

Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary

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Abstract

In many estuaries, maxima in turbidity and abundance of several common species of zooplankton occur in the low salinity zone (LSZ) in the range of 0.5–6 practical salinity units (psu). Analysis of zooplankton abundance from monitoring in 1972–1987 revealed that historical maxima in abundance of the copepod *Eurytemora affinis* and the mysid *Neomysis mercedis*, and in turbidity as determined from Secchi disk data, were close to the estimated position of 2 psu bottom salinity. The copepod *Sinocalanus doerrii* had a maximum slightly landward of that of *E. affinis*. After 1987 these maxima decreased and shifted to a lower salinity, presumably because of the effects of grazing by the introduced clam *Potamocorbula amurensis*. At the same time, the copepod *Pseudodiaptomus forbesi*, the mysid *Acanthomysis* sp., and amphipods became abundant with peaks at salinity around 0.2–0.5 psu.

Plausible mechanisms for maintenance of these persistent abundance peaks include interactions between variation in flow and abundance, either in the vertical or horizontal plane, or higher net population growth rate in the peaks than seaward of the peaks. In spring of 1994, a dry year, we sampled in and near the LSZ using a Lagrangian sampling scheme to follow selected isohalines while sampling over several complete tidal cycles. Acoustic Doppler current profilers were used to provide detailed velocity distributions to enable us to estimate longitudinal fluxes of organisms. Stratification was weak and gravitational circulation nearly absent in the LSZ. All of the common species of zooplankton migrated vertically in response to the tides, with abundance higher in the water column on the flood than on the ebb. Migration of mysids and amphipods was sufficient to override net seaward flow to produce a net landward flux of organisms. Migration of copepods, however, was insufficient to reverse or even greatly diminish the net seaward flux of organisms, implying alternative mechanisms of position maintenance.

Zooplankton in estuaries are often distributed by species along a salinity gradient (Miller 1983; Laprise and Dodson 1994). In many northern temperate estuaries a group of planktonic species occupies the low salinity zone (LSZ), a region just seaward of the limit of salinity intrusion, commonly the site of an estuarine turbidity maximum (ETM) or entrapment zone (Peterson et al. 1975; Arthur and Ball 1979; Simenstad et al. 1990). This group of species includes the calanoid copepod *Eurytemora affinis* (e.g., Katona 1970; Heinle and Flemer 1975; Bousfield et al. 1975; Miller 1983; Soltanpour and Wellershaus 1984; Orsi and Mecum 1986; Runge and Simard 1990; Simenstad et al. 1990), mysids (Siegfried et al. 1979; Runge and Simard 1990), and fish larvae (Fortier and Leggett 1983; Dauvin and Dodson 1990; Dodson et al. 1989; Jones et al. 1990; Bennett 1997). In

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some estuaries exotic species such as the copepod *Pseudodiaptomus* spp. have become established in the same salinity range (Cordell et al. 1992; Kimmerer and Orsi 1996).

The aggregation of these species at the same salinity region in many estuaries could have several proximate causes. A strong influence of hydrodynamics is suggested by the frequent presence of an ETM close to the maxima of abundance and the location of the maxima near the landward limit of stratification, where physical conditions change from riverine to estuarine. A biological cause of these maxima is suggested by the co-occurrence of several species in the same region and by differences in chemical and biological environment between the ETM and surrounding regions.

An interaction between hydrodynamics and behavior or population dynamics could result in abundance maxima through several mechanisms. These mechanisms can be illustrated by considering the longitudinal transport or flux of planktonic organisms or particles past a point along the estuarine channel. This flux can be described as

$$\text{Flux} = \overline{\langle UCA \rangle} \equiv \overline{\langle \bar{U} \rangle \langle \bar{C} \rangle} + \overline{\langle U' C' \rangle} A \quad (1)$$

where U is velocity along the channel (positive is landward), C is the concentration of particles (or abundance of organisms), and A is cross-sectional area. The overbar indicates averaging over time, and the brackets indicate averaging

Table 1. Summary of mechanisms for maintenance of an abundance or turbidity peak or for reversal of seaward net flux of organisms or particles. Letters in bold are used to refer to these mechanisms in the text.

Basic mode of transport	Tidal (flood/ebb) T , greater concentrations in areas of high velocity on flood over ebb	Tidal (slack water) TS , greater concentration near bottom during landward density current pulses	Residual R , greater concentration where residual currents are landward or internal concentration mechanisms
Horizontal mechanisms H	Concentration elevated through shoal-channel exchanges	Concentration elevated through shoal-channel exchanges, par- ticularly near slack water due to phase differences	Residuals created by (1) interaction of nonlinearities in flow and basin ge- ometry; (2) lateral asymmetry in freshwater input or meteorological forcing; or (3) energy flux diver- gence minimum (Jay et al. 1990)
Vertical mechanisms V	Concentration elevated by: (1) resuspension due to ebb-flood asymmetry in near-bed shear stress, or (2) negatively buoy- ant particles interact with ebb-flood asymmetries in ver- tical mixing	Negatively buoyant particles sink during slack water be- cause vertical mixing is weak, and are transported during pulse	Negatively buoyant particles interact with gravitational circulation
Mechanisms requiring biological behavior B	(1) Vertical migration off the bottom on flood elevates con- centration, or (2) migration higher in water column on flood exposes organisms to higher velocity	Organisms migrate into lower layers when vertical mixing is weak and are transported dur- ing pulse	Organisms adjust buoyancy or vertical swimming speed to remain in layer with landward residual transport in gravitational circulation cell
Net production or loss of particles or mate- rials P	Not applicable	Not applicable	(1) Higher growth or reproductive rate of organisms, or aggregation of par- ticles, in the maximum than else- where, or (2) lower mortality of or- ganisms or disaggregation of particles in the maximum than else- where

over the cross-sectional area. The righthand part of Eq. 1 is a decomposition of U and C into sectionally and time-averaged values (lefthand term) and variations about the averaged values U' and C' (righthand term). Variation in cross-sectional area A with tide is ignored (thereby neglecting terms such as Stokes drift). In this paper we consider temporal fluctuations in U' and C' on time scales from hours to weeks, so more rapid temporal fluctuations are considered dispersive.

Over time scales of several days the tidally averaged net flow in San Francisco Bay can be positive because of spring-neap variations in tidal energy and atmospheric forcing. Nonetheless, over a time scale longer than a few days (\bar{U}) must be negative because of net freshwater flow. If the concentration C is constant or fluctuates randomly, the average value of the righthand term in Eq. 1 will be zero, and the flux of particles will be seaward. To maintain a maximum in concentration at some location in the estuary requires a mechanism for overcoming the net seaward flux caused by the net flow and dispersal down the concentration gradient. Any mechanism that causes the U' and C' to covary positively on the seaward side of the maximum can cause landward transport supporting the maximum.

Numerous mechanisms exist to transport nonliving or planktonic particles against the mean flow to produce maxima (Table 1). These involve three basic modes of transport:

tidal processes in which temporal correlations of U' and C' occur over a substantial part of the tidal cycle; slack-water processes in which U' and C' are spatially correlated during brief periods near slack water; and residual processes in which U' and C' are spatially correlated over long time periods. Mechanisms for each of these modes of transport may occur in either the horizontal or vertical planes or may require biological behavior, which we assume for small organisms is in the vertical direction only. An additional class of mechanisms exists for the formation of maxima, by which the net production of living or nonliving particles exceeds losses to advection and dispersion (Rogers 1940; Ketchum 1954).

We are attempting to resolve these mechanisms with respect to plankton in the northern reach of the San Francisco estuary (Fig. 1) and in this paper focus on vertical and behavioral mechanisms. Before 1988, a persistent ETM co-occurred with high chlorophyll levels and high abundance of *E. affinis* and *Neomysis mercedis*, while the introduced copepod *Sinocalanus doerrii* was very abundant at a slightly lower salinity (Orsi and Mecum 1986). In 1987, the introduced clam *Potamocorbula amurensis* became very abundant in the northern estuary, and by 1988 the abundance maxima of the above zooplankton species had become lower and had shifted landward (Kimmerer and Orsi 1996). In addition, *Pseudodiaptomus forbesi* became abundant in 1988

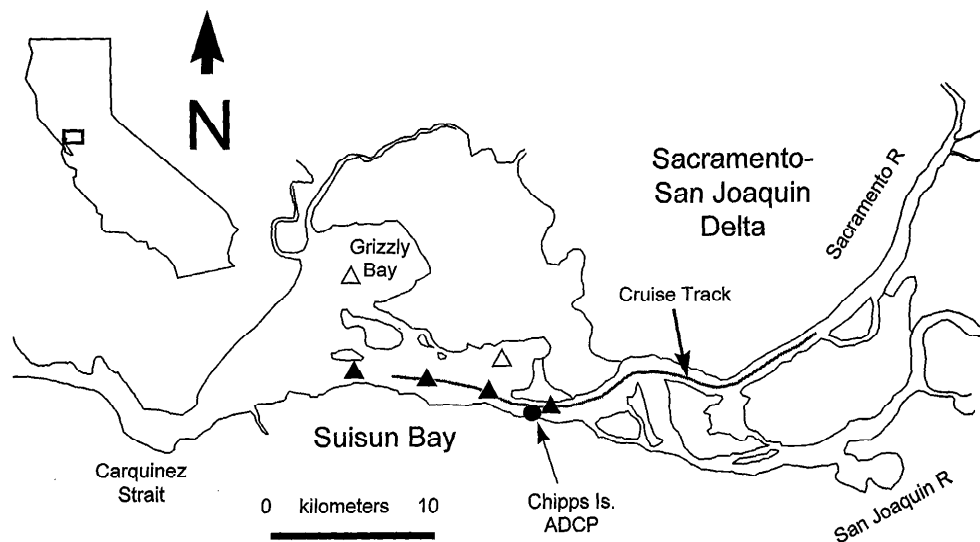


Fig. 1. Map of study area with range of positions on cruises A–C shown as a solid line. Also shown are the location of the acoustic Doppler current profiler at Chipps Island and the stations used for comparing zooplankton abundances over shoals (open triangles) and channels (solid triangles).

and established a maximum at about 1 practical salinity unit (psu) salinity (Kimmerer and Orsi 1996). The introduced mysid *Acanthomysis* sp. also became abundant at about the same salinity in the early 1990s (Orsi and Mecum 1996).

Although the positions and sizes of the maxima and even the identity of the most common species changed in 1987–1988, the question remains: how do these species maintain their maxima? This paper examines the interaction between the physical environment and the vertical movement of zooplankton in the LSZ of the northern San Francisco estuary. We use data gathered during spring 1994 to show that all of the abundant taxonomic groups underwent tidally oriented vertical migration, which for some taxa was sufficient to offset net seaward transport. We use historical data to show that abundance maxima were persistent and more closely tied to the LSZ than to geographic position. We also present evidence on the LSZ as habitat for these organisms and discuss how they are able to maintain that position and what advantages they might obtain. Our study differs from previous such studies in the number of different taxa observed to migrate tidally and in the application of acoustic Doppler current profiler (ADCP) data to estimate longitudinal fluxes.

Methods

Analysis of existing data—Data from zooplankton surveys from 1972 through 1993 obtained from the California Department of Fish and Game (CDFG; J. Orsi and L. Mecum, pers. comm.) were analyzed for the presence and position of maxima in turbidity, chlorophyll (measured since 1976), and abundance of several species of zooplankton. Sampling methods are discussed fully in Orsi and Mecum (1986, 1996), Kimmerer et al. (1994), and Kimmerer and Orsi (1996). Samples used in this analysis were taken with a 154- μm -mesh, 10-cm-diameter Clarke-Bumpus net towed

obliquely from the bottom to the surface. In most years surveys were taken once in March and November and twice in each month from April through October. Data were trimmed to include only months sampled biweekly and only stations in main channels. Surface-specific conductance, measured at each station, was converted to salinity using the equation of state for seawater (UNESCO 1981). The inverse of secchi disk depth was used as a measure of light extinction coefficient; these admittedly crude measurements provide the only long-term historical data on turbidity of the northern estuary.

Zooplankton analyses focused on species known to be abundant at salinities of 0.2–6 psu. The copepod *E. affinis* and the mysid *N. mercedis* were present in all years, and the copepods *S. doerrii* and *P. forbesi* became abundant in 1979 and 1989, respectively. Because the abundance of chlorophyll and all zooplankton species except *P. forbesi* declined sharply in 1988, we analyzed data for all but *P. forbesi* only before 1988. Data from individual surveys were included in the analyses if the data included at least 20 stations in channels (the maximum was 37 but most had 25–30 stations) and the range of salinity covered was at least 0.2–5.6 psu (the median range was 0.07–10.7 psu). This resulted in data from up to 212 surveys for some variables (Table 2).

For each variable y (inverse secchi depth, chlorophyll concentration, and abundance of each zooplankton taxon) in each survey, the position of the peak value of y as distance up the axis of the estuary was determined as follows. First, y was \log_{10} transformed after adding a constant (0 for chlorophyll and inverse secchi depth, 0.1 for mysids, 10 for copepods). This introduces error in some samples because detection limits vary with the abundance of other species in the samples, and occasionally there were anomalous zeros at intermediate stations. Therefore data points for which y was zero were omitted from the initial analysis unless they

Table 2. Frequency of occurrence of peaks in abundance meeting the criteria in the text for each variable and median salinity value at the peaks.

Variable	Number of cases		Percent meeting criteria	Median salinity (psu)
	Total	Meeting criteria		
Turbidity	212	192	91	1.52
Chlorophyll	168	132	79	1.01
<i>E. affinis</i>	212	212	100	1.96
<i>N. mercedis</i>	212	209	99	1.59
<i>S. doerrii</i>	129	118	91	0.21
<i>P. forbesi</i>	72	55	76	0.43

were in the upper or lower 10% of the range of distance, insuring against the procedure failing because of errors introduced by a few, low values at intermediate stations. A robust smoothing technique (the lowess procedure in S-PLUS; Venables and Ripley 1994) was fitted using a span parameter equal to the largest gap in the distance data (median 8 km). These values were interpolated to equally spaced values of distance, then the resulting curve was smoothed using a running median with twicing (Venables and Ripley 1994). Finally, the distance corresponding to the highest peak in the curve was taken as the position of the abundance or concentration peak. Peaks were not included when the coefficient of determination of the final curve, including all data points, was <0.1 . The results of this procedure were compared with peaks detected visually in data for *E. affinis*; the median absolute difference was 1.4 km, and 92% of the differences were less than 5 km, suggesting that the algorithm for peak identification was unbiased.

The same procedure was used to determine the locations of peaks with respect to distance in kilometers up the main channel of the estuary. The location of each peak was then compared to X_2 , the estimated distance up the main channel from the mouth of the estuary to where daily-average bottom salinity is 2 psu (Jassby et al. 1995). The value X_2 was calculated for the median date of each survey by interpolation among continuous monitoring stations or, to fill in missing data, by time-series regression on the log of freshwater flow into the estuary (Jassby et al. 1995). It provides a useful index of the distance of saltwater intrusion into the estuary. In addition to locations of peaks, we determined the locations of various percentiles of the population on each survey in terms of distance up the estuary, as a measure of spread of the population.

We also assessed the potential for shoals to be source regions for zooplankton (as they can be for phytoplankton; Cloern et al. 1983) and determined potential net population growth rates of zooplankton species. Abundance data for *E. affinis* and *N. mercedis* at two shallow stations (3 m mean depth) were compared with data taken from the same surveys at four nearby channel stations (12 m; Fig. 1). The means of data from shallow and deep stations for each survey ($N = 281$, 16 yr) were calculated and the differences were examined by paired Mann-Whitney U -test.

Sampling and analysis in 1994 field study—The sampling program included continuous in situ monitoring of currents using an ADCP at the edge of the main shipping channel at river kilometer 74 (Fig. 1), and three cruises in spring 1994. Cruises of the R/V *San Carlos* occurred on 18–19 April (cruise A, neap tide), 26–27 April (B, spring tide), and 17–18 May (C, neap tide). Sampling was designed to be Lagrangian, with stations identified by salinity rather than geographic location. During each cruise, the vessel cycled for 27–28 h among three channel stations defined by a surface-specific conductance of approximately 1, 3, and 6 mS cm^{-1} (stations 1, 3, and 6, approximately 0.5, 1.6, and 3.3 psu salinity). Each station was visited once per tidal cycle starting at station 6, with the timing set to arrive at station 3 (the LSZ station) near the maximum flood and ebb. Station 3 was also visited as close as possible to slack water on most tides. Median depth during sampling was 12.7 m (range 9–18 m).

The vessel was equipped with a 1,200-kHz broadband ADCP that was used to provide instantaneous velocity profiles. Salinity and temperature were determined by vertical profiles with a Seabird CTD. Samples were taken for macrozooplankton (mysids and amphipods) with 60-cm, 0.5-mm-mesh opening-closing Bongo nets with flow meters, towed near the bottom and at about the middle of the water column; on cruise C only bottom samples were taken. An additional fixed Bongo net was towed 1 m below the surface. Nets were towed for 10 min, then samples were fixed in 5% formaldehyde in surface water. The depth of the deep nets was calculated from the amount of wire out and the wire angle. On cruise B a depth recorder was used to verify the calculated depths that were generally accurate to within 1 m.

Samples were taken for mesozooplankton (all stages of copepods) with a 100-liter min^{-1} submersible pump equipped with a noncollapsible intake hose and discharging into a 30-cm-diameter, 35- μm mesh net. Samples of about 0.6 m^3 were taken at the same depths as net samples and, in 8 of 50 profiles, at intermediate depths. Volume sampled and flow rate were determined using a flow meter calibrated by timing the filling of a bucket. Mesozooplankton samples were preserved in 2–5% formaldehyde.

Pump samples were taken at the same depths for chlorophyll, either filtered whole or size-fractionated using a 10- μm -mesh screen before filtration. Glass-fiber filters (GF/C) were folded, placed in small envelopes, and frozen for transport and storage. Chlorophyll samples were extracted using a mixture of acetone, DMSO (dimethylsulfoxide), and water in a ratio of 9:9:2, and read on a Turner Designs model 10 fluorometer calibrated with pure chlorophyll.

Macrozooplankton samples were subsampled if necessary using a plankton splitter, and mysids (*N. mercedis* and the introduced *Acanthomysis* sp.) and total amphipods were counted under a dissecting microscope. Mesozooplankton samples were subsampled as necessary using a splitter or a piston pipette, and copepods were counted and identified to species and major life stage.

Vertical movement of macrozooplankton was analyzed using abundance in the 1-m depth stratum, which varied strongly with time. This value reflects not only the vertical distribution in the water column but also the movement of

these epibenthic organisms off the bottom. Abundance at 1 m depth was used in exploratory analyses with tidal velocity, day versus night, cruise, and station (nominal specific conductance) as independent variables. The final analysis comprised an analysis of covariance with velocity and day versus night as covariates; none of the interaction terms were significant. Data did not generally meet the assumptions of least-squares modeling because of several apparent outliers, so we used a robust generalized linear model procedure that reduces the influence of outliers (S-PLUS; Venables and Ripley 1994). In all statistical analyses, we examined residuals for violations of assumptions of the models used, including (where appropriate) a normal distribution and a lack of autocorrelation in the residuals.

For mesozooplankton, the mean depth of the center of mass was calculated from the vertical distribution of abundance at each station and expressed as a proportion of the water column depth. Following exploratory analyses, regression models were determined as above with velocity as the independent variable and including day versus night where necessary (*see Results*). Relationships between mean depth and velocity did not appear to vary among stations. *E. affinis* and copepodites of *S. doerrii* were insufficiently abundant during cruise C, and *P. forbesi* during cruise A, to include those data in the analysis. Chlorophyll data (total and $>10 \mu\text{m}$) were analyzed similarly to mesozooplankton.

We estimated the longitudinal fluxes of total macrozooplankton and total copepods for April–June using abundance data and hourly velocity profiles from the fixed ADCP at Chipps Island (Fig. 1). Total abundance was used rather than abundance of individual species to minimize the error in parameter estimates; slopes of relationships to velocity were similar within these major groups, although diel variability differed somewhat among copepod species. First we fit the abundance data to a multiple linear regression model including depth as proportion of the water column, velocity, and for macrozooplankton, day versus night. Because residuals from least-squares regression were nonnormally distributed, the model was fitted using a robust method in the S-PLUS programming environment (generalized linear model with robust fit; Venables and Ripley 1994). This model was then used to calculate predicted abundance values at each depth and time step. The sum of the products of velocity and abundance were used to calculate a flux in organisms $\text{m}^{-2} \text{s}^{-1}$, which is the rate at which organisms pass the sampling point per unit cross-sectional area. ADCP velocity data were extrapolated to the surface (about 1.5 m or three depth bins) using the value in the uppermost 0.5-m-depth bin. Data were extrapolated from the deepest value to zero at the bottom (1.9 m or about four bins) assuming a 1/6-power law.

Results

Historical data—Turbidity, zooplankton abundance, and to some extent chlorophyll were generally at maximum levels at or near 2 psu salinity (Fig. 2). Examples A–E were from a single survey (second survey in July 1987), selected at random from surveys in 1972–1987 in which significant peaks were detected for all variables. Figure 2F, for *P. for-*

besi, was taken at random from surveys in 1989–1993 and is for the first survey in August 1992. Peaks meeting the criteria were detected in 76–100% of the surveys with enough data (Table 2). Peaks in abundance of *P. forbesi* and chlorophyll concentration were found much less frequently than peaks in turbidity or abundance of other taxa, and many of the chlorophyll peaks were at low salinity.

Peak locations in terms of distance up the axis of the estuary were closely correlated with X_2 for most variables (Fig. 3, Table 3). Chlorophyll concentration and abundance of *E. affinis* and *P. forbesi* had regression slopes that differed significantly from 1 (Table 3). The relationship for *P. forbesi* is based on many values at the upper end of the range and few at the low end of the range of X_2 , because drought prevailed for most of the time (1989–1993) when *P. forbesi* was abundant. Peaks for turbidity, *E. affinis*, and *N. mercedis* were nearly always close to X_2 , while those for *S. doerrii* and *P. forbesi* tended to occur further landward, and chlorophyll peaks were scattered (Table 3).

Both *E. affinis* and *N. mercedis* were more abundant at channel than shoal stations on average. Median values for *E. affinis* were 590 and 850 m^{-3} for shallow and deep stations, respectively, and the difference was significant ($P < 0.0001$, $N = 281$, Wilcoxon paired sign-rank test). For *N. mercedis*, medians were also significantly different ($P < 0.0001$) at 2.9 and 14.4 m^{-3} , respectively.

Results of 1994 field studies—ADCP profiles taken from the fixed station during April–June 1994 showed no sign of gravitational circulation, as demonstrated by the continuous seaward direction of tidally filtered velocities in the top and bottom depth bins (Fig. 4; *see also* Monismith et al. 1996). Shipboard ADCP measurements (not shown) showed instantaneous velocities to be unidirectional throughout the water column, even close to slack water.

Chlorophyll concentration and abundance of several zooplankton species declined with increasing salinity (Fig. 5) on the three cruises and in routine monitoring surveys taken over the same time period. The principal exception was *Acanthomysis* sp., which was most abundant at intermediate salinity (Fig. 5F). The distributions of chlorophyll and of species abundant before 1988 (Fig. 5A–C,E) were markedly different in height and location from those observed in earlier years before the spread of *P. amurensis* (Figs. 2, 3).

Egg ratios of copepods and ratios of neonates to total mysids were used as indices of birth rate. Egg ratio of *E. affinis* (Fig. 6A) declined with distance seaward only on cruise C ($P < 0.01$, analysis of variance). Egg ratio of *P. forbesi* (Fig. 6B) increased over time but did not vary significantly among stations ($P > 0.5$, analysis of variance). The ratio of mysids in the 2-mm (smallest) length category to adult mysids did not vary among stations for *N. mercedis* (Fig. 6C, $P = 0.1$, analysis of variance); although this ratio varied among stations for *Acanthomysis* (Fig. 6D, $P < 0.05$), it was not higher in the LSZ than seaward.

All categories of macrozooplankton, including total macrozooplankton, amphipods, and both mysid species, varied positively in abundance at 1 m depth by day versus night and with tidal current velocity (Fig. 7, Table 4). Slopes of the three taxa were essentially identical, although day–night

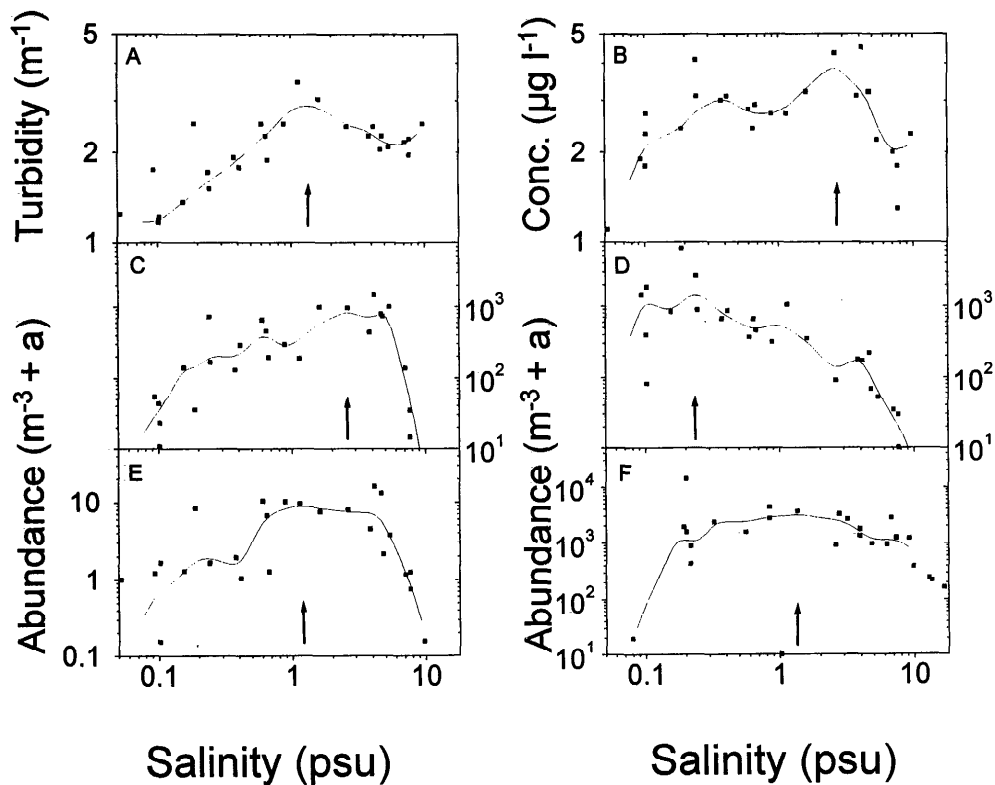


Fig. 2. Relationship to salinity of selected variables from single surveys: A, turbidity (m^{-1}); B, chlorophyll ($\mu\text{g liter}^{-1}$); C, *E. affinis* (m^{-3}); D, *N. mercedis* (m^{-3}); E, *S. doerrii* (m^{-3}); F, *P. forbesi* (m^{-3}). Points are individual data, lines are lowess fits to the data used to determine peaks, and arrows give the positions of the calculated peaks (see Methods).

differences were greater for amphipods than for either of the mysids.

Among the copepods, mean depth of all species varied with tidal velocity with a positive slope, but there were differences among life stages and by day versus night for some (Table 5, Fig. 8). *E. affinis* adults (Fig. 8A) and copepodites (Fig. 8B; cruises A, B only) had significant slopes of mean depth versus tidal velocity only by day; the same was true for *P. forbesi* adults (Fig. 8C). *P. forbesi* copepodites had a significant slope by both day and night (Fig. 8D). Mean depth of *S. doerrii* adults and copepodites varied significantly with tidal velocity both day and night (Fig. 8E,F; cruises A, B only). Variability was considerable in all of these data, but residuals from these regressions were uncorrelated with any of the environmental or other variables available; thus, this variance remains unexplained and may be heavily influenced by patchiness and sampling error.

Mean depth and water-column mean concentration of chlorophyll (Fig. 9) showed no significant variation with tidal velocity, either as total chlorophyll or as chlorophyll larger than $10 \mu\text{m}$ (not shown). The mean depth of chlorophyll concentration was below mid-depth.

A multiple linear regression fit to the abundance of macrozooplankton included tidal velocity averaged over the water column, depth (expressed as a fraction of the water column depth), day versus night, and the interaction between depth and day versus night (Table 6). The correlation of

predicted and observed values was 0.72. The tidally filtered flux of macrozooplankton calculated from this model was positive, i.e., landward (Fig. 10A). The flux calculated assuming a uniform vertical distribution of macrozooplankton was seaward (Fig. 10A).

For copepods the model included station (i.e., nominal salinity), depth, velocity, and the interaction between depth and velocity (Table 7). The correlation of predicted and observed values was 0.74. However, the resulting tidally filtered flux was seaward, and nearly identical to that resulting from a uniform distribution of copepods in the water column (Fig. 10B).

Discussion

Mechanisms for maxima—Abundance maxima of several zooplankton species were consistently located close to or slightly landward of the 2 psu isohaline. Our study examined evidence for each of the mechanisms depicted in Table 1, except for horizontal mechanisms in cell H–R (i.e., row H, column R), for which we have few data. Density pulses that could result in slack-water transport (column TS) were not observed either in the shipboard or shore-based ADCPs. Gravitational circulation was never detected in the residual velocity profiles, and calculations using the ADCP data from the fixed station suggested that the ebb–flood asymmetry in velocity was insufficient to produce landward movement

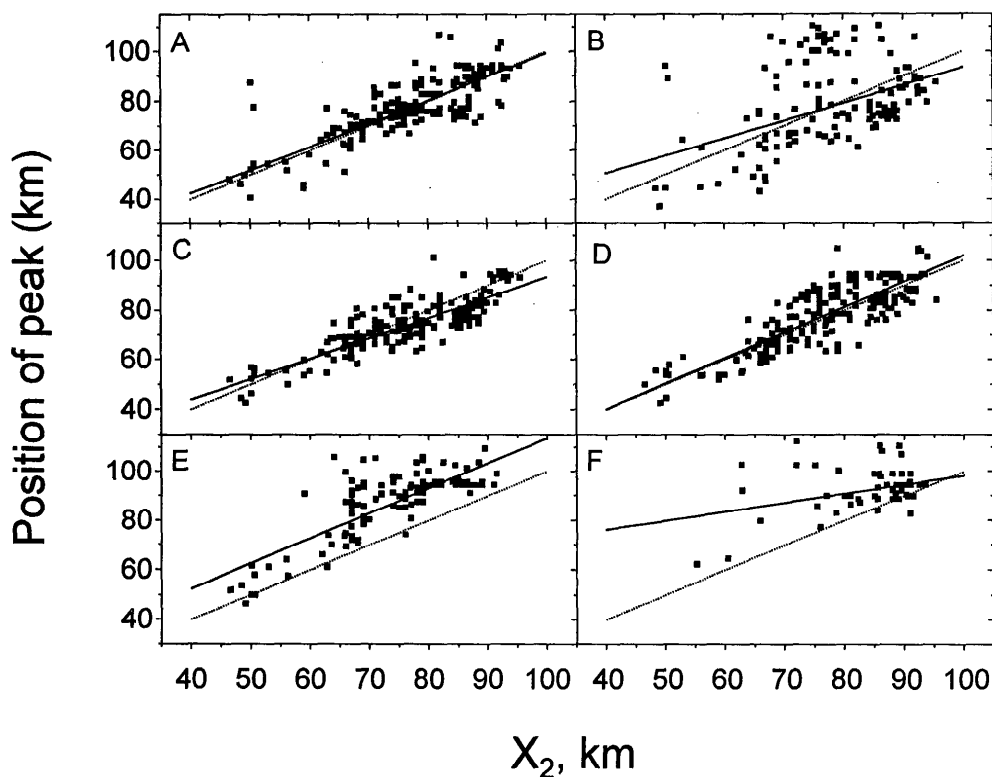


Fig. 3. Position of peaks in river kilometers versus X_2 on date at the midpoint of each survey for A, turbidity; B, chlorophyll; C, *E. affinis*; D, *N. mercedis*; E, *S. doerrii*; F, *P. forbesi*. Solid lines are fitted to the data using generalized linear models with a robust fitting procedure (see Table 3); dashed lines give the 1:1 slope.

even for particles or organisms concentrated near the bottom (mechanisms V–R and B–R). We therefore focus on tidal mechanisms (column T) and net production (P–R).

Peaks in chlorophyll often occurred near 2 psu before 1988. These peaks may have been due in part to exchange between productive shoal regions and adjacent channels (mechanisms H–T or H–R; Cloern et al. 1983). Although the shoals are probably still more productive than the channels, this effect is no longer detectable because of the high grazing losses in Suisun Bay (Alpine and Cloern 1992). The current continuous decline in chlorophyll from freshwater through the LSZ suggests that any mechanism for retention is over-ridden by consumption in and west of Suisun Bay.

Table 3. Robust regression statistics for peak positions (km) versus X_2 and median width of the peaks (distance between location of 5th and 95th percentiles of the raw data).

Variable	<i>N</i>	Slope \pm SE	Intercept \pm SE	<i>r</i>	Median width (km)
Turbidity	192	0.95 \pm 0.04	4.6 \pm 3.3	0.79	24
Chlorophyll	132	0.71 \pm 0.12	22 \pm 9	0.42	25
<i>E. affinis</i>	212	0.83 \pm 0.03	10.6 \pm 2.6	0.84	9
<i>N. mercedis</i>	209	1.03 \pm 0.04	-1.2 \pm 3.3	0.84	11
<i>S. doerrii</i>	118	1.02 \pm 0.07	11.8 \pm 5.0	0.78	15
<i>P. forbesi</i>	55	0.37 \pm 0.12	61 \pm 10	0.39	17

For zooplankton, some of the potential mechanisms listed above can be addressed with existing data. Tidal resuspension (mechanism V–T) is discussed below under mechanism B–T (demersal migration). For the shoals to provide source material to the channels (mechanism H–T or H–R) would

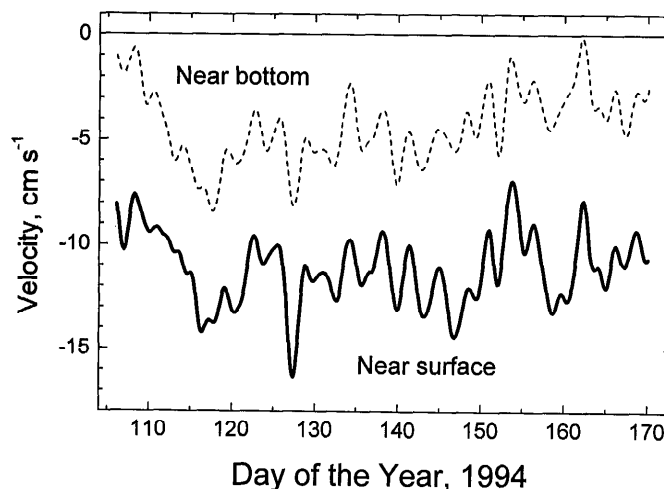


Fig. 4. Tidally filtered (i.e., net or residual) velocities along the axis of the channel at Chipps Island from the fixed acoustic Doppler current profiler for the near-surface (solid) and near-bottom (dashed) depth bins.

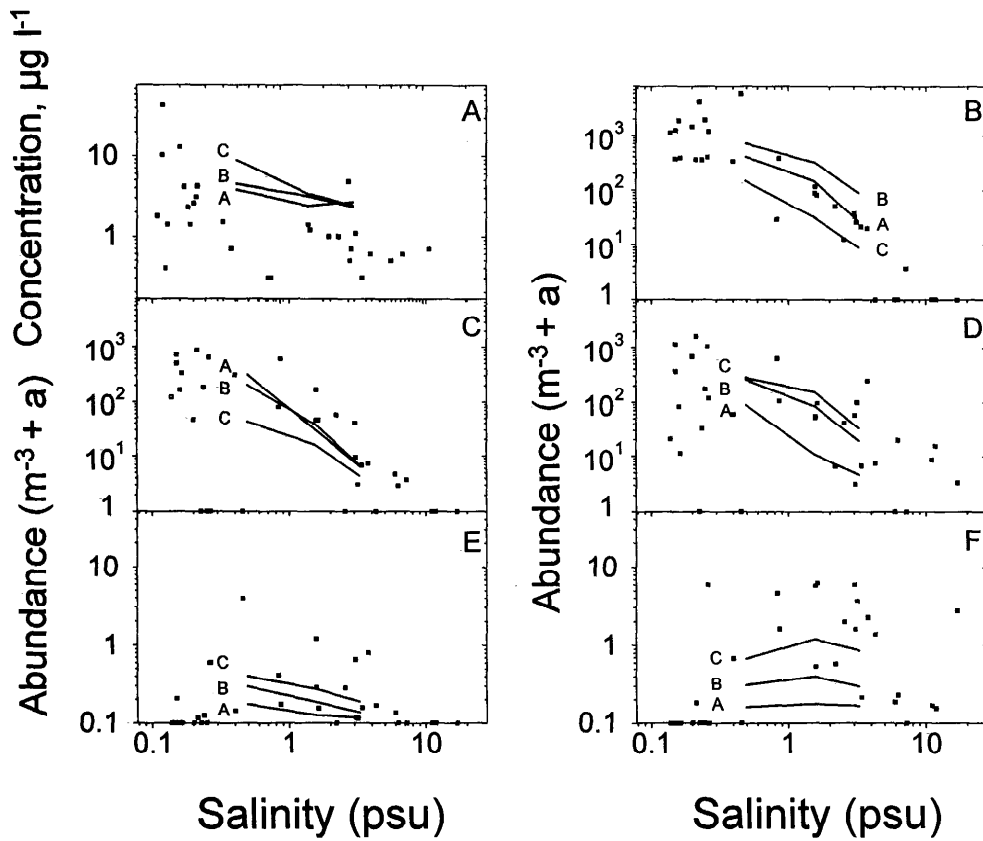


Fig. 5. Chlorophyll concentration and abundance of zooplankton in spring of 1994 versus salinity from routine monitoring surveys (points) and 1994 cruises A–C (lines, with letters identifying cruises). The constant *a* was 10 for copepods and 0.1 for mysids. A, chlorophyll; B, *E. affinis* adults; C, *S. doerrii* adults; D, *P. forbesi* adults; E, *N. mercedis*; F, *Acanthomysis* sp.

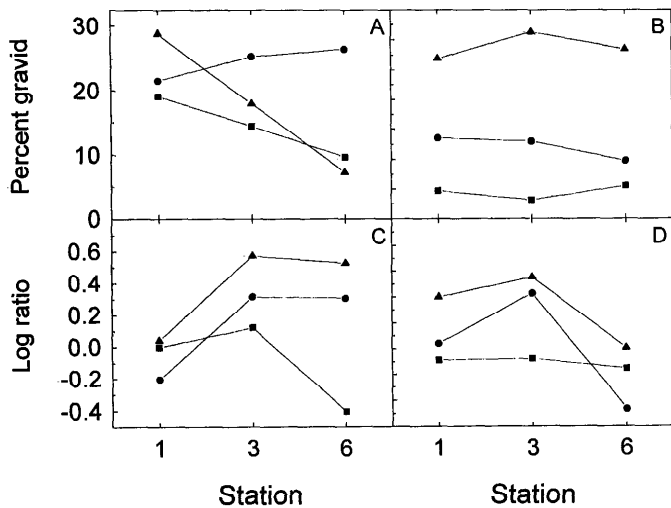


Fig. 6. Population ratios by cruise (symbols connected by lines: ■, cruise A; ●, B; ▲, C) and station. A, B, percentage of female copepods that are gravid; A, *E. affinis*; B, *P. forbesi*; C, D, log of ratio of abundance of 2-mm mysids to adult mysids; C, *N. mercedis*;

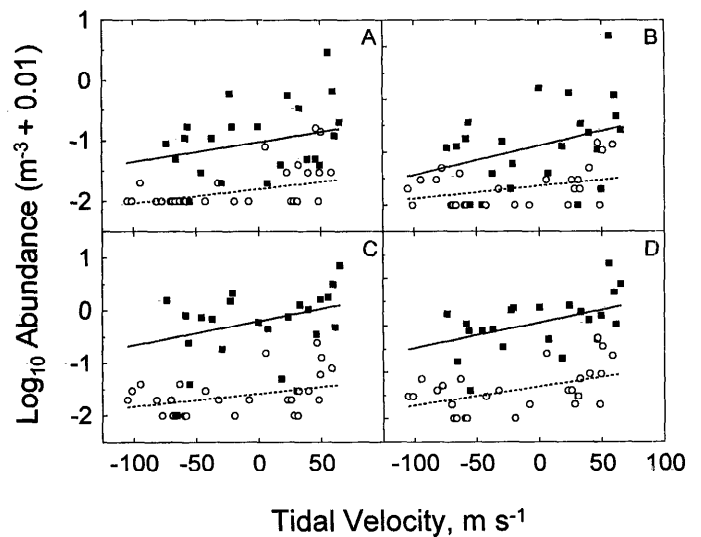


Fig. 7. Abundance of macrozooplankton at 1 m depth by day (open) and night (closed) versus water column mean tidal velocity. A, *N. mercedis*; B, *Acanthomysis* sp.; C, amphipods; D, total zooplankton. Lines are robust regression models; dashed line, day; solid line, night; all regressions were significant (see results of analyses of covariance, Table 4).

Table 4. Regression statistics for robust analyses of covariance of log abundance of macrozooplankton at 1 m depth versus tidal velocity and day versus night. Correlation is between the fitted value and the response variable.

Taxon	Velocity		Day versus night		Correlation
	Value	P	Value	P	
<i>N. mercedis</i>	0.003	0.006	-0.34	<0.0001	0.68
<i>Acanthomysis</i> sp.	0.004	0.010	-0.36	0.0001	0.63
Amphipods	0.003	0.013	-0.68	<0.0001	0.81
Total macrozooplankton	0.0045	0.001	-0.66	<0.0001	0.82

require abundance of zooplankton to be higher on the shoals. This was not the case; both *E. affinis* and *N. mercedis* were generally more abundant at channel than nearby shoal stations.

Higher growth or reproductive rate or lower mortality (mechanism P-R) in the LSZ compared with other areas could produce the observed effect. Elevation of growth or reproductive rates would require a more favorable food environment in the LSZ than elsewhere. Chlorophyll peaks have not been consistently colocated with peaks in zooplankton abundance and often are far removed (Fig. 3), suggesting a decoupling between phytoplankton and zooplankton production. In our 1994 field studies particulate organic matter was elevated, and bacterial production was more associated with particles, in and seaward of the LSZ than landward (Hollibaugh and Wong in press). Thus, the feeding environment for zooplankton may be enhanced in and seaward of the LSZ (Morris et al. 1978; Frenette et al. 1995) even in the absence of substantial elevations in chlorophyll (e.g., Bousfield et al. 1975).

The egg ratios of female copepods do not suggest lower birth rates seaward except for *E. affinis* in cruise C (Fig. 6A). That effect could be due to reduced food supplies caused by grazing by *P. amurensis*, although previous analyses of egg ratios have not shown a decline due to *P. amurensis* or a relationship with chlorophyll or salinity (Kimmerer et al. 1994; Kimmerer and Orsi 1996). Therefore it is unlikely that per-capita birth rates decrease greatly seaward of the LSZ. Furthermore, although chlorophyll levels were typically higher in the LSZ than seaward, at least until 1987

levels were high enough that food limitation of *E. affinis* was rare (Kimmerer et al. 1994).

Abundance of *N. mercedis* appears to be food limited (Orsi and Mecum 1996), which may imply a higher net population growth landward of the LSZ where chlorophyll concentrations were higher. However, ratios of young to total mysids were not greater in or landward of the LSZ than seaward (Fig. 6C,D). Either net population growth rate was not higher landward than seaward, or longitudinal mixing was rapid enough to obscure variation in age structure resulting from higher birth rates landward of the LSZ.

Increased mortality rates seaward of the LSZ could occur due to increased salinity or increased predation. Mortality rates are very difficult to measure in an estuary (Peitsch 1993) and have not been determined in San Francisco Bay. The salinity responses of growth of both *E. affinis* and *N. mercedis* indicate that both species can thrive in salinities well outside the range in which they are most abundant (Heubach 1969; Katona 1970; Roddie et al. 1984). The maximum feeding rate of *E. affinis* occurs at a salinity of 15 psu (Powell and Berry 1990). Furthermore, their responses have different thresholds, with *E. affinis* more tolerant of high salinities than *N. mercedis* (Heubach 1969; Katona 1970; Roddie et al. 1984), yet their peaks in terms of salinity have been close to each other. Thus, mortality due to osmotic stress is an unlikely contributor to the observed patterns.

Higher predation rates seaward relative to the LSZ could be due either to greater abundance of predators or higher per-capita predation rates. Visual predators may be less successful at finding planktonic prey in the LSZ because of the higher turbidity, but we have no data on success rates of visual predators.

Before 1987, predators more abundant seaward of the LSZ included the copepod *Acartia* spp., which can prey on copepod nauplii but is too small to prey on any life stage of *N. mercedis*. The mean abundance of adult *Acartia* was on the order of 500 m⁻³ at a mean salinity of about 6 psu, where the mean abundance of *E. affinis* reached 25% of its peak before 1987. At a clearance rate of *E. affinis* nauplii of 30 ml *Acartia*⁻¹ d⁻¹ (Landry 1978; Lonsdale et al. 1979; Stoecker and Egloff 1987; Kimmerer and McKinnon 1989), the mortality rate on early nauplii would be 1.5% d⁻¹. The generation time of *E. affinis* is about 15–30 d at the temperatures in the bay, of which about 35% is spent as a nau-

Table 5. Mean log abundance for copepods and regression statistics for robust regressions of mean depth of center of mass of copepods versus tidal velocity. Correlation is between the fitted value and the response variable.

Species	Stage	Cruise	Log abundance (mean±95% CL)		Data included	Slope±95% CL	Correlation
			Day	Night			
<i>E. affinis</i>	A	All	2.0±1.2	2.1±1.4	Day	0.0012±0.0004	0.47
<i>E. affinis</i>	C	A, B	2.8±0.9	2.9±0.9	Day	0.0008±0.0003	0.50
<i>S. doerrii</i>	A	A, B	1.5±1.4	1.7±1.4	All	0.0017±0.0004	0.42
<i>S. doerrii</i>	C	A, B	2.0±1.0	2.1±0.9	All	0.0018±0.0003	0.73
<i>P. forbesi</i>	A	B, C	1.8±1.1	2.2±1.2	Day	0.0015±0.0006	0.48
<i>P. forbesi</i>	C	B, C	2.0±1.5	2.1±1.2	All	0.0013±0.0004	0.46

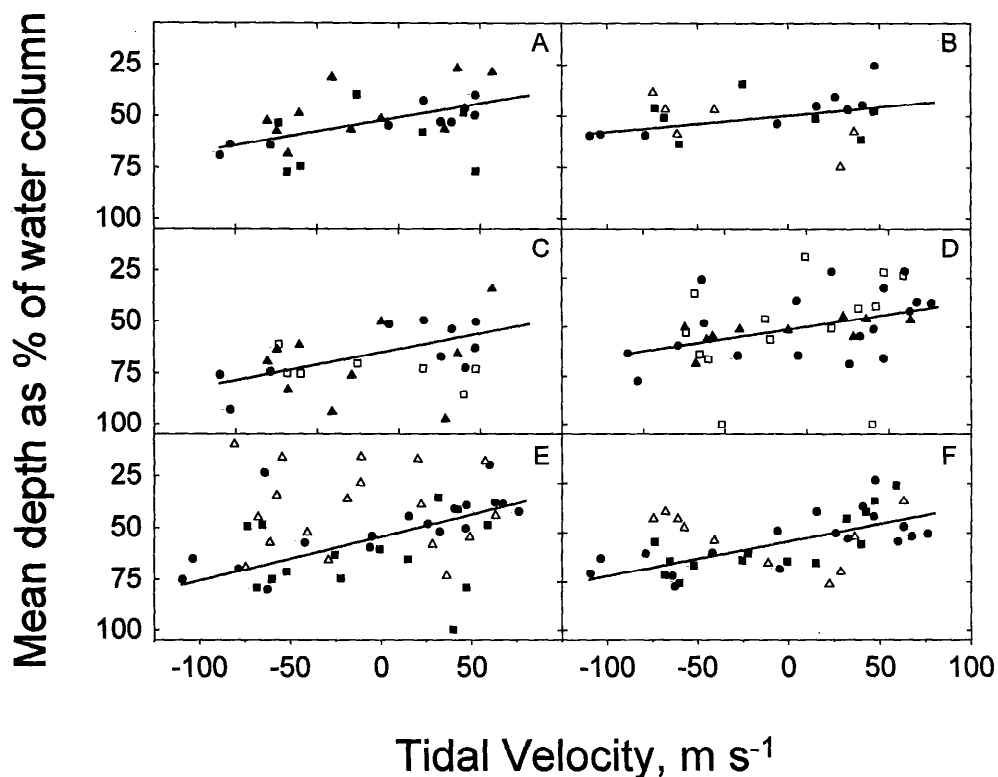


Fig. 8. Mean depth as percentage of water column taken from surface to the deepest sample versus water-column mean tidal velocity for three copepod species: left column, adults; right column, copepodites. A, B, *E. affinis* (daytime only); C, D, *P. forbesi* (daytime only for adults; day and night for copepodites); E, F, *S. doerrii*. Symbols as in Fig. 6 except that open symbols were not included in regressions. All regression lines are robust regression models; corresponding least-squares regression was significant in all cases (Table 5).

plus (Heinle and Flemer 1975) and perhaps 20% as an early nauplius. Thus, mortality to the entire population due to predation by *Acartia* would comprise about $0.2\% \text{ d}^{-1}$, which seems negligible. Data on abundance of planktivorous fish are available but have not yet been analyzed.

Since 1987 the consumption rate of nauplii by *P. amurensis* may have been sufficient to elevate mortality of *E. affinis* in Suisun Bay and west, i.e., generally seaward of the LSZ. The peak in abundance of *E. affinis* has shifted landward and, during summer months, this species has been absent. Its apparent replacement, *P. forbesi*, has a peak that is generally landward of the LSZ and less consistent than the earlier peaks in *E. affinis* (Fig. 3F). Thus, although mechanisms for position maintenance may not have changed qualitatively, the current abundance maximum of copepods could be supported by elevated predation rates to seaward, but that was not the case before 1987.

Tidal migration—Of the six taxa of zooplankton examined, all moved in synchrony with the tides during at least part of the day, and all moved in a direction that would retain them in the estuary (i.e., up on flood, down on ebb). The same pattern was observed in this study for species of larval fish that do not disperse ontogenetically to the shallows (Bennett 1997). Although this movement could have been

passive, the diel differences in vertical distribution suggest active migration.

Numerous examples are available in the literature of tidally oriented migration by zooplankton, particularly larval forms of benthic or demersal organisms but also including copepods and larval fish (Cronin and Forward 1979; Fortier and Leggett 1983; Forbes and Benfield 1986; Kimmerer and McKinnon 1987; Laprise and Dodson 1989; Hough and Naylor 1991; Morgan et al. 1997). *N. mercedis* has been known to migrate vertically on a diel cycle (Heubach 1969; Siegfried et al. 1979; Orsi 1986), and Orsi (1986) reported a tidal component to its migration pattern.

The macrozooplankton, comprising mysids and amphipods, appeared to have a pattern of vertical migration that was sufficient to reverse seaward mean transport and move them landward (Fig. 10). This is consistent with mechanism B-T1 above. There being little or no evidence supporting the other mechanisms for retention of the macrozooplankton, we conclude that these species are retained in the maximum by tidal migration. There was no evidence for a different response of these species to tidal velocity among the three stations. This was unexpected, because tidal migration in freshwater would move zooplankton away from their maximum. However, our 1-mS cm^{-1} station may not have been far enough landward to encompass the landward limit of the

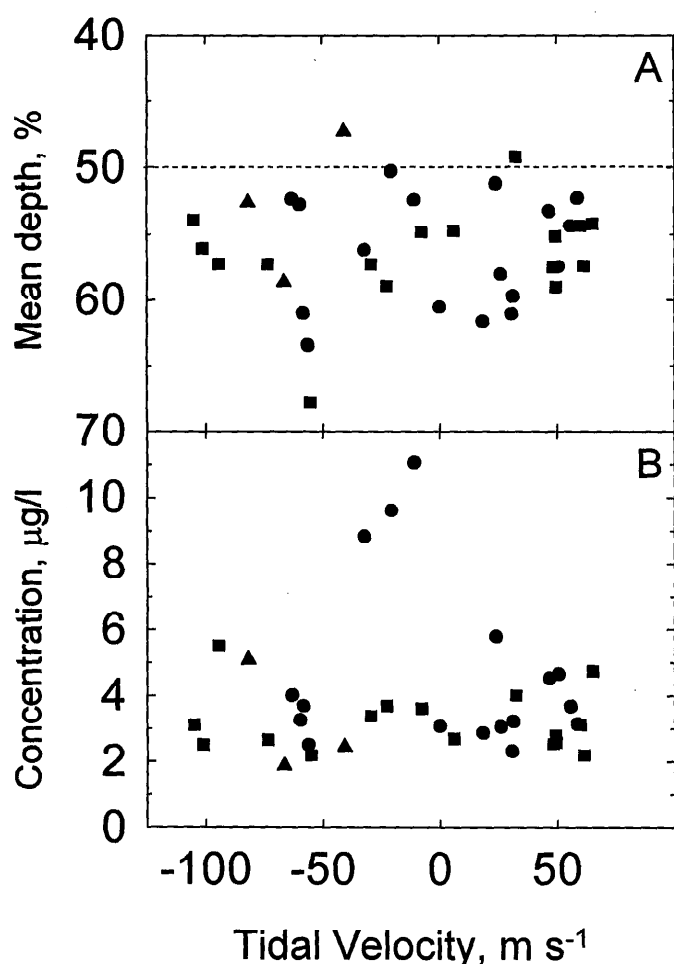


Fig. 9. Mean depth of center of mass (top) and water-column mean values (bottom) for chlorophyll. Symbols as in Fig. 9.

migratory pattern, judging from the present longitudinal distributions of zooplankton (Fig. 5).

The behavior of the estuarine copepods of the northern San Francisco estuary was rather different from that reported from other estuaries. In many estuaries, *E. affinis* adults are essentially epibenthic (Heinle and Flemer 1975; Vuorinen 1987; Simenstad et al. 1990). In some estuaries, *E. affinis* migrates diel off the bottom, and later stages, especially gravid females, are particularly rare in the water column by day, apparently to avoid visual predation (Vuorinen 1987).

Table 6. Coefficients with standard errors and significance for multiple linear regression for macrozooplankton used to estimate flux.

Term	Estimate	SE	Significance
Intercept	-0.78	0.085	<0.001
Water-column mean velocity	0.0024	0.001	<0.001
Depth as fraction of water column	1.55	0.16	<0.001
Day versus night	-0.75	0.085	<0.001
Depth × day versus night	0.86	0.16	<0.001

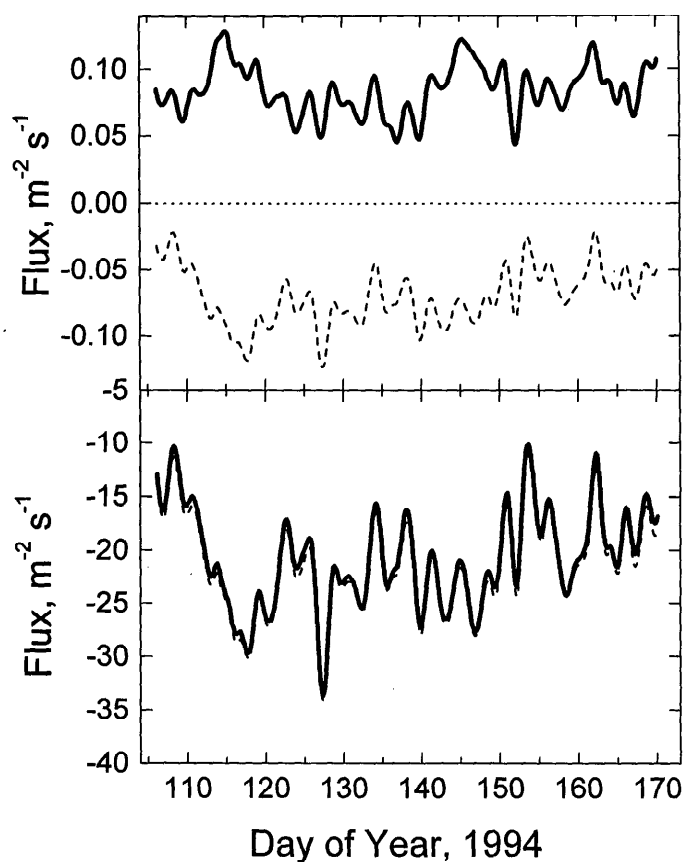


Fig. 10. Calculated longitudinal flux per unit cross-sectional area of A, macrozooplankton (total amphipods and mysids); and B, total copepods. Solid line, tidally filtered values calculated using a multiple linear regression model for the abundance of zooplankton. Dashed line, tidally filtered values calculated assuming uniform distribution in the water column.

In our study, *E. affinis* was equally abundant in the water column throughout the day and night and on all tides. *P. forbesi* also varied from the usual pattern for its genus, in which the larger stages and particularly the gravid females remain near the bottom by day (Fancett and Kimmerer 1985; Cordell et al. 1992). Fancett and Kimmerer (1985) found that adults of *P. cornutus* attached themselves to pieces of bottom detritus by means of long setae on the antennules and showed that this strategy was effective at reducing the influence of visual predation. These strategies appear not to

Table 7. Coefficients with standard errors and significance for multiple linear regression for copepods used to estimate flux.

Term	Estimate	SE	Significance
Intercept	-0.078	0.051	NS*
Station (factor)			<0.0001
Water-column mean velocity	0.0021	0.0009	0.02
Depth as fraction of water column	0.18	0.09	0.036
Velocity × depth	-0.0043	0.0016	0.008

* NS, not significant.

operate in the northern San Francisco estuary. Presumably, the high turbidity (the 1% light level averages about 0.7 m) reduces the effectiveness of visual predators in much of the water column, so that these energetically expensive strategies are unnecessary.

In contrast to macrozooplankton, copepods were not more abundant in the water column during the flood than during the ebb, so their behavior is consistent with mechanism B-T2. However, this movement was insufficient to reverse the seaward transport. Therefore it appears that the present-day peaks in abundance may be due to the spatial gradient in predation by *P. amurensis*. The cause of the peaks occurring in the LSZ before 1987 and the advantage conferred by the observed vertical migration remain unknown.

This study has demonstrated both the value and the difficulty of performing field studies in estuaries while attempting to follow water masses. The observed patterns were unambiguously related to tidal flows and not to advection of a spatially variable depth pattern past a point. This reinforces our belief that, for pelagic populations, the saline parts of the estuary are better described with reference to salinity than to geographic position (see Laprise and Dodson 1993) and that future studies should consider a similar Lagrangian approach to analyzing such systems.

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