Tidal migration and retention of estuarine zooplankton investigated using a particle-tracking model

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Abstract

We used hydrodynamic and particle-tracking models to investigate vertical movement of plankton and resulting retention in the San Francisco Estuary. The hydrodynamic model was UnTRIM, a three-dimensional, unstructured grid model, which had been calibrated to historical conditions in this estuary for 1994–1997, a period of widely varying hydrology. Intensive field studies of hydrodynamics and vertical movements of organisms during 1994–1996 provided input data for the models. The particle-tracking model was run with 14 alternative behaviors for three 45 d periods of contrasting hydrology. The behaviors included passive behavior, several simple tidal migration patterns, and several sinking speeds. Vertical positions of migrating and sinking particles resembled those seen in the field studies for copepods and epibenthos, respectively. Passive particles were advected from the estuary at rates that depended on freshwater flow. All of the non-passive behaviors caused retention of the particles in the low-salinity region of the estuary under some flow conditions. Tidal migration was very effective at maintaining position, but model results and a re-examination of the field data suggested that migration speed should increase with increasing freshwater flow. Continuous sinking was also effective at retention, particularly in deep areas of low tidal velocity. We conclude that the vertical distributions observed in the field studies were a result of active patterns of movement, that these patterns can result in retention, and that retention in a bathymetrically complex estuary can be understood only in the context of the full time-varying three-dimensional flow field.

Planktonic organisms in estuaries face a continual challenge: they must overcome dispersive and advective losses. Each population of estuarine plankton has a core geographic region or range of salinity in which it is able to thrive, and other regions where it does not thrive or from which a return to the population center is unlikely. The imperative for population maintenance is to maintain abundance in the core region.

Several mechanisms have been proposed that could maintain planktonic populations in estuaries. High population growth rate in the population center could overcome advective and dispersive losses (Ketchum 1954). Although such a mechanism may work for rapidly growing organisms such as phytoplankton, it is an unlikely mechanism for mesozooplankton, which have lower potential population growth rates (Barlow 1955; Hough and Naylor 1991). Behavior that keeps organisms near the bottom, where they are less likely to be entrained in unfavorable flows, could also minimize losses (Rogers 1940). This mechanism is viable, as many estuarine organisms are demersal, and some even have mechanisms for clinging to the bottom and avoid washout by tidal or flood flows (Jacobs 1968; Sheehy and Greenwood 1989; Ueda et al. 2004). Moreover, plankton populations could be maintained in estuaries if dispersion continually reseeds regions where advection has reduced abundance (Speirs and Gurney 2001).

Another mechanism for retention or directed transport is through tidally timed vertical migration. This behavior reaches its extreme in tidal stream transport (Greer Walker et al. 1978), in which the organisms remain on the bottom or move to the margins when currents are unfavorable and enter the water column when currents are favorable, which could be into or out of an estuary depending on the ontogenetic stage of the organism. Tidal stream transport works by ratcheting an organism in one direction with a favorable current and holding it near or on the bottom when the current direction is unfavorable. This behavior has been reported in a wide variety of fish and decapod larvae (Creutzberg 1961; Greer Walker et al. 1978; Forward and Tankersley 2001). It is common and may be ubiquitous among organisms that migrate into or out of strongly tidal estuaries.

Most estuarine holoplankton remain within the water column throughout the tidal cycle, yet populations typically have their highest density over some region of the estuary or range of salinity, implying a mechanism for retention or concentration (Jacobs 1968). For estuaries with strong freshwater discharge, the mechanism would have to limit or reverse seaward transport by the resulting net flow. Among several proposed mechanisms for retention under these conditions, the most likely is tidal vertical migration by which the organisms are on average higher in the water column during flood than during ebb (Wooldridge and Erasmus 1980). This behavior would take advantage of reduced seaward transport, or net landward transport, in the lower part of the water column during ebb and maximize transport landward during flood.

For clarity we use "tidal migration" to mean behavior in which the organisms move entirely within the water column, as opposed to "tidal stream transport," in which

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Table 1. Reports of tidal migration in estuarine holoplankton. This includes a few reports of no migration, but does not include reports of tidal stream transport in which the organisms are absent or much less abundant in the water column on the ebb than on the flood. TVM, tidal vertical migration.

Taxa	Location	Remarks	Reference
Copepods	Georgia, U.S.A.	Eulerian, one station every 2 h for 11 d. <i>Acartia tonsa</i> more abundant at surface on flood, near bottom at high slack. Nauplii appeared to be passive.	Stickney and Knowles 1975
Copepods, mysids	Sundays, South Africa	Eulerian, one night, six stations. Apparent TVM in some species, but sample size small.	Wooldridge and Erasmus 1980
Mysid	San Francisco, U.S.A.	Eulerian, hourly for \sim 24 h at each of two stations. Apparent diel migration and possible TVM, but not statistically tested.	Orsi 1986
Copepod	Westernport, Australia	Four days, one night; Lagrangian sampling on 2 d. TVM in <i>Acartia fancetti</i> but not in <i>Paracalanus indicus</i> , a peritic species.	Kimmerer and McKinnon 1987
Copepods	Conwy, UK	Eulerian, nine occasions inferred; three depths. <i>Eurytemora affinis</i> more abundant and higher in water column on flood than ebb. Copepods have circatidal endogenous rhythms of activity.	Hough and Naylor 1991, 1992b
Amphipods	Conwy, UK	Eulerian, four night tidal cycles. <i>Gammarus zaddachi</i> more abundant and higher in the water column on flood than ebb; higher activity around high tide.	Hough and Naylor 1992 <i>a</i>
Ciliates	Southampton, UK	Eulerian, one complete and one partial tidal cycle. <i>Mesodinium rubrum</i> at surface on flood, avoided on ebb.	Crawford and Purdie 1992
Copepods	Columbia, U.S.A.	Eulerian and Lagrangian, many days. TVM in E. affinis.	Morgan et al. 1997
Copepods, macroplankton	San Francisco, U.S.A.	Three 30 h cruises each of 3 yr, two boats in 1995 and 1996. Lagrangian in 1994–1995, Eulerian in 1996. TVM in adults and copepodites of <i>Acartiella sinensis, E. affinis,</i> <i>Pseudodiaptomus forbesi, Sinocalanus doerrii</i> ; deep distribution in <i>Tortanus dextrilobatus</i> and macroplankton	Kimmerer et al. 1998, 2002
Copepods	Jiulong, China	Eulerian, cruises monthly for 1 yr. Four of five copepod species migrated tidally; <i>Calanus sinicus</i> , a neritic rather than estuarine resident, did not.	Shang et al. 2007
Copepods	Chikugo, Japan	Eulerian over three periods. <i>Sinocalanus sinensis</i> copepodites and nauplii migrated tidally day and night; all stages of <i>Pseudodiaptomus inopinus</i> migrated tidally by day but rose into the water column at night.	Ueda et al. 2010
Copepods	Seine, France	Tidal migration in <i>E. affinis</i> shown in high-frequency Eulerian sampling over five daytime tidal cycles; adults and copepodites migrated but nauplii did not.	Schmitt et al. 2011

the organisms leave the water column during unfavorable currents. Both behaviors have been reported in a wide variety of planktonic organisms (Forward and Tankersley 2001; Table 1).

Most studies of tidal migration or near-bottom residence have been field or laboratory studies showing evidence of tidal migratory patterns or activity patterns (Cronin and Forward 1979; Crawford and Purdie 1992), although a few theoretical or modeling studies have investigated the outcomes of various migration patterns (Show 1980; Hill 1991; Manuel and O'Dor 1997). Retention through tidal migration is rarely in doubt when the water column is stratified and baroclinic flow is strong (Cronin 1982); however, in unstratified waters the effectiveness of tidal migration depends on the details of the circulation pattern (Kimmerer and McKinnon 1987). Although tidal migration is likely energetically expensive and therefore of selective advantage only if it retains organisms, there have been few clear demonstrations that it is effective in unstratified or periodically stratified waters.

A particle-tracking study on the St. Lawrence Estuary demonstrated that vertical movements of particles representing plankton were very effective in retaining and even concentrating particles in certain locations of the estuary (Simons et al. 2006). In that study, sinking or tidal migration sufficient to put particles in the deeper layer resulted in strong retention. However, retention was much more effective when aided by baroclinic circulation.

More generally, though, few studies have linked the vertical distributions of organisms observed in the field to inferred behaviors and to the presumed retention within the estuary. A modeling study showed that tidal movements were essential for matching modeled and observed spatial distributions of Acartia tonsa in a small Texas lagoon (Show 1980). A previous study of tidal vertical migration in the San Francisco estuary included nine 30 h periods of frequent depth-stratified sampling (Bennett et al. 2002; Kimmerer et al. 2002; Hobbs et al. 2006) to estimate the center of mass of the plankton populations as a fraction of the depth of the water column. Bottom-mounted acoustic Doppler current profilers were used to determine contemporaneous vertical profiles of tidal velocity. Evidence for tidal migration was detected for several species of copepod and larval fish. However, two-dimensional (2D; vertical and longitudinal) Eulerian calculations showed that tidal migration was insufficient to overcome net seaward flow because the water



Fig. 1. Model domain in the San Francisco Estuary and coastal ocean (inset) and region of interest for this study showing bathymetry. Letters and rectangles show locations where vertical distributions of particles were sampled, at approximate distances of: (A–F) 76, 64, 56, 46, 36, and 26 km up the axis of the estuary.

column was unstratified. This led the authors to conclude that "(t)o resolve this issue will require modeling studies of the interaction of behavior with the three-dimensional flow field" (Kimmerer et al. 1998). Likewise, Lane et al. (1997) concluded that net fluxes smaller than a few percent of tidal oscillations could not be resolved by intensive field measurements without a numerical model.

Here, we cast the results of that earlier study (Kimmerer et al. 1998, 2002) in a Lagrangian framework. We used a three-dimensional (3D) hydrodynamic model with a particle-tracking model to determine tidal behaviors that mimicked the observed vertical distributions of plankton. We then assessed the outcomes of these behaviors in terms of retention under three different flow scenarios.

Methods

Study area and data—The focus of our study was the northern San Francisco Estuary, particularly Suisun Bay and surrounding waters (Fig. 1). Suisun Bay is shallow with a mean depth of ~ 5 m and a bimodal depth distribution with extensive shoals < 5 m deep and two channels ~ 10 m deep. Immediately to the west the channel

deepens to ~ 30 m in Carquinez Strait as the estuary cuts through part of the Coast Range before broadening again into San Pablo Bay, which links to the south to San Francisco Bay and the Pacific Ocean. To the east of Suisun Bay lies the California Delta, a network of tidal channels, largely freshwater, that separate islands used mainly for agriculture.

The climate is Mediterranean, with generally wet winters and dry summers, and freshwater flow is highly variable. Most freshwater flow entering the estuary comes from the Sacramento River and, to a lesser extent, the San Joaquin River, which meet to form the Delta. Winter–spring flows typically rise following periods of storms and snowmelt, whereas flow during the dry season is under the control of massive state and federal water management projects that store water in winter–spring and release it to be diverted from the southern Delta in summer. Freshwater flow determines the extent of the salinity gradient; during dry periods brackish water penetrates into the western Delta, whereas during floods it extends no further than San Pablo Bay (Fig. 1), about 50 km seaward.

Because it is shallow and tidal currents are strong, much of Suisun Bay is usually well mixed, but Carquinez Strait to the west is stratified in salinity most of the time, and the channels in Suisun Bay can be stratified periodically except during high-outflow conditions. This situation results in a persistent null zone near the sill located landward of the Strait, where baroclinic circulation and an associated turbidity maximum are persistent seaward and intermittent landward of the sill (Schoellhamer 1998, 2001). Cells of baroclinic circulation have been found in the Sacramento River near the confluence with the San Joaquin River (Nichol 1996), and on some occasions in the northern channels of Suisun Bay (Schoellhamer 2001).

Data for freshwater flow (net Delta outflow) were obtained from the Dayflow accounting program (www. water.ca.gov/dayflow). Long-term data on zooplankton abundance were obtained from the Interagency Ecological Program, which has sampled monthly throughout the northern estuary since 1972 (Orsi and Mecum 1986). These data were used to determine the distributions of planktonic organisms in salinity space. We focused principally on the copepod Eurytemora affinis, a member of a species complex found in most north temperate estuaries (Lee 2000). This copepod has a population center around salinity 2 (practical salinity scale) in this and many other estuaries (Schmitt et al. 2011). Since 1987 E. affinis has been abundant only in winter-spring, and it disappears from the plankton by June each year (Kimmerer and Orsi 1996; Winder and Jassby 2011), so we used data from 1972 to 1986 for this analysis, including May-October when this species was most abundant.

Model—The UnTRIM San Francisco Bay–Delta Model (MacWilliams et al. 2008; MacWilliams and Gross 2013; M. MacWilliams unpubl.) was applied to simulate hydrodynamics for a period spanning from 01 April 1994 through 01 April 1997. The model domain extends from the Pacific Ocean through all of San Francisco Bay and the entire California Delta (Fig. 1). The model takes advantage of the grid flexibility allowed in an unstructured mesh by varying grid cell sizes. The horizontal grid resolution is \sim 1 km at the ocean boundary and ~ 400 m at the mouth of the estuary, decreasing with distance in the landward direction to 50–75 m in the western Delta and 10–50 m in the narrower channels of the central and southern Delta. The vertical grid resolution is 1 m to a depth of 20 m, below which it increases gradually from 1 to 5 m. The grid contains 129,946 horizontal grid cells and $> 10^6$ 3D grid cells. A description of the model boundary conditions and the results of the model calibration and validation are presented in MacWilliams et al. (2008; M. MacWilliams unpubl).

The flexible integration of staggered-grid hydrodynamics particle-tracking model (FISH–PTM) is a 3D particletracking model that estimates particle trajectories using 3D hydrodynamic information from UnTRIM. Instantaneous values of water level, velocity, and eddy diffusivity were archived to files at a half-hour interval. The backward Itô stochastic differential equation (La Bolle et al. 2000) was used to estimate particle trajectories. Node velocities were estimated from the velocities normal to cell faces using the nRT2 method described by Wang et al. (2011). Velocity



Fig. 2. (A) daily freshwater flow into the estuary from the Sacramento–San Joaquin Delta during model runs for low (L), medium (M), and high (H) flows. (B) Freshwater flow (left axis, thick line) and position of the salinity 2 isohaline as distance up the axis of the estuary (X2, right axis, thin line). Tick marks at top indicate sampling dates in 1994–1996; vertical bands indicate periods modeled using the PTM identified by flow range with letters L, M, H.

was then interpolated from node velocity values to particle locations by the method of generalized barycentric coordinates (Meyer et al. 2002). The time step for both advection and diffusion was chosen such that displacements in a time step do not exceed vertical or horizontal cell spacing. The particle tracking method is first-order accurate in time and space.

We selected three 45 d periods from the 1994–1997 simulation period for particle-tracking analysis to obtain a range of realistic flows (Fig. 2). The periods were: low flow starting 17 April 1994, with median freshwater flow at the 16th percentile of all daily flows from 1955 through 2012; medium flow, starting 17 August 1995, with median flow at the 61st percentile; and high flow, starting 01 January 1995, with median flow at the 95th percentile. Note that these periods are unrelated to the sampling periods (Fig. 2), which were selected in relation to the phenology of larval fish.

Particles were given one of 14 behaviors (Table 2), including neutrally buoyant or passive behavior, constant sinking at several speeds, and tidal migration at several speeds. Tidal direction was established for each grid cell at each time step based on the flow velocity in relation to the orientation of the channel axis. Particles that migrated

Table 2. Particle behaviors used in model runs. Each behavior was run for all three flow scenarios, and all behaviors remained constant for the entire run. Behaviors with abbreviations are explored in Table 3 and Figs. 4, 8; those without abbreviations were eliminated from further analysis because they were essentially redundant (*see* Methods). Behaviors in bold are shown as examples in Figs. 3, 6, and 7.

Identifier	Behavior	Abbreviation	Velocity (mm s ⁻¹)
Α	Neutrally buoyant	Passive	—
В	Sink if above 1 m from bottom; otherwise neutral	—	-0.5
С	Sink	Sink 0.5	-0.5
D	Sink if above 1 m from bottom, otherwise neutral	_	-0.5
Е	Sink	Sink 1	-1.0
F	Sink if above 1 m from bottom, otherwise neutral	_	-1.0
G	Sink	Sink 2	-2.0
Н	Sink if above 1 m from bottom, otherwise neutral	—	-2.0
Ι	Tidal migration; swim up on flood, down on ebb	Tidal 0.25	± 0.25
J	Tidal migration	Tidal 0.5	± 0.5
Κ	Tidal migration	Tidal 1	± 1.0
\mathbf{L}	Tidal migration biased downward	Tidal B 0.5	+0.25, -0.75
Μ	Tidal migration biased downward	Tidal B 1	+0, -1.0
Ν	Tidal migration biased downward, neutral if $ u < 0.20$ m s ⁻¹	—	+0.25, -0.75

tidally moved up at the selected speed during floods and down during ebbs. Three of the tidal behaviors were biased, with sinking speed on the ebb greater than rising speed on the flood.

Several behaviors had two versions; for example, all of the sinking behaviors had alternatives in which the particles would become passive if they were within 1 m of the bottom. This was intended to prevent particles from becoming stuck in low-velocity near-bottom locations. However, the results from these runs did not differ noticeably from those without this restriction, so those data are not presented or discussed further. A biased tidal migration scheme was tried in which migration ceased around slack water, in an attempt to reduce artifacts that were apparently due to particles being at their shallowest position late in the flood and deepest position late in the ebb, which offset the tidal migration pattern from that of the tidal currents (see Discussion). This modification to the original biased migration scheme likewise had no noticeable effects on the outcome and is not discussed further. We also focused much of our analytical attention on a few example behaviors (Table 2). Passive behavior was used as a null model. The sinking behavior with the slowest sinking speed (0.5 mm s⁻¹) was selected to roughly match observed vertical distributions of macroplankton and epibenthos (Kimmerer et al. 2002). The slower of the two biased tidal migration behaviors was selected as the one that resulted in the closest match of vertical movement from all model output to the mean of all of the field data

Particles were released at the first time step of the simulation in a pattern intended to mimic the distribution relative to salinity of the copepod *E. affinis*. This allowed us to use the rate of loss of particles from this salinity range as an intuitive, quantitative measure of the efficacy of each behavior for retention. An alternative would have been to seed the particles randomly within the domain, but in that case, most of the particles would have been far removed from the region of interest in the northern estuary, and interpretation would have been difficult.

To set up the releases, a series of salinity bins was established: < 0.05, then in 13 logarithmically equal steps from 0.05 to 1, then by 1 to 34 (i.e., 1, 2, 3, ..., 32, 33, 34), and > 34. The low-salinity bins were intended to give good resolution in the region of interest for the copepods without having excessive bins in other regions. The volume of water in each salinity bin was determined from output of the hydrodynamic model. Next, for each release (behavior) group the proportion of particles in each salinity range was determined from the distribution of E. affinis with respect to salinity. Approximately 80,000-100,000 particles were released for each behavior, and target densities for each salinity range were calculated from the numbers of particles and the proportion in each salinity range. All particles were released only in the northern portion of the model domain (i.e., from San Pablo Bay east). The number of particles released in each grid cell was calculated based on the salinity in the cell and the volume of the cell to achieve, on average, the desired density of particles (m^{-3}) in each salinity range. All particles were released at cell centers.

Analysis of PTM output—The location (x, y, z) of each particle was reported every half hour along with salinity of the grid cell surrounding the particle and its velocity. Postprocessing steps extracted information relevant to this analysis. Six sampling sites (Fig. 1) were set up and, for each flow scenario, three of the six were selected from the region with the highest particle density. At each half-hour reporting time, the vertical positions of all particles within each site were used to calculate the depth of the center of mass of all particles within the site. Across all model runs and behaviors, these samples contained 1-1579 (median 124) particles. This sampling mimicked the field sampling for zooplankton, except that the exact position of every particle was known, whereas the zooplankton distributions were determined from vertically stratified net or pump samples (Kimmerer et al. 2002).

The height above bottom of the center of mass of particles as a fraction of water column depth (scaled from 0

at the bottom to 1 at the surface) was then plotted against velocity (flood is positive) for each half-hour reporting time. A smoothed line was fitted to the data to aid in interpretation; we used a generalized additive model with a spline smoother (Hastie and Tibshirani 1990) weighted by the number of particles in each reporting time. We also computed a linear fit with the same weighting, to allow comparison of slopes with the results of field sampling.

Since only a handful of behaviors was modeled, we attempted to bracket the range of likely vertical migration speeds and did not expect to model the exact speed at which the organisms were moving. Furthermore, the actual swimming speeds are likely to vary temporally and spatially, and our field data show some evidence of this, as discussed below. For these reasons we did not attempt a statistical test of the correspondence of vertical movements of particles with those of organisms. Rather, we relied on the fact that our range of particle movements bracketed the range of observed movements and examined the consequences for longitudinal movement from the range of behaviors.

The final distribution of particles in salinity space should resemble that of copepods if the retention mechanism is reasonably accurate, although variation in reproduction and mortality with salinity would also influence the spatial distribution of copepods and would alter their distribution relative to that of particles with identical behavior. We used the salinity of each particle's cell, together with the number of particles divided by the volume in each salinity bin, at the end of the run to determine a resource use function (Manly et al. 2002). This was compared graphically with the distribution of copepods in salinity space. A more formal comparison was not attempted because of the probable effect of birth and mortality on the distributions of copepods.

Over the model run, particles may leave the model domain through the ocean boundary, leave the domain through the diversion pumps in the southern Delta, or remain within the domain inside or outside a selected range of salinity. The fraction of particles that leave the domain or "escape" the selected range toward higher salinity over time could be considered losses to the population. Thus, if the retention mechanism were effective, this loss would be small in relation to typical mortality values for these copepods (on the order of 1–10% d⁻¹; Hirst and Kiørboe 2002). We calculated loss rates as

$$L = 100 \frac{d(\ln[N(t)])}{dt}$$
(1)

where L is the daily percentage of particles that were lost, N(t) is the number of particles remaining in the domain and below the salinity limit, and the rate of change was determined by linear regression of the log-transformed number of particles remaining. Note that loss rates were not constant under the high-flow scenario, but this provides an easy way to compare among scenarios. For most model runs the selected salinity limit was 10. We also used several alternative salinity limits (15, 20, and 25) as a sensitivity check.

Results

Eddy diffusivity values estimated by UnTRIM varied strongly with tidal phase and stratification and ranged from on order of molecular viscosity (10⁻⁶ m² s⁻¹) in strongly stratified areas up to 0.1 m² s⁻¹ in energetic unstratified areas. Therefore the effectiveness of behavior in moving the center of mass of particles away from the middepth varied with position and tidal phase. Nevertheless, the vertical distributions of particles showed strong effects of behavior that manifested as movement of the depth of the center of mass calculated from all particles in each sample. These movements were related to alongchannel velocity, both sampled at locations in Fig. 1. Results for the three example behaviors at selected sampling sites (Fig. 3) show that centers of mass of passive particles were clustered around middepth at all tidal velocities, as expected. The total number of particles sampled for the passive behaviors (left column of Fig. 3) was generally less than those for other behaviors because passive particles rapidly dispersed seaward, especially in the high-flow scenario. The smaller sample size at each reporting time resulted in greater vertical variation in centers of mass for the passive behavior in the high-flow scenario compared with other scenarios.

Centers of mass of sinking particles remained below middepth with a U-shaped distribution by which they were higher in the water column during both strong ebb and flood than at lower tidal velocities. The biased tidal migration behavior resulted in a rotation of the distribution relative to that of sinking particles, so that particles were deeper in the water column on the ebb than on the flood. In the migrating cases, there was hysteresis such that data traced a cyclical pattern from deep at the beginning of the flood to shallow at the end of the flood and to the beginning of the ebb, and eventually deep at the end of the ebb (Fig. 3).

Each of the examples in Fig. 3 and data for the remaining sample sites and selected behaviors (Table 2) were characterized by spline curves (Fig. 4) to illustrate how patterns changed with flow and location. In all but the passive cases the shapes of the relationships differed among flows, sample sites, and to some extent swimming or sinking speed. Centers of mass of passive particles had slight responses to velocity, but the directions were inconsistent. Centers of mass of sinking particles were consistently below middepth and, for low and medium flows, U-shaped. For particles that migrated tidally, centers of mass were mostly higher on the flood than the ebb. Increases in sinking speed beyond 0.5 mm s⁻¹ had relatively small effects on vertical distributions (Fig. 4 for Sink 0.5, 1, and 2). Increases in tidal migration speed steepened some of the relationships of depth of center of mass to tidal velocity (Fig. 4 for Tidal 0.25, 0.5, and 1 and the two biased behaviors).

Linear regressions of the scaled depth of center of mass on tidal velocity weighted by the number of particles passing through the sample site during each 30 min time step were determined for each of the curves in Fig. 4 (Table 3). Linear regression is clearly inappropriate for



Fig. 3. Location of center of mass of particles as a fraction of the water column depth vs. tidal velocity (positive landward) for three selected behaviors during the three flow periods for particle sampling locations B (low or medium flow) or E (high flow; Fig. 1). The areas of symbols indicate the number of particles included in calculating each data point, scaled in all panels by the key shown in the top center panel. Lines include linear regressions (thin lines) and smoothing spline curves (thick lines), both modeled with weighting by the number of particles represented by each point. Arrows in the upper right panel show hysteresis as demonstrated by separate smoothing spline curves for increasing (lower) and decreasing (upper) velocity, shifted up and down for clarity and linked to a segment of the regression line for comparison.

some of the data, notably those from sinking behaviors at low and medium flows, with their U-shaped patterns. Nevertheless, we present these as indices of the responses of the particles to velocity, and for comparison with slopes determined from vertically stratified samples of zooplankton, which averaged around 0.1 (m s⁻¹)⁻¹ (Kimmerer et al. 2002). Slopes of these regressions were consistently positive for the tidal migration behaviors (Table 3); that is, the center of mass tended to be deeper on the ebb than on the flood. This was not the case for the passive or sinking behaviors, for which the regression slopes were usually different from zero owing to the large sample sizes, but inconsistent in sign among locations and flow scenarios (Table 3).

In all scenarios the horizontal movements of most particles were dynamic on tidal and longer timescales. Maximum 1 d excursions of individual particles in distance along the axis of the main channel were 10–25 km (10th and 90th percentiles), with the greatest excursions for the passive case and the highest flow. The different behaviors resulted in great differences in the final spatial distributions of particles, relative to the initial distributions, after 45 d (Fig. 5). Passive particles were spread throughout the entire estuary and out into the coastal ocean. Concentrations in the ocean were low, but a large fraction of the particles was outside the estuary, and many had left the model domain. For the Sink 0.5 behavior, particles were concentrated in channels of Suisun Bay and the western Delta, with a few hot spots in channels of Suisun Marsh. The particles apparently accumulated there because the channels were relatively deep, and the particles oscillated within a few model grid cells. Each particle continued to move horizontally and vertically, with excursions to the surface; thus, these particles were not stuck but were trapped by hydrodynamic processes. For the Tidal B 0.5 behavior, particles moved further landward than in either of the other two cases and did not appear to become trapped to as great an extent as in the Sink 0.5 case.

Concentrations of particles by salinity bin at the end of the 45 d run (Fig. 6) differed substantially between the passive behavior and other behaviors shown. At all three flows, most of the passive particles were at high salinity, but because of the much larger volumes at high salinity, notably in the ocean part of the domain, the concentrations



Fig. 4. As in Fig. 3 for all locations and nine behaviors, with only the spline curves (Fig. 3) shown and axes and data omitted for clarity. Underlined behaviors and sampling locations are shown in detail in Fig. 3.

there are low. Also, particles that had left the domain at the ocean or landward boundary did not contribute to calculated concentration. At low flow (Fig. 6A) the Tidal B 0.5 and Sink 0.5 behaviors both resulted in a broad peak between salinities of 0.4 and 6. The anomalous peak in particle density for the Sink 0.5 behavior at salinity ~ 8.5 was largely a result of the accumulation in Suisun Bay and Suisun Marsh (Fig. 5). At medium flow (Fig. 6B) the peaks resulting from the tidal and sinking behaviors separated, with that from the tidal behavior at a somewhat lower salinity. At high flow, both the tidal and sinking behaviors resulted in peaks in density at salinity above ~ 3 , but densities were low because many particles were in the large, high-salinity region.

Distributions in salinity space of *E. affinis* from longterm monitoring plotted in Fig. 6 matched moderately well with the Tidal B 0.5 behavior at low and medium flows. Data were not available to match the high-flow condition because the limited geographic range of the monitoring program meant that few samples were taken outside of the freshwater region of the estuary when flow was high.

The time course of particle locations in salinity and geographic space shows great differences among the three selected behaviors and among the three flow periods (Fig. 7). Passive particles rather quickly moved seaward, even in the low-flow case. By day 20 at low flow, more than half of the passive particles had reached salinity > 20 or had left the model domain at the seaward boundary. As flow increased, this transport accelerated, as is evident

around day 15 in the high-flow case when flow increased sharply (Fig. 2A). Sinking particles at low and medium flow appeared to reach an equilibrium, with most of the particles in salinity 0.5–10. At high flow about half of the particles were in the 10–20 salinity bin. Tidally migrating particles in the low-flow case moved landward, and significant numbers became entrained in water diversions in the south Delta. At medium flow the particles stayed mostly in the low-salinity zone, whereas at high flow they moved rapidly seaward following the flow pulse.

All nine of the sinking or swimming behaviors that were analyzed resulted in reduced rates of loss compared with loss rates of the passive behavior for at least some flows (Eq. 1; Fig. 8). The sinking behaviors were effective in reducing losses to very low levels, except under the highest flow. The tidal migration behaviors were most effective if the migration speed increased with increasing flow. For example, tidal migration at only 0.25 mm s⁻¹ sufficed to overcome advection at low flow, but only the 1 mm s^{-1} tidal migration speed was effective at high flow. The biased tidal migration behaviors were somewhat more effective than the pure tidal behaviors at the same speeds. At high flow the 1 mm s⁻¹ swimming speed was considerably more effective than 0.5 mm s^{-1} . Loss rates with alternative salinity limits (10, 15, or 25 vs. 10 in Fig. 8) declined as salinity limits increased, but the relative differences from the corresponding passive cases were similar, and the values in Fig. 8 were strongly correlated with corresponding values with the alternative salinity limits (r = 0.97-0.99).

Table 3. weighted by n	Slopes w. umber of	ith 95% confidenc f particles, for each	e limits of linear h flow and sampl	regressions of de e site (Fig. 1) and	spth of center of a subset of beha	mass of particle aviors. The slope	s as a fraction o es are organized	of the height of by row and col	the water colu lumn as in Fig.	nn vs. velocity 4.
Flow	Site	Passive	Sink 0.5	Sink 1	Sink 2	Tidal 0.25	Tidal 0.5	Tidal 1	Tidal B 0.5	Tidal B 1
Low	А	0.022 ± 0.003	-0.018 ± 0.008	-0.011 ± 0.01	-0.011 ± 0.009	0.079 ± 0.005	0.132 ± 0.009	0.22 ± 0.021	0.076 ± 0.007	0.047 ± 0.012
	в	-0.004 ± 0.003	0.022 ± 0.009	0.033 ± 0.011	0.032 ± 0.011	0.034 ± 0.004	0.066 ± 0.006	0.183 ± 0.016	0.044 ± 0.006	0.074 ± 0.010
	C	-0.016 ± 0.002	-0.012 ± 0.006	-0.013 ± 0.008	-0.013 ± 0.008	0.031 ± 0.004	0.076 ± 0.007	0.146 ± 0.011	0.048 ± 0.005	0.050 ± 0.007
Medium	Α	0.024 ± 0.005	-0.008 ± 0.007	-0.001 ± 0.008	-0.001 ± 0.008	0.082 ± 0.005	0.138 ± 0.008	0.238 ± 0.013	0.079 ± 0.006	0.047 ± 0.009
	в	-0.016 ± 0.006	0.023 ± 0.009	0.041 ± 0.011	0.042 ± 0.011	0.017 ± 0.005	0.052 ± 0.007	0.143 ± 0.010	0.032 ± 0.006	0.061 ± 0.009
	C	-0.014 ± 0.005	0.006 ± 0.007	0.005 ± 0.008	0.006 ± 0.008	0.006 ± 0.004	0.028 ± 0.004	0.064 ± 0.007	0.024 ± 0.003	0.046 ± 0.005
High	D	0.028 ± 0.014	0.002 ± 0.010	-0.007 ± 0.009	-0.010 ± 0.009	0.123 ± 0.017	0.226 ± 0.021	0.550 ± 0.029	0.139 ± 0.016	0.133 ± 0.013
	Щ	0.013 ± 0.015	-0.081 ± 0.010	-0.085 ± 0.01	-0.084 ± 0.010	0.064 ± 0.015	0.128 ± 0.018	0.311 ± 0.023	0.057 ± 0.012	0.039 ± 0.012
	Ц	0.025 ± 0.007	-0.047 ± 0.008	-0.047 ± 0.008	-0.046 ± 0.008	0.034 ± 0.007	0.052 ± 0.008	0.102 ± 0.011	0.022 ± 0.007	0.014 ± 0.008

of tidal migration in a stratified water column, and such migration would be unlikely without a selective advantage to the organisms that expend the energy to migrate. Exceptions to tidal migration are informative in this regard. Two copepod species collected abundantly in tidal migration studies but not observed to migrate tidally were neritic species (i.e., not resident in the respective estuaries; Calanus sinicus, Paracalanus indicus; Table 1). Presumably retentive or other behavioral responses to tidal currents would lack selective advantage for neritic species. Although the link from behavior through hydrodynamics to retention is logical, it has rarely been made quantitatively. Most reports have simply assumed that tidal migration

Tidal migration may be ubiquitous in estuarine holoplankton, at least in regions where river flow induces net seaward movement. Several reports have presented field evidence of tidal migration, although that evidence is based on only a handful of species and rests on small sample sizes in some cases (Table 1). Retention is a logical consequence

would result in retention, and some even refer to the migration itself as retention without having demonstrated retention by analyzing the interaction of the flow field with vertical position of the organisms (Hough and Navlor 1991). Thus, analyses such as that presented here and a handful of previous reports (Kimmerer and McKinnon 1987; Simons et al. 2006) are necessary to make quantitative links between tidal behavior and retention and to determine whether retention is a necessary outcome of tidal migration.

An analytical model by Hill (1991) determined the conditions under which tidal migration could result in retention. Net landward transport of a particle through tidal vertical migration was maximized with perfect phasing of vertical position with the tide, maximum shear in the vertical velocity profile, and maximum amplitude of the migration. Shear is greatest where the water column is strongly stratified and net flow reverses at depth. Amplitude is maximized in tidal stream transport, by which organisms move to the bottom and achieve zero velocity when the current flows in the unfavorable direction. The borderline cases occur where vertical movements are subtle or limited (e.g., because of vertical turbulence) and where shear occurs only through straining of the water column in the absence of stratification.

Two field studies took the next step by calculating the likely net transport or retention resulting from migration. Tidal migration by the copepod Acartia fancetti was sufficient to effect retention in a channel of an unstratified marine bay (Kimmerer and McKinnon 1987; see McKinnon et al. 1992 for species identification). This demonstrated that baroclinic circulation was not essential for retention by tidal migration, although freshwater input to that bay was very low and therefore seaward transport by advection was negligible. Conversely, tidal migration by copepods in the upper San Francisco Estuary was insufficient, and no amount of migration within the water column would have been sufficient, to overcome net seaward transport as determined by 2D Eulerian calculations (Kimmerer et al. 1998, 2002).

Discussion



Fig. 5. Initial and final distributions of particles as concentrations on a log scale (right) under the low-flow scenario. (A) initial particle distributions. (B) Passive behavior. (C) Sink at 0.5 mm s⁻¹ (Down 0.5). (D) Tidal migration biased downward, speed 0.25 mm s⁻¹ up on flood and 0.75 mm s⁻¹ down on ebb (Tidal B 0.5).

Here we have shown that tidal migration similar to that observed in the field can be highly effective at reducing losses from zooplankton population centers. The principal difference between the earlier 2D calculations and the results of 3D modeling is that the entire flow field is involved in the interaction between vertical position and horizontal motion. This is not surprising, as aggregations due to interactions between vertical and horizontal movements have been observed many times (e.g., at fronts [Franks 1992] or sills [Gagnon and LaCroix 1983]). The upper San Francisco Estuary is bathymetrically complex, with multiple channels, some deeply incised, numerous backwaters, and extensive shoals. Baroclinic circulation occurs in cells of deeper water such as Carquinez Strait (~ 30 m deep), especially during neap tides (Monismith et al. 2002), and in shallower channels off the main channel where tidal flows are weaker (Schoellhamer 2001). Thus, the factors that influence the retentive effects of tidal vertical migration (Hill 1991) are highly variable in space and time in this estuary.

Similar results were obtained in a 3D modeling study of the St. Lawrence Estuary (Simons et al. 2006). The two estuaries are somewhat similar in bathymetric complexity, but the St. Lawrence is substantially deeper, and therefore stratification and baroclinic circulation are apparently more frequent; indeed, baroclinic circulation was an essential feature of retention in that modeling study (Simons et al. 2006).

Patterns of vertical movement—Did the copepods really migrate actively? Based on our particle-tracking results, it seems they did. Passive particles had positive slopes of vertical distribution vs. velocity in several instances, including at all three sampling sites in the high-flow scenario (Table 3). Confidence limits of these small slopes did not include zero in most cases, but that was a consequence of the large number of data points. The main point is that these slopes were not always positive and were much smaller than those resulting from the tidal migration. They are probably a consequence of the skewed spatial distribution of particles at release (Fig. 5A) interacting with the variable bathymetry.

It is also possible that placement of sampling sites near bathymetric features that aggregate organisms that sink



Fig. 6. Final distributions of particle concentrations in salinity space and distributions of copepods (*Eurytemora affinis*) during (A) low, (B) medium, and (C) high-flow conditions for the three behaviors shown in Figs. 3 and 5. Copepod densities are not plotted for high flow because there were too few samples in brackish to saline water.

can result in apparent vertical migration. Our vertical profiles showed considerable differences in patterns of vertical movement for migrating or sinking particles among rather closely spaced sampling sites, with the strongest movements often occurring at the deeper sampling sites (Fig. 4; Table 3), suggesting an effect of bathymetry or reduced vertical mixing due to stratification in deeper locations. However, the sampling schemes for the previous field studies involved a variety of sampling arrangements under a variety of flow conditions and were Lagrangian during 2 of the 3 yr of the study (Kimmerer et al. 2002). This essentially rules out artifacts, although it may help to explain the variability in results among sampling cruises.

The swimming speeds assigned to the particles seemed reasonable. Most aquatic organisms can maintain swim-

ming speeds of 1 body length s^{-1} (~ 1 mm s^{-1} for the copepods in this study) for long periods, and copepods are capable of burst swimming of nearly 1000 times that speed. Tidal migration speed of *A. fancetti* in an Australian bay was estimated at about 1 body length s^{-1} , and it is possible that planktonic organisms use the turbulence structure of the water column to aid, rather than hinder, their movements (Kimmerer and McKinnon 1987).

The two groups of active behaviors, continuous sinking and tidal migration, resulted in very different vertical positions and relationships of the center of mass with velocity (Figs. 3, 4; Table 3). Continuous sinking at all speeds resulted in mean depths well below the midpoint of the water column and in U-shaped patterns of mean depth with tidal velocity, except at the highest freshwater flow.



Fig. 7. Particle fates for the conditions in Fig. 3: fraction of the particles in several salinity bins, past the ocean boundary, or lost to entrainment in diversion flows from freshwater.

These patterns of vertical distribution vs. velocity resembled those of epibenthic organisms including mysids, amphipods, and the shrimp *Crangon franciscorum (see* fig. 9 in Kimmerer et al. 2002) and likely arose from the increase in turbulent mixing at high positive or negative velocities, which overcame the settling of these particles to some extent. For the epibenthic organisms in the estuary, the U-shaped pattern may have been amplified by tidally stimulated swimming activity (Cronin and Forward 1979; Hough and Naylor 1992*a*) and were further modified by diel variability in depth distributions.

Tidal migration resulted in the particles being higher in the water column on the flood than on the ebb (Fig. 4), and these distributions steepened as the swimming speed increased (Table 3). Adding a bias toward sinking in the vertical movements caused the vertical distribution of center of mass to resemble a mixture of those from the unbiased tidal migration behavior and the sinking behavior. This reduced the range in mean depth between maximum flood and maximum ebb, and therefore also the slope of mean depth vs. velocity, but also caused particles to spend more time in the deeper part of the water column.

The principal difference between the vertical movements of particles and those observed for copepods in the field was the hysteresis evident in the particle movements (Fig. 4). The rules for particle movement were very simple: particles moved upward any time the water velocity was in a flood direction in their grid cell and downward when the water was ebbing. Since it took some time for vertical position to change, the particles were deep in the water column well into the flood and shallow well into the ebb, and they reached their ultimate positions late on each tide. This means that the position of the center of mass of particles was not fully synchronous with respect to tides, reducing the effectiveness of their vertical movements at effecting retention (Hill 1991).

We re-examined the copepod data for hysteresis and did not find it. The copepods appeared to be moving so that their position, not their velocity, was well-synchronized with the tidal currents and therefore optimal for retention (Hill 1991).

This suggests that our movement rules were too simplistic. A more realistic rule in retrospect would have been for movement to reverse as the tidal current decelerated. As an alternative, we tried simply making the particles passive when tidal current speed was less than 0.20 m s^{-1} , but that change had little effect. Likewise, movement rules that included avoidance of the surface or the bottom had little influence on vertical position and were not explored further. Avoidance of the surface and diel migration away from the surface are common behaviors. Although these have been implicated in retention (Crawford and Purdie 1992 for ciliates), these behaviors are likely to be effective in retention only in a water column with shallow stratification.

Consequences for horizontal distribution and retention— Both sets of non-passive behaviors resulted in very patchy horizontal distributions of particles at any one time



Fig. 8. Loss rates of particles by flow condition for nine behaviors, as percent per day. Particles were considered lost if they crossed the ocean boundary, were diverted from the freshwater reach of the estuary, or arrived at and remained in salinity > 10. Underlined behaviors are those presented in Figs. 3, 6, and 7. The y-axis scales are the same in all three panels.

(Fig. 5). Despite the similarity of tidally averaged positions in salinity space between initial distributions and final distributions for some behaviors (Fig. 6), the actual final positions of particles were much less homogeneous than the initial distributions. For example, sinking particles were concentrated in sections of deep channels and in certain areas of shoal, notably in northern Suisun Bay, as well as small channels (Fig. 5C). Vertically migrating particles were somewhat more broadly distributed but still patchy (Fig. 5D). The patchy distribution of particles was likely a result of the interaction between vertical movements and the highly variable bathymetry in the estuary, which is a likely source of patchiness in zooplankton distributions.

In striking contrast to the outcomes for non-passive behavior, passive particles were lost from the system at rates that were high compared with typical population growth rates of planktonic organisms (Fig. 8). Loss rates of passive particles increased with freshwater flow as a result of the increase in residual flow through the estuary. The final distributions of passive particles indicated a center of mass well to seaward of the release area (Fig. 6).

At low and intermediate flow, most of the behaviors resulted in substantial reduction of losses to higher salinity (Figs. 6–8); however, there were important differences in the interactions of these behaviors with freshwater flow. At the lowest flow, losses for the 1 mm s^{-1} tidal migration behavior were about half those of passive particles and much larger than those of the other behaviors. This result came about because the particles ratcheted into freshwater, where they became entrained in flows of freshwater pumped out of the estuary; by contrast, seaward losses for this behavior were negligible.

At intermediate flow the 0.25 mm s⁻¹ tidal migration behavior became less effective than the behaviors with more rapid swimming speeds. Turbulent mixing overcame this rather weak swimming, resulting in small changes in the relationship of center of mass with current velocity (Table 3). All of the other behaviors effectively eliminated advective and dispersive losses at this flow (Fig. 8).

At high freshwater flow, the sinking behaviors remained effective, but some of the tidal migration behaviors became much less so (Fig. 8). Presumably the tidal behaviors generally did not hold the particles in the deeper layer long enough to overcome net seaward transport in the more rapidly moving surface layer. Tidal migrations at 1 mm s⁻¹, with and without bias, were the only tidal behaviors that kept the loss rate below 5% d⁻¹, although the loss rate for the 1 mm s⁻¹ biased tidal migration was the lowest among all behaviors.

Freshwater flow at least as high as that in our high-flow scenario occurs frequently in the San Francisco Estuary, with a return period of flows above the maximum in our study period of 138 days. There are three possible outcomes for zooplankton during these periods.

- (1) The zooplankton may undergo a period of depressed abundance and slow recovery after a high-flow period. The highest flow year was 1983, when flow exceeded the median of our high-flow period for a total of 104 d (80 consecutive). Abundance of copepods during 1983 was not particularly depressed compared with that in earlier or later years (Winder and Jassby 2011). Furthermore, there is little relationship between copepod abundance and freshwater flow in the estuary (Kimmerer 2002).
- (2) Copepod populations could recover rapidly through high population growth. Populations of two estuarine copepod species recovered their abundance after floods through a combination of position maintenance near the bottom in deep channels and rapid population growth after the floods (Ueda et al. 2004). High population growth rate of copepods after floods in the San Francisco Estuary is unlikely because these floods occur most often in winter to early spring when temperature and phytoplankton production, and therefore maximum growth rates of copepods, are low.
- (3) Copepods may adjust their behavior with changes in freshwater flow. It is unlikely that they can detect freshwater flow directly, but they could adjust their behavior based on salinity. This seems likely, although based on limited evidence. There are many examples of ontogenetic reversal of the direction of tidal stream transport in estuarine organisms (Forward and Tank-



Fig. 9. Data from the 1994 to 1996 field study reformatted (Kimmerer et al. 2002). Boxplots show medians, quartiles, and extreme values of slopes of depth of center of mass as a fraction of water column depth vs. velocity for each year. Letters indicate corresponding values for individual species with x values jittered for readability: A, *Acartia* spp.; E, *Eurytemora affinis*; P, *Pseudodiaptomus forbesi*; S, *Sinocalanus doerrii*. Values in circles are from the westernmost of two vessels (*see* Discussion).

ersley 2001). Tidal migration of *E. affinis* varied in strength with location relative to the population center in a Welsh estuary (Hough and Naylor 1991). Additionally, the apparent strength of tidal migration in the 1994–1996 studies varied with freshwater flow if location is taken into account (Fig. 9). The slopes of depth of center of mass vs. tidal velocity were bimodal during the high-flow year (1995), with steeper slopes in samples taken from the more landward of the two vessels used in the Lagrangian sampling scheme that year. The more seaward vessel was often in shallower water with strong tidal currents and wind waves, likely resulting in reduced ability of the copepods to maintain vertical position.

The sinking behaviors resulted in retention under all flow conditions, more so than the tidal migration behaviors. Particularly at low flow, a substantial amount of this retention occurred in marsh sloughs. This was not an artifact of the way the model moves particles, but rather a consequence of the interaction of behavior and hydrodynamics as represented by the model. It is consistent with the accumulation of fine, slowly settling sediment particles in backwaters and shoals, except that sediment can be cohesive once deposited, whereas the particles never settled to the bottom and remained there, but continually moved vertically and horizontally.

Trapping, such as that observed for sinking particles, is probably uncommon for organisms such as mysids that tend to remain near the bottom. These organisms are relatively strong swimmers, and we presume that they, too, can modify their behavior to achieve some objective. Uncommon or not, an aggregation of macroplankton in small areas such as this would presumably attract predators and therefore might not be observed in field data. Horizontal distributions of particles and plankton—The tidal migration behaviors resulted in peaks of particle density at salinities between ~ 0.5 and 5 near the landward limit of the salinity-derived density gradient and therefore the buoyancy gradient necessary for stratification. Although this was close to the peak abundance of one copepod species (Fig. 7), there are three additional factors to be considered when interpreting these results.

- (1) The migratory behavior driving these distributions was detected in copepodites and adults. Nauplii may be too small to swim continually at rates necessary for substantial shifts in the center of mass in this estuary, although nauplii have also been reported to migrate tidally (Ueda et al. 2010). The vertical distributions of nauplii were not determined during the 1994–1996 field studies. The actual distributions of copepods is likely to depend on passive drifting of nauplii for the duration of these stages (typically a week or two; Kimmerer and Gould 2010) and migration during copepodite (duration also a week or two) to adult (duration usually a few weeks) stages (Stickney and Knowles 1975; Schmitt et al. 2011). A lack of migration in nauplii would dilute the retentive effect of the migration.
- (2) Copepods hatch, adjust their behaviors, and die, but particles are sterile, unchanging (in our model), and immortal. Spatially variable birth or mortality likely play a key role in spatial distributions. Spatial (or salinity-based) adjustments in behavior (Hough and Naylor 1991; Seuront 2006; Ueda et al. 2010) likely cause adjustments of position as freshwater flow changes and alters the salinity and velocity field.
- (3) Not all copepods are retained in the same salinity range. E. affinis was most abundant where the particles were retained through tidal migration, and it is most abundant at salinities of 0.5-5 in most temperate estuaries of the northern hemisphere (Schmitt et al. 2011). However, other copepods are most abundant at other salinities; for example, in the San Francisco Estuary, Pseudodiaptomus forbesi, which had much the same migratory behavior as E. affinis (Kimmerer et al. 2002), is much more abundant in freshwater than in the low-salinity zone (Kimmerer et al. 1998). Limnoithona tetraspina has a broad peak in abundance at salinity = 5-10, implying somewhat different behaviors, perhaps cessation of migration below a certain salinity. Tortanus dextrilobatus abundance peaks at salinity ~ 10 , and this copepod did not migrate but remained near the bottom (Kimmerer et al. 2002), which our results suggest would result in a higher mean salinity (Fig. 6).

The efficacy of tidal vertical migration for retention has been accepted rather uncritically based on evidence that until recently has been fairly scant (Table 1). Many of the previous field studies have sampled only one or a few tidal cycles. Only a handful of previous attempts have been made to determine how tidal migration works: the simple modeling by Kimmerer and McKinnon (1987) to determine that tidal migration could overcome dispersive losses; the analytical modeling by Hill (1991) showing the conditions under which tidal migration could lead to retention; and the 3D modeling by Simons et al. (2006), which showed that tidal migration could retain plankton in the St. Lawrence Estuary. We have added to this record by showing that both near-bottom positioning and tidal migration are highly effective, although in different ways, at retaining particles, and presumably plankton, in a dynamic estuary at various flows and with spatially variable stratification.

Previous results and our conclusions raise the question: what environmental cues stimulate the vertical movement in organisms that do not go to the bottom on the ebb? We are unaware of studies of these cues, apart from speculation (Forward and Tankersley 2001). The observation that the direction of vertical movement can vary depending on longitudinal position (Hough and Naylor 1992*b*) suggests the estuarine plankton are responding to immediate cues rather than merely entraining an endogenous rhythm with the phasing of tidal currents. Selective pressure to maintain position must be enormous, and planktonic organisms should at least be able to distinguish a strong tidal flow from slack water because of the differences in turbulence. How they tell ebb from flood remains a mystery.

Acknowledgments

We thank M. Weaver and two anonymous reviewers for helpful comments. This work was supported by a grant from the U.S. Department of the Interior (R10AC20074).

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Associate editor: Thomas R. Anderson

Received: 05 September 2013 Accepted: 01 January 2014 Amended: 27 January 2014