—stations 17 and 21 and South Bay—stations 24 and 30; Fig. 1). All samples were collected during the day. In order to sample a broad size range of zooplankton, at each station slow vertical hauls (10 m min<sup>-1</sup>) were made from near bottom to surface with a 73 µm-mesh, 0.5 m-diameter plankton net. The mesh size was chosen to approximate the 64 µm mesh used in an earlier study of the SFE of by Ambler *et al.* (Ambler

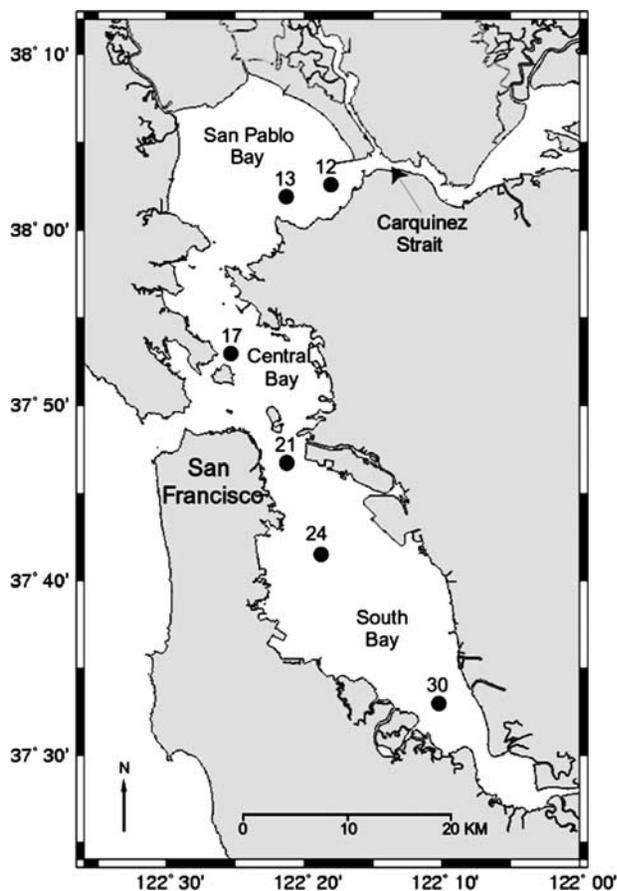


Fig. 1. Map of the San Francisco Estuary. Sampling stations are indicated by the closed circles.

*et al.*, 1985) and to ensure the collection of early and late stages of target organisms, such as copepods. Samples were concentrated and preserved in a 5–10% formaldehyde seawater solution. Sample volume was calculated using a calibrated low-speed flowmeter.

Hydrographic data were collected simultaneously by the San Francisco Water Resources division of the USGS using a Sea-bird Electronics™ Conductivity-Temperature-Depth (SBE 9 CTD) instrument. Stratification indices were calculated by subtracting surface measurements from bottom measurements of salinity, temperature and sigma-t. In addition to hydrographic data, we obtained an index of the outflow from the Sacramento-San Joaquin delta from the California Department of Water Resources (DWR) (<http://cdec.water.ca.gov/cgi-progs/iodir/wsihist>) and the multivariate ENSO index (MEI), a basin-wide climatological index, from the National Oceanic and Atmospheric Administration's Climate Diagnostics Center, (<http://www.cdc.noaa.gov/people/klaus.wolter/MEI/>). We lagged the MEI by 4 months because other studies in the NE Pacific have identified a temporal lag between the MEI and local biological response (Hooff and Peterson, 2006).

Adult holoplanktonic taxa such as copepods were usually identified to species. However, the *Acartia* subgenus *Acartiura* cannot be reliably identified to species on the west coast of North America (Bradford, 1976). We believe that there are several closely related species within this region, but they cannot be separated by standard morphological techniques, but will only be discriminated through genetic studies or by using more subtle microscopic characters that have not yet been identified. Thus, the ability to identify *Acartia* subgenus *Acartiura* in the NE Pacific still awaits a thorough taxonomic revision. Meroplankton such as invertebrate larval stages were usually identified to order or family level. Younger life history stages (e.g. copepod nauplii and eggs) that could not be identified to the level of specificity of the adults were not included in the analyses.

Mesozooplankton (>73 µm) counts were converted to abundance (individuals m<sup>-3</sup>) and log (x + 1) transformed. Species richness and Shannon-Weiner's diversity index were calculated for each sample and means were compared among bay, season and years using three-way ANOVAs. Contour plots were made using the triangulation with linear interpolation method in SURFER v. 8.07.

## Community analysis

### Cluster analysis

Mesozooplankton communities were identified through cluster analysis, which grouped samples based on

similarities in taxon presence and abundance. Rare taxa (present in <5% of the samples) and one sample (representing a freshwater zooplankton community) that was identified through PCOrd's outlier analysis function were removed prior to the analysis. Similarities between 106 samples with abundances for 70 taxa were measured by relative Euclidean distance measure using Ward's linkage method (McCune and Grace, 2002). The resulting matrix was used to generate a dendrogram with 0.93% chaining (Supplement 1 in the Supplementary Material online). The dendrogram was scaled to both percentage of information remaining and Wishart's (Wishart, 1969) objective function. Groups were identified by pruning to 25% retained information. Dufrière and Legendre's (Dufrière and Legendre, 1997) method of choosing the level of pruning was consulted, but qualitative criteria were also employed for selecting a final pruning level that would better facilitate presentation and discussion of results.

### Indicator species

To identify taxa representative of the different clusters, we employed Indicator Species Analysis (ISA) (Dufrière and Legendre, 1997). ISA assigns each taxon cluster-specific indicator values (IV), ranging from 0 (no indication) to 100 (perfect indication) based on their faithfulness and exclusiveness to that cluster. Monte Carlo randomization was used to assess the statistical significance of the IVs (alpha = 0.01). Following Keister and Peterson (Keister and Peterson, 2003), we further defined best indicators of a cluster as species whose IV for that cluster was at minimum five times greater than for any other cluster.

### Ordination

We used Non-metric Multidimensional Scaling to identify relationships between mesozooplankton communities (clusters) and environmental variables. The Sørensen (Bray-Curtis) distance measure was used. In addition to the environmental data and indices, spatial variables (station latitude, station longitude, and, as an approximation of distance to the mouth of the estuary, distance to the Golden Gate Bridge) were included in the analysis. The number of dimensions that most adequately described the data was chosen to minimize the final stress (a measure of the goodness-of-fit of points in the *k*-dimensional solution to the actual samples in *n*-dimensional space) and retain statistical significance with respect to dimensionality. All multivariate analyses were conducted using PC-Ord v. 5.10 (McCune and Mefford, 2006).

## RESULTS

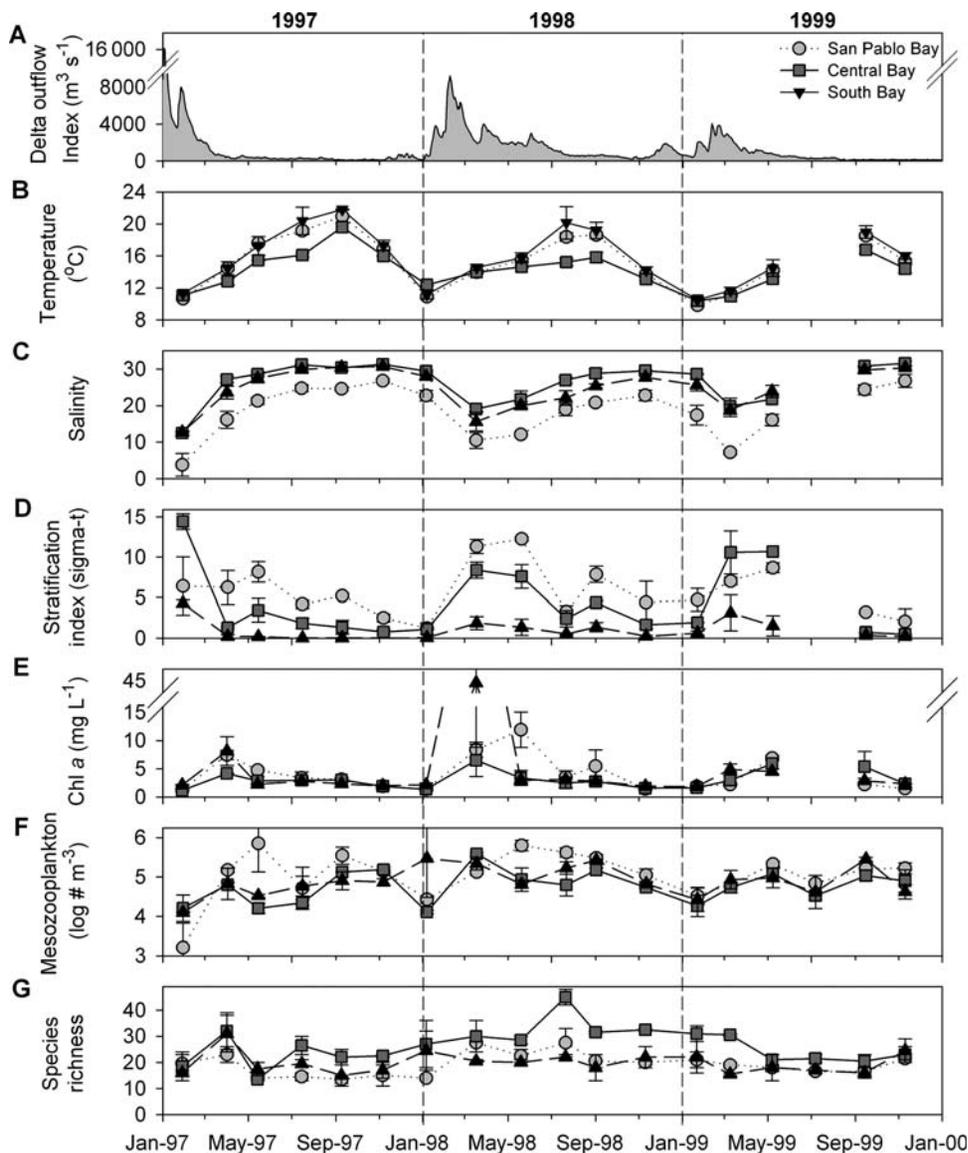
### Spatial and temporal patterns

#### *Hydrography and chlorophyll a*

Strong estuary-wide seasonal fluctuations in temperature and salinity were observed during the time period of this study. Salinity decreased for ~2 month periods in the spring that overlapped with periods of high flow from the Sacramento and San Joaquin Rivers (Fig. 2A). The change in temperature in the estuary was more

gradual and not as strongly correlated with river outflow through the delta, peaking in late summer and reaching a minimum during the winter (Fig. 2B). Inter-annual variation in these patterns appeared small (however, note that salinity and temperature data are unavailable from July 1999).

The California DWR categorized flows from the Sacramento River as ‘wet’ [Water Year (WY) Index  $\geq 9.2$ ] for the WYs 1996–1997, 1997–1998 and 1998–1999. Flows from the San Joaquin River were categorized as ‘wet’ (WY Index  $\geq 3.8$ ) for WYs 1996–1997



**Fig. 2.** Seasonal and inter-annual patterns of hydrographic and biological parameters from San Francisco Estuary. Values represent averages from the two stations in each bay (San Pablo, Central, and South) per cruise (1–3 days in duration). (A) Delta outflow (<http://cdec.water.ca.gov/cgi-progs/iodir/wsihist>). Dashed line shows average outflow through the delta (1956–2010). (B) Temperature, (C) salinity, (D) stratification index, (E) chlorophyll, (F) mesozooplankton abundance (individuals  $m^{-3}$ ) and (G) species richness. Error bars are  $\pm$  SE.

and 1997–1998 and ‘above normal’ ( $3.1 < \text{WY Index} < 3.8$ ) for WY 1998–1999 (<http://cdec.water.ca.gov/cgi-progs/iodir/wsihist>). Discharge from the Sacramento and San Joaquin rivers was greatest for the 1997–1998 WY and less for the 1996–1997 and 1998–1999 WYs. One of the largest daily river discharges since the DWR began recording in 1955 occurred in early January 1997. Annual patterns in outflow through the delta reflected wet-dry seasons, though in 1998, high outflows persisted well into summer.

Environmental conditions in Central Bay were consistent with its position near the mouth of the estuary and resulting marine influence. Water temperature was generally colder and fluctuated less than at other stations (Fig. 2B). Salinity was generally high ( $\sim 30$ ) in summer and autumn, dropping to  $< 20$  during the wet season (Fig. 2C). Stratification appeared seasonal and related to the degree of outflow through the delta (Fig. 2D).

Both South and San Pablo Bays experienced greater fluctuations in temperature than Central Bay and were generally warmer in the spring and autumn (Fig. 2B). South Bay closely resembled Central Bay in water column average salinity but experienced very little water column stratification (Fig. 2D). Conversely, San Pablo Bay’s salinity was consistently five or more psu lower than Central Bay and it was frequently stratified.

Estuary-wide chlorophyll *a* was highest in spring months (Fig. 2E). There were no strong differences in chlorophyll *a* among the bays, though Central Bay generally had the lowest values. In March of 1998 a bloom was observed in South Bay.

### Zooplankton

In total, 149 taxa were identified (Supplement 2 in the Supplementary Material online). Mean estuary-wide mesozooplankton density was  $18.7 \times 10^5$  individuals  $\text{m}^{-3}$ . Average abundances were lower ( $1.42 \times 10^5$  ind.  $\text{m}^{-3}$ ) in the wet season compared with the dry season ( $2.34 \times 10^5$  ind.  $\text{m}^{-3}$ ) ( $F_{(1,101)} = 5.01$ ,  $P = 0.027$ ). Estuary-wide total mesozooplankton abundance was highest in 1998, particularly for stations nearest the mouth ( $F_{(2,101)} = 4.60$ ,  $P = 0.012$ ; Fig. 2F). Abundance was generally higher in San Pablo Bay than in South and Central Bays ( $F_{(2,101)} = 3.15$ ,  $P = 0.047$ ).

Species richness and diversity did not vary among seasons but were higher in Central Bay ( $F_{(2,103)} = 15.42$ ,  $P < 0.001$ , Fig. 2G; and  $F_{(2,103)} = 10.73$ ,  $P < 0.001$ , respectively) than in both North and South Bays, particularly in 1998. Species richness was higher in 1998 than in other years ( $F_{(2,89)} = 10.04$ ,  $P < 0.001$ ).

Table I: Axes correlations. Values shown are  $r^2$ . Strong correlations are in bold, notable moderate correlations are italicized

	Axes		
	1	2	3
Julian date	0	0.001	0.001
Latitude	<i>0.175</i>	0.030	0.015
Longitude	0.000	<i>0.399</i>	0.000
Distance to GG	0.074	<b>0.492</b>	0.002
Delta outflow	0.124	0.050	0.034
MEI	0.020	0.023	0.012
Depth	<i>0.189</i>	0.064	0.003
Chlorophyll	0.084	0.007	0.003
Oxygen	0.020	0.020	0.086
SPM	<i>0.287</i>	0.002	0.006
Salinity	<b>0.692</b>	0.000	0.000
Temperature	0.047	<i>0.309</i>	0.025
Sigma-t	<b>0.694</b>	0.007	0.000
Density stratification	<i>0.389</i>	0.059	0.000
Four-month-lagged MEI	0.048	0.003	<i>0.299</i>

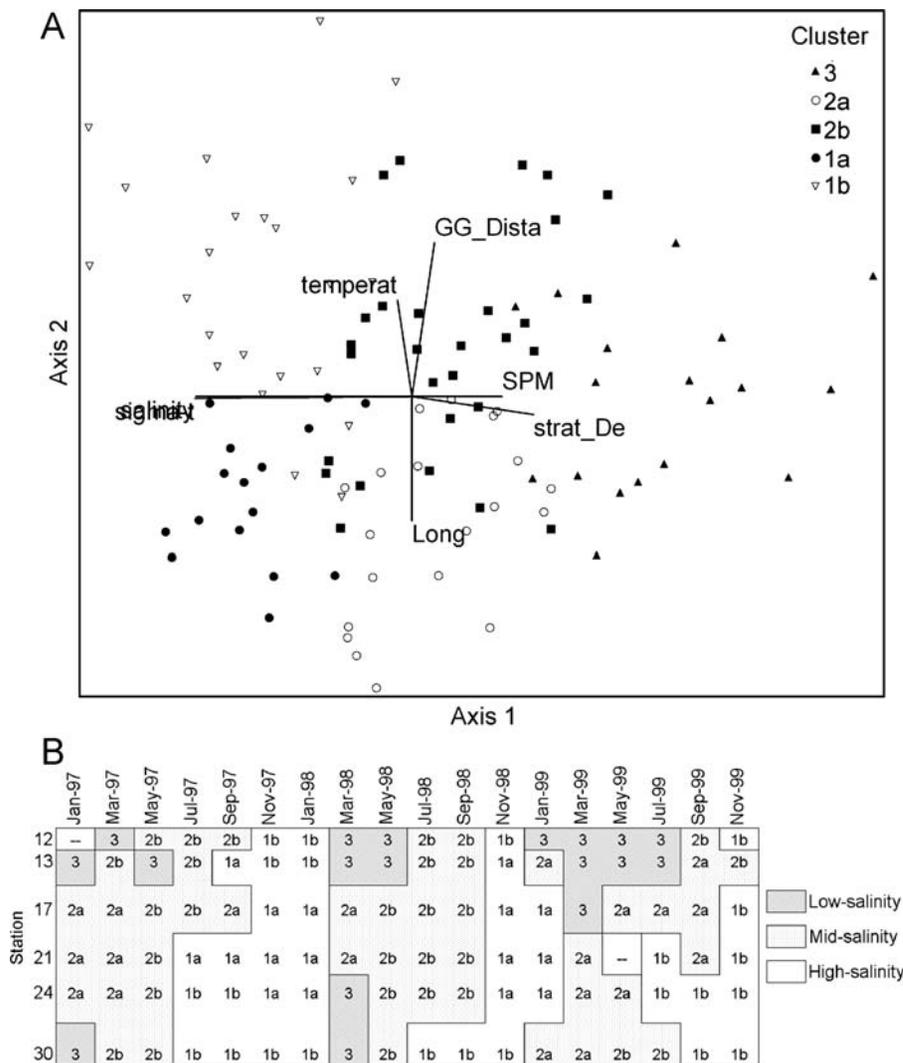
### Community structure (multivariate analyses)

A 3D ordination solution relating to 82.7% of the variation between samples was chosen based on a moderate stress value of 15.6. The final instability was 0.0001. Axis 1 represented 39.9% of the variance and was related to a gradient of river flow, with correlations with density ( $r^2 = 0.694$ ), salinity ( $r^2 = 0.692$ ), stratification ( $r^2 = 0.389$ ), suspended particulate matter ( $r^2 = 0.287$ ) and latitude ( $r^2 = 0.175$ ) (Table I). Axis 2 was primarily represented by distance to marine influence (i.e. the mouth of the estuary at the Golden Gate) ( $r^2 = 0.492$ ), longitude ( $r^2 = 0.399$ ) and temperature ( $r^2 = 0.309$ ) and represented 23.5% of variation. Axis 3 represented 19.3% of the variation in community structure. It was most strongly correlated to the lagged MEI ( $r^2 = 0.299$ ).

Cluster analysis identified five primary groups of samples based on similarities in mesozooplankton taxa presence and abundance. These groups were separated along axis 1 into low, mid and high salinities (Fig. 3A). Mid- and high-salinity groups (clusters 1 and 2) were further separated by cool and warm temperature (a and b, respectively) along axis 2. Lower temperature clusters, 1a and 2a, were restricted to areas nearest the mouth. Environmental parameters and indicator species associated with each cluster are reported in Table II and Supplement 3 in the Supplementary Material online, respectively.

#### Cluster 1

The high-salinity assemblage followed a similar trend each year, with initial restriction to the southern three stations and subsequent expansion to the northernmost



**Fig. 3.** Multivariate analyses. **(A)** Ordination joint plot from non-metric multidimensional scaling with sample units labeled by cluster. Environmental variables that were strongly associated ( $r^2 > 0.2$ ) with axes 1 and 2 are overlaid as vectors. Vector length and direction indicates relative strength of the correlation with the axes. *Abbreviations:* Distance to marine influence (GG\_Dista), longitude (Long), density stratification (strat\_De), suspended particulate matter (SPM), temperature (temperat), and, overlaid on each other, salinity and density (sigma-t). **(B)** Spatio-temporal plot of sample units labeled by cluster. Communities are grouped by salinity category (low, mid, high). Subcategories 'a' and 'b' represent 'cold' and 'warm', respectively.

*Table II: Mean  $\pm 1$  SE characteristics of zooplankton clusters. Total abundances in brackets are calculated without two extremely high Oikopleura dioica abundances*

Cluster	Abundance ( $\times 10^3$ ind. $m^{-3}$ )	Species richness	Diversity (Shannon)	Chlorophyll ( $mg L^{-1}$ )	Salinity	Temperature ( $^{\circ}C$ )	Oxygen	SPM
1a	310 $\pm$ 233 (74 $\pm$ 21)	23.3 $\pm$ 2.4	1.6 $\pm$ 0.2	2.0 $\pm$ 0.2	29.3 $\pm$ 0.5	14.5 $\pm$ 1.1	7.9 $\pm$ 0.2	11.3 $\pm$ 1.4
1b	106 $\pm$ 19	17.7 $\pm$ 1.0	1.1 $\pm$ 0.1	2.3 $\pm$ 0.2	27.6 $\pm$ 0.8	16.8 $\pm$ 0.8	7.4 $\pm$ 0.1	18.1 $\pm$ 4.0
2a	107 $\pm$ 24	24.2 $\pm$ 1.5	1.3 $\pm$ 0.1	4.0 $\pm$ 0.5	22.3 $\pm$ 1.4	13.3 $\pm$ 0.6	8.6 $\pm$ 0.2	15.9 $\pm$ 3.3
2b	262 $\pm$ 113 (150 $\pm$ 24)	24.1 $\pm$ 1.4	1.3 $\pm$ 0.1	3.3 $\pm$ 0.4	24.6 $\pm$ 0.7	16.4 $\pm$ 0.4	7.7 $\pm$ 0.1	16.0 $\pm$ 3.6
3	172 $\pm$ 39	19.7 $\pm$ 1.2	1.1 $\pm$ 0.1	10.5 $\pm$ 3.6	13.2 $\pm$ 1.9	13.4 $\pm$ 0.6	9.4 $\pm$ 0.3	45.5 $\pm$ 7.1

station by late autumn. During the dry season of 1998, the high-salinity assemblage was not present in Central Bay until after September, compared with 1997 and

1999 when it arrived prior to July. In 1997 and 1998, there was a high-salinity low-temperature cluster, 1a, found primarily in Central Bay and the northern part

of South Bay during summer (1997 only) and autumn (Fig. 3B). This was a largely neritic species grouping. In 1999, cluster 1a was absent, and was replaced by the high-salinity high-temperature cluster, 1b, that had previously occurred primarily in San Pablo and South Bays.

#### Cluster 2

The mid-salinity assemblage was present in Central Bay and northern South Bay in January 1997 (Fig. 3B). This assemblage expanded to dominate South Bay until May, after which it was restricted to the northern half of the bay as the high-salinity assemblage took over South Bay. The mid-salinity assemblage disappeared by November. In 1998, this assemblage appeared later, first in Central Bay in March then expanding to dominate South Bay by May, and remained the most prevalent assemblage over the lower SFE until after November. In 1999, the mid-salinity assemblage appeared in January at stations 13 and 30 and dominated the southern 3 stations from March through May, after which it was present in north Central and San Pablo Bays. Cluster 2a generally preceded the appearance of the high-temperature cluster, 2b, which was the most frequently sampled cluster. In 1999, cluster 2a was not replaced by 2b and remained in the bay until September.

#### Cluster 3

The low-salinity cluster 3 occurred least frequently. It was restricted primarily to San Pablo Bay during the wet season but also occurred infrequently in South Bay during winter of 1997 and 1998 (Fig. 3B).

### Taxon-specific patterns

#### *Dominant holoplankton other than copepods*

The suborder Tintinnia was the most abundant and frequently occurring taxon collected from the lower estuary, occurring over the entire temperature and salinity range. Tintinnia abundances averaged  $2.10 \times 10^4$  ind.  $m^{-3}$  and peaked during the spring and autumn in North and Central Bay (Fig. 4A). Their abundances were greatest in 1998 and 1999.

*Oikopleura dioica* was more abundant and occurred across a greater range in the lower estuary during autumn and winter months. However, it was consistently absent from station 30 (Fig. 4B). During the spring and summer it was present primarily near the mouth of the estuary with the exception of a peak abundance of  $3.71 \times 10^6$  ind.  $m^{-3}$  at site 12 in May 1997.

The phylum Rotifera was among the most abundant taxa sampled in the SFE. Their abundance peaked

throughout the estuary from late winter through spring (Fig. 4C). During the dry season, the distribution of rotifers became more restricted towards the mouth. Rotifers were most abundant during the spring of 1998.

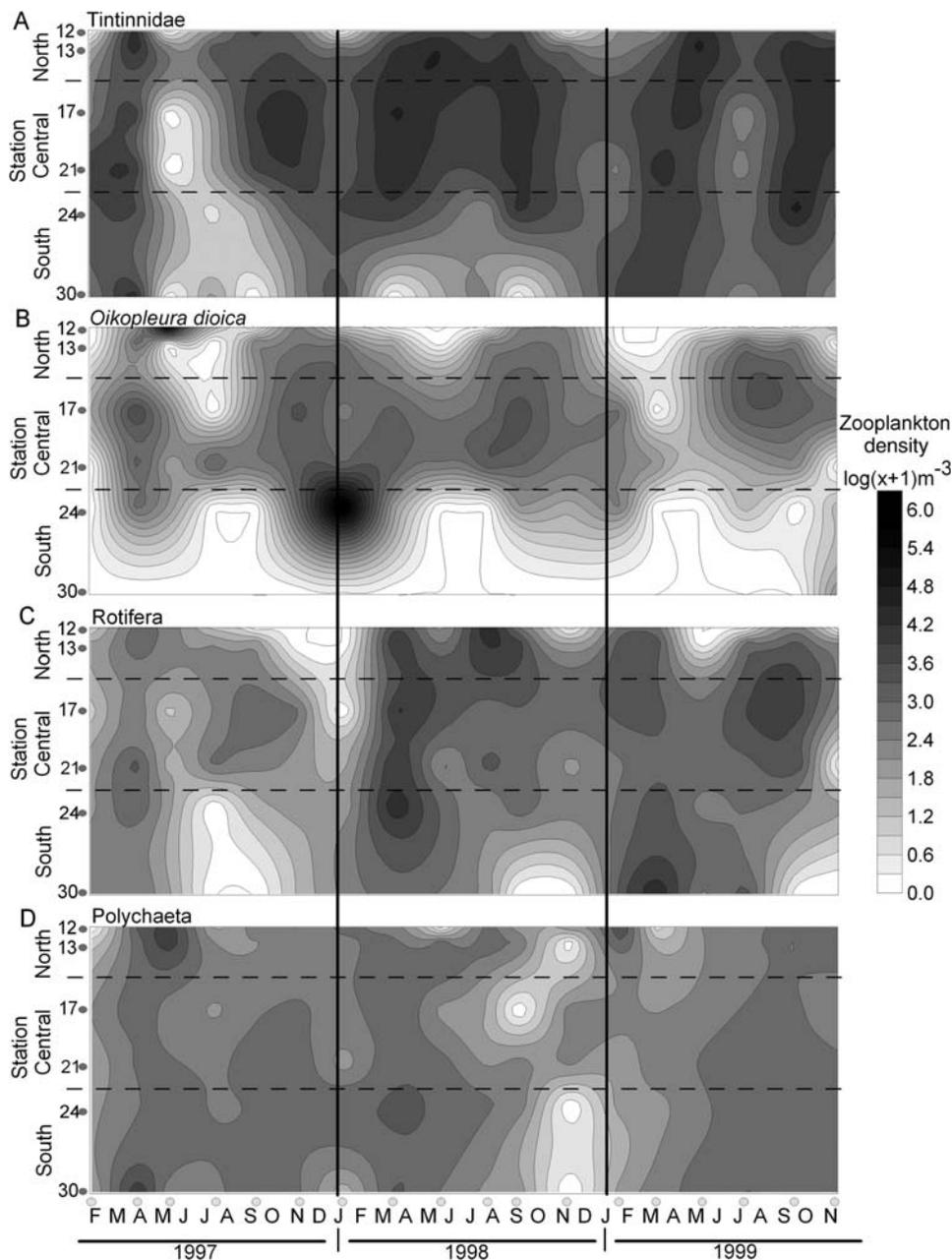
Polychaetes were present throughout the SFE, but their distribution was difficult to characterize and did not appear to have a strong seasonal cycle. The large decrease in abundance during autumn of 1998 is notable, as this decrease did not occur in 1997 or 1999 (Fig. 4D).

#### *Meroplankton*

The most abundant meroplankton sampled were bivalves, gastropods and spionids (polychaetes). Bivalve larvae had an average abundance of  $2.37 \times 10^3$  ind.  $m^{-3}$  and were most abundant in San Pablo Bay, with pulses occurring in early spring in South Bay. Bivalves appeared to increase in abundance in 1998 (Fig. 5A). Gastropod larvae showed a strong seasonal signal, having estuary-wide abundance peaks in late summer and autumn (Fig. 5B). Gastropoda was an indicator taxon of the high-salinity communities (clusters 1a,b) and their distribution showed a similar progression of first being abundant in South Bay during summer and expanding northward to San Pablo bay during autumn. Larval spionids showed large inter-annual fluctuations in their spatial and temporal distribution (Fig. 5C). During 1997, they were abundant primarily in South Bay. During 1998 they had high abundances throughout the estuary from late spring through the end of the year. They were present at similar densities in 1999, but occurred only in the autumn.

#### *Copepods*

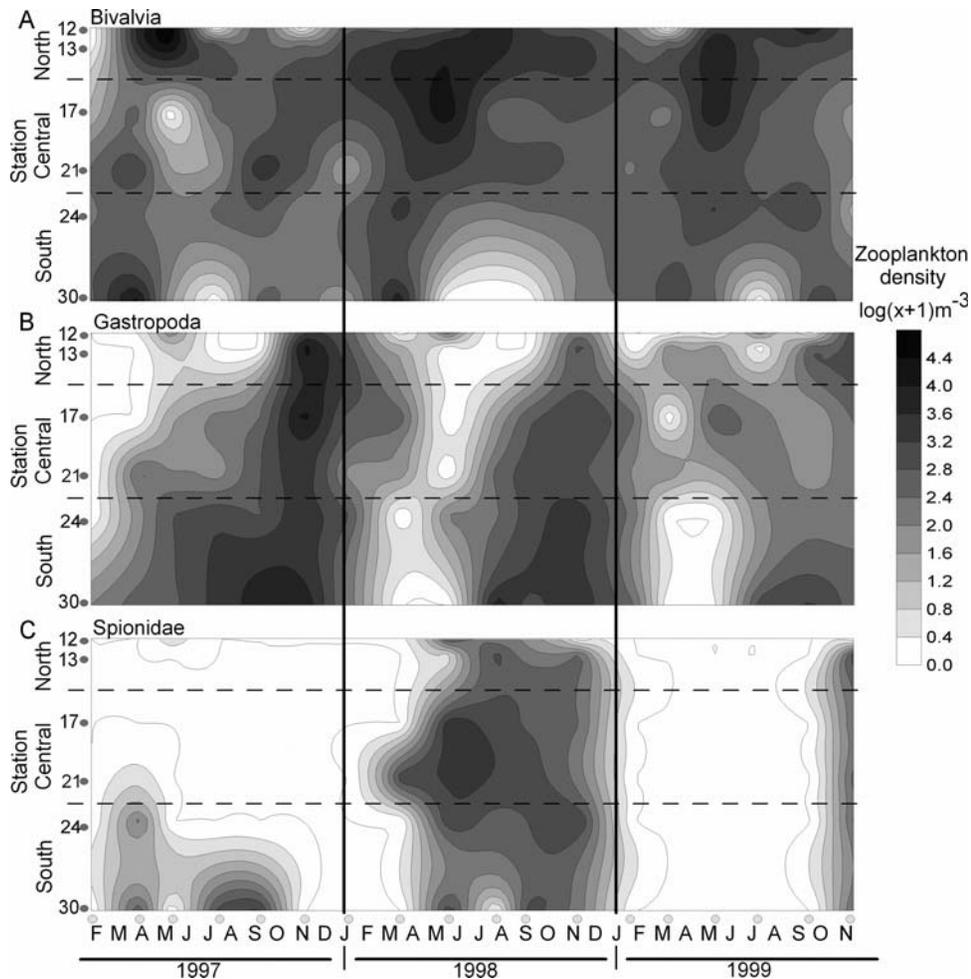
High-salinity communities were characterized by high abundances of both indigenous and non-indigenous copepods. We saw two large peaks in abundance of the neritic calanoid, *Paracalanus* sp., in Central Bay, the first in late autumn 1997–winter 1998, and the second in autumn 1998 (Fig. 6A). *Paracalanus* sp. was an indicator of cluster 1a, as was the neritic poecilostomatid, *Oncaea similis*, found primarily in Central Bay (Fig. 6A and B). The harpacticoid, *Euterpina acutifrons* and the non-indigenous calanoid, *T. dextrilobatus*, were also indicative of cluster 1a. In 1997 and 1998, *E. acutifrons* was present in Central Bay year-round, with a peak abundance exceeding  $5.0 \times 10^3$  ind.  $m^{-3}$  occurring during the autumn, accompanied by a cross-bay expansion (Fig. 6C). This species was notably absent in 1999. Cluster 1b was strongly indicated by the presence of *Acartia californiensis* (Fig. 6D). The temporal and spatial distribution of this species was strongly related to river flow, being absent when outflow was high (Fig. 6D). With the exception of November 1999, their



**Fig. 4.** Spatio-temporal plots of  $\log(x + 1)$  abundances of individual taxonomic groups. The  $y$ -axis is latitudinal with station locations indicated by darkened circles. The  $x$ -axis is time, with sampling dates indicated by open circles. Note differing color scales for each set of panels. (A) Tintinnidae, (B) *Oikopleura dioica*, (C) Rotifera, (D) Polychaeta.

distribution was largely restricted to South Bay. The non-indigenous *P. marinus* and *O. davisae* were abundant in both high salinity clusters. *Pseudodiaptomus marinus* appeared first in South Bay and expanded northward through autumn, then disappeared around the time of the onset of the wet season (Fig. 7A). *Pseudodiaptomus marinus* abundance decreased from 1997 to 1999, but peaked in abundance at  $2.60 \times 10^3$  ind.  $m^{-3}$  in San

Pablo Bay in November 1999. The non-indigenous cyclopoid copepod *O. davisae* was the second most abundant taxon, with a maximum abundance of  $4.4 \times 10^5$  ind.  $m^{-3}$  and an average abundance of  $2.97 \times 10^4$  ind.  $m^{-3}$ . During summer months *O. davisae* was the most abundant taxon sampled in both San Pablo and South Bays (Fig. 7B), and its abundance in Central Bay was second only to that of tintinnids.

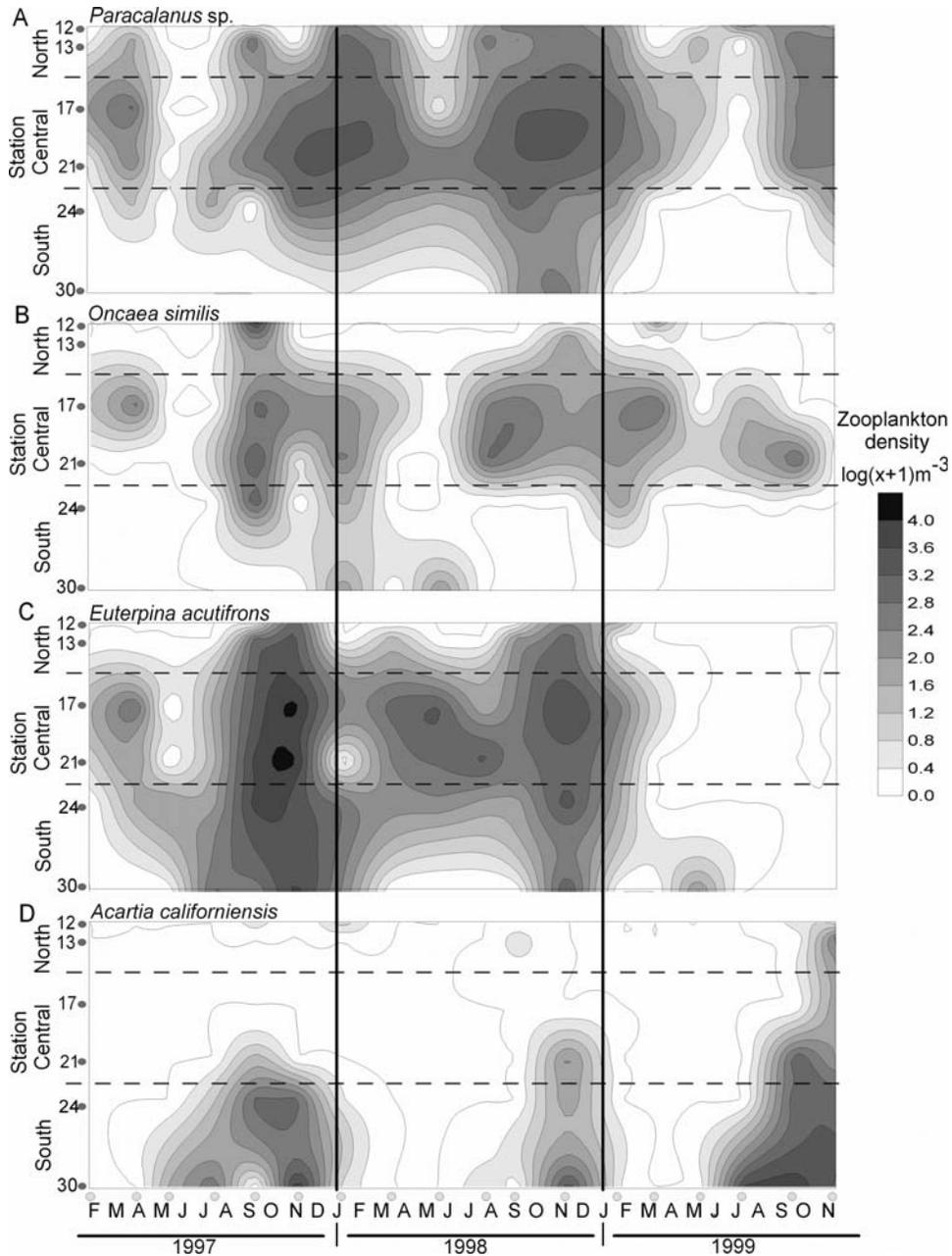


**Fig. 5.** Spatio-temporal plots of  $\log(x+1)$  abundances of individual meroplankton groups. The y-axis is latitudinal with station locations indicated by darkened circles. The x-axis is time, with sampling dates indicated by open circles. (A) Bivalvia, (B) Gastropoda, (C) Spionidae.

The mid-salinity low temperature cluster (2a) was characterized by the presence of calanoids, *Acartia tonsa* and *Acartia (Acartiura)* spp., whereas the mid-salinity high-temperature cluster (2b) was characterized by the non-indigenous cyclopoids, *O. davisae* and *L. tetraspina*. *Acartia (Acartiura)* spp. was one of the most abundant taxa sampled. They were seasonally absent from south South Bay during the period when water temperatures reached their maximum (Fig. 7C). They were also absent from station 12 when salinity was at its lowest. *Acartia (Acartiura)* spp. were particularly abundant estuary-wide during 1999. *Limnoithona tetraspina* was the third most abundant mesozooplankton species in SFE. They were abundant year-round in San Pablo Bay and seasonally abundant in Central and South Bays. *Limnoithona tetraspina* was also an indicator taxon of the low salinity cluster, and their distribution was strongly related to river flow. During months of high river output, the range of *L. tetraspina* expanded toward the

mouth of SFE from both San Pablo and South Bays (Fig. 7D). In spring 1998 they had high abundances across the estuary. Salinities during this period were lower than in 1997 and 1999.

There were several other non-indigenous calanoids associated with low salinity conditions. *Eurytemora affinis* was a strong indicator of the low salinity cluster and was present in San Pablo Bay during periods of high outflow through the delta (Fig. 8A, Supplement 4 in the Supplementary Material online). *Sinocalanus doerrii* largely co-occurred with *E. affinis*, with the exception of a peak in abundance at station 30 in March 1998 (Fig. 8B). *Pseudodiaptomus forbesi* were found in low abundances (Fig. 8C). During March 1998 they occurred across the lower estuary and in July 1999 they had a peak abundance of  $51 \text{ ind. m}^{-3}$  in San Pablo Bay. There was no apparent seasonal pattern in distribution or abundance of the predatory calanoid, *T. dextrilobatus* (Fig. 8D). They were consistently abundant in San Pablo and South Bays



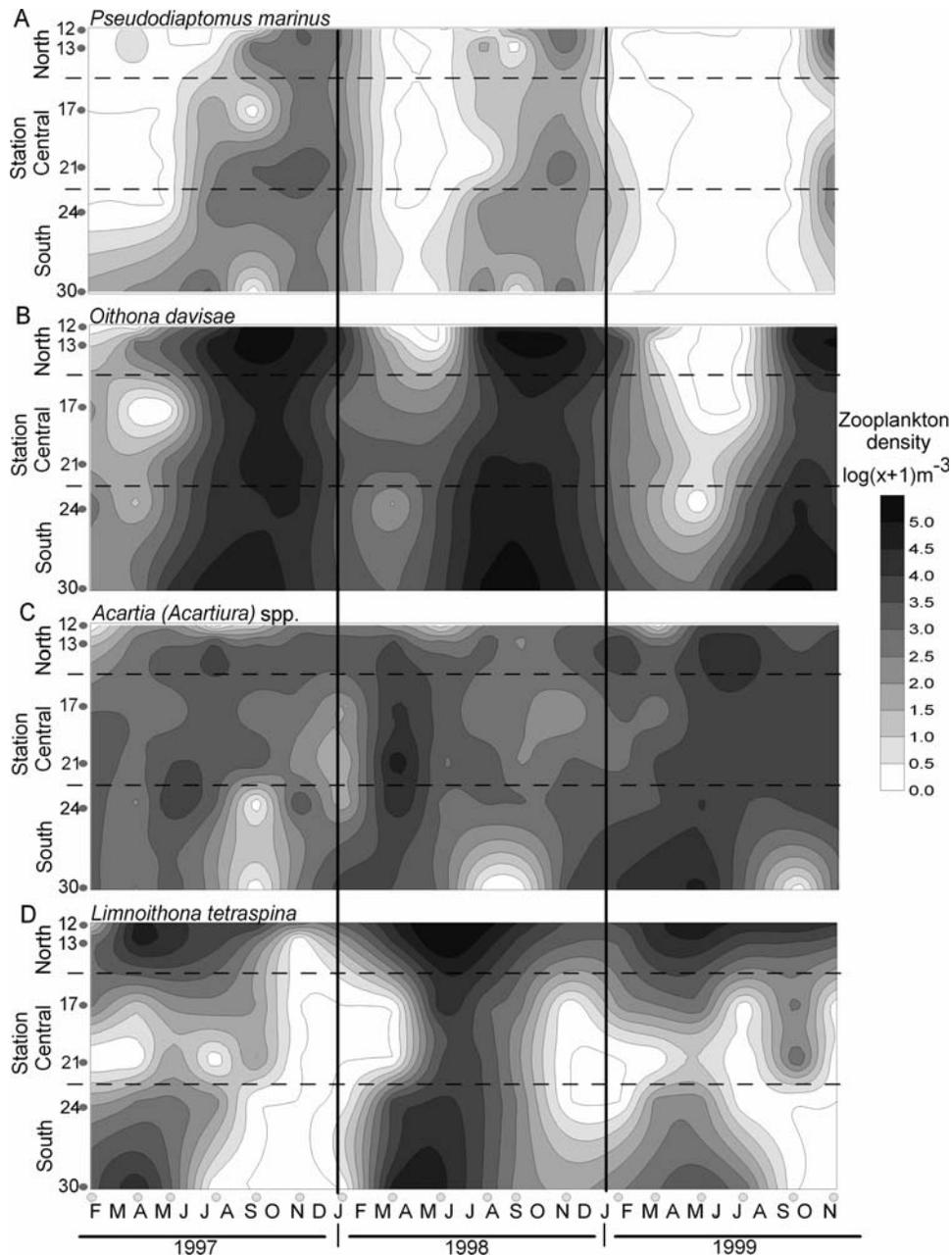
**Fig. 6.** Spatio-temporal plots of  $\log(x + 1)$  abundances of individual taxonomic groups. The  $y$ -axis is latitudinal with station locations indicated by darkened circles. The  $x$ -axis is time, with sampling dates indicated by open circles. (A) *Paracalanus* sp., (B) *Oncaea* sp., (C) *Euterpina* sp., (D) *Acartia californiensis*.

and reached peak abundances of  $10^3 \text{ m}^{-3}$ . They were most abundant in 1998, extending across the estuary during the summer.

## DISCUSSION

We observed dramatic changes in the mesozooplankton ( $>73 \mu\text{m}$ ) of the lower SFE, including shifts in spatio-

temporal patterns, ENSO effects and the prevalence of non-indigenous species. Over the period of our study, the lower SFE experienced above average freshwater input, resulting in lowered salinities estuary-wide. The marine influence on the estuary was also likely heightened in 1997 and 1998 due to increased sea level associated with El Niño. A seasonal progression was seen in the mesozooplankton community clusters that was related to salinity, distance to marine influence and

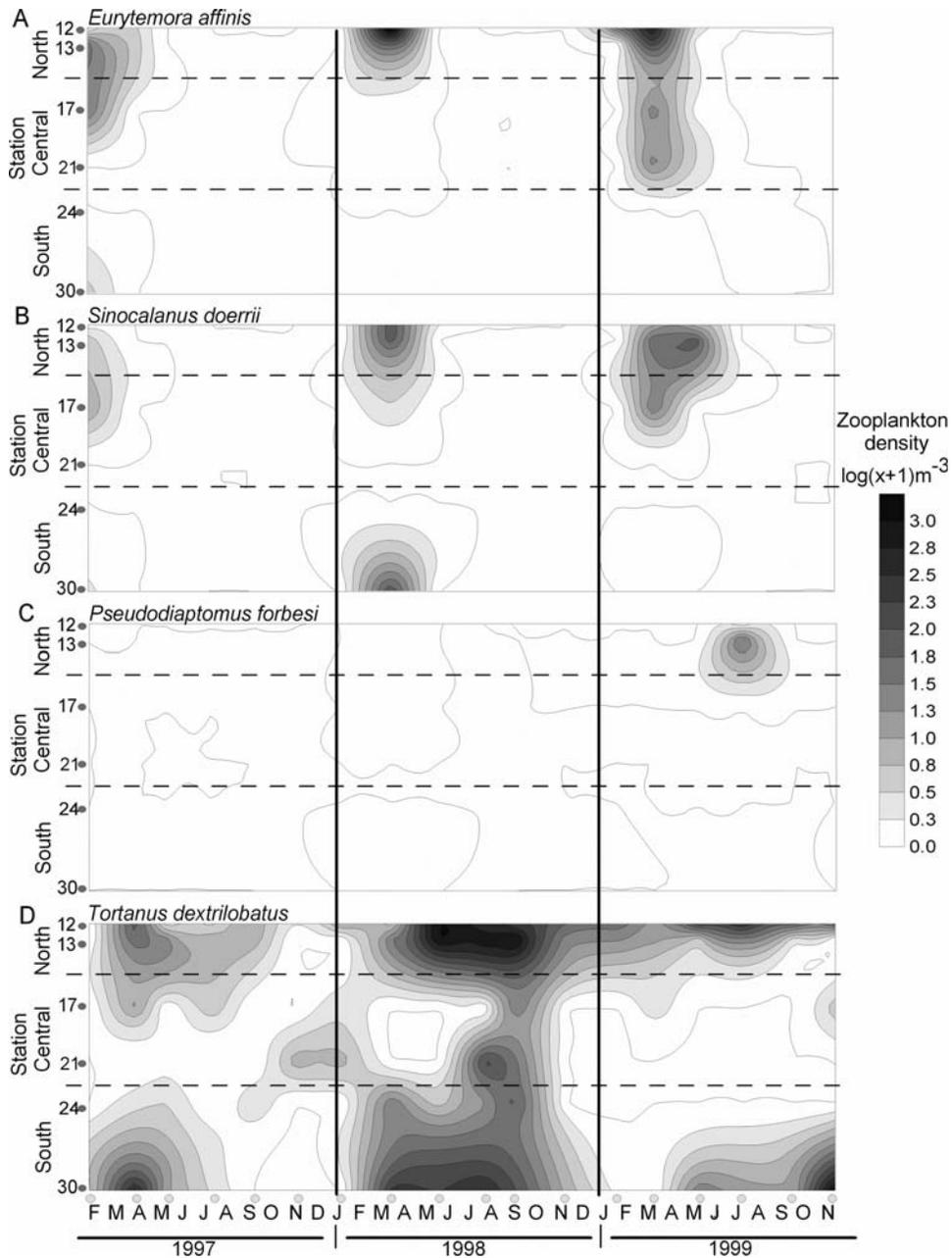


**Fig. 7.** Spatio-temporal plots of  $\log(x+1)$  abundances of individual taxonomic groups. The  $y$ -axis is latitudinal with station locations indicated by darkened circles. The  $x$ -axis is time, with sampling dates indicated by open circles. (A) *Pseudodiaptomus marinus*, (B) *Oithona davisae*, (C) *Acartia (Acartiura) spp.*, (D) *Limnoithona tetraspina*.

temperature. The mesozooplankton was numerically dominated year-round by tintinnids. Within the metazoans, *O. davisae* dominated during the dry season, and during the wet season, dominance was split spatially with *O. dioica* dominating the seaward extent of the lower estuary and *L. tetraspina* dominating the landward extent. This is indicative of a long-term (16–19 years) shift in the dominance from (presumed) native calanoid copepods to non-indigenous (Asian) cyclopoid copepods.

### Mesozooplankton community dynamics

We identified five primary mesozooplankton communities present in the lower SFE from 1997 to 1999 whose distributions were related to salinity, distance to marine influence and temperature. Because water temperature in the SFE is influenced by atmospheric and oceanic conditions, in addition to freshwater input, temperature and salinity gradients are often uncoupled.



**Fig. 8.** Spatio-temporal plots of  $\log(x + 1)$  abundances of individual taxonomic groups. The  $y$ -axis is latitudinal with station locations indicated by darkened circles. The  $x$ -axis is time, with sampling dates indicated by open circles. (A) *Eurytemora affinis*, (B) *Sinocalanus doerrii*, (C) *Pseudodiaptomus forbesi*, (D) *Tortanus dextrilobatus*.

This uncoupling was apparent during our study and resulted in distinct zooplankton communities between wet/dry seasons and cold/warm seasons.

When grouped by salinity, zooplankton communities showed a predictable spatial and temporal progression through the estuary. With the onset of the wet season and high river outflow through the delta, cluster 3 appeared in the lower estuary (San Pablo Bay, and to a

lesser extent, South Bay). At stations near the mouth, the mid-salinity assemblage was present. As outflow through the delta declined, mid-salinity clusters first expanded to the north and south, and then were restricted further north, until being fully replaced by the high-salinity dry season assemblage.

When grouped by temperature, communities showed a similar though less predictable progression between

cold and warm seasons. Horizontal gradients in mesozooplankton communities related to temperature were often observed with stations nearer the mouth having cold water communities and landward stations having warm water communities. Cluster 1a, the warmest of the cold water clusters, appeared during the dry season and preceded cluster 2a in the Central Bay. Cluster 2a was present in the Central Bay when freshwater input (outflow through the delta and presumably flow into South Bay) was high and cluster 3 was present to the north and south, suggesting that cluster 2a was the result of mixing or stratification of clusters 1a and 3 (Cluster 2a was frequently sampled from a stratified water column). The retreat of cold water clusters northward to San Pablo Bay and their replacement in the south by high-temperature clusters coincided with reduction in outflow through the delta.

In terms of freshwater flow entering the delta, 1998 was one of the three wettest years between 1956 and 2000 (Kimmerer, 2002). The average estuary-wide salinity in 1998 was slightly below that in 1997 and 1999, and the decrease was most apparent in the dry season (July–December). During the dry season of 1998, the high-salinity assemblage was not present in Central Bay until after September, compared with 1997 and 1999 when it arrived prior to July. The later appearance of cluster 1a in 1998 than in 1997 could be explained by the longer duration of high outflow through the delta that occurred in 1998. Persistence of the low-salinity community in San Pablo Bay in 1999 was surprising, since this was the driest of the 3 years. Cold water clusters were also more prevalent in the estuary than in the previous 2 years. Cluster 1a did not appear during the dry season. Instead, cluster 2a persisted into the autumn and was replaced by the warm water cluster, 1b. La Niña conditions during 1999 may have resulted in decreased presence of neritic species (cluster 1a) due to reduced oceanic influence compared with the previous 2 years.

Despite different hydrography and circulation patterns, San Pablo and southern South Bay followed similar progressions in their zooplankton communities: cluster 3 to 2b to 1b as freshwater discharge decreased and the bays warmed. However, there was a difference in the two locations in the persistence of these communities, with cluster 3 persisting longest in San Pablo Bay, and cluster 1b persisting longest in South Bay. In contrast, mesozooplankton communities at stations near the mouth of the estuary were less predictable. While there was a repeated shift between mid-salinity and high-salinity assemblages, reflecting wet and dry seasons, respectively, the warm–cold identity of the cluster varied widely.

As in previous studies elsewhere, we found that spatio-temporal variation in estuarine zooplankton communities is associated with a suite of environmental variables representing the effect of season and the alternating prominence of coastal and riverine influences e.g. temperature, salinity, freshwater input and distance from oceanic or riverine input. For instance, in the Westerschelde estuary, Belgium and the Netherlands, spatial variation was related to a horizontal chlorinity (salinity) gradient and temporal variation related to a seasonal temperature gradient (Soetaert and Van Rijswijk, 1993). In Mission Bay, San Diego, and the Senegal River Estuary, Senegal and Mauritania, spatial variation in species composition was related to distance to marine or continental influence, depending on the season (Champalbert *et al.*, 2007; Elliott and Kaufman, 2007). In the lower SFE, micronekton and macrozooplankton communities were also correlated with distance from marine influence and, to a lesser extent, salinity (Gewant and Bollens, 2005). In our study, variation in mesozooplankton was much more strongly related to salinity (axis 1, Table I), perhaps reflecting a greater fidelity of mesozooplankton to water masses than micronekton or macrozooplankton.

Elliott and Kaufmann (Elliott and Kaufmann, 2007) attributed inter-annual variation in mesozooplankton community composition in Mission Bay, California to differences in rainfall. In the SFE, inter-annual environmental variability is often explained by patterns in rainfall and river discharge (Cloern and Nichols, 1985), which is to some extent reflected in the mesozooplankton, e.g. in the timing of the appearance of cluster 3 and in the variable presence of mid- and high-salinity assemblages. Based on the magnitude of river flow, however, we would not have predicted the persistence of cluster 3 in San Pablo Bay in 1999. This may have been caused by the coupling of decreased seaward advection of cluster 3 due to reduced river flow and reduced evaporation caused by relatively low temperatures occurring during a La Niña year.

Biological forcing could also be an important driver of zooplankton community structure in the lower SFE, but this was difficult for us to assess given the data available. With regard to food resources, we only had chlorophyll *a* data, a very crude measure of phytoplankton availability to zooplankton. Previous studies in the SFE indicate that the quantity and quality of specific types of food would be expected to affect variation in zooplankton composition (Rollwagen-Bollens and Penry, 2003; Gifford *et al.*, 2007). Predation is another biological force that is well known to affect zooplankton dynamics (e.g. Brooks and Dodson, 1965; Steele and Frost, 1977; Verity and Smetacek, 1996), but was not measured in

our study. In the SFE, there is clear seasonal and regional variation in composition of macrozooplankton and micronekton, potential predators of mesozooplankton (Gewant and Bollens, 2005), and Hooff and Bollens (Hooff and Bollens, 2004) demonstrated a significant impact of the predatory copepod, *T. dextrilobatus*, on copepod populations in the estuary, particularly on *Acartia* (*Acartiura*). Nevertheless, our analyses, based on the data available, indicate strong physical forcing as the primary influence on variation in zooplankton communities in the lower SFE.

### Patterns of individual taxa

Compared with other estuaries, SFE is considered to have a low level of primary production (Cloern, 1996; but see Cloern *et al.*, 2007), giving microzooplankton heightened importance in planktonic food webs as prey for omnivorous copepods (Rollwagen-Bollens and Penry, 2003; Gifford *et al.*, 2007; Rollwagen-Bollens *et al.*, 2011). Though our sampling protocol only collected larger (73–200  $\mu\text{m}$ ) microzooplankton, tintinnids were the most abundant taxon sampled. In the SFE, ciliates were important food sources for *Acartia* spp. when phytoplankton were not blooming (Rollwagen-Bollens and Penry, 2003) and tintinnids, specifically, were found to make up a large percentage of the prey ingested by first feeding larval herring, *Clupea pallasii* (Bollens and Sanders, 2004).

Various microzooplankton taxa, such as rotifers, increase in abundance with increasing freshwater flow in the upper SFE (Kimmerer, 2002). Our sampling in the lower SFE also showed that rotifers were more abundant during the spring, particularly in 1998, suggesting increased abundance with freshwater inflow. While a similar pattern occurred with bivalve larvae, gastropod larvae were more abundant during dry periods. Tintinnid abundances did not appear to be directly affected by freshwater inflow and peaked twice per year, once in spring and again in autumn.

Copepods typically dominate the mesozooplankton (Verity and Smetacek, 1996) of marine waters; however, appendicularians are also often abundant (Gorsky and Fenaux, 1998). While not mentioned in the results of the 1980–1981 survey of San Francisco Bay by Ambler *et al.* (Ambler *et al.*, 1985), *Oikopleura dioica* was one of the most abundant species sampled by us during 1997–1999. Appendicularians have extremely rapid growth rates and can form dense blooms (Alldredge, 1982; Gorsky and Fenaux, 1998). *Oikopleura dioica* plays a different trophic role than do most copepods, ingesting smaller (<25  $\mu\text{m}$ ) phytoplankton and bacteria (Tønnesson *et al.*, 2005). Appendicularians are also a

potentially important food source for both larval and adult fish (Mousseau *et al.*, 1998; Prokopchuk and Sentyabov, 2006), and eggs and juveniles are fed on by calanoid copepods (López-Urrutia *et al.*, 2004).

The abundance of some copepod species (*P. marinus* and *E. acutifrons*) appeared related to El Niño and La Niña patterns, likely a result of variation in sea level and oceanic input to the estuary. As reported by Ambler *et al.* (Ambler *et al.*, 1985), neritic copepod taxa (cluster 1a) occurred most frequently in Central Bay during the dry season, likely due to decreased seaward advection by river flow.

In 1980, *Acartia clausi* was the dominant wet season copepod and spanned the lower SFE (Ambler *et al.*, 1985). *Acartia* (*Acartiura*) spp. in our study [identified as *A. clausi* *s.l.* by Ambler *et al.* (Ambler *et al.*, 1985)] were an order of magnitude lower in abundance. We did, however, see the same pattern of seasonal decline of *Acartia* (*Acartiura*) spp. from South Bay during the dry season, as well as from station 12 when salinities were at their lowest. Ambler *et al.* (Ambler *et al.*, 1985) noted that there appeared to be little spatio-temporal overlap between *A. clausi* *s.l.* and *A. californiensis* in the SFE, analogous to the seasonal succession of *Acartia hudsonica* and *A. tonsa* observed in estuaries of the eastern USA (Sullivan *et al.*, 2007). In Tomales Bay, California, another low-inflow estuary near the SFE, a similar pattern was seen by Kimmerer (Kimmerer, 1993), with *A. californiensis* abundant in the inner bay during warmer temperatures and replaced by *Acartia* (*Acartiura*) spp. (tentatively identified as *A. hudsonica*) in cooler conditions. While *A. californiensis* was also abundant in South Bay in the dry seasons during our study, we saw a large amount of overlap between the two species, particularly in 1999, though *A. californiensis* had a much narrower salinity range (20–32) than *Acartia* (*Acartiura*) spp. (7–32). Over the dry season, *A. californiensis* had both average and peak abundances an order of magnitude lower than those reported by Ambler *et al.* (Ambler *et al.*, 1985). While these lower abundances may have been caused by our sampling wetter years than did Ambler *et al.* (Ambler *et al.*, 1985), this does not explain the decreased abundance of *Acartia* (*Acartiura*) spp.

*Oithona davisae* was the dominant copepod species during the dry season in our study (Fig. 7B, Supplement 2 in the Supplementary Material online). In 1980, Ambler *et al.* (Ambler *et al.*, 1985) reported that *O. davisae* was the third most abundant taxon during the dry season, after *A. californiensis*. It was most abundant in South Bay, but was most frequently observed in Central Bay (Ambler *et al.*, 1985). We found this species was abundant across the lower SFE, with decreased abundances and frequencies of occurrence near the

mouth. *Oithona davisae* is considered a thermophilic species, and the observed seasonal and along-estuary patterns of abundance may be due to higher egg production rates of *O. davisae* at higher temperatures (Uye and Sano, 1995).

*Limnoithona tetraspina* was the most abundant copepod species sampled during the wet season, with highest abundances in San Pablo Bay and South Bay (Fig. 7D). While Ambler *et al.* (Ambler *et al.*, 1985) did not identify most cyclopoids below the level of order, it is likely that *L. tetraspina* was not present during 1980, as its introduction has been estimated to have occurred near the time of its first detection in 1993 (Orsi and Ohtsuka, 1999). This non-indigenous copepod has previously been noted as abundant in low-salinity regions of the upper SFE (Bouley and Kimmerer, 2006), and our results indicate that its range extends to much higher salinities, with abundances  $>10^3$  ind.  $m^{-3}$  occurring at salinities as high as 30.

Several other non-indigenous copepods were associated with low salinities, including *Sinocalanus doerrii*, *T. dextrilobatus*, *E. affinis*, *A. sinensis* and *P. forbesi* (Fig. 8). Of these, *T. dextrilobatus* was the most abundant and had the widest temporal range. *Eurytemora affinis* and *S. doerrii* were present in the lower SFE only during high river flow. The restriction of *E. affinis* to a narrow temporal window in spring was also seen by Kimmerer and Orsi (Kimmerer and Orsi, 1996) between 1988 and 1995, and was attributed to the introduction of the clam, *Corbula amurensis*. Unlike the distribution reported by Orsi and Ohtsuka (Orsi and Ohtsuka, 1999), *S. doerrii* overlapped the downstream range of *E. affinis* and was found in salinities ranging between 6 and 18. *Pseudodiaptomus forbesi* was only abundant in San Pablo Bay in late spring 1999, a seasonal peak consistent with Kimmerer and Orsi (Kimmerer and Orsi, 1996).

### ENSO effects

In addition to warmer sea surface temperatures, El Niño events are associated with increases in sea surface height (Ryan and Noble, 2007) and precipitation. Variability in the strength of these forcings may explain variation in the composition of mesozooplankton in the lower SFE, such as the increased prevalence of high-salinity clusters we observed in late summer and autumn 1997 (Fig. 3B). Decreases in coastal zooplankton and changes in species composition associated with El Niño events (McGowan *et al.*, 1998; Schwing *et al.*, 2002) do not appear to have occurred in the SFE, as abundances in 1998 (the El Niño year) were higher than during 1999 or 1997. As found in other studies (e.g. Hidalgo and Escribano, 2001; Hooff and Peterson, 2006), we saw increases in species richness associated

with El Niño. Notably, we did not see any perturbation of the seasonal succession of dominant copepods, which may be predicted to occur with water temperature changes associated with El Niño (Hopcroft *et al.*, 2002). This stability in the presence of ENSO-related environmental variability may indicate the resilience of estuarine organisms to short-term environmental change (Palomares-García and Gómez-Gutiérrez, 1996).

Another possible ENSO effect is the enhancement of secondary production due to increased freshwater flows that cause increased water column stability and primary production. In south San Francisco Bay, water column stratification is necessary for bloom formation because it allows phytoplankton to stay in the photic layer and decoupled from benthic grazers (Cloern, 1991; Koseff *et al.*, 1993). Similar positive effects of freshwater flow on production can extend to higher trophic levels in other estuarine and near coastal systems (Cloern, 1996; Reaugh *et al.*, 2007; Schlacher *et al.*, 2008). This may have resulted in the increased abundances of mesozooplankton we observed in the lower SFE during El Niño.

### Non-indigenous species

Eight copepod taxa that were frequently sampled in 1997–1999 were not noted in 1980 (Table III). Three of these taxa (*T. dextrilobatus*, *A. sinensis*, and *P. marinus*) are non-indigenous calanoids that almost certainly would have been identified to the level of genus by Ambler *et al.* (Ambler *et al.*, 1985) had they been present. *Tortanus dextrilobatus* reached densities of  $10^3 m^{-3}$ , which Bollens *et al.* (Bollens *et al.*, 2002) found notable as being particularly high for a planktonic carnivore. Results from feeding experiments using *O. davisae* and *Acartia (Acartiura)* spp. as prey items suggested that *T. dextrilobatus* prefers the larger calanoids as prey and has a significant predatory impact on copepods in the lower SFE (Hooff and Bollens, 2004). Competitive interactions between non-indigenous and native copepod species may also have ramifications for higher trophic levels without affecting total copepod abundance. For instance, Meng and Orsi (Meng and Orsi, 1991) showed that, though decreases in abundance of *E. affinis* have been offset (and likely exacerbated) by *Sinocalanus doerrii*, the differing behaviors of the two calanoids cause large differences in their availability to first feeding striped bass.

The lower SFE is now home to a largely Asian assemblage of copepods. Previously dominant calanoids of the genus *Acartia* and *Acartia (Acartiura)* are now less abundant than the non-indigenous oithonid cyclopoids *O. davisae* and *L. tetraspina*. The copepod community associated with low salinities in the SFE is comprised of

Table III: Seasonal occurrence of copepod taxa with distinct regions of the lower San Francisco Estuary: 1980 vs. 1997–1999

Copepod Taxa	1997–1999 (present study)						1980 (Ambler <i>et al.</i> )					
	Jan–May			June–Dec			Jan–May			June–Dec		
	CB	SO	SP	CB	SO	SP	GG	SO	SP	GG	SO	SP
<i>Oithona davisae</i>	78	100	67	94	100	89	53	1	16	45	25	12
<i>Limnoithona tetraspina</i>	56	88	100	50	39	94	—	—	—	—	—	—
<i>Acartia (Acartiura) spp.</i>	100	100	94	100	72	94	a	a	a	a	a	a
<i>Euterpina acutifrons</i>	67	47	11	67	56	33	—	—	—	—	—	—
<i>Paracalanus sp.</i>	78	41	56	83	44	67	61	10	38	81	11	50
<i>Pseudodiaptomus marinus</i>	28	53	33	67	72	50	—	—	—	—	—	—
<i>Acartia californiensis</i>	0	29	6	28	78	28	7	0	0	9	83	50
<i>Acartia tonsa</i>	83	53	44	100	56	94	na	na	na	na	na	na
<i>Oncaea similis</i>	50	29	6	39	11	17	30	1	0	54	5	8
<i>Tortanus dextrilobatus</i>	28	65	83	33	56	89	—	—	—	—	—	—
<i>Eurytemora affinis</i>	28	12	61	6	0	0	0	17	44	0	11	4
<i>Corycaeus anglicus</i>	56	12	6	56	6	11	46	10	16	36	5	20
<i>Coullana canadensis</i>	11	29	28	0	6	6	—	—	—	—	—	—
<i>Acanthocyclops vernalis</i>	17	6	56	0	0	0	—	—	—	—	—	—
<i>Pseudobryda sp.</i>	6	6	56	0	0	0	—	—	—	—	—	—
<i>Microsetella sp.</i>	28	12	6	39	11	0	38	7	22	18	10	4
<i>Epilabidocera longipedata</i>	61	59	33	28	17	28	na	na	na	na	na	na
<i>Sinocalanus doerrii</i>	17	18	56	0	0	0	0	1	11	0	0	0
<i>Calanus pacificus</i>	22	35	11	6	0	0	na	na	na	na	na	na
<i>Acartiella sinensis</i>	11	18	28	0	6	22	—	—	—	—	—	—
<i>Tortanus discaudatus</i>	33	35	0	22	11	6	na	na	na	na	na	na

Taxa present in >25% of samples in a given region/season are listed in order of greatest mean abundance (Central Bay, CB; Golden Gate, GG; South Bay, SO and SP, San Pablo Bay). ‘—’ indicates that the taxon was not mentioned in Ambler *et al.* (Ambler *et al.*, 1985). Note, however, that Ambler *et al.* (Ambler *et al.*, 1985) did not identify most harpacticoid taxa. ‘na’ indicates that the taxon was mentioned in Ambler *et al.* (Ambler *et al.*, 1985) but occurrence was not reported.

<sup>a</sup>Taxonomic discrepancy—Ambler *et al.* (Ambler *et al.*, 1985) referred to *A. clausi*.

species that occur in Chinese and Korean estuaries, e.g. *L. tetraspina*, *Sinocalanus doerrii*, *T. dextrilobatus*, and *P. forbesi* (Orsi *et al.*, 1983; Orsi and Ohtsuka, 1999). The only other record we found of several of these species co-occurring is from the lower Columbia River Estuary, Oregon and Washington (Cordell *et al.*, 2008; Bollens, unpublished data), where they were likely introduced through discharge of ballast water from SFE (Cordell *et al.*, 2008; Simkanin *et al.*, 2009). The copepod community in the SFE associated with high salinities was strikingly similar to that reported in Japanese estuaries, where dominant taxa include *O. davisae*, *Acartia (Acartiura) omorii*, *P. marinus* and *Paracalanus spp.* (Uye and Liang, 1998; Islam *et al.*, 2006). In contrast, copepod communities in other estuaries along the US West Coast bear little resemblance to the SFE. For instance, to the south of SFE, Mission Bay, California (a location with only sporadic freshwater input) is dominated by *A. californiensis*, *Oithona similis*, and *Oithona oculata* (Elliott and Kaufmann, 2007), though the presence of *P. marinus* has been noted (Fleminger and Kramer, 1988).

Oithonids are smaller than calanoids, and represent a change in the size structure of the copepod community in the SFE. Uye (Uye, 1994) found a similar

decrease in copepod community median size, and dominance of *O. davisae*, when comparing Tokyo Bay, Japan, to both historical records from the same location and to Osaka Bay, Japan, and associated this change with increased levels of eutrophication, potentially due to an increase in the relative importance of flagellates compared with diatoms in primary production. While there is diet overlap between oithonids and some larger copepods, oithonids are raptorial feeders and target primarily motile prey such as ciliates and flagellates, whereas calanoids such as *Acartia* prefer large diatoms (Uchima, 1988; Atkinson, 1996; Gifford *et al.*, 2007). While diatoms dominate the phytoplankton community of the SFE (Cloern and Dufford, 2005), increased climatic variability beginning in the late 1970s has caused a decrease in diatom carbon in the northern SFE (Lehman, 2004). This decrease was further exacerbated by the introduction of the clam *C. amurensis* in 1987 (Alpine and Cloern, 1992). We could not find any information regarding changes in the relative importance of motile microplankton versus diatoms to primary production in the SFE, but blooms of dinoflagellates have been recorded since 1999 during autumn and winter (Cloern *et al.*, 2005; Cloern *et al.*, 2007), coinciding with

periods of peak *O. davisae* abundance. Increases in oithonid abundance may also be aided by reduction in calanoid numbers due to predation of calanoid nauplii by *C. amurensis* (Kimmerer *et al.*, 1994).

In addition to smaller size, oithonids also differ from calanoids in terms of their mode of swimming (Paffenhöfer, 1993) and their escape response (Drenner and McComas, 1980), and Bouley and Kimmerer (Bouley and Kimmerer, 2006) hypothesized that these attributes might reduce the susceptibility of oithonids to visual predators, specifically juvenile fish, compared with calanoids. Purcell *et al.* (Purcell *et al.*, 2007) suggested that by being detrimental to fish populations, reduction in the size structure of copepod communities is beneficial to non-visual predators, such as jellyfish. In Fukuyama Harbor, Japan, oithonid populations are likely influenced by gelatinous predators (Uye and Sano, 1995). While low-salinity regions of the SFE did not historically support populations of jellyfish (Rees and Gershwin, 2000) and they were not commonly found in the lower estuary by our sampling, populations of several non-indigenous species of hydromedusae originally from the Black Sea were discovered in the SFE in the 1990s (Rees and Gershwin, 2000; Mills, 2001).

## CONCLUSIONS

Between 1980–1981 and 1997–1999, a dramatic shift occurred in the mesozooplankton community of the lower SFE. Most notable, abundances of the historically seasonally dominant copepods, *A. californiensis* and *Acartia (Acartiura)* spp., decreased, and were replaced by two smaller, non-indigenous (Asian) cyclopoids, *O. davisae* and *L. tetraspina*, and the appendicularian, *O. dioica*, as the dominants. In addition, inter-annual differences between El Niño and La Niña periods were substantial and appeared related to variable strengths of riverine and oceanic forcing. Impacts of changing zooplankton composition on higher trophic levels in the lower SFE are unknown but likely to be significant (e.g. Bollens *et al.*, 2002; Hooff and Bollens, 2004), especially when considering the behavioral and ecological differences between native calanoid and non-indigenous oithonid copepods (e.g. Uye, 1994).

## SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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