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Persistence of Tidally-oriented Vertical Migration by Zooplankton in a Temperate Estuary

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ABSTRACT: Tidal vertical migration by zooplankton is a common phenomenon in estuaries, usually associated with landward movement of meroplankton or position maintenance of holoplankton. Little is known about the persistence of this behavior, its spatial variability, or its response to changing environmental conditions. We extended a previous study of tidal movements of zooplankton in the low-salinity zone (LSZ) of the San Francisco estuary in 1994 to include data from two additional years with very different hydrology. Freshwater flow during sampling in 1995 was about 7-fold greater than in 1994; the LSZ was about 28 km further seaward, and gravitational circulation in the LSZ was strong. In 1996 freshwater flow and LSZ position were intermediate but, because the LSZ was in shallower water in 1996 than in 1995, gravitational circulation was uncommon. Behavior of copepods in both years was similar to that reported in 1994 with some tidal migration observed during most cruises. An exception was the introduced carnivorous copepod *Tortanus dextrilobatus*, which did not migrate and maintained a position deep in the water column (1995 only). In 1996, mysids mainly stayed near the bottom with evidence for vertical migration from only 1 of 6 data sets, whereas amphipods migrated slightly on a diel schedule; these behaviors contrasted with the tidal migration observed in 1994. The bay shrimp *Crangon franciscorum* did not appear to migrate, but was more abundant in the water column during both ebb and flood, suggesting passive vertical dispersal. Zooplankton did not appear to maintain position by interactions with lateral circulation cells. The results for copepods suggest rigidity in behavior with little or no relaxation of the vertical movement in 1995 when strong gravitational circulation would have made upstream movement relatively easy. Mysids and amphipods altered their behavior depending on local conditions related to freshwater flow.

Introduction

Populations of estuarine species often occur in distinct, sometimes narrow, salinity ranges (Miller 1983; Laprise and Dodson 1994). To maintain population maxima in a particular salinity range requires a mechanism for overcoming advective and dispersive losses. This need is particularly acute for planktonic and epibenthic organisms because of their limited swimming ability.

Various mechanisms available to planktonic populations for overcoming seaward advection can be aggregated into three categories (Kimmerer et al. 1998): mechanism 1, net population growth sufficient to overcome advective and dispersive losses (Rogers 1940; Ketchum 1954; Speirs and Gurney 2001); mechanism 2, spatial correlation of a vertically or laterally variable distribution pattern with a residual flow field; and mechanism 3, correlation of vertical position with velocity at the tidal time scale.

The oligohaline or low-salinity zones (LSZ) of estuaries are of particular interest because they are frequently where several abundant species of plankton and epibenthos, as well as larval and juvenile fish (e.g., Bousfield et al. 1975; Fortier and Leggett 1983; Dodson et al. 1989; Dauvin and Dodson 1990; Jones et al. 1990; Runge and Simard 1990; Kimmerer et al. 1998, 2001), are most abundant. These regions represent approximately the landward limit of penetration of sea salt into estuaries and the landward limit of haline stratification. In many estuaries the oligohaline region includes a null zone and an estuarine turbidity maximum (ETM; e.g., Jones et al. 1990). The general theory of the formation of these ETMs holds that residual two-layer flow, or gravitational circulation, occurs seaward of a null zone at a salinity of approximately 2 psu, resulting in accumulation of particles and planktonic organisms according to mechanism 2 above (Postma and Kalle 1955; Peterson et al. 1975; Arthur and Ball 1979; Morgan et al. 1997), although this theory oversimplifies the time-dependence and nonlinearities that are important in trapping particles (Jay and Musiak 1994).

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In some estuaries the null zone theory may have limited applicability in the vicinity of the LSZ. Some zooplankton species maintain positions at a salinity below 1 psu, where stratification is infrequent and gravitational circulation should be rare. In the absence of bathymetric constrictions the longitudinal density gradient, which drives gravitational circulation, is less steep at 2 psu than at higher salinity (Monismith et al. 1996, in press). Strong tidal currents in shallow water tend to suppress stratification and inhibit gravitational circulation (Geyer 1993). Spring-neap variation in tidal shear stresses may result in spring-neap variation in stratification and gravitational circulation (Monismith et al. 1996). Variation in gravitational circulation at a longer time scale may occur due to movement of the LSZ in response to variation in freshwater flow (Jassby et al. 1995). In an estuary of varying bathymetry the LSZ can move between shallow and deep water, altering the propensity for gravitational circulation to occur and producing ETMs that are positioned by geography instead of salinity (Schoellhamer 2001).

Where bi-directional residual flow fields such as gravitational circulation do not occur, behavioral mechanisms can still reduce dispersive and advective losses (mechanism 3). Tidally-oriented migration by estuarine organisms is a common behavior, particularly in larval forms of benthic or demersal organisms but also in copepods, mysids, and larval fish (Cronin and Forward 1979; Cronin 1981; Fortier and Leggett 1983; Forbes and Benfield 1986; Orsi 1986; Kimmerer and McKinnon 1987; Laprise and Dodson 1989; Hough and Naylor 1991; Morgan et al. 1997; Kimmerer et al. 1998).

In river-dominated estuaries, seaward residual currents driven by river flow add an advective loss term to estuarine resident populations. As river flow increases, advective transport increases, which should exacerbate the problem of position maintenance. Although in some estuaries gravitational or other residual flow patterns may increase in strength with increasing river flow, the rate of increase can be small (Monismith et al. in press). The literature is silent on the extent to which vertical migration behavior, or the resulting retention, changes as river flow increases.

We previously documented tidally-oriented vertical migration in all 6 taxa of planktonic organisms studied in 1994 in the LSZ of the San Francisco estuary (Kimmerer et al. 1998). Those results were obtained in a drought year when the LSZ was continuously in the shallow regions of Suisun Bay and western Sacramento-San Joaquin delta (Fig. 1) and gravitational circulation did not occur. That study gave rise to three additional questions addressed here: do organisms of the LSZ consistently migrate vertically in response to tides, is the extent of tidal vertical migration related to freshwater flow, and does the migratory behavior vary laterally in a way that might influence retention? Here we compare the previous results with results from 1995, a high-flow year, and 1996, a year of intermediate flow, to address these questions.

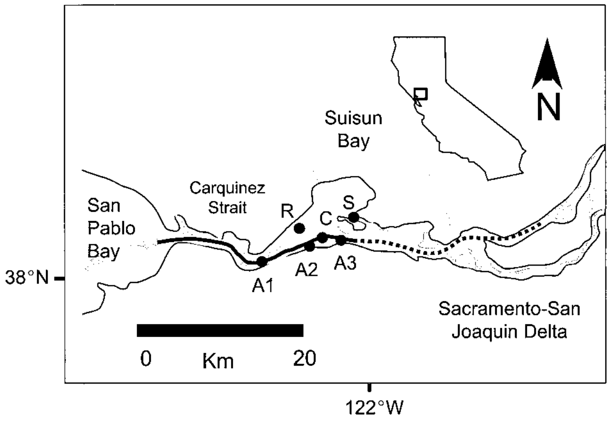

Fig. 1. Map of the northern San Francisco estuary showing locations discussed in the text with water deeper than 10 m shaded. Solid line—range of cruise tracks during 1995; dotted line—range of cruise tracks in 1994. Symbols near the center of the figure are locations of ADCPs (A1, A2, A3) and sampling locations for 1996: R = Reserve fleet; C = Ship channel, S = Suisun Cut. ADCPs were also located close to R and C.

Methods

STUDY SITE AND MONITORING DATA

The study site was the northern San Francisco estuary (Fig. 1). This well-studied estuary is characterized by a moderate tidal range (1–2 m) and highly variable river flow owing mainly to extreme seasonal and interannual variability in precipitation (Nichols et al. 1986). Zooplankton of the brackish region of the San Francisco estuary is considered an east Asian fauna owing to the large number of introduced species (Orsi and Ohtsuka 1999).

Data from long-term monitoring programs of the Interagency Ecological Program for the San Francisco Estuary (unpublished data) were used to determine the salinity ranges of common zooplankton and epibenthic crustaceans collected in this study and to provide information on chlorophyll distribution in the northern estuary. Methods used in these monitoring programs have been described elsewhere (Hatfield 1985; Orsi and Mecum 1986; Lehman 1992; Kimmerer et al. 1998). Data included abundance data for the shrimp *Crangon franciscorum* taken from the San Francisco Bay study (Hatfield 1985), mysids and selected species of adult copepods from the zooplankton monitoring program (Orsi and Mecum 1986), and chlo-

TABLE 1. Comparison of sampling locations and methods, and of general conditions, during the three years of the study.

Sampling Condition	1994	1995	1996
General location	Eastern Suisun Bay	Carquinez Strait	Central Suisun Bay
General design	Lagrangian, 1 vessel	Lagrangian, 2 vessels	Eulerian, 2 vessels
Specific location	Cycling between 1, 3, 6 mS cm^{-1}	Eastern vessel, c. 2 psu at 10 m depth; seaward vessel ~5 km to the west	Station C and either R or S
Cruise start dates	A: 18 April B: 26 April C: 17 May	A: 6 June B: 14 June C: 17 July	A: 3 June B: 13 June C: 20 June
Sampling schedule	Cycle once per tide, sample at 3 depths	Hourly at 3 depths	Hourly at 3 depths
Sampling methods	Opening-closing nets, 150-μm mesh	Pump discharging through 200-μm net	Fixed nets, 200-μm mesh
Freshwater flow	Low	High	Intermediate
Gravitational circulation	None	Frequent	Infrequent
Taxa examined	Several copepods, mysids, amphipods	Adult copepods only	Two copepods, mysids, amphipods, bay shrimp

rophyll concentration from the zooplankton and water quality programs, which were combined starting in 1995 (Orsi and Mecum 1986; Lehman 1992). Chlorophyll data were plotted against salinity for 1972–1986 and 1988–1998; a decrease in chlorophyll concentration from the first to the second period has been attributed to benthic grazing by the clam *Potamocorbula amurensis,* introduced in 1986 (Alpine and Cloern 1992).

Abundance of copepods and epibenthic macroinvertebrates from 1994–1998 was used to develop graphs of distribution with respect to salinity as follows. Most of the zooplankton monitoring stations are in freshwater, while most of the data for *C. franciscorum* came from high-salinity stations. To minimize bias in salinity distributions due to the distribution of sampling effort, we divided available data into 25 bins of salinity and averaged abundance within each bin. The number of data points per bin either increased (*C. franciscorum*) or decreased (copepods and mysids) linearly from low to high salinity, with a minimum bin size of 20. Bins were then adjusted so tied salinity values all fell in the same bin. Salinity and abundance were then averaged within bins, and abundance was converted to cumulative relative abundance.

For all years we obtained freshwater flow data from the Interagency Ecological Program's Dayflow water accounting program (unpublished data). The position of the salt field was indexed by X_2, the estimated daily average distance up the main channel from the mouth of the estuary to where bottom salinity is 2 psu (Jassby et al. 1995). X_2 was determined from freshwater flow by a time-series regression (Jassby et al. 1995).

FIELD SAMPLING

The general design in 1994–1996 was to sample in and near the LSZ for vertical distribution over a 24-h to 30-h period. We sampled on 3 different dates each year (Cruises A–C, Table 1) during late spring-early summer so as to capture larval fish of interest (Bennett et al. in press). Although methods differed somewhat among years (Table 1) , we believe the differences in results were due more to environmental conditions than differences in sampling methods.

Sampling in 1994 was described by Kimmerer et al. (1998). In 1995 we used two vessels, R/V *San Carlos* and *Turning Tide,* in an attempt to follow water masses as identified by salinity. *San Carlos* followed approximately 2 psu at a depth of 10 m, and *Turning Tide* maintained a position approximately 5 km to seaward. Positions were not maintained precisely because wind often moved vessels out of the channel into shallower water. Sampling on R/V *Turning Tide* was terminated early during Cruise A because of equipment problems, so data from that cruise are insufficient to test for vertical movement. Zooplankton was collected with submersible pumps equipped with flow meters, discharging into 150-μm mesh nets. Pumps had mean flow rates of 0.7 (*San Carlos*) and 0.2 m^3 min^{-1} (*Turning Tide*), and sample volumes were 0.7–2 m^3. Samples were pumped from 1 m below the surface, mid-depth, and 1 m above the bottom (or a maximum of 25 m) in an hourly rotation to obtain one set of samples each hour when possible.

The sampling scheme for 1996 used fixed stations, since data from 1994 and 1995 revealed little dependence of depth distributions on salinity. Stations were chosen so tidal currents would move the 2 psu isohaline past the stations on each tidal cycle. One station was occupied by R/V *San Carlos* in the ship channel of Suisun Bay (station C), and the other by R/V *Turning Tide* in one of two locations in the northern channel (Stations R and S; Fig. 1). The sampling scheme was simplified: we took samples using 75-cm diameter, 200-μm mesh nets fished at 3 depths. Two nets were fished from a single wire, one at about 1 m off the bottom and the other at mid-depth. The nets did not open or close; although the nets were deployed quickly, some contamination by shallow plankton undoubtedly occurred, and we did not correct for it. A third net was fished 1 m below the surface from a separate wire. Each net was equipped with a flow meter for measuring volume filtered. When time permitted we took an additional oblique tow to corroborate the total abundance from the three stratified tows.

In both years we subsampled with a splitter or piston pipette to obtain ~100 *Pseudodiaptomus forbesi* adults, and counted adults (1995) or adults and copepodites (1996) of all copepods found. Data for adults and copepodites were combined after examination of the data revealed no apparent difference in their vertical distributions. In 1996 larger subsamples were taken for mysids and amphipods (target count of 50), and *C. franciscorum* was counted in entire samples (25% subsample in one case). All data were reduced to abundance per cubic meter in each depth stratum.

Salinity/temperature profiles were taken from each vessel with a Seabird SBE-19 profiler every 10 (1995) or 20 (1996) min. During 1996 Cruise A on R/V *San Carlos* an electrical failure resulted in a complete loss of data. We filled in salinity data using a regression of data from the remaining cruises on salinity from a nearby U.S. Bureau of Reclamation fixed station.

Velocity data used included tidally-filtered, vertically binned data for detection of gravitational circulation and vertically-averaged hourly mean data for analysis of vertical movements of plankton. Data were obtained from fixed Acoustic Doppler Current Profilers (ADCP) stations at 1-m depth intervals. In 1995 ADCP stations were located at stations A1 and A2 (Fig.) . Since A1 was closer to Carquinez Strait, the deepest part of this region of the estuary, we used data from that station to detect gravitational circulation. This data record contained several gaps but none during cruises. After four gaps of 1–7 d had been filled in using harmonic analysis, hourly means were filtered to remove variation at the tidal and shorter time scale (Godin 1972), and data for the cruise dates were extracted for plotting and analysis. Data from 1-m depth had anomalous periods of strong landward velocity during late summer, and data from 2 m had consistently stronger seaward current vectors than bins above or below it. We used data only from 3 m and deeper in analysis of the plankton data and the data from A2 for analysis of variation at the tidal time scale.

ADCP data were available during 1996 from stations A3, R, and S (Fig. 1). Infrequent small data gaps were ignored, since they occurred well outside the time period of the field sampling. Data were averaged into hourly bins, then either filtered as above for detecting gravitational circulation, or averaged over the water column for analysis of variation at the tidal time scale.

DATA ANALYSIS

We detected tidally-oriented migration of copepods by least-squares regression of mean depth as a percentage of the water column depth versus water-column mean tidal velocity as before (Kimmerer et al. 1998). This mode of analysis required a full suite of samples at each depth; sample points were missed either because of missing samples due to difficulties in the field, or because of low abundance in some samples. To account for high variability in total abundance in the water column, particularly in 1996, we weighted mean depth data by the square root of mean water-column abundance in performing the regressions. For larger organisms (mysids, amphipods, and shrimp, 1996 only) we analyzed both mean depth and total abundance in the water column. Examination of plots and tests of differences among cruises using analysis of covariance generally revealed differences in intercept and sometimes slope, so we analyzed cruises separately. Analysis of covariance was also used to examine differences between day and night distributions, and between adult and juvenile copepods.

All analyses were conducted after graphical exploratory analyses (Cleveland 1993) using the S-Plus statistical language (Venables and Ripley 1997). Regressions were by ordinary least squares if the data met assumptions of normality, homoscedasticity, and lack of autocorrelation in residuals, and were not unduly influenced by single points. These assumptions were tested by examining various diagnostic plots. None of the statistically-significant models reported here contained significant autocorrelation in the residuals. In cases requiring regressions of two variables both measured with substantial error we applied geometric mean regression (Ricker 1973), under the assumption that errors in both variables were of similar relative magnitude (see Prairie et al. 1995).

Results

ENVIRONMENTAL CONDITIONS

The common zooplankton species differed in salinity range (Fig. 2). The copepods *Tortanus dextrilobatus* and *Acartiella sinensis* had median salinity values of about 10 and 2 psu, whereas the other common species had median values below 1 psu. The bay shrimp *C. franciscorum* was abundant at

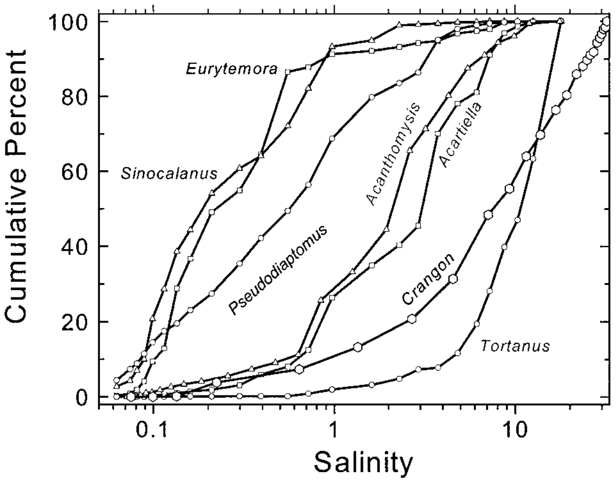

Fig. 2. Salinity distributions of common species of copepods and epibenthic crustaceans as cumulative percent relative abundance based on mean abundance in each of 25 salinity bins during 1994–1998.

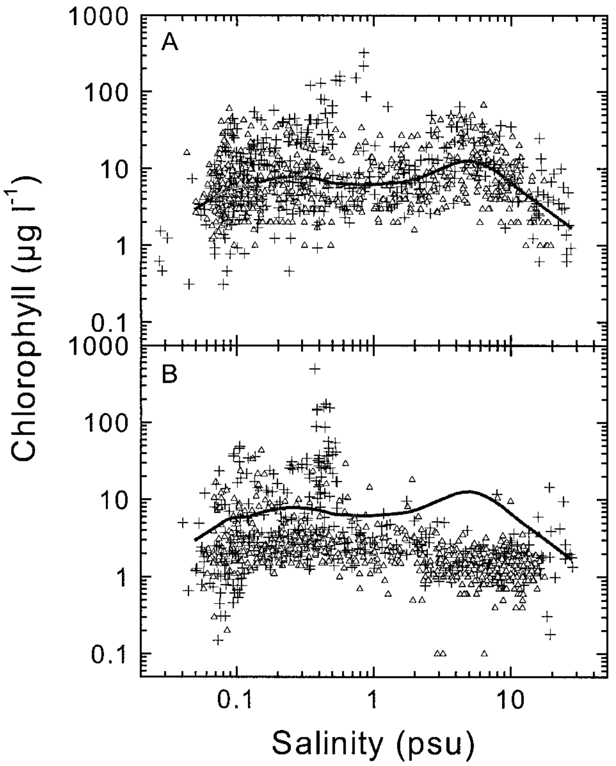

Fig. 3. Chlorophyll concentrations from two monitoring programs in the northern estuary versus salinity for May through September in 1972–1986 (A) and 1988–1998 (B). Crosses are data from Interagency Ecological Program (IEP) zooplankton monitoring; triangles are data from IEP water quality monitoring. Data have been sampled to obtain a total of 1,000 points out of 6,649 (A) and 3,520 (B). Lines are locally-weighted least-squares regression with a span of 0.2 (Venables and Ripley 1997) fit to the data in A above S = 0.05 for comparison of patterns between the two periods.

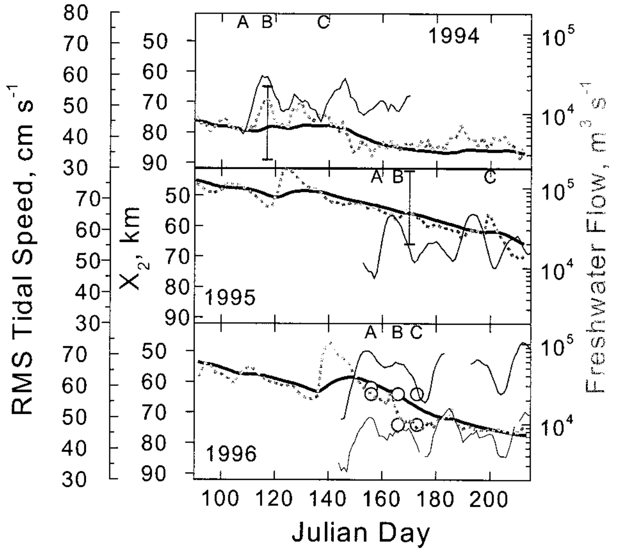

Fig. 4. Environmental conditions during cruises for 1994, 1995, and 1996. Heavy solid lines, X_2 (left axis); heavy dotted lines, freshwater flow scaled to X_2 according to relationship in Jassby et al. (1995) (right axis); thin solid lines, root-mean square tidal current speed at ADCP station near sampling station (outer left axis). Tidal current data for 1996 from Stations C (top) and S (bottom). Letters indicate cruise dates; error bars and circles give sampling positions in kilometers on the X_2 axis as a range for all three cruises (1994, 1995) or as discrete station locations for each cruise (1996).

higher salinity and over a broader range of salinity than most of the other taxa.

Chlorophyll concentrations often showed a local maximum at around 5 psu before 1987 (Fig. 3a). During 1988–1998 chlorophyll was generally about 3-fold to 10-fold lower at salinity between 0.5 and 20 psu than previously, and a consistent and occasionally steep spatial gradient was set up with higher chlorophyll at salinity below than above 1 psu (Fig. b).

The three years of the field study encompassed nearly the extreme of hydrologic conditions in the estuary (Fig. 4). The first year, 1994, was dry with X_2 about 80–82 km during the cruises, 1995 was wet with X_2 of 55–60 km during the cruises, and intermediate flow in 1996 put X_2 at an intermediate position of around 65–70 km during the cruises. These three ranges put our sampling regime in three very different hydrodynamic environments (Fig. 1): the transition between eastern Suisun Bay and the Sacramento-San Joaquin delta in 1994, western Suisun Bay through Carquinez Strait in 1995, and central Suisun Bay in 1996. The tidal excursion is about 5–25 km depending on tidal phase and location.

Tidal energy, as represented by root-mean-square tidal current velocity at ADCP stations near the sampling sites, varied with the spring-neap cy-

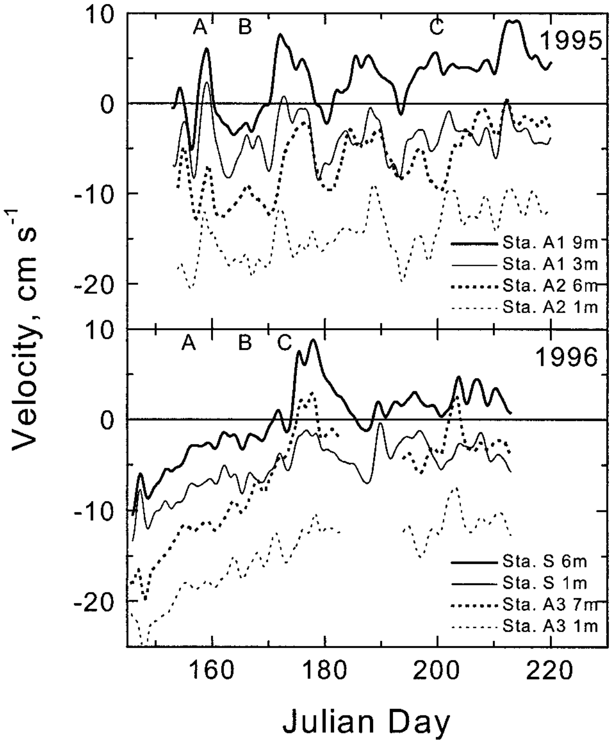

Fig. 5. Time series of tidally-filtered velocity data from near-surface and near-bottom ADCP bins at two stations in 1995 (top) and 1996 (bottom). Positive velocities are eastward, or upstream relative to river flow. Letters indicate cruise dates.

cle and among cruises, mainly because of differences in sampling location (Fig. 4). In 1996 tidal energy was substantially lower in the northern channel than the ship channel of Suisun Bay. Since in 1994 and 1995 the sampling locations did not usually coincide with the ADCP locations, the rms tidal speed data are more useful for within-year than between-year comparisons. Spring-tide conditions prevailed during 1994 and 1995 Cruise B and 1996 Cruise A, neap tides during 1994 and 1995 Cruises A and C and 1996 Cruise C, and intermediate tides during 1996 Cruise B (Fig. 4).

Tidally-filtered near-surface and near-bottom velocities from fixed ADCP's showed that gravitational circulation was most frequent in deep water or at high salinity. In both 1995 and 1996, residual near-bottom currents became progressively more positive (landward) as the season progressed and salinity increased (Fig. 5). During most of June–July 1995, gravitational circulation was frequent at station A1, as indicated by the generally landward bottom current and seaward near-surface current (3 m depth). At the shallower, more easterly station A2, gravitational circulation was nearly absent, and near-bottom residual currents were strongly seaward during the sampling cruises. In 1996 gravitational circulation occurred in July at station S but only for brief periods at A3; although both stations are about the same depth, the tidal prism and therefore tidal velocities are smaller at S than A3. Gravitational circulation was not detected at either station during the cruises.

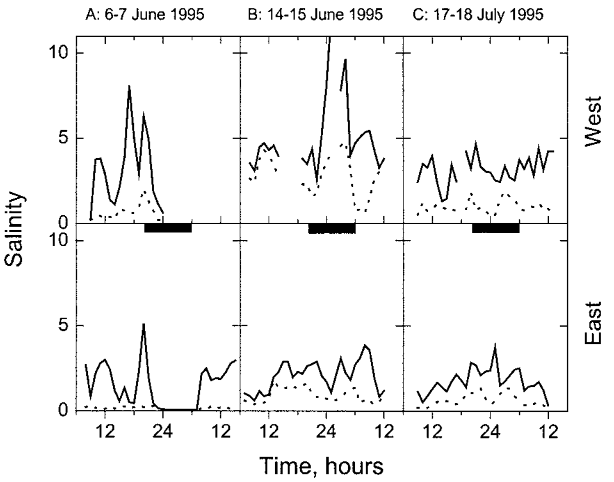

Fig. 6. Salinity data for 1995 cruises. Bottom row, data from R/V *San Carlos* (eastern vessel); top row, data from R/V *Turning Tide,* nominally 5 km to the west. Lines show salinity near the surface (heavy line) and in the deepest sample (dotted line). Dark bars indicate times of darkness.

In 1995 the two vessels attempted to drift with the tides between western Suisun Bay and the western end of Carquinez Strait and, on Cruise B, into San Pablo Bay (Fig. 1). This meant sampling in water that varied in depth between 10 and 35 m. As a result of this variation, bottom salinity varied between nearly freshwater and 16 psu, and salinity at 10 m depth was highly variable as well (Fig. 6). Stratification was strong in the deeper channels, particularly on Cruise A when tidal mixing was weakest. Some of the variability in Fig. 6 was due to difficulties in keeping the vessels on moving stations in this dynamic environment, particularly with the pumps deployed. On Cruise A, R/V *San Carlos* (East) moved into a region of nearly freshwater during the flood tide and eventually had to be repositioned.

In 1996 both vessels occupied fixed stations, so salinity varied as the salt field moved past the sampling location. Stratification was strong during periods of elevated salinity, particularly in the northern channel, and tended to be somewhat stronger on ebbs than on floods (Fig. 7).

In 1995 only copepods were abundant enough to be analyzed for vertical distribution. In 1996 we collected sufficient copepods, mysids, amphipods (ship channel only), and bay shrimp, *C. franciscorum.* Figure 8 gives three examples of the vertical distributions found on these cruises, along with ve-

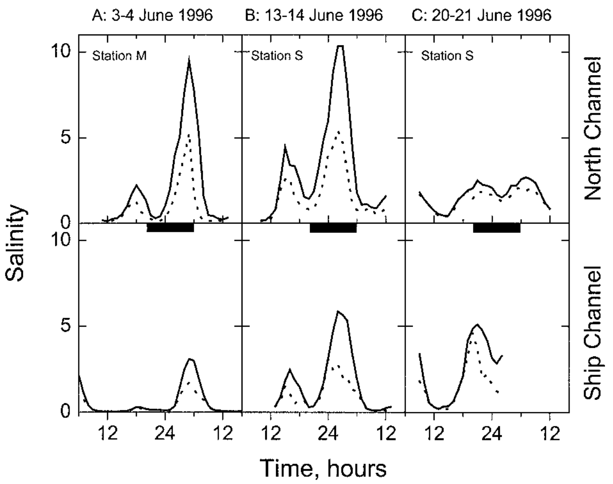

Fig. 7. Salinity data as in Fig. 6 for 1996 cruises. Top row, data from R/V *Turning Tide,* positioned in the northern channel (Station R or S); bottom row, data from R/V *San Carlos* in the ship channel (Station C). Lines as in Fig. 6.

locity, salinity, and abundance data. Analysis of these data is presented below. Examples are given in Fig. 8a and b for the copepod *P. forbesi* from Cruise C in 1995 (west) and 1996 (ship channel), and in Fig. 8c for mysids (mostly *Acanthomysis bowmani*) from Cruise C in 1996 (ship channel). Tidal migration is evident in the generally greater abundance of copepods near the surface on the flood and greater abundance near the bottom on the ebb, although the pattern is subtle especially in Fig. 8b. Mysids generally stayed near the bottom with few in the near-surface samples at any time and only a slight tendency to be higher in the water column on the flood than on the ebb.

Figure 9 gives examples for various taxa from various cruises to illustrate the range of patterns in the relationships between vertical position and tidal velocity. Figure 9a and b show contrasting relationships with velocity for *P. forbesi* (also *Eurytemora affinis* from 1995 Cruise A east), one in which the relationship is strong and significant and the other in which it is absent. Mysids (Fig. 9c) generally showed no pattern except for a tendency to be most abundant near the bottom, although in this particular example mysids were slightly further off the bottom during stronger currents in either direction. Amphipods (mostly *Gammarus daiberi*; Fig. 9d), collected in abundance only in the ship channel in 1996, had a diel component to their movements but no tidal component, and were very close to the bottom by day. *C. franciscorum* (Fig. 9e,f) were usually higher in the water column by night than by day and often higher in the water column on strong floods and strong ebbs, resulting in U-shaped curves of vertical distribution (e.g., Fig. 9f).

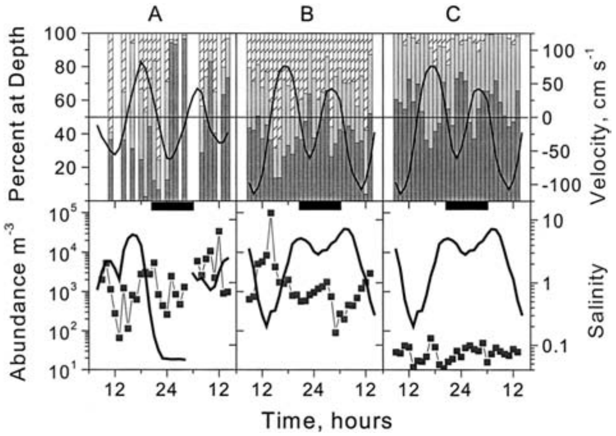

Fig. 8. Examples of vertical distribution results with environmental and abundance data. Top row, percent of the population in each of 3 depth bins: near-surface (hatched bars), mid-depth (light gray), and near-bottom (dark gray), and velocity from the nearest ADCP station (lines, right axis). Bottom row, abundance (squares, left axis) and salinity (line, right axis). Letters are for identification only and do not indicate cruises: A) *Pseudodiaptomus forbesi* from 1995 Cruise A East; B) *P. forbesi* from 1996 Cruise C North; C) mysids from 1996 Cruise C North.

DATA ANALYSIS

Mean abundance from oblique tows taken in 1996 was correlated with the mean abundance from stratified tows, and geometric mean regression slopes were not significantly different from 1 (Table 2). This gives confidence that the stratified samples provided a representative sample of the entire water column.

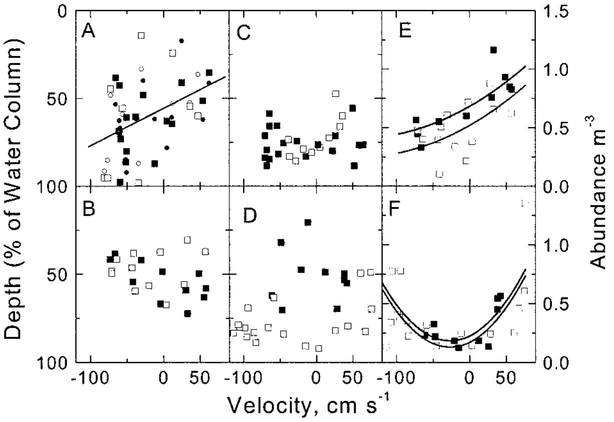

Fig. 9. Example plots of vertical distribution (center of mass as percent of water column depth) versus tidal velocity. A) *P. forbesi* (squares) and *Eurytemora affinis* (circles) from 1995 Cruise A East; B) *P. forbesi* from 1996 Cruise B northern channel; C) Mysids from 1996 Cruise C northern channel; D) Amphipods from 1996 Cruise C, ship channel; E) *Crangon franciscorum* from 1996 Cruise B northern channel; F) *C. franciscorum* from 1996 Cruise C ship channel. Solid symbols are night, open are day. Lines are: A, linear regression for *P. forbesi* data; E and F, quadratic regressions for day (lower line) and night (upper line).

TABLE 2. Comparison of oblique and stratified samples for different taxa, 1996 only. Values given are intercepts and slopes (±95% CI) for regressions where the independent variable was the log mean abundance in the water column from stratified samples, and the dependent variable was the log abundance from a single oblique tow taken immediately after the stratified tows. Abundance values were increased by 1 (*Sinocalanus doerrii*) or 0.1 (mysids, amphipods, and *Crangon franciscorum*) to allow for zeros.

Taxon	Intercept	Slope
Pseudodiaptomus forbesi	−0.33 ± 0.51	1.14 ± 0.18
Sinocalanus doerrii	0.30 ± 0.48	0.86 ± 0.31
Mysids	0.16 ± 0.32	0.91 ± 0.27
Amphipods	0.02 ± 0.21	0.99 ± 0.21
Crangon franciscorum	0.12 ± 0.13	1.10 ± 0.30

The metric used to detect vertical movement was the center of mass of the population as a percentage of the water column depth, rather than total abundance in the water column. In 1995, total abundance in the water column of the abundant copepod species did not vary on a diel basis or with tidal velocity ($p > 0.1$ in each case, linear regression or *t*-test as appropriate; degrees of freedom for each test can be determined from Fig. 10). In 1996 total abundance in the water column was less useful than in 1994 or 1995 as a measure of vertical movement off the bottom, because total abundance varied with salinity and therefore tidal stage (e.g., Fig. 8b bottom row).

Mean depth of center of mass of copepods had no diel signal in any of these data sets, nor did the relationship of mean depth to velocity vary by day versus night (analysis of covariance, $p > 0.1$ in each case, degrees of freedom 1 or 2 less than in Fig. 10). Depth of the center of mass of copepods was related to water-column mean velocity linearly or unrelated to velocity (Fig. 9a,b). Slopes of regressions of mean depth on water-column mean velocity for copepods in all three years are summarized in Fig. 10. *P. forbesi* showed evidence of tidal vertical migration on 8 of 12 occasions when a sufficient sample was obtained (generally at least 18). The values from 1995 Cruise B were near zero from both vessels (Fig. 10) . This was a time of high tidal energy (Fig. 4) and samples were taken in a region of changing bathymetry, suggesting that turbulent mixing might have prevented the copepods from maintaining vertical position. However, across all of the data, the slopes of vertical distribution versus velocity were unrelated to rms current speed. In 1996, *P. forbesi* appeared to migrate vertically on a tidal cycle in the ship channel (station C, Fig. 1) as found in 1994. In the northern channel, copepods did not appear to migrate and their vertical distribution seemed random. The velocity range was smaller in the northern channel than in the ship channel (Fig. 4), which may have made detection of the signal more difficult.

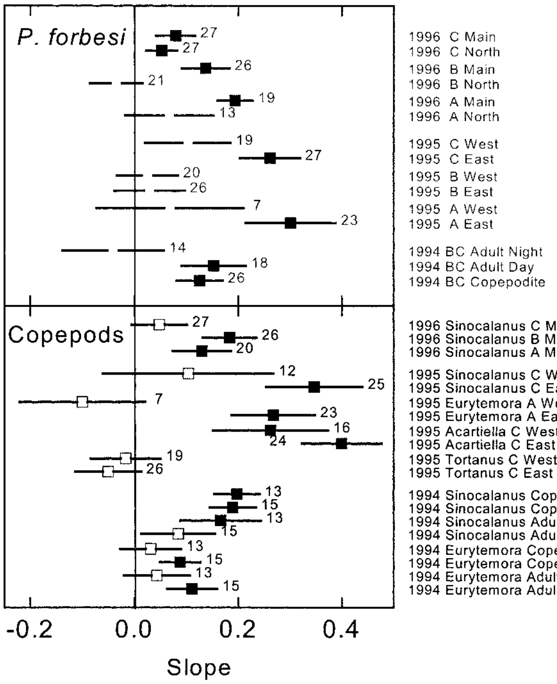

Fig. 10. Summary of results of regressions of weighted mean depth of copepods versus tidal velocity. Symbols are slopes ± 1 standard error, and numbers give degrees of freedom; filled symbols, significantly different from 0 ($p < 0.05$, 1-tailed *t*-test), open symbols, not significant. Top, results for *P. forbesi*; bottom, results for various copepod species. Data are identified by year, genus (bottom panel only), cruise, and location except for 1994, when life stage and day/night are given.

The other species of copepod were present only on some cruises (Fig. 10). *E. affinis* had almost identical behavior to *P. forbesi* during 1995 Cruise A (east only). *Sinocalanus doerrii* appeared to migrate tidally in data from the eastern vessel but not the western vessel (only 14 points). *A. sinensis* showed evidence of tidal vertical migration in data from both vessels. In contrast, *T. dextrilobatus* did not appear to migrate tidally, although data from the eastern vessel suggested a diel component of migration (not shown). This copepod was generally uncommon in surface samples and most abundant in near-bottom samples. In 1996 the only abundant copepod besides *P. forbesi* was *S. doerrii,* counted only in samples from the ship channel. It had a significant relationship between mean depth and velocity during Cruises A and B but not C (Fig. 10).

In contrast to results from 1994, neither mysids nor amphipods appeared to migrate consistently in response to tides. Mysids were most abundant in the near-bottom samples and uncommon in surface samples; in the ship channel 59% of the mys-

TABLE 3. Regression results for mysids, amphipods, and *Crangon franciscorum,* 1996 data only. Coefficients are given with 95% confidence intervals. Where two values of the coefficients are given, they refer to coefficients for a second-order polynomial transformation of the independent variable (Venables and Ripley 1997).

Site	Cruise	Taxon	Independent	df	Coefficient	p
North	A	Mysids	Velocity	13	0.03 ± 0.17	0.7
North	B	Mysids	Velocity	21	0.03 ± 0.08	0.5
North	C	Mysids	Velocity	27	0.07 ± 0.10	0.17
Main	A	Mysids	Velocity	23	0.02 ± 0.05	0.5
Main	B	Mysids	Velocity	20	0.01 ± 0.08	0.7
Main	C	Mysids	Velocity	19	15 ± 4, 16 ± 4	<0.0001
Main	A	Amphipods	Day/Night	21	10.8 ± 4.0	<0.0001
Main	B	Amphipods	Day/Night	21	11.9 ± 6.5	0.003
Main	C	Amphipods	Day/Night	25	15.0 ± 10.1	<0.0001
North	A	*C. franciscorum*	Velocity	9	0.2 ± 0.7, −0.5 ± 0.6	0.2
			Day/Night		−0.4 ± 0.2	0.004
North	B	*C. franciscorum*	Velocity	19	0.7 ± 0.4, 0.1 ± 0.4	0.0007
			Day/Night		0.1 ± 0.1	0.06
North	C	*C. franciscorum*	Velocity	25	0.03 ± 0.4, 0.9 ± 0.4	0.002
			Day/Night		0.06 ± 0.08	0.2
Main	A	*C. franciscorum*	Velocity	22	0.1 ± 0.6, 0.6 ± 0.7	0.1
			Day/Night		0.1 ± 0.1	0.2
Main	B	*C. franciscorum*	Velocity	22	0.2 ± 0.4, 0.5 ± 0.4	0.0001
			Day/Night		0.16 ± 0.08	0.0008
Main	C	*C. franciscorum*	Velocity	25	0.3 ± 0.5, 0.9 ± 0.5	0.001
			Day/Night		0.03 ± 0.1	0.6

ids were collected in the near-bottom samples and 3% in the near-surface samples, while in the northern channel 53% were collected near-bottom and 8% near-surface. Slopes of mean depth versus tidal velocity were slightly positive in the ship channel on Cruises B and C, although during Cruise C the best fit was to a quadratic curve (Table 3). There was no diel effect for mysids on any cruise at either station (analysis of covariance, $p > 0.1$). Amphipods were most abundant in near-bottom samples and had a weak diel migration but no tidal migration (Table 3, ship channel only). Amphipods were abundant only at a salinity below about 1 psu.

The mean abundance in the water column of bay shrimp, *C. franciscorum,* was generally higher at night and on strong flood and ebb currents. The best fits to the data for all cruises was a quadratic curve, except that data were insufficient for Cruise A in the northern channel (Table 3) . In all cases the minimum in the quadratic curve was negative, indicating a greater tendency for shrimp to rise off the bottom on a flood than on an ebb at the same current speed.

Discussion

PATTERNS FOR COPEPODS

Selective tidal stream transport is best documented for meroplankton including larvae of benthic crustaceans (Cronin and Forward 1979) and demersal fish (Harden Jones et al. 1979). Although there seems to be general acceptance of this pattern in the literature for meroplankton (e.g., Power 1997), the number of cases in which tidal vertical migration by holoplankton has been demonstrated is small, and many of these studies involved a relatively small number of samples or a narrow range of hydrographic conditions (e.g., Wooldridge and Erasmus 1980; Orsi 1986; Kimmerer and McKinnon 1987; Hilmer and Bate 1991; Hough and Naylor 1991, 1992a; Crawford and Purdie 1992; Schlacher and Wooldridge 1994; Wang et al. 1995; Morgan et al. 1997; Kimmerer et al. 1998). A general pattern of tidal migration for position maintenance by holoplankton has not been demonstrated.

We previously showed that all 6 taxa of the zooplankton studied migrated vertically in synchrony with tides, i.e., mechanism 3 above (Kimmerer et al. 1998). We also presented evidence incompatible with mechanisms 1 (higher reproductive rate or lower mortality in the LSZ) or 2 (interaction of vertical distribution with residual flow). Here we have examined temporal persistence in these patterns and developed some information on lateral variability.

Results presented here show some important differences among years and variability in responses of several taxa. Differences among years may have been at least partly due to differences in methods, particularly the use of an Eulerian sampling scheme in 1996. In general Lagrangian schemes help to prevent aliasing of advective and migratory patterns and may be preferable for examining tidal migration (Kimmerer et al. 1998). We used an Eulerian scheme in 1996 to avoid some of the logistical and sampling problems encountered in previous years, and to keep our sampling locations close to fixed ADCPs. Although this scheme precluded the use of abundance in the near-surface samples as a metric for migration by mysids and amphipods, mean position in the water column served as an adequate and unambiguous substitute.

If the differences in patterns among years are not an artifact of sampling methods, they can be used to infer some key points about the plasticity of behavior of the different organisms sampled. Copepods as a group, except for *T. dextrilobatus,* migrated tidally much of the time and with a similar pattern (Fig. 10). This behavioral pattern was relatively unresponsive to large variations in freshwater flow and the resulting wide range of salinity distributions (Fig. 2). The pattern may have been obliterated by strong tidal currents at some times (e.g., Fig. 10, 1995 Cruise B) and was undetected when sample sizes were small or velocity ranges narrow. Otherwise, the tidal migration pattern did not vary with any of the environmental factors measured. This apparent rigidity of behavior contrasts both with the behavior of other crustaceans (see below) and with results suggesting that endogenous rhythms of activity of *E. affinis* varied with sampling location and phase of the spring-neap tidal cycle (Hough and Naylor 1991, 1992b).

The migratory behavior of the copepods is not consistent, but also not responsive to changes in freshwater flow, salinity, or stratification. The adequacy of this behavior for position maintenance remains to be determined. Previous analyses showed that migration within the water column was apparently insufficient to maintain position in an unstratified water column (Kimmerer et al. 1998), but the same may not be true when the water column is stratified.

The general pattern of copepod vertical distribution seemed anomalous compared with other estuaries. For the most part, *P. forbesi* and, when abundant, *E. affinis* were well-distributed throughout the water column with an intermittent and rather subtle pattern of tidal vertical migration resulting in relatively small shifts in mean depth. Elsewhere members of the *E. affinis* species complex (Lee 2000) and members of the genus *Pseudodiaptomus* migrate on a diel basis and often remain on or near the bottom by day (Heinle and Flemer 1975; Fancett and Kimmerer 1985; Vuorinen 1987; Walter 1987; Simenstad et al. 1990; Cordell et al. 1992; Jerling and Wooldridge 1992; Morgan et al. 1997). Seaward in the San Francisco estuary *Pseudodiaptomus marinus* is more abundant at night than by day, suggesting a diel migration pattern similar to that observed for this species and its congeners elsewhere (Kimmerer unpublished data). The difference in behavior between these species in the LSZ of the San Francisco estuary and similar species elsewhere may be due to the high turbidity of the entire northern estuary (Kimmerer et al. 1998). If the vertical migration behavior is a response to planktivory by fish (Fancett and Kimmerer 1985; Vuorinen 1987), then regions of high turbidity may provide refuges where migration is unnecessary.

Our limited results for tidal migration of *E. affinis* in 1994 and 1995 also contrast with those from similar studies in the Columbia River ETM. There, *E. affinis* was more abundant in the water column on the flood than on the ebb (Morgan et al. 1997), implying an epibenthic behavior. Hough and Naylor (1992b) found that this species had an endogenous swimming rhythm that was phased to the tides but in a variable way, possibly related to position maintenance. Similar endogenous rhythms could result in the vertical patterns seen in both the Columbia River studies and our studies. The reason for the differences in vertical movement and distribution between these two rather similar estuaries remains unknown.

The longitudinal position of the maximum of *E. affinis* also contrasts with previous studies and appears to have changed in the San Francisco estuary. This species worldwide appears to be highly variable in genetic affinities (Lee 2000) and in salinity range and morphology (Busch and Brenning 1991) as well as migratory pattern. The center of abundance in the San Francisco estuary in recent years has occurred at salinity < 0.5 (Fig. 2), whereas the earlier salinity peak was around 2 (Kimmerer et al. 1998). This landward shift appears to have coincided with the spread of the introduced clam *Potamocorbula amurensis,* which was implicated in the decline of this species in the LSZ (Kimmerer et al. 1994; Kimmerer and Orsi 1996), but the mechanism that would increase abundance in freshwater is unknown. Members of the *E. affinis* complex have colonized freshwater from estuaries elsewhere (Lee 1999).

PATTERNS FOR MACROZOOPLANKTON

Mysids and amphipods, analyzed only in 1994 and 1996, showed a striking contrast to copepods in their response to different freshwater flow regimes. Tidal vertical migration was strong in 1994, a low-flow year, and weak to absent in 1996 under conditions of intermediate flow. In both years both of these taxa remained near the bottom with about half of the animals collected in the bottom net. Although based on data from only two years, this suggests some plasticity in behavior of these animals. Positioning near the bottom would result in landward transport only under conditions of strong gravitational circulation or ebb-flood asymmetry, which was not common during the sampling cruises (Fig. 5 and Kimmerer et al. 1998). Since sampling stations in the ship channel in 1996 were within a tidal excursion of the deeper waters of Carquinez Strait, where gravitational circulation was frequent in 1995 (Fig. 5) and 1996 (not shown), mysids and amphipods collected at the sampling stations were presumably exposed to gravitational circulation part of the time in 1996, resulting in at least the potential for position maintenance without the need for energetically-expensive migration.

The tidal behavior of *C. franciscorum* has not been examined before in the San Francisco estuary. The life history of this shrimp differs markedly from that of the other species examined, which are permanent residents of the LSZ. Adult shrimp migrate seaward to the lower estuary or coastal ocean to spawn, and juveniles recruit to the estuary in spring, moving landward over time as they grow (Hatfield 1985). *C. franciscorum* has a broader distribution in space and salinity (Fig. 2) than the other species. As with mysids and amphipods, a behavior by which shrimp remain near the bottom would move them landward over time in the brackish to saline regions of the estuary, but not landward of the LSZ. This outcome is consistent with their distribution in salinity space (Fig. 2). The movement off the bottom observed during strong currents may be passive, or it may reflect an activity rhythm stimulated by turbulence as suggested for blue crab larvae by Welch et al. (1999).

EFFECTS OF MIGRATORY PATTERNS

Stratification and density-driven currents were generally greatest near the end of the ebb and beginning of the flood (low-later slack). A migratory pattern by which animals moved into the bottom layer toward the end of the ebb would be most effective at moving the animals landward. We saw no behavior that appeared to match this pattern. To the extent that organisms responded to tidal velocities, they appeared to do so in response to the existing velocities instead of anticipating changes.

Previous reports have documented retention of zooplankton due to interactions between vertical position and persistent lateral circulation patterns such as large-scale tidal eddies (Trinast 1975; Alldredge and Hamner 1980; Wooldridge and Erasmus 1980). The influence of lateral variability on retention was not fully resolved by our sampling, but data from 1996 are pertinent. To produce aggregation due to lateral variability would require an interaction between vertical migration of the copepods and substantial lateral variability in current profiles. Residual velocities at the surface and near-bottom had similar patterns in the northern and ship channels in 1996, although somewhat less dominated by seaward net flow in the northern channel (Fig. 5). This implies that lateral residual circulation was weak, at least at the scale of the entire Suisun Bay. Migratory behavior appeared somewhat weaker in the northern channel than the ship channel (Fig. 10), possibly in response to the reduced seaward residual flow, but this does not suggest that substantial lateral aggregations should be expected. General patterns of abundance were similar at the two locations.

Although we have extensive evidence showing some degree of persistence of various behaviors, we are unable to determine how these translate to position maintenance. Migration by mysids and amphipods in 1994 was sufficient to overcome net seaward velocities, but migration by copepods was not (Kimmerer et al. 1998). Analysis based on Eulerian current data did not take into account the variability in water depth, and vertical variation in current velocity to which copepods would be exposed. Based on the results presented here, the variable bathymetry in the northern San Francisco estuary may play a key role in position maintenance. The frequency and duration of exposure to gravitational circulation may determine the outcome of a particular behavior. To resolve this issue will require modeling studies of the interaction of behavior with the three-dimensional flow field.

An additional, unresolved issue is the advantage for zooplankton to remain in or landward of the LSZ. In many estuaries chlorophyll concentrations or bacterial activity, and therefore the food environment, are enhanced in the LSZ (e.g., Vincent et al. 1996), possibly increasing reproductive success of zooplankton. Another potential advantage is increased turbidity, which may confer advantages in avoidance of predation by visually-feeding planktivores. Both of these effects could help to compensate for losses to seaward advection (Ketchum 1954). Neither of these advantages appears to apply to the LSZ of the San Francisco estuary. Since 1988, chlorophyll concentration has been lower in the LSZ compared to the freshwater delta (Fig. 3), and the size distribution of the phytoplankton in 1994 (Kimmerer unpublished data) indicated a shift toward smaller cells compared with earlier measurements in the region (Cole et al. 1986). Bacterial production in April–October decreased slightly with increasing salinity in the northern estuary, with no sign of a peak in the LSZ (Hollibaugh and Wong 1996). Previous analyses showed no difference in egg ratios of egg-carrying copepods in and out of the LSZ (Kimmerer et al. 1994). There is no clear advantage to being in the LSZ in terms of several measures of potential food concentration. The turbidity maximum reported by Kimmerer et al. (1998) may be ephemeral, possibly related to consistent sampling near the end of the flood tide during the long-term monitoring program (Schoellhamer 2001). Therefore, the advantage to zooplankton of maintaining position in and landward of the LSZ remains unknown.

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