

Macrozooplankton and Micronekton of the Lower San Francisco Estuary: Seasonal, Interannual, and Regional Variation in Relation to Environmental Conditions

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ABSTRACT: Macrozooplankton and micronekton are intermediaries linking lower trophic levels (e.g., phytoplankton and mesozooplankton) to higher ones (e.g., fishes and birds). These organisms have not been extensively studied in the San Francisco Estuary (SFE), California. The objective of this study was to determine the distribution and abundance of macrozooplankton and micronekton in the SFE and to describe how these vary seasonally, interannually, and regionally in relation to environmental variables. Water column macrozooplankton and micronekton were sampled monthly from September 1997 to December 2000 at 6 stations spanning North, Central, and South Bays using a Methot Trawl. The macrozooplankton and micronekton in the lower SFE were dominated by 4 fishes and 7 invertebrates that comprised 98% of the total catch. Correspondence analyses revealed 4 groups of species that exhibited similar patterns of distribution and abundance. The assemblages changed between the wet and dry seasons and with distance from the coastal ocean. Based on abundance patterns, the dominant taxa in the lower SFE can be classified as: organisms spawned from common members of neritic assemblages that use mostly North Bay and that are abundant during the dry season (*Clupea pallasii*, *Spirinchus thaleichthys*, *Porichthys notatus*); estuarine-dependent organisms with broad distributions in the estuary year-round (*Crangon franciscorum*, *Crangon nigricauda*, *Engraulis mordax*); resident species remaining within the estuary but occurring mostly in South Bay during the wet season (*Palaemon macrodactylus*, *Symydotea laticauda*, *Neomysis kadiakensis*); and gelatinous species (*Pleurobrachia bachei*, *Polyorchis* spp.) occurring in all three bays with a single peak in abundance in December and January in North and South Bays. The variation in distribution, abundance, and composition of macrozooplankton and micronekton was related to life history strategies, distance from the coastal ocean, and season.

Introduction

Estuaries are generally characterized as areas of high biological productivity rich in planktonic and nektonic species (Day and Yáñez-Arancibia 1985; McHugh 1985; Mallin and Paerl 1994; Emmett et al. 2000). The San Francisco Estuary (SFE), California, has historically provided essential habitat for larger predatory fish species including *Oncorhynchus tshawytscha* (Chinook salmon), *Acipenser medirostris* (green sturgeon), and *Morone saxatilis* (striped bass) and also has supported large numbers of migrating waterfowl and many species of marine mammals. The SFE is the largest estuary on the west coast of North America, receiving freshwater from the Sacramento and San Joaquin Rivers to the east (the watershed drains nearly 160,000 km² or 42% of California's land area) and having a marine influence from the Pacific Ocean

to the west via the Golden Gate (Conomos et al. 1985).

The production of pelagic food webs depends on the successful transfer of energy from lower trophic levels to higher trophic levels, accomplished by midsize, intermediate consumers: macrozooplankton and micronekton (Marais 1983; deSylva 1985; Mallin and Paerl 1994; Hartmann and Brandt 1995). Macrozooplankton and micronekton include both fish and invertebrate species. Macrozooplankton are distinguished by their size (generally > 2 mm) and micronekton by their ability to swim against currents. Studies conducted in the SFE by Hatfield (1985) and Siegfried and Kopache (1980) concluded that macrozooplankton are an important food source for *M. saxatilis*, *A. medirostris*, and *Leptocottus armatus* (staghorn sculpin); Barry et al. (1996) found that the local distribution of these fish in nearby Elkhorn Slough was in part regulated by the distribution of their prey. Salinity and temperature define the boundaries for many aquatic animals and are subject to temporal (seasonal, interannual) and spatial (regional) variation in the SFE. Abundance of many fish species, including *Spirinchus thaleichthys* (long-

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fin smelt), *O. tshawytscha*, and *M. saxatilis*, correlate with freshwater outflow (Stevens and Miller 1983; Armor and Herrgesell 1985; Pearson 1989; Baxter et al. 1999; Matern et al. 2002). Hatfield (1985) also concluded that the distribution and abundance of the native crangonid shrimp species (*Crangon franciscorum*, *C. nigricauda*, and *C. nigromaculata*) were directly affected by the rate and duration of freshwater discharge.

Studies on the pelagic ecology of the SFE have focused heavily on the primary producers (Cloern 1979, 1996; Cloern et al. 1985; Alpine and Cloern 1992; Jassby et al. 1996) and fishes, particularly in the brackish to freshwater reaches of the estuary (Armor and Herrgesell 1985; Herbold and Moyle 1989; Meng and Orsi 1991; Meng et al. 1994). The San Francisco Bay Study was initiated in 1980 to collect data on the distribution and abundance of larger fish and invertebrate species throughout the SFE (Baxter et al. 1999). Mesozooplankton of the lower SFE have also been a focus of recent studies (Ambler et al. 1985; Bollens et al. 2002; Purkerson et al. 2003; Rollwagen Bollens and Penry 2003; Hooff and Bollens 2004). Missing from the literature is research on the community ecology of the macrozooplankton and micronekton of the SFE and their critical role as intermediaries in the transfer of energy between secondary producers and the higher trophic levels of the estuary.

The objective of this study was to determine the spatial and temporal variability in abundance and community composition of macrozooplankton and micronekton in the lower SFE. The following questions are addressed: What are the most abundant species of macrozooplankton and micronekton in the lower SFE, how do their abundances vary seasonally, interannually, and regionally, and how do changes in the community composition of macrozooplankton and micronekton relate to environmental conditions (i.e., salinity and temperature) in the lower SFE?

Materials and Methods

STUDY SYSTEM

The five separate regions of the SFE are the Sacramento-San Joaquin Delta, Suisun Bay, North (San Pablo) Bay, Central Bay, and South Bay, each of which exhibits somewhat different hydrological conditions determined by its position relative to marine and freshwater sources. This report is concerned only with North, Central, and South Bays, which we refer to collectively as the lower SFE (Fig. 1). North Bay is in close proximity to the delta, is heavily influenced by the freshwater of the Sacramento and San Joaquin Rivers, and is generally less saline than either Central or South Bays. South Bay

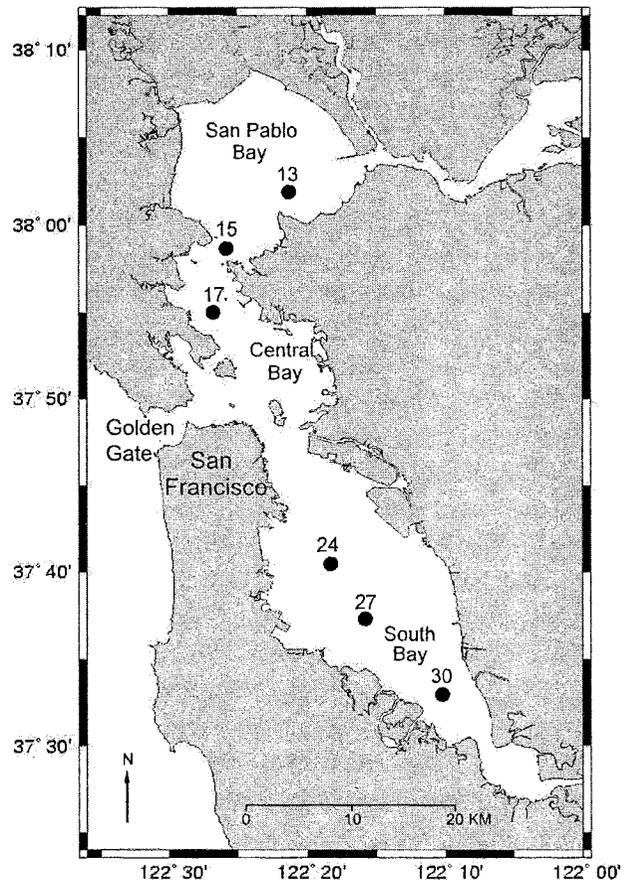


Fig. 1. San Francisco Estuary, showing the location of the six stations (13, 15, 17, 24, 27, and 30) sampled in this study.

lacks significant freshwater inflow and on average is the most shallow bay, resulting in relatively poor circulation and flushing. Central Bay is connected to the Pacific Ocean in the west via the Golden Gate and is more heavily influenced by saltwater than either North or South Bays. Both North and South Bays have extensive shoals (< 3 m) incised by a natural channel scoured by freshwater runoff and tidal movements. Central Bay, although smallest in surface area, is far deeper (average = 11 m), containing the greatest volume of water (Conomos et al. 1985).

The SFE is influenced by a Mediterranean climate with a significant portion of the runoff occurring in the 6-mo wet season from November through April. Most of the freshwater is delivered to the estuary during the wet season followed by snowmelt runoff from the Sierra Nevada snow pack as temperatures rise during spring and summer (Cloern and Nichols 1985).

FIELD SAMPLING

Water column macrozooplankton and micronekton were sampled monthly aboard the R/V *Ques-*

tuary from September 1997 to December 2000 at six stations spanning North, Central, and South Bays (Fig. 1). The United States Geological Survey (USGS) Water Quality of San Francisco Bay program previously designated these stations as part of their long-term monitoring program. The stations follow the naturally occurring channel from the Delta to South Bay (<http://sfbay.wr.usgs.gov/access/wqdata/>).

Macrozooplankton and micronekton samples were collected using a Methot Trawl with a mouth area of 4 m² and a mesh size of 3 mm (Methot 1986). The conical nylon net extends 5 m to a cod-end designed to protect captured organisms from being damaged while under tow. The bridle cables attach at two points, leaving the mouth relatively unobstructed. A steel depressor bar suspended below the frame keeps the opening of the net perpendicular to the flow. Volume filtered was calculated using the product of mouth area and distance traveled as determined by a General Oceanic flow meter suspended in the center of the net.

The net was lowered to a depth of 1 m above the bottom and retrieved in a stepwise, oblique manner. The net was towed for 30 min at 1.5–2.0 knots. Volumes filtered ranged from 5,000 to 7,000 m³.

All tows were completed at night, beginning approximately 1 h after sunset to reduce net avoidance. Due to the large distances between our stations in the three embayments, it was necessary to partition the effort over two consecutive nights, sampling stations 13, 15, and 17 on the first night and stations 24, 27, and 30 on the second night (Fig. 1).

Catches were immediately removed from the net and preserved in a 5–10% formalin-seawater solution for later analysis. In the laboratory all specimens were identified to the lowest taxonomic level possible, enumerated, and measured for standard length using a dissecting Leica MZ6 microscope. For large catches of any one species, a random subsample of 50 individuals was measured for total length.

Hydrographic data, including salinity and temperature, were obtained from the USGS Water Quality Sampling program online database (<http://sfbay.wr.usgs.gov/access/wqdata/>). The monthly macrozooplankton-micronekton sampling schedule was set to coincide as closely as possible with the USGS cruises, although in some cases there was a lag of several days.

DATA REDUCTION AND STATISTICAL ANALYSES

To identify temporal and spatial variations in community composition, we used the indirect eigenvector ordination Correspondence Analysis

(CA). CA uses a reciprocal averaging algorithm to generate both species and sample scores that effectively display primary environmental gradients within the community (Gauch 1982). For multivariate analyses, we used the computer software PC-ORD version 4.27 (McCune and Mefford 1999). Correlation analysis of environmental variables and axis scores was applied to aid in the interpretation of sample and species distribution along the two major axes of the CA, including temperature, salinity, station distance from the Golden Gate, and a seasonal metric representing the wet and cold versus dry and warm seasons. This latter metric was calculated using the formula: $\sin(360/365 \times \text{Julian day})$, where we set day 0 as November 1, the first day of the wet season. The equation assigned each Julian day a value between 1.00 to –1.00 according to the position on the sin wave (e.g., maximum wetness and coldness [1.00] on February 1 and maximum dryness and warmth [–1.00] on August 1).

Results

MACROZOOPLANKTON AND MICRONEKTON COMMUNITY COMPOSITION AND ABUNDANCE

A total of 267,996 individuals comprising 69 taxa of macrozooplankton and micronekton were collected in 214 tows between September 1997 and December 2000. The 11 most abundant species accounted for 98% of the total catch, and consisted of 4 fish and 7 invertebrate taxa (Table 1). The top 4 species made up 90% of the catch, including the ctenophore *Pleurobrachia bachei*, *Engraulis mordax* (northern anchovy), the valviferon isopod *Synidotea laticauda*, and *S. thaleichthys*. Of the most abundant species, the only year-round resident is the introduced Caridean shrimp, *Palaemon macrodactylus*. The other ten species are seasonal residents (*C. franciscorum*, *C. nigricauda*, *E. mordax*, *S. thaleichthys*, *Porichthys notatus* [plainfin midshipman], *Clupea pallasii* [Pacific herring], *P. bachei*, and *Polyorchis* spp.) or information on their life histories is incomplete (*Neomysis kadiakensis* and *S. laticauda*).

Densities of total macrozooplankton and micronekton ranged from near zero to a maximum of 1,759 individuals 1,000 m⁻³, and exhibited marked spatial and seasonal variability. All three bays most often exhibited the highest abundances in summertime, with a second peak in late fall, most notably in South Bay (Fig. 2). Minima in abundance occurred mostly in the spring (February, March, and April), except for South Bay. Abundances in North Bay, particularly in 1998, remained high from May to August and then declined in the fall months with a small spike in winter. Central Bay showed lowest overall abundances with small peaks in May and June and during the winter, but mark-

TABLE 1. Mean length and standard error (in parentheses) of macrozooplankton and micronekton identified during the study period, ranked in terms of total numbers. n = number measured, total number = number collected. Taxa listed without a mean length were damaged or only one specimen was captured. *Taxon that are (≤ 10 specimens) are listed in the footnote.

Taxon	Common Name	Mean Length (mm)	n	Total Number
<i>Pleurobrachia bachei</i>	Ctenophore	8 (0.07)	1,193	92,190
<i>Engraulis mordax</i>	Northern anchovy	60 (0.24)	8,953	57,676
<i>Synidotea laticauda</i>	Isopod	15 (0.04)	5,103	54,351
<i>Crangon franciscorum</i>	Bay shrimp	44 (0.13)	6,028	32,906
<i>Spirinchus thaleichthys</i>	Longfin smelt	46 (0.28)	2,352	10,631
<i>Crangon nigricauda</i>	Blacktail shrimp	28 (0.16)	2,614	4,915
<i>Polyorchis</i> spp.	Medusae	16 (0.23)	798	3,246
<i>Palaemon macrodactylus</i>	Pile shrimp	30 (0.16)	1,323	3,217
<i>Porichthys notatus</i>	Plainfin midshipmen	40 (0.74)	1,461	1,958
<i>Clupea pallasii</i>	Pacific herring	51 (0.70)	660	1,421
<i>Neomysis kadiakensis</i>	Mysid	17 (0.10)	1,121	1,358
<i>Lepidogobius lepidus</i>	Bay goby	36 (0.47)	465	506
<i>Alienacanthomysis macropsis</i>	Mysid	13 (0.05)	378	482
<i>Crangon nigromaculata</i>	Blackspotted shrimp	31 (0.67)	389	466
<i>Sardinops sagax</i>	Pacific sardine	69 (0.84)	326	462
<i>Heptacarpus stimpsoni</i>	Stimpson's shrimp	19 (0.22)	289	334
<i>Spirinchus starksi</i>	Night smelt	55 (0.77)	310	310
<i>Atherinops affinis</i>	Topsmelt	65 (1.33)	199	226
<i>Parophrys vetulus</i>	English sole	34 (2.05)	207	207
(Fam.) <i>Nereididae</i>	Polychaete	33 (5.29)	31	163
<i>Gnorimosphaeroma oregonensi</i>	Isopod	8 (0.09)	94	102
<i>Aurelia</i> sp.	Medusae	215 (10.52)	43	97
Unknown mysid	Mysid	11 (0.18)	64	72
<i>Genyonemus lineatus</i>	White croaker	83 (8.66)	65	67
<i>Tridentiger trignocephalus</i>	Chameleon goby	35 (1.24)	23	58
<i>Citharichthys stigmaeus</i>	Speckled sandab	28 (0.92)	52	55
<i>Acanthomysis bowmani</i>	Mysid	11 (0.28)	45	52
<i>Eutonina indicans</i>	Medusae	19 (0.81)	22	36
<i>Callianassa</i> sp.	Ghost shrimp	35 (2.15)	26	32
<i>Alosa sapidissima</i>	American shad	74 (2.70)	30	31
<i>Atherinopsis californiensis</i>	Jacksmelt	77 (11.07)	31	31
<i>Leptocottus armatus</i>	Pacific staghorn sculpin	71 (6.91)	28	29
Unknown polychaete	Polychaeta			24
<i>Decapod megalops</i>	Megalopae			24
<i>Acanthogobius flavimanus</i>	Yellowfin goby	83 (5.01)	16	21
<i>Lepidopsetta bilineata</i>	Rock sole	27 (2.21)	17	21
<i>Aequorea</i> spp.	Medusae			19
<i>Oncorhynchus</i> spp.	Salmon spp.	64 (9.54)	18	18
<i>Syngnathus leptorhynchus</i>	Bay pipefish	130 (13.65)	15	17
<i>Lampetra ayresi</i>	River lamprey	150 (7.22)	15	15
<i>Acanthomysis aspera</i>	Mysid	11 (0.59)	8	14
<i>Symphurus atricaudus</i>	California tonguefish	62 (5.65)	13	13
<i>Dorosoma petenense</i>	Threadfin shad	94 (3.44)	12	12
	Total specimens		267,996	

* *Morone saxatilis*, *Cymatogaster aggregate*, (O.) *Opisthobranchia*, *Isopsetta isolepis*, *Leuresthes tenuis*, *Ilypnus gilberti*, *Lampetra tridentate*, *Capprellia* spp., *Liparis pulchellus*, *Sphaeroma pentodon*, *Clevelandia ios*, *Chrysaora fuscescens*, (Fam.) *Myliobatidae*, *Hippoglossus stenolepis*, *Citharichthys sordidas*, *Foersteria purpurea*, *Phanerodon furcatus*, *Sagitta* sp., *Gasterosteus aculeatus*, *Hippoglossina stomata*, *Icelinus cavifrons*, *Microgadus proximus*, *Sebastes pinneger*, *Platichthys stellatus*, *Ammodytes hexapterus*, and *Thysanoessa spinifera*.

edly lower abundances during the spring and fall. Peak abundances in South Bay usually occurred in late summer (July and August), declined in September, then peaked again in December, and minimum densities consistently occurred in early summer (May and June).

HYDROGRAPHY

The hydrography of the SFE reflects the seasonality of precipitation and runoff. Increased flows

from winter storms approaching the Pacific Ocean begin in early November, and peak flows in February and March often reflect the snowmelt from local mountain ranges. The 6-mo wet season typically ends by April, followed by 6 mo of little to no precipitation and reduced freshwater input (e.g., delta input; Fig. 3). In 1998, a strong El Niño year, springtime flows were the highest recorded during this study ($9,000 \text{ m}^3 \text{ s}^{-1}$) and appreciable flows continued through June.

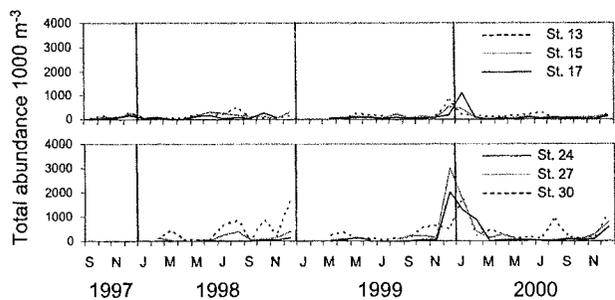


Fig. 2. Abundance of macrozooplankton and micronekton in the San Francisco Estuary, 1997–2000. No data were collected in South Bay prior to December 1997 as indicated by an asterisk. Data points with numbers refer to stations not sampled during cruise.

The seasonal variation in the magnitude and duration of freshwater flows directly effected the salinity and temperature gradients within the SFE. Mean water column salinity ranged from 4 to 32 psu, with minima occurring in February and March and maxima occurring in October (Fig. 4). Regional variation was less for salinity than for temperature, but still striking, with Central Bay stations generally more saline and North Bay stations less saline. Variation in mean water column temperature for all six stations ranged from 10°C to 22°C and followed a seasonal pattern with maxima in August and minima in March. Low temperatures persisted from January to April, followed by a rapid increase during May and June, with temperatures remaining high through October and then falling sharply in November and December. Regional variation in temperature was also marked, with South Bay being notably warmer, particularly during summer, and Central Bay stations being the coldest.

ORDINATION ANALYSIS

Reciprocal averaging (RA) of log-transformed species abundance data indicated that distance from the Golden Gate and seasonality (winter and

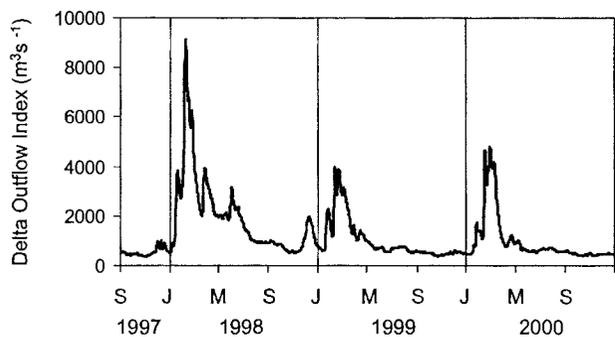


Fig. 3. Delta outflow index from September 1, 1997 to December 31, 2000. Data from (<http://www.iep.ca.gov/dayflow/index.html>).

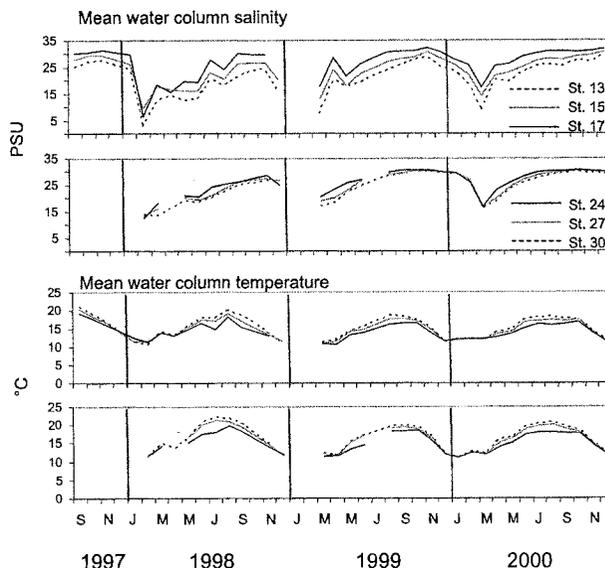


Fig. 4. Mean water column salinity and temperature for San Francisco Estuary, 1997–2000.

spring versus summer and fall) can account for variation in the abundance of macrozooplankton and micronekton in the SFE. RA scores along axis one show a clear separation between the wet season (November 1–April 30) and dry season (May 1–October 31; Fig. 5), and were significantly correlated with the sin function metric (seasonality), temperature, and distance from the Golden Gate (Table 2). Axis two scores were significantly correlated with station distance from the Golden Gate,

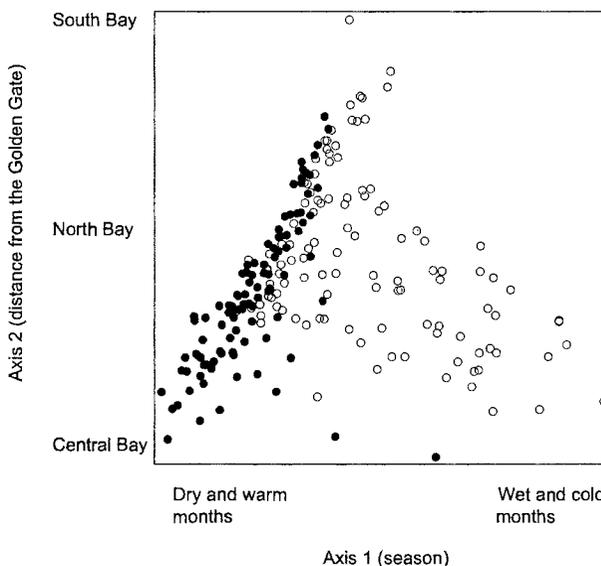


Fig. 5. Reciprocal averaging ordination of the 214 samples collected during this study. Closed points represent samples collected during May 1 to October 31, and open points represent samples collected during November 1 to April 30.

TABLE 2. Correlation matrix comparing environmental variables and reciprocal averaging scores of axis one and axis two. R values are shown with significant correlations denoted with asterisks (* $p < 0.05$, ** $p < 0.01$).

	RA Scores		Distance	Seasonality	Salinity
	Axis One	Axis Two			
Temperature	-0.546**	0.047	-0.155*	-0.869**	0.296**
Salinity	-0.067	-0.387**	-0.148*	-0.316**	
Seasonality	0.688**	0.198**	-0.001		
Distance	-0.156**	-0.435**			

salinity, and seasonality. Samples from Station 30 in South Bay (located the greatest distance from the Golden Gate, 30 km) scored the highest on axis two, and samples collected at station 17 (the closest station to the Golden Gate, 8 km) had the lowest axis two score (Fig. 6).

Ordination of species scores (Fig. 7) illustrated the same environmental gradients by grouping taxa with similar seasonal abundance and regional distribution patterns. Species that scored high on axis one were more abundant during the wet season. Species with high scores on axis two were more abundant at stations in South Bay, and those with low axis two scores were most abundant in Central Bay. The coefficient of determination of the correlations between ordination distances in the original n -dimensional space was 0.335 for the first axis and 0.205 for the second axis, accounting for a cumulative 54% of the variance.

SPATIAL AND TEMPORAL PATTERNS OF INDIVIDUAL TAXA

C. pallasi abundances (Fig. 8) consistently peaked in May or June, then rapidly declined and remained low (< 1 individual 1000 m^{-3}) during Au-

gust to April in 1999 and 2000, but abundances in 1998 were extremely low throughout the year. *C. pallasi* were captured primarily in North Bay (stations 13 and 15) and were largely absent from South Bay (stations 27 and 30). In June 2000, the range extended further south into Central Bay, with large catches at station 24.

The seasonal abundance pattern of *S. thaleichthys* was similar to *C. pallasi*, with a large peak in June and a second peak in August or September, except in 2000 when the second peak was absent (Fig. 8). Abundance declined less rapidly, with minima occurring for 6 mo from October to April. *S. thaleichthys* was narrowly distributed within the lower SFE and was almost exclusively captured in North Bay at stations 13, 15, and 17.

P. notatus had a single annual peak of abundance in September or October and was rarely caught from December to July (Fig. 8). In August, densities increased, with large catches in September, October, and November. The highest densities were recorded in Central Bay at stations 17 and 24, and the lowest at stations 13, 27, and 30.

Densities of *C. franciscorum* were low from September to April, then increased sharply in May and remained high through August, sometimes with a

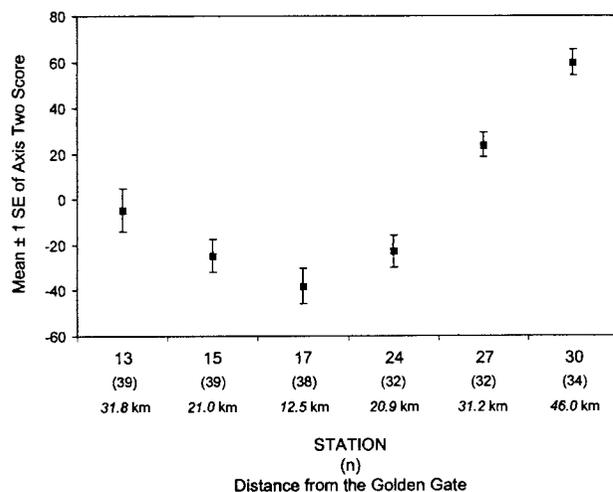


Fig. 6. Mean (\pm SE) score of axis two ordinations for each sampling station. The number in parentheses (n) below each station number is the sample size. The number in italics is the distance of that station from the Golden Gate.

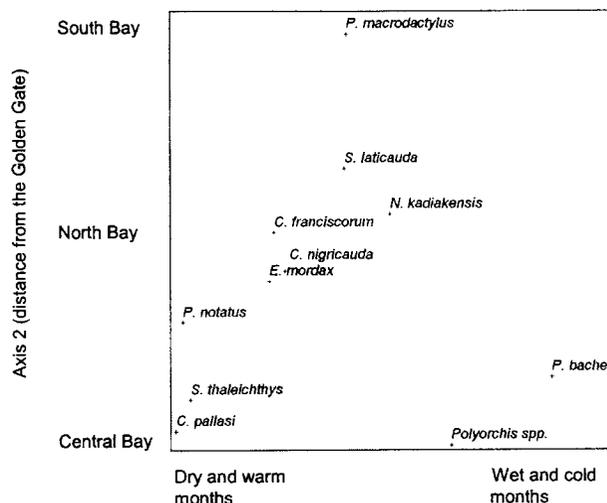


Fig. 7. Reciprocal averaging ordination of the eleven most abundant macrozooplankton and micronekton.

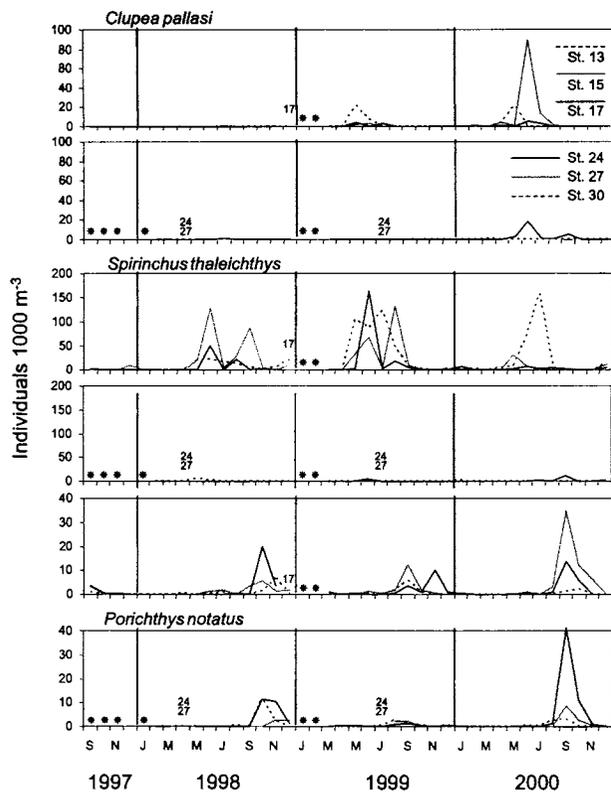


Fig. 8. Abundance of *Clupea pallasii*, *Spirinchus thaleichthys*, and *Porichthys notatus* in San Francisco Estuary, 1997–2000.

smaller peak in December (Fig. 9). The greatest densities occurred at stations 13 and 30, and were consistently very low in Central Bay, except in 1998 when large catches were recorded at all stations.

E. mordax was abundant throughout the study, with large catches at all six stations (Fig. 9). There were two periods of maximum abundance, March to May and August to October, with lower abundances recorded in June and July and also in January and February. *E. mordax* was most abundant in North Bay (station 15) and South Bay (stations 27 and 30). The lowest abundances generally occurred at stations 13 and 24.

The seasonal pattern of abundance of *C. nigricauda* also had two peaks, May to July and October to December (Fig. 9). Seasonal minima generally occurred in August and September and again in March and April. *C. nigricauda* were most common in the southern reaches of North Bay (station 15), often extending into Central Bay (station 17). In 2000, large numbers appeared in March and April in South Bay (station 30), and in December densities increased sharply at all stations except station 24.

P. macrodactylus showed peak abundances twice a year (i.e., an early peak in February and March and a lesser peak in July and August). Season lows

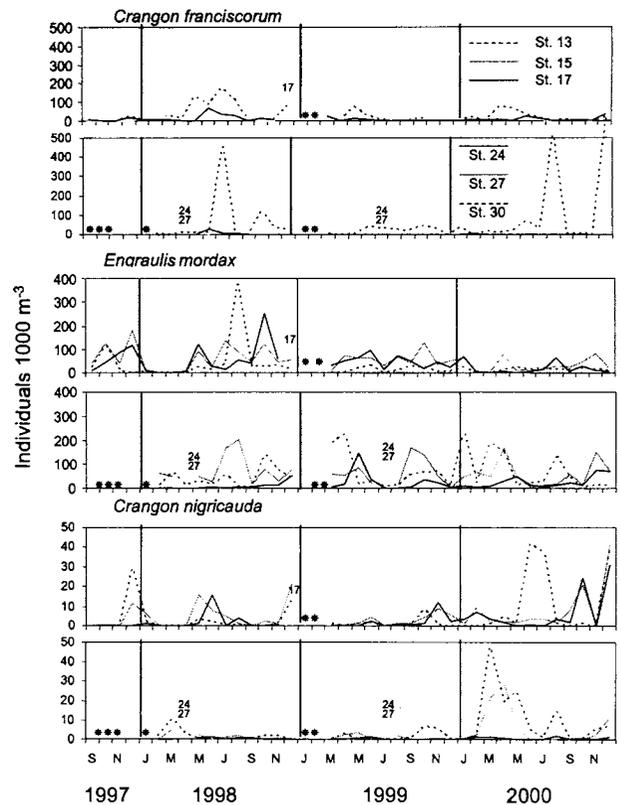


Fig. 9. Abundance of *Crangon franciscorum*, *Engraulis mordax*, and *Crangon nigricauda* in San Francisco Estuary, 1997–2000.

occurred in May and June and again in September to December (Fig. 10). Most individuals were caught in South Bay (station 30) and were largely absent in Central Bay. In 1998 large numbers occurred at stations 13, 15, and 17 in February, March, and April. In 1999, no station recorded catches greater than 5 individuals $1,000\text{ m}^{-3}$ until October.

S. laticauda was very abundant from October to January, reaching densities of 1,500 individuals $1,000\text{ m}^{-3}$ (Fig. 10). In March, catches declined sharply and remained low through July, increased slowly in August and September, and peaked in December or January. *S. laticauda* were confined almost entirely to South Bay at station 30, with small densities sampled at station 13 and 27 in December.

The mysid, *N. kadiakensis*, was most abundant during January to April and was rarely caught between June and November (Fig. 10). During the spring peak, individuals appeared at all stations except station 30; in 1998 individuals were present in all three bays, including station 30.

P. bachei was only abundant in the winter (December and January) and was absent the remainder of the year (Fig. 11). The largest catches of *P.*

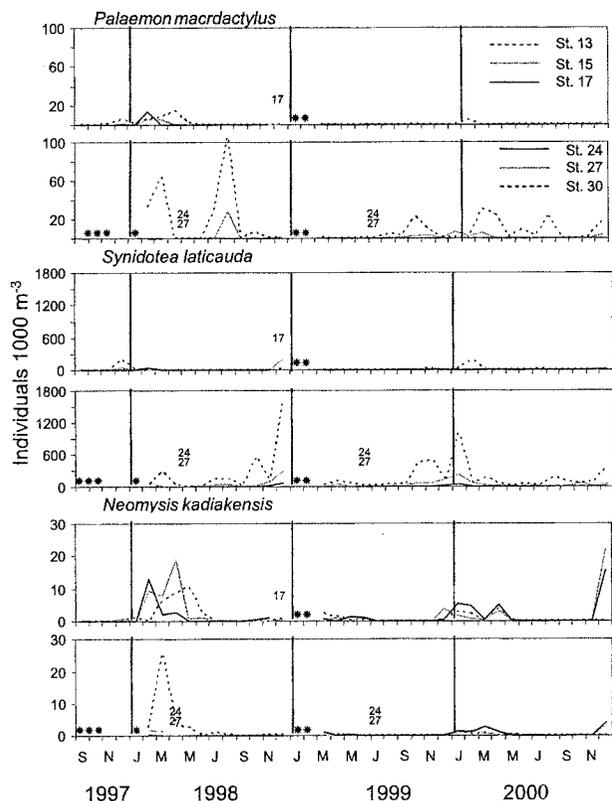


Fig. 10. Abundance of *Palaemon macrodactylus*, *Synidotea laticauda*, and *Neomysis kadiakensis* in San Francisco Estuary, 1997–2000.

bachei were captured in the winter of 1999–2000, where abundances exceeded 1,700 individuals $1,000\text{ m}^{-3}$. During this peak, large numbers were recorded at all six stations, with the largest catches occurring at stations 24 and 27.

The hydrozoan jellyfish, *Polyorchis* spp., was abundant only during November and December although largely absent during the winter of 1998–1999. They most commonly occurred in Central Bay (station 17), but on one occasion (November–December 1999) reached maximum densities (> 70 individuals $1,000\text{ m}^{-3}$) in North Bay (station 13 and 15; Fig. 11).

Discussion

The community composition of macrozooplankton and micronekton in the lower SFE is dominated by 4 fish and 7 invertebrate species. All 4 fish species as well as 3 Caridean shrimp have been identified as major constituents of the adult fish and invertebrate communities in SFE, as determined by other midwater trawl sampling (Aplin 1967; Armor and Herrgesell 1985; Moyle et al. 1986; NOAA 1990; Baxter et al. 1999). The two gelatinous species, *P. bachei* and *Polyorchis* spp., re-

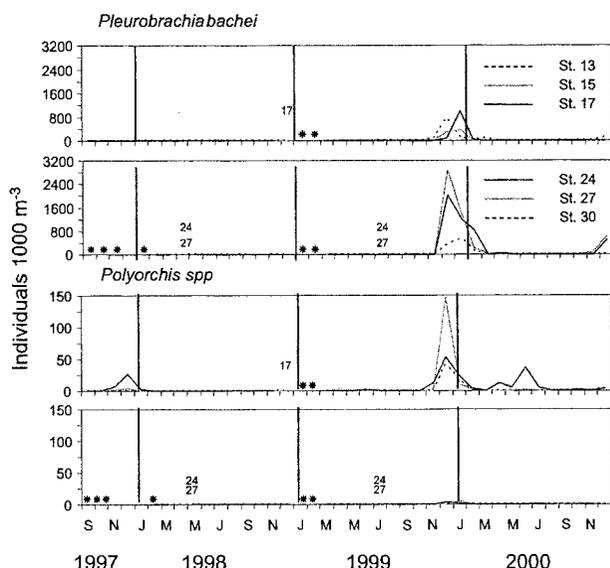


Fig. 11. Abundance of *Pleurobrachia bachei* and *Polyorchis* spp. in San Francisco Estuary, 1997–2000.

main understudied within northern California estuaries, although they have been the focus of several studies in southern California (e.g., La Jolla Bight and Newport Bay, see Hirota 1974 and Cronk 1982). The mysid *N. kadiakensis* and the isopod *S. laticauda* are known to occur in SFE, but have not been quantitatively studied (Menziés and Miller 1972; Orsi and Knutson 1979; but see Dean et al. 2004).

POPULATION ANALYSES OF DOMINANT TAXA

Estuaries tend to be dominated by relatively few species, often categorized by their seasonal occurrence and dependence on the estuarine ecosystem (e.g., transients or residents; Holt and Strawn 1983; Musick and Colvocoresses 1985; Felley 1987; Keller et al. 1999; Kirby-Smith et al. 2001). This is apparently also true for the SFE.

Summer peaks of *S. thaleichthys* and *C. pallasii* in May and June were most likely the result of young of the year produced from spawning in winter (Armor and Herrgesell 1985). The highest densities of age-0 *C. pallasii* and *S. thaleichthys* occur in May, often in the North and Central Bays (Baxter et al. 1999). These two taxa showed very similar patterns of temporal and spatial variability. Large catches of small juveniles of *P. notatus* were recorded in September and October following their spawning in June and July (Watson 1996; Baxter et al. 1999). For each of these 3 species, the lower SFE is used as a spawning ground, where eggs are deposited on submerged substratum, and again later as a nursery for rearing larvae and juveniles. The adults do not remain within the bay, exiting shortly after

laying their eggs (Armor and Herrgesell 1985). The populations of adult *C. pallasii* (pelagic) and *P. notatus* (demersal) are both considered marine, spending their adult lives in the coastal ocean (Arora 1948). The *S. thaleichthys* is classified as an anadromous species, spawning in freshwater or slightly brackish water, and then emigrating to neritic environments as they mature (Baxter et al. 1999).

The two crangonid shrimp species, *C. franciscorum* and *C. nigricauda*, also use the estuary to spawn during longer reproductive seasons (often 5–6 mo), with gravid females present year-round (Hatfield 1985). Most crangonid shrimp larvae hatch in early spring in the saline reaches of Central Bay and adjacent coastal waters, then migrate up the estuary as post-larvae and use the shallows of North and South Bays as early juveniles. As they mature, the larger juveniles migrate into the channels, returning to the ocean as adults (Israel 1936; Wahle 1982; Baxter et al. 1999). The short lifespan and dependence on the SFE help explain the broad distribution within all subembayments and occurrence throughout the year.

E. mordax, like the *Crangon* spp., was broadly distributed within the lower SFE and common in all months. The coastal population, which extends from Vancouver, British Columbia, to central California (McHugh 1951), is very common in bays and estuaries, using inshore habitats during the two spawning periods, February to April and July to September (McGowan 1986; Wang 1986). Baxter et al. (1999) observed broad distributions and high abundances of *E. mordax* in the lower SFE. The long spawning season and close proximity of the lower SFE to the coastal ocean help explain the dominance of *E. mordax* in our catches.

There are no quantitative studies on the ecology or population biology of *S. laticauda* within SFE or adjacent estuaries (Rafi and Laubitz 1990); it has been suggested that this isopod is restricted to the warmer, less saline reaches of the SFE (Menzies and Miller 1972). Our data show the distribution of *S. laticauda* to be centered in South Bay, with a small peak in North Bay during the winter months. Except for this smaller, secondary peak in North Bay, our data are not consistent with the physiochemical boundaries described by Menzies and Miller (1972). The mysid *N. kadiakensis* was distributed in North and Central Bays during the peak of the wet season, January to April, and were near their maximum length (Mauchline 1980). Orsi and Knutson (1979) determined that the seasonal abundance patterns of the mysid *Neomysis mercedis*, a common mysid found in and near the low-salinity zone of the estuary, were the direct result of reproductive events. Carlson and Matern (2000) con-

cluded that *N. kadiakensis* showed peak abundances in February and March in Suisun Bay. Orsi and Knutson (1979) rarely found other species of mysids in North, Central, or South Bays, and *N. kadiakensis* also dominates the mysid community in the tidal marshes of China Camp in North Bay (Dean et al. 2004).

The introduced Caridean shrimp *P. macrodactylus* is the only shrimp species whose life cycle is thought to be completed entirely within the SFE. Although it follows a similar life history pattern to the previously discussed two crangonid species, adult *P. macrodactylus* do not migrate out of the estuary (Siegfried 1980). Recruitment of new individuals spawned in winter is the likely source of peak abundances in spring. *P. macrodactylus* exhibited a lower tolerance to increased salinities than either *Crangon* spp. and was rarely caught in Central Bay. Most individuals were captured in South Bay and a few were captured in North Bay (station 13). This distribution is consistent with Baxter et al. (1999), who reported large catches in Suisun Bay and South Bay. In February 1998, large flooding probably displaced the population west into North Bay. It is probable that we undersampled the northern SFE population, which is often centered further upstream than our sampling, e.g., within Suisun Bay and the west Delta (Baxter et al. 1999).

The two gelatinous species, *P. bachei* and *Polyorchis* spp., showed very strong seasonal occurrence patterns, being captured exclusively in the late fall and winter months, during periods of high salinity, and then disappearing by early spring. Both species have been identified as conspicuous members of the marine zooplankton community and have extensive geographic ranges along the neritic eastern Pacific Coast (Hirota 1974; Arai and Brinckmann-Voss 1980). The ctenophore *P. bachei* grows within specific temperature limits and can position itself (via vertical migration) within optimal temperatures; lateral transport is probably the result of local oceanic and wind driven currents and tidal forcing, which advect organisms from coastal to estuarine habitats (Hirota 1974; Cronk 1982).

COMMUNITY COMPOSITION

Four groups of species were identified, based on similar patterns of distribution and abundance: organisms spawned from common members of neritic assemblages that use primarily North Bay and that are abundant during the dry season (*C. pallasii*, *S. thaleichthys*, *P. notatus*); estuarine-dependent organisms with broad distributions in the estuary and year-round occurrence (*C. franciscorum*, *C. nigricauda*, *E. mordax*); resident species remaining within the estuary and occurring most commonly in South Bay during the wet season (*P. macrodactylus*,

S. laticauda, *N. kadiakensis*); and two gelatinous species occurring in all three bays, with a single peak in abundance in December and January in North and South Bays (*P. bachei*, *Polyorchis* spp.).

We observed the three neritic fish species, *C. pallasii*, *S. thaleichthys*, and *P. notatus*, using the lower SFE as a nursery and relatively quickly emigrating back to the Pacific Ocean. Felley (1987) determined that the distribution of estuarine forms in a Louisiana estuary was driven by their life history patterns, with many species appearing seasonally for only short periods of time. In southern California, Allen (1982) found strong correlations of reproductive adult fish with temperature and abundance, suggesting they were seeking preferable spawning habitat (see also Horn and Allen 1985; Desmond et al. 2002). Weinstein (1985) also concluded that transient species recruited from the ocean were primarily using the estuary as a nursery and accounted for > 70% of the total numbers of individuals in Chesapeake Bay.

C. franciscorum, *C. nigricauda*, and *E. mordax* exhibited multiple spawning episodes (based on length frequency data not shown) and were one of the dominant taxa in all three lower SFE sub-bayments (but particularly in North and South Bays) with juvenile and adult individuals abundant year-round.

P. macrodactylus has been classified as a resident species, distributed near the freshwater source entering North Bay (Newman 1963; Sitts and Knight 1979). From its similar distribution and seasonal abundance patterns, and position on axis one, it seems likely that *S. laticauda* should be considered a resident as well. The classification of *N. kadiakensis* remains unclear, given its more ubiquitous distribution within the lower SFE (although our largest catches occurred in North and South Bays).

It seems appropriate to categorize the gelatinous species *P. bachei* and *Polyorchis* spp. as marine, given their common occurrence outside the Golden Gate, although it remains unresolved whether large numbers were advected into the bay by wind or tidally driven currents or if they bloomed within the bay from a resident seed population. The appearance of peak abundances in North and South Bays, but not Central Bay, which is most proximate to the coastal ocean, is particularly noteworthy. Hirota (1974) and Cronk (1982) concluded that individual *P. bachei* captured inshore most likely originated from neritic populations. Both species showed a strong seasonal pattern in the lower SFE, being present in late fall and early winter when bay salinities are near maxima and seaward moving surface currents are at a minimum, supporting the hypothesis that these individuals originated from a neritic source.

HYDROLOGIC EFFECTS ON COMMUNITY COMPOSITION

In most estuarine environments variation in community composition occurs seasonally and can be related to several underlying environmental gradients. Physiochemical parameters (salinity and temperature) are commonly correlated with estuarine species distribution, often defining their geographical boundaries (Saiki 1997). Holt and Strawn (1983) concluded that the seasonal variation in fish assemblages in Trinity Bay, Texas, was driven by changes in temperature; they were able to differentiate cold and warm season assemblages using cluster analyses of community composition data. Desmond et al. (2002) also identified temperature as the underlying environmental gradient that explained the most variation in fish assemblages between estuaries in southern California (see also Horn and Allen 1985). Our ordination analysis of dominant taxa revealed that axis one was significantly correlated with temperature. We interpreted this correlation as a predictor of the community composition of macrozooplankton and micronekton in the lower SFE. Species-specific axis scores (Fig. 7) from *S. thaleichthys*, *C. pallasii*, and *P. notatus* were markedly lower than for other species and represent a separation point between the fishes and invertebrates, suggesting the fishes are more strongly correlated to temperature. This has been suggested to affect the timing of reproductive events of marine species in a European estuary (Drake et al. 2002).

Changes in the composition of macrozooplankton and micronekton were also evident along the axis of the estuary (i.e., distance from the Golden Gate), underscoring the importance of proximity to the coastal ocean. In Pamlico Sound, North Carolina, Ross and Epperly (1985) found that distance from the estuary mouth and salinity were the primary factors determining fish assemblage composition. CA of nekton assemblages of the Calcasieu estuary, Louisiana, revealed three major species groups that were bound by distance from the mouth of the estuary and salinity (Felley 1987). Yoklavich et al. (1991) also recorded a change in the composition of fish species in Elkhorn Slough, California, noting a large decrease in the similarity between stations located near the mouth of the slough and stations upstream.

As a result of the 1997–1998 El Niño, freshwater flow into the SFE increased substantially in February 1998 and remained high for several months, lowering salinities in North and Central Bays to less than 9 psu. The most significant source of freshwater flow into the SFE is through the San Joaquin and Sacramento River system in the northeast. Sev-

eral large creeks in South Bay contribute freshwater as well during strong rain storms. Kimmerer (2002) analyzed a 34-yr (1967–2000) data set and found the abundance of several species of macrozooplankton and micronekton (*C. franciscorum*, *C. pallasi*, and *S. thaleichthys*) to be positively correlated with freshwater flow in the SFE. During the very high flow rates in spring 1998 we observed increases in abundance of several invertebrate species, but a decrease in abundance of fish species. Desmond et al. (2002) suggested that irregular disturbances, such as flooding events, have a beneficial effect on the invertebrate assemblages of three southern California estuaries; they reported large peaks in abundance after such events. Armor and Herrgesell (1985) concluded that large pulses of freshwater into SFE, resulting from major storms, displaced most fish species downstream, perhaps exiting the Golden Gate and moving into the Gulf of the Farallones.

It is also possible that the increased abundance we observed was an in situ response to the stimulation of production of the pelagic food web. During the very high flow period of spring 1998 we saw an increase in abundance of *P. macrodactylus* and *N. kadiakensis*, and in summer 1998 high densities of *C. franciscorum* and *C. nigricauda* extended well into Central Bay. A notable exception to this pattern was *P. bachei* and *Polyorchis* spp.; these gelatinous taxa were less abundant during this high flow period. Bollens et al. (1999) showed a positive response of secondary producers (i.e., copepods and other mesozooplankton) to increased chlorophyll during this period of greater than usual freshwater input and water column stability. We hypothesize that this fuel increased production in the macrozooplankton and micronekton.

We identified 82 taxa of macrozooplankton and micronekton in the SFE, of which 11 accounted for 98% of the total abundance. We observed that the greatest variation in abundance of macrozooplankton and micronekton occurred seasonally, with the highest abundances usually occurring in summer (with a secondary peak sometimes occurring in late fall), and lowest abundances occurring in spring. Correspondence analysis of community composition showed that sample scores of axis one were significantly correlated with a seasonal gradient between the wet season and dry season (and temperature); sample scores of axis two were significantly correlated to distance from the Golden Gate and salinity. We found that much of the variation in distribution, abundance, and composition of macrozooplankton and micronekton in the lower SFE could be explained by distance from the coastal ocean (Golden Gate) and seasonality (winter and spring versus summer and fall).

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