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Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone

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Abstract

We investigated the degree of flexibility in retention strategies of young fishes in the low-salinity zone (LSZ) of the San Francisco Estuary during years of highly variable river flow. We conducted depth-stratified sampling over three full tidal cycles in each year from 1994 to 1996. In 1994, exotic striped bass (*Morone saxatilis*), native longfin smelt (*Spirinchus thaleichthys*), and exotic yellowfin goby (*Acanthogobus flavimanus*) migrated tidally, occurring near the surface on flood tides and near the bottom on ebb tides. This strategy may have facilitated retention, because landward residual currents were absent in this drought year. During 1995, this behavior persisted for striped bass and yellowfin goby, even though landward residual currents were present under high river-flow conditions. In moderate river-flow conditions (1996), longfin smelt again migrated tidally, whereas at another station adjacent to shallow bays, longfin smelt, striped bass, and native delta smelt (*Hypomesus transpacificus*) migrated on a reverse diel cycle, occurring near the surface by day and at depth by night. Reverse diel migration may facilitate horizontal transport and retention. Therefore, young fishes appeared to be behaviorally flexible in different environmental conditions to maximize retention. Vertical migrations may also enhance feeding success because zooplankton prey similarly migrated in the LSZ. Our study underscores the value of interdisciplinary studies in a variety of environmental conditions to decipher the range of organism behaviors promoting transport and retention in optimal habitats.

The mechanisms underlying the vertical distribution of aquatic organisms have fascinated researchers throughout the last century (Murray and Hjort 1912; Hutchinson 1967; Forward 1988; Neilson and Perry 1990). Promoted by the interplay between the physical environment and organism behavior, vertical distributions can enhance transport to and retention in nursery habitats (Boehlert and Mundy 1988; Shanks 1995). Deciphering these complex relationships continues to provide fundamental challenges for population ecology, the designation of essential habitats for fisheries, and conservation of aquatic biodiversity (Jones et al. 1999; Swearer et al. 1999). In estuaries, many invertebrates and

fishes migrate vertically in ways that facilitate immigration or retention (Miller et al. 1985; Boehlert and Mundy 1988). Species are often abundant just seaward of the margin of salinity intrusion in estuaries, which is frequently a region of maximum turbidity, referred to as the oligohaline or low-salinity zone (LSZ) (Dodson et al. 1989; Simenstad et al. 1994; Kimmerer et al. 1998; Sirois and Dodson 2000). The widespread occurrence of this pattern has led to a conceptualization of the LSZ as an important nursery habitat for zooplankton and early life stages of fishes (Miller et al. 1985; Sirois and Dodson 2000; North and Houde in press).

A variety of mechanisms can enhance retention of zooplankton and fishes in the LSZ (Kimmerer et al. 1998). To be retained, organisms must overcome advection seaward due to river flow as well as tidal dispersion. Organisms may accumulate in high abundance by (1) maintaining rapid population growth or accumulation rates within the LSZ relative to predation and advective or dispersive losses (McGurk 1989; Pace et al. 1992); (2) migrating laterally to the shoals on ebb tides and to channel habitats on flood tides using diel or tidal cues (Wooldridge and Erasmus 1980); (3) sinking passively in vertically stratified waters (Sclafani et al. 1993), or swimming downward into net landward residual flow resulting from gravitational circulation (Weinstein et al. 1980; Laprise and Dodson 1989a); and (4) migrating upward on the flood and downward into lower velocity flow, or to the bottom, on the ebb (Laprise and Dodson 1989b; Rowe and Epifanio 1994). Of these four mechanisms, vertical migra-

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tion behavior is frequently studied. Often, in estuaries with semidiurnal or diurnal tidal cycles, a diel rhythm coincides with tidal migrations such that movements to surface waters occur on nightly flood tides with organisms remaining at depth during daytime ebbs (Weinstein et al. 1980; Christy and Morgan 1998; Forward et al. 1998; Jenkins et al. 1998; Kimmerer et al. 1998).

The degree to which retention strategies are fixed by endogenous rhythms or are variable behavioral responses remains unresolved. Position maintenance strategies often switch during ontogeny in response to changes in physiology and habitat requirements (Laprise and Dodson 1989a,b, 1990). This phenomenon is well described for fishes that are spawned offshore and subsequently enter estuaries (Boehlt and Mundy 1988; Shanks 1995). However, for particular early life stages several field and laboratory studies identified endogenous rhythms in estuarine zooplankton and larval invertebrates (Forward 1988; Hough and Naylor 1992; Tankersley and Forward 1994) as well as fishes (Gibson 1978; Wipplhauser and McCleave 1988; Forward et al. 1998). Behavioral plasticity in migration strategies is also documented for zooplankton (Forward 1988; Bollens and Frost 1991) and thought to be prevalent in fishes (Neilson and Perry 1990). Flexibility in migration strategies may result from phenotypic plasticity at the level of the individual, or from a behavioral polymorphism at the cohort or population level with plasticity manifesting as the result of rapid selection for specific behaviors in different environmental conditions (Cousyn et al. 2001). If behavioral plasticity of either form is a characteristic feature of estuarine organisms, then migration strategies need to be evaluated over a wide variety of environmental conditions to understand relationships between hydrodynamics and behavioral mechanisms that can promote retention.

In the San Francisco Estuary, previous studies indicated that some zooplankton and young (larval and juvenile) fishes maintain peak abundance in or near the LSZ (Herbold et al. 1992; Moyle et al. 1992; Kimmerer et al. 1998). Furthermore, the degree of retention in this low-salinity and nursery habitat is considered a potentially important mechanism regulating recruitment success and population dynamics. Annual abundances of several fish species are statistically associated with the seasonal magnitude of freshwater flow and longitudinal position of the LSZ (Jassby et al. 1995; Bennett and Moyle 1996). Previous work on potential retention mechanisms indicated that larval striped bass (*Morone saxatilis*) remained at depth in the LSZ regardless of tidal direction or time of day, and that longfin smelt (*Spirinchus thaleichthys*) were abundant in surface waters as yolk-sac and young postlarvae and occurred progressively deeper as they grew larger (Wang 1986; Fujimura 1991). These findings are consistent with those from the Chesapeake Bay estuary, where larval striped bass have been observed to occur regularly in the lower two-thirds of the water column (Kernehlan et al. 1981; Chesney 1993). North and Houde (2001) recently showed that younger postlarvae were positioned near the surface while older postlarvae were positioned near the bottom. Therefore, larval striped bass and juvenile longfin smelt typically occur at depth to presumably use residual

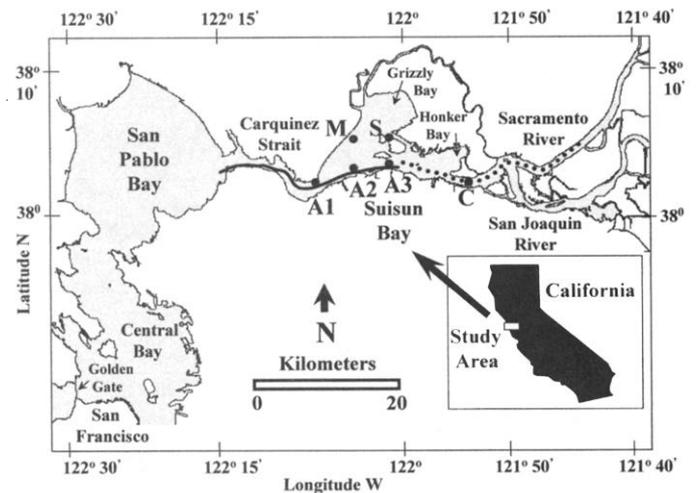


Fig. 1. Study area in the San Francisco Estuary showing sampling and acoustic Doppler current profiler locations. The 1994 cruise tracks are shown by dotted line and 1995 cruises by solid line. Sampling locations in 1996 are shown in the north channel near the reserve fleet (M) and Suisun Cut (S) and in the ship channel near middle ground (A3). Dopplers were also located near S and A3 in 1996, near Benicia (A1) and Bulls Head (A2) in 1995, and near Chippis Island (C) in 1994.

landward transport produced by gravitational circulation for position maintenance.

In this paper, we investigate the degree of flexibility in behavioral responses by native and exotic species to changing hydrodynamics to shed light on mechanisms that may contribute to the nursery habitat potential of the LSZ in the San Francisco Estuary (Herbold et al. 1992; Moyle et al. 1992; Jassby et al. 1995; Bennett and Moyle 1996). This work was part of an interdisciplinary investigation to evaluate the potential relationships between the hydrodynamics of the LSZ and the abundance and vertical distribution of zooplankton and young fishes under a range of freshwater river-flow conditions. Previously we have shown that during low freshwater flow (drought) residual landward currents at depth were absent and mysids, amphipods, and copepods underwent tidally oriented vertical migrations (Kimmerer et al. 1998). Here we report on the interactions of LSZ hydrodynamics and vertical distributions of young fishes during a 3-yr period that included low, moderate, and high freshwater flow conditions. Each year we conducted depth-specific sampling for young fishes over three full (24 to 30 hr) tidal cycles. We describe flexibility in vertical migration strategies by a group of exotic and native species under different environmental conditions and locations, as well as switching of migration tactics between native and nonnative estuaries. Specifically, we test the hypothesis of Neilson and Perry (1990) that behavioral strategies in fishes can be plastic responses to changing environmental conditions to facilitate retention in optimal habitats.

Methods

Study area and species life histories—The San Francisco estuary (Fig. 1) is the largest estuarine system on the Pacific

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

Sampling	1994	1995	1996
General location	Eastern Suisun Bay and Sacramento River	Carquinez Strait and western Suisun Bay	Central Suisun Bay
Freshwater flow	Low	High	Moderate
Gravitational circulation	None	Frequent	Infrequent
General design	Lagrangian, one vessel	Lagrangian, two vessels	Eulerian, two vessels
Specific location	Cycling between 1, 3, 6 mS cm ⁻¹	Following ca. 2 psu at 10-m depth	One vessel in north channel (Fig. 1, M, S) and one in ship channel (Fig. 1, MG)
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 three depths	Hourly at three depths	Hourly at three depths
Sampling methods	Opening-closing nets, 150- μ m mesh	Pump discharging through 200- μ m net	Fixed nets, 200- μ m mesh
Fish taxa examined	Five species	Two species	Six species

coast of the United States. The estuary is morphologically complex, formed by the Sacramento and San Joaquin river systems, which drain through a large delta, then via a series of subembayments into the Pacific Ocean at the Golden Gate north of San Francisco. The hydrology is dominated by highly variable river flow that changes in response to extreme seasonal and interannual variability in precipitation, releases of freshwater from upstream impoundments, as well as exports of freshwater from the delta (Nichols et al. 1986; Monismith et al. 1996). Tidal mixing is strong throughout the San Francisco Estuary, where the tidal currents at the mouth of the estuary are approximately 2.0 m s⁻¹ driven by a tidal range of about 1.75 m. In the Suisun Bay study area (Fig. 1), the tidal currents are on the order of 1.0 m s⁻¹ (Monismith et al. 1996). The estuary is also characterized by a broad array of exotic species, of which several are abundant in the LSZ (Bennett and Moyle 1996; Kimmerer and Orsi 1996).

The assemblage of young fish associated with the LSZ is dominated by three exotic species and three species native to the San Francisco Estuary. Of the exotic species, striped bass (*M. saxatilis*) are the dominant piscivore of the estuarine food web. An important sport fish, they were introduced into the estuary in 1879 from the eastern United States. Striped bass are anadromous, spawning in the freshwater reaches of the Sacramento and San Joaquin rivers from April to May. Larvae develop as they are carried seaward by river flow to accumulate slightly landward of the LSZ (1–2 psu salinity). Survival from the egg to juvenile stage is correlated with river flow and the longitudinal position of the LSZ (Jassby et al. 1995; Kimmerer et al. 2001). Yellowfin goby, *Acanthogobius flavimanus* (Brittan et al. 1970), and Shimofuri goby, *Tridentiger bifasciatus* (Matern and Fleming 1995), were first discovered in 1963 and 1986 respectively. Native to Asian estuaries, they were probably introduced with the ballast water of ships (Matern and Fleming 1995; Bennett and Moyle 1996). Both species are euryhaline, spawning in rock piles or burrows when water temperatures rise in late spring and summer along the shoreline and slough habitats adjoining the LSZ. Pelagic larvae settle near

the bottom and presumably disperse laterally to shoal and slough habitats (Matern and Fleming 1995; P. Moyle, University of California, Davis, pers. comm.). Of the native species, prickly sculpin (*Cottus asper*) is a common freshwater species whose larvae are carried by river flow into the LSZ during early spring. Postlarvae settle to the bottom and eventually disperse laterally and landward to freshwater (Kresjsa 1967). Prickly sculpin lack a functional swim bladder throughout life. Longfin smelt (*S. thaleichthys*) and delta smelt (*Hypomesus transpacificus*) are semianadromous, spawning in the tidal freshwater delta. Longfin smelt spawn in late February–March whereas delta smelt spawn during March–May. Declining abundance of both species in recent years has raised considerable concern, especially for delta smelt, which is currently listed as a threatened species under the Federal and State Endangered Species Acts.

Sampling—The overall study design was similar in 1994–1996, with differences in sampling schedule and methods. We sampled during spring–early summer, when the majority of larval fishes were present within or near the LSZ. Each year, sampling cruises occurred on three different dates over complete tidal cycles (24–30 h). Depth-specific samples were taken hourly at 1 m below the surface, middepth, and near bottom. Differences in sampling design and methods among years (Table 1) were chosen in part to account for high variation in seasonal flow, which positioned the LSZ in morphologically distinct areas of the estuary (Fig. 1).

Sampling in 1994 was quasi-Lagrangian, with stations identified by salinity rather than geographic location, alternating among nominal surface specific conductance of 1, 3, and 6 mS cm⁻¹, once each per tidal cycle. Three cruises on the R/V *San Carlos* were scheduled to coincide with two predicted neap tides (cruises A and C) and one spring tide (cruise B). Depth-specific samples for young fishes and macrozooplankton (mysids and amphipods) were taken using paired 60-cm opening-closing nets (150- μ m mesh) fitted with flow meters, and towed for 10 minutes at 2–4 knots. Concurrent sampling and enumeration of mesozooplankton (copepods) are described in Kimmerer et al. (1998, 2002).

In 1995, sampling was Lagrangian in that the R/V *San Carlos* followed a salinity of approximately 2 psu near the bottom and the R/V *Turning Tide* was positioned about 5 km seaward (Fig. 1). These positions were not precisely maintained because of rigorous field conditions. Three sampling cruises then occurred on two neap tides and one spring tide. Submersible pumps fitted with flow meters with mean flow rates of $0.7 \text{ m}^3 \text{ min}^{-1}$ on the R/V *San Carlos* and $0.2 \text{ m}^3 \text{ min}^{-1}$ on the R/V *Turning Tide* were used to take 10–15-min depth-specific samples. Pumped water was filtered through a $200\text{-}\mu\text{m}$ mesh net for young fishes and macrozooplankton. Maximum pumping depth was 25 m. Few fishes were caught on the R/V *Turning Tide*. Comparisons of our samples with fish catch in routine plankton-net surveys at similar dates and locations (R. Baxter, California Department of Fish and Game, pers. comm.) suggest that the lower pumping rate on the R/V *Turning Tide* was not sufficient to effectively sample young fishes. Similarly, many postlarval and juvenile longfin smelt probably avoided the pump intake on the R/V *San Carlos*. Data from only the R/V *San Carlos* are presented here.

Moderate river-flow rates in 1996 maintained the LSZ within Suisun Bay, a morphologically complex subembayment composed of two primary channels divided by a sequence of shoals and small islands. We used two vessels to sample simultaneously in the north channel and the ship channel of Suisun Bay (Fig. 1). In addition, examination of data from 1994 to 1995 indicated that salinity had little influence on the depth distributions of young fishes or zooplankton (Kimmerer et al. 1998), so we sampled at fixed stations. The R/V *San Carlos* sampled in the ship channel (station A3, Fig. 1) and the R/V *Turning Tide* sampled in the north channel at station M during cruise A, and station S during cruises B and C. With this sampling design, the 2 psu isohaline was tidally advected past each station. Sampling for young fishes and zooplankton was depth specific as before, but simplified, and used 75-cm diameter, $200\text{-}\mu\text{m}$ mesh nets. The nets remained open throughout towing, and, although retrieval time was minimized and maximum towing depths were less than 10 m, some contamination probably occurred. No corrections for this were estimated.

Each year, vertical profiles of salinity and temperature were monitored with a Seabird SBE-19 CTD before and after each deployment of the nets. Currents were continuously monitored with acoustic Doppler current profilers (ADCP). In 1994, we used a fixed ADCP located near Chipps Island (C, Fig. 1), and in 1995 fixed ADCP stations were located at Benicia bridge (A1) and Bulls Head (A2) (Fig. 1), with data from the Bulls Head station used to calculate mean water-column velocity (Kimmerer et al. 2002). In 1996, fixed ADCPs were located near the reserve fleet (M), Suisun Cut (S), and middle ground (A3) (Fig. 1). In all years, currents were also monitored while sampling using a 1,200-kHz broadband ADCP mounted on the ship.

In all years, contents of the nets were fixed in 5–10% formaldehyde and subsequently stored in 70% ETOH. All fishes (larvae, juveniles) were sorted from the samples, identified (Wang 1986), and measured with a dissecting scope fitted with an ocular micrometer (standard length, $\pm 0.1 \text{ mm}$). As a quality control measure, all larval smelt ($<15 \text{ mm}$) and

larval cyprinid identifications were subsequently verified by J. C. S. Wang (National Environmental Services). In 1996, we estimated the amount of detrital material by measuring the height of settled material in each of the sample jars and calculated volumes.

Data analysis—Potential vertical movements of fishes and copepods were evaluated in several steps. First, fish abundance ($\text{No.} \times 10^{-3} \text{ m}^3$) at depth was plotted according to fish standard length (SL) classes to examine the potential influence of ontogeny on vertical position. Second, tidal and diel influences on vertical position were evaluated by calculating the mean depth of the center of fish or copepod mass as a percent of the water column, essentially mean depth weighted by abundance at the three depths sampled (Kimmerer et al. 1998). Third, after exploratory analyses, regression models were constructed using mean depth with tidal velocity, day versus night, and cruise within years as independent variables. Because total abundance varied considerably among tows, mean depth was weighted by the square root of mean abundance. Finally, we included mean depth with tidal velocity and day versus night in linear regressions. In some instances, data were insufficient for day versus night comparisons. Where data were not normally distributed and exhibited outliers, we used robust linear regressions (Venables and Ripley 1997). We then examined residuals for normality and autocorrelation. All statistical analyses were performed using S-Plus (Venables and Ripley 1997).

Results

Physical conditions—Estuarine hydrology over the three years of study varied considerably with respect to freshwater river flow and longitudinal position of the LSZ (Figs. 1, 2). Mean flow from April through July in 1994 was $6.2 \pm 2.7 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ (drought year), $65.6 \pm 36.5 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ in 1995 (wet year), and $28.2 \pm 21.2 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ in 1996 (moderate year) (Fig. 2). This positioned the LSZ in geographically distinct regions of the estuary as represented by the differences among our sampling cruise tracks in 1994 (western Suisun Bay and lower Sacramento River, about 80–82 km from the Golden Gate) and 1995 (Carquinez Strait and western Suisun Bay, 55–60 km), and fixed sampling positions in 1996 (Suisun Bay, 65–70 km) (Fig. 1). Although we selected sampling dates to occur near predicted spring and neap tides during the larval fish season, tidal energy, as characterized by the root mean square of tidal height, indicates that during 1994 and 1995 we sampled on or near neap tides that occurred during periods of strong overall tidal energy, and in 1996 we sampled during true neap conditions only during cruise C (Fig. 2). This suggests that the energy available for water-column mixing was generally high throughout our study.

Gravitational circulation and stratification are strongly controlled by the interaction between the baroclinic pressure gradients, which are created by the horizontal salinity gradient, and vertical shear (mixing), which tends to both short-circuit gravitational circulation and destratify the water column (Monismith et al. 1996). Since both the baroclinic

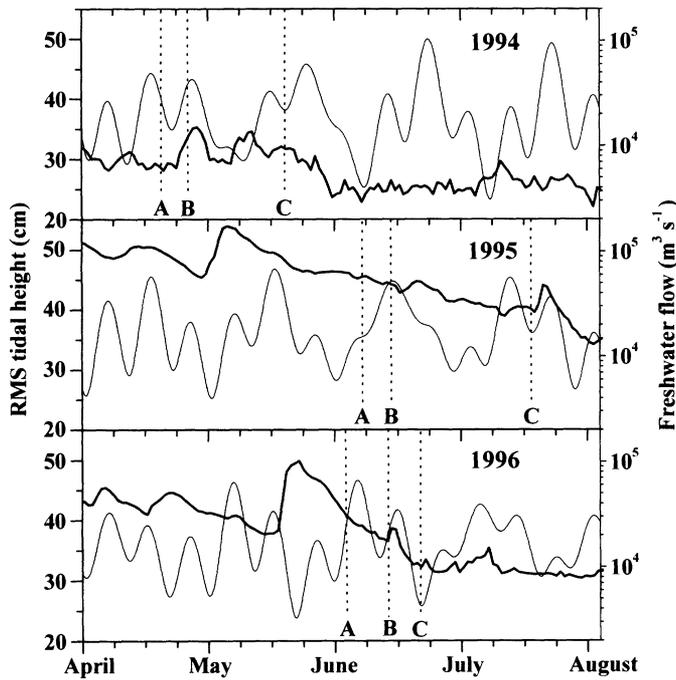


Fig. 2. Physical environmental conditions during the 1994, 1995, and 1996 sampling seasons. Thin solid line shows root mean square (rms) of tidal height, and freshwater flow is shown by heavy solid line. Cruise dates (A, B, C) are shown by vertical dotted lines.

pressure gradients and vertical mixing scale with depth, gravitational circulation and stratification are also dependent on depth. With a uniform depth, this would imply an increasing tendency for stratification to develop as freshwater flow increases and the salinity gradient is compressed, but in the San Francisco Estuary the effect of variable bathymetry dominates (Monismith et al. 1996). In our study, large differences in the mean longitudinal position of the LSZ among years resulted in radically different water depth, and therefore stratification and gravitational circulation. Sampling depths ranged from 8 to 15 m in 1994 in the ship channel at the eastern end of Suisun Bay and lower Sacramento River. In 1996, depths were similar and ranged from 7 to 11 m in the north channel (M, S, Fig. 1) and 8 to 12 m in the ship channel near middle ground (A3, Fig. 1). However, in 1995, as we followed 2 psu bottom salinity, our position ranged from western Suisun Bay (10 m) through Carquinez Strait (up to 32 m) across a sill at Benicia (A1, Fig. 1). Some of the variability in depth can also be attributed to difficulties in maintaining vessel position in the channel during deployment of the submersible pumps, as indicated by a period of nearly fresh water recorded during cruise A (Fig. 3).

With reduced freshwater flow and shallower depth, gravitational circulation was not detected in 1994 (Monismith et al. 1996; Kimmerer et al. 1998) as supported here by the slight differences in surface and bottom water salinity (Fig. 3). These results contrast with those from 1995. Because of the deep water column in Carquinez Strait, stratification and gravitational circulation were frequent, particularly during cruise A in 1995 (Fig. 3) (Kimmerer et al. 2002). In 1996,

gravitational circulation was intermittent and generally occurred during periods of maximum salinity, and therefore salinity stratification, at our fixed sampling stations (Fig. 3) as tidal currents moved the LSZ past our position (Kimmerer et al. 2002).

Fish catch—Although a total of 29 species were collected over the 3 yr of study, six species, striped bass, longfin smelt, yellowfin goby, shimofuri goby, prickly sculpin, and delta smelt together comprised 98% of the catch. Larval stages comprised the majority of individuals in the catch among years, although higher numbers of juvenile longfin smelt (>20 mm SL), delta smelt (>20 mm SL), and yellowfin goby (>15 mm SL) were collected in 1996 (Figs. 4, 5). A small number of fish eggs were identified as striped bass. The spatiotemporal distributions of these six species among cruises and years generally reflected their respective spawning seasons and previous knowledge of their distribution with respect to the LSZ (Wang 1986; Herbold et al. 1992) such that the catch of longfin smelt and prickly sculpin declined in cruise C, 1994 (17–18 May), and few larval fishes were sampled during cruise C, 1995 (18–19 July). In 1996, total fish catch in the north channel was about threefold greater than in the shipping channel, with about a fourfold difference between sites in the striped bass catch (Fig. 5). Longfin smelt catch was similar between sites, although in the ship channel sufficient numbers of delta smelt and yellowfin goby were only caught during cruise B (13–14 June) and cruise C (20–21 June), respectively.

The fish catch among years was generally lower at higher salinity (>5 psu), except for prickly sculpin and shimofuri goby, and (in 1996) generally associated with higher volumes of detrital material in the samples (Fig. 3). Detrital material increased at lower bottom salinity (Pearson $r = -0.354$, $P = 0.001$) and was also correlated with the abundances of striped bass (Pearson $r = 0.412$, $P = 0.000$), longfin smelt (Pearson $r = 0.261$, $P = 0.016$), delta smelt (Pearson $r = 0.343$, $P = 0.001$), and yellowfin goby (Pearson $r = 0.277$, $P = 0.010$). Prickly sculpin (Pearson $r = 0.150$, $P = 0.171$) and shimofuri goby (Pearson $r = 0.221$, $P = 0.042$) were less associated with detrital material in comparison with the other species.

Vertical distributions—The six most abundant species exhibited interspecific and ontogenetic differences in vertical distribution profiles. Prickly sculpin, shimofuri goby <10 mm, longfin smelt <10 mm, delta smelt <15 mm, and yellowfin goby <7 mm occurred primarily in the surface waters in all cruises (Figs. 4–5). In comparison, striped bass, longfin smelt >10 mm, delta smelt >15 mm, and yellowfin goby >7 mm were most abundant at depth. Two of these four species had clear size-related depth profiles (Figs. 4–5), such that most longfin smelt >10 mm and yellowfin goby >7 mm were caught at depth. Although only 17 delta smelt were collected in 1994, the majority of fish over 15 mm were collected in the near-bottom samples (Fig. 4). In contrast, delta smelt were primarily surface-oriented in 1996 but became more abundant at depth as they grew larger (Fig. 5). These ontogenetic patterns of vertical distribution match closely the ontogeny of swim-bladder development with lar-

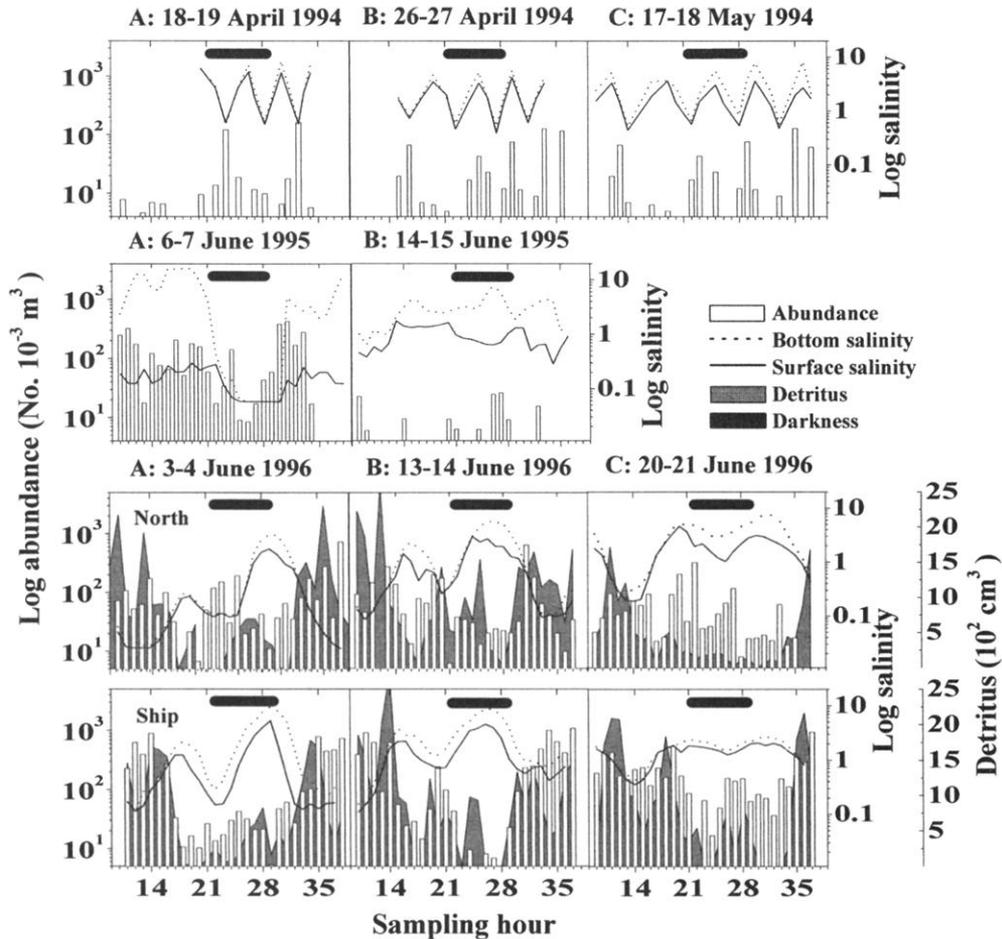


Fig. 3. Total fish abundance ($\text{No.} \times 10^{-3} \text{ m}^{-3}$) with surface and bottom salinity during each cruise 1994–1996. Also shown in 1996 are the volumes of detrital material in samples.

val length; striped bass develop swim bladders at about 5 mm, longfin smelt at 10 mm, delta smelt at about 15 mm, yellowfin goby at 7 mm, and shimofuri goby at about 10 mm (Wang 1986). Prickly sculpin lack a functioning swim bladder (Wang 1986). Because of these observations, subsequent analyses of vertical migration behavior were restricted to species and life stages with developed swim bladders for which adequate data were available.

Vertical distribution among cruises in 1994–1995 suggested fishes were migrating vertically on a tidal cycle. Striped bass and yellowfin goby were generally concentrated at middepth and near-bottom during ebb tides and near the surface during flood tides during each cruise (shown for striped bass in Fig. 6). Mean depth of abundance in the water column for striped bass and yellowfin goby among all cruises in 1994–1995 was significantly associated with tidal velocity and not associated with a diel pattern (Fig. 8, Table 2). Longfin smelt exhibited a similar pattern in 1994, while few were caught in 1995 (Fig. 8, Table 2). Results were similar for *Pseudodiaptomus forbesi*, the overall dominant copepod in the catch and important prey item, which also migrated vertically. Mean depth of *P. forbesi* abundance in the water column was significantly associated with tidal ve-

locity and time of day among all cruises in 1994 and with tidal velocity in 1995 (Table 3, Kimmerer et al. 1998, 2002).

In contrast, vertical distributions in 1996 at the north channel sites suggested evidence of reverse diel migration and no apparent relationship to tidal direction, whereas in the ship channel distributions were less discernable. In the north channel, striped bass, longfin smelt, and delta smelt were generally abundant in the surface waters during the day, and at depth during the night during each cruise (shown for longfin smelt in Fig. 7). However, distributions for yellowfin goby were highly variable (Fig. 8). In the ship channel, longfin smelt generally occurred in the surface waters during flood tides and at depth during ebb tides (Fig. 7). Mean depth of longfin smelt abundance is statistically associated with tidal velocity with no influence of a diel pattern at the shipping channel site (Fig. 8, Table 2). Mean depth of abundance for other species was unrelated to tidal direction or a diel pattern (Table 2), and few delta smelt or yellowfin goby were caught during the night (Fig. 8). *P. forbesi* vertical distributions were not associated with either velocity or time of day at the north channel site but were significantly associated with tidal velocity at the ship channel site (Table 3).

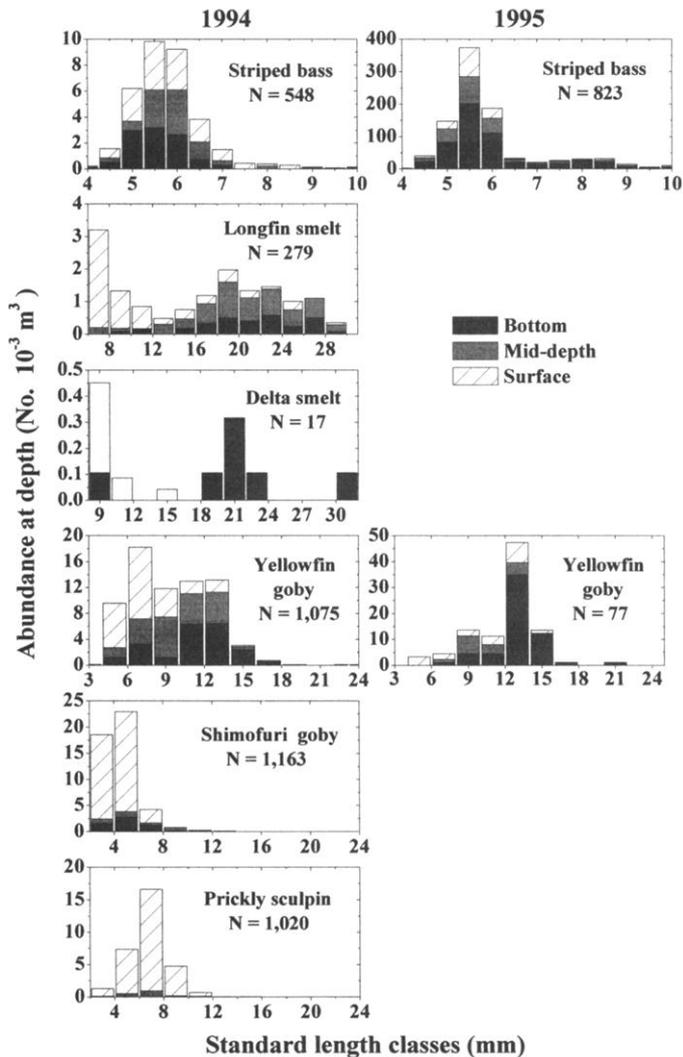


Fig. 4. Vertical partitioning of abundance at depth (No. $\times 10^{-3} \text{ m}^3$) according to larval length in near surface, mid-depth, and near bottom samples among cruises in 1994 and 1995. Note: only two species were caught in sufficient abundance in 1995.

Discussion

Young fishes migrated vertically and maintained position in the LSZ of the San Francisco Estuary, switching between two strategies depending on freshwater flow and longitudinal position of the LSZ. Abundances of four fish species and estimated volume of detrital material were highest at the lower end of the range of salinity sampled in the LSZ. These results support previous observations (Herbold et al. 1992; Moyle et al. 1992) showing that an assemblage of young fishes occupies the turbid landward margin of the LSZ. Most of these species with developed swim bladders consistently migrated vertically in response to tidal direction during drought conditions (1994) when the LSZ was positioned in eastern Suisun Bay and the Sacramento River, as well as during flood conditions (1995) when the LSZ was seaward in Carquinez Strait (Fig. 1). These tidally oriented vertical migrations lacked a diel component and persisted in spite of

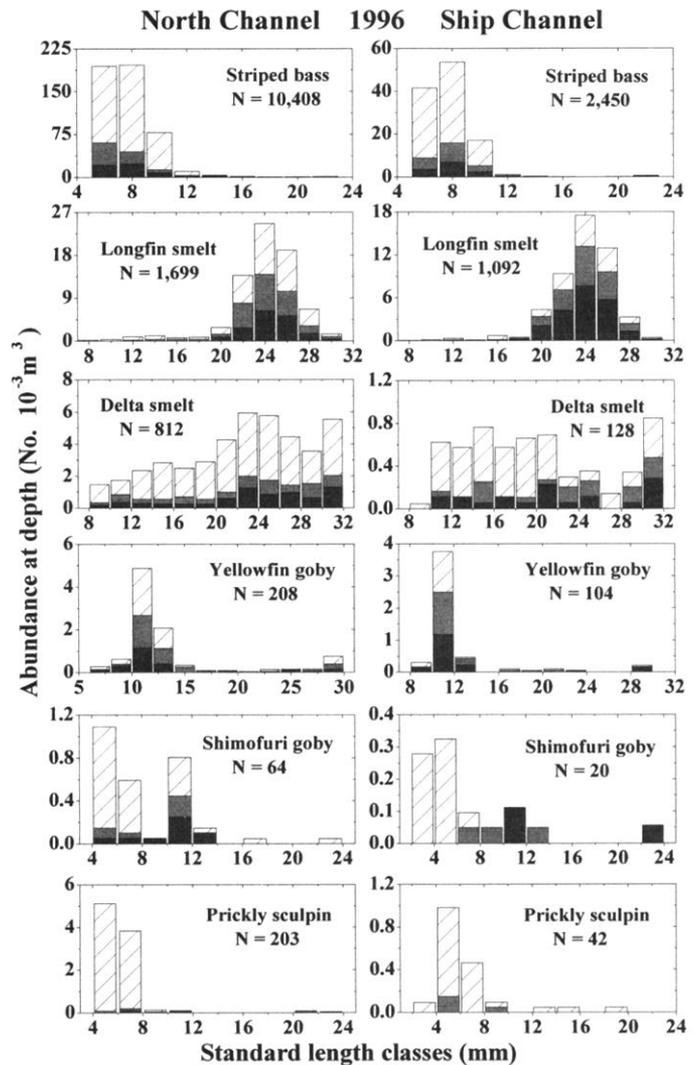


Fig. 5. Vertical partitioning of abundance according to larval length in near surface, mid-depth, and near bottom samples among cruises in 1996. Legend is the same as in Fig. 4.

large differences in river flow and hydrodynamics between these years. In contrast, during moderate freshwater flow conditions when the LSZ was positioned in the morphologically complex central Suisun Bay (Fig. 1), fishes exhibited reverse diel migrations at the north channel sites such that they were more abundant at the surface by day and at depth by night. Concurrently, at the ship channel site longfin smelt migrated tidally as in 1994 and 1995. These findings clearly show that these fishes (particularly longfin smelt) can employ alternative migration strategies when river-flow changes the position of the LSZ.

The pattern of reverse diel migration exhibited by three fish species at the north channel in 1996 may reflect horizontal exchange with the shoals and marsh. Reverse diel migration can result from active selection of near surface waters during the day and random dispersal or sinking at night (Neilson and Perry 1990). This strategy has been hypothesized to improve feeding success because light levels for visually foraging fishes are higher near the surface; the

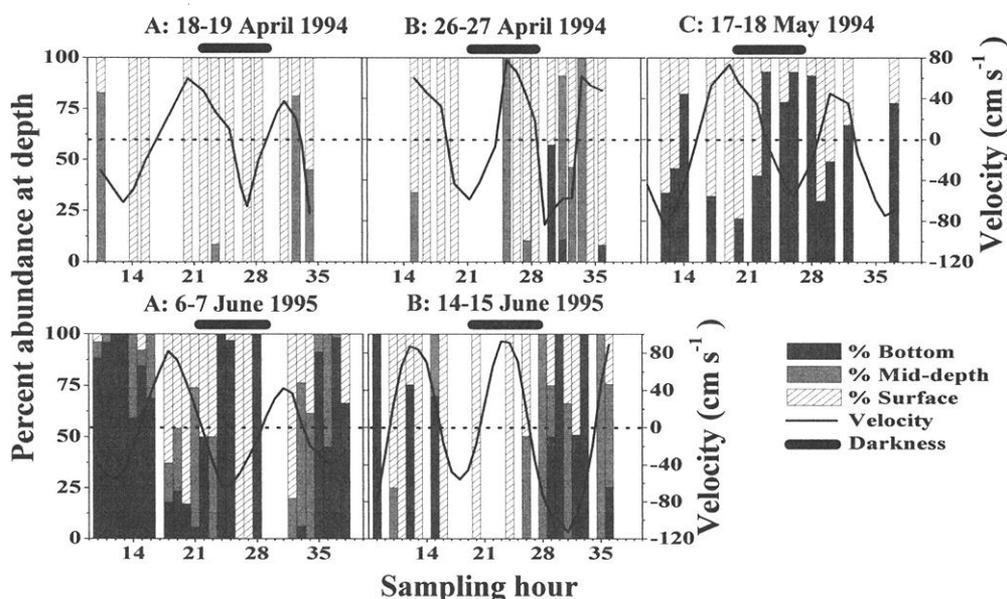


Fig. 6. Examples of percent of total abundance for striped bass in near surface, middepth, and near-bottom samples during cruises in 1994 and 1995, with water-column mean tidal velocity from the Chippis Island ADCP (1994) and Bulls Head ADCP (1995).

strategy has also been hypothesized to help these fishes avoid predation (Ohman et al. 1983; Jenkins et al. 1998). Stomach content and laboratory observations of the endangered delta smelt suggest they are visual foragers and do not feed nocturnally (Bennett et al. unpubl. data). However, overall densities of prey were lower near the surface during the daylight (Kimmerer et al. 2002). *P. forbesi* is a primary prey item but was randomly positioned with respect to depth, tidal velocity, and daylight in the north channel (Table 3, Kimmerer et al. 2002). In addition, juvenile delta smelt were observed in higher densities and were generally larger in shallow Honker and Grizzly Bays (Fig. 1) than in the ship channel in 1996 (Aasen 1999). Moreover, recent hydrodynamic studies indicate that Suisun Cut (Fig. 1) in the north channel serves as a main conduit for tidal exchange between these shallow bays (Burau et al. unpubl. data). These studies

suggest delta smelt move with tidal currents between these shallow bays. Our study supports this scenario, because delta smelt were generally larger and approximately six times more abundant in our samples from the north channel than the ship channel (Fig. 5). Therefore, the pattern of reverse diel migration reported here may be the result of surface orientation of fishes during daylight, which would promote horizontal exchange with shallow bays and dispersion during the night. This strategy would also promote retention in the LSZ through horizontal rather than vertical patterns of movement (Wooldridge and Erasmus 1980) and could enhance feeding success for delta smelt as well as other fishes (Aasen 1999; M. Nobriga, California Department of Water Resources, unpubl. data).

Comparisons of the vertical distributions of young fishes between naturalized and native estuaries provide further ev-

Table 2. Regression results for mean depth of abundance of larval fishes versus water column velocity and time of day for cruises pooled by year and site.

Species	Year (site)	df	Velocity			Day vs. night		
			Value	SE	P	Value	SE	P
Striped bass	1994	27	0.45	0.07	0.0000	8.43	6.94	0.24
	1995	39	0.38	0.12	0.004	9.61	14.8	0.52
	1996 (north)	73	0.002	0.031	0.96	24.9	4.88	0.0000
	1996 (ship)	70	0.01	0.07	0.91	7.02	13.7	0.61
Longfin smelt	1994	25	0.32	0.12	0.015	2.09	11.1	0.85
	1996 (north)	78	0.01	0.03	0.76	19.4	3.50	0.0000
	1996 (ship)	71	0.11	0.04	0.002	2.33	4.97	0.64
Delta smelt	1996 (north)	59	0.03	0.04	0.36	46.9	6.99	0.0000
	1996 (ship)	21	0.098	0.088	0.29	—	—	—
Yellowfin goby	1994	36	0.28	0.07	0.0002	9.10	6.74	0.18
	1995	22	0.41	0.09	0.0002	—	—	—
	1996 (north)	57	0.01	0.06	0.88	1.73	7.57	0.82
	1996 (ship)	12	0.03	0.14	0.81	—	—	—

Table 3. Regression results for mean depth of abundance of the copepod, *Pseudodiaptomus forbesi*, versus water column velocity and time of day for cruises pooled by year and site in 1996.

Year (site)	df	Velocity			Day vs. night		
		Coeff	SE	P	Coeff	SE	P
1994	39	0.094	0.04	0.03	5.2	2.3	0.03
1995	79	0.13	0.04	0.004	0.13	2.4	>0.1
1996 (north)	65	0.02	0.02	0.4	1.1	1.4	>0.1
1996 (ship)	77	0.14	0.02	<0.0001	3.1	1.6	0.6

idence of plasticity in behavioral responses. Although we are unaware of information on the vertical distributions of yellowfin goby and shimofuri goby in their native estuaries, striped bass larvae have not been previously reported to undertake vertical migrations. In the Hudson river estuary, investigators have hypothesized that vertical movements may occur on diel basis (Smith 1988), and in the Chesapeake postlarval striped bass appear to occur regularly in the lower two-thirds of the water column (Kernehan et al. 1981; Chesney 1993; E. Houde pers. comm.). Recently, North and Houde (2001) have shown that striped bass larvae post-yolk-sac stage (probably before swim-bladder inflation) were near the surface on flood tides, whereas older larvae were at depth. Residual landward currents are a more consistent feature of the Hudson and Chesapeake estuaries than the San Francisco Estuary, such that vertical migration may not be necessary for position maintenance. Fujimura (1991) found no evidence of vertical migration during a drought year in vertically stratified abundance data on striped bass larvae from an entire tidal cycle. However, without concurrent hydrodynamic data the reasons for this are unclear.

Our results suggest that the retention strategies for postlarval striped bass and longfin smelt are not fixed; however,

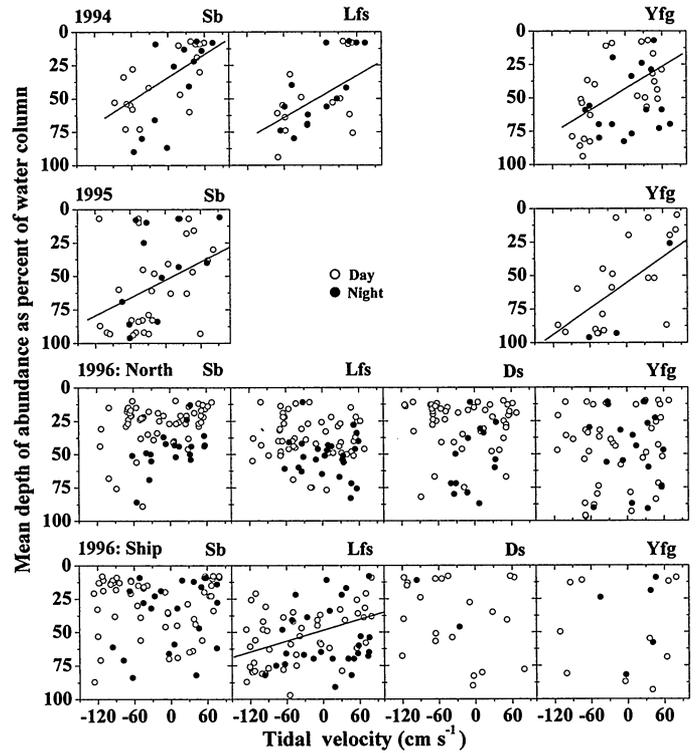


Fig. 8. Mean depth of abundance as a percent of the water column in day and night samples with tidal velocity for striped bass (Sb), longfin smelt (Lfs), delta smelt (Ds), and yellowfin goby (Yfg) for cruises pooled by year, and for the north channel and ship channel sampling sites in 1996. Lines are significant linear or robust regressions (see also Table 2).

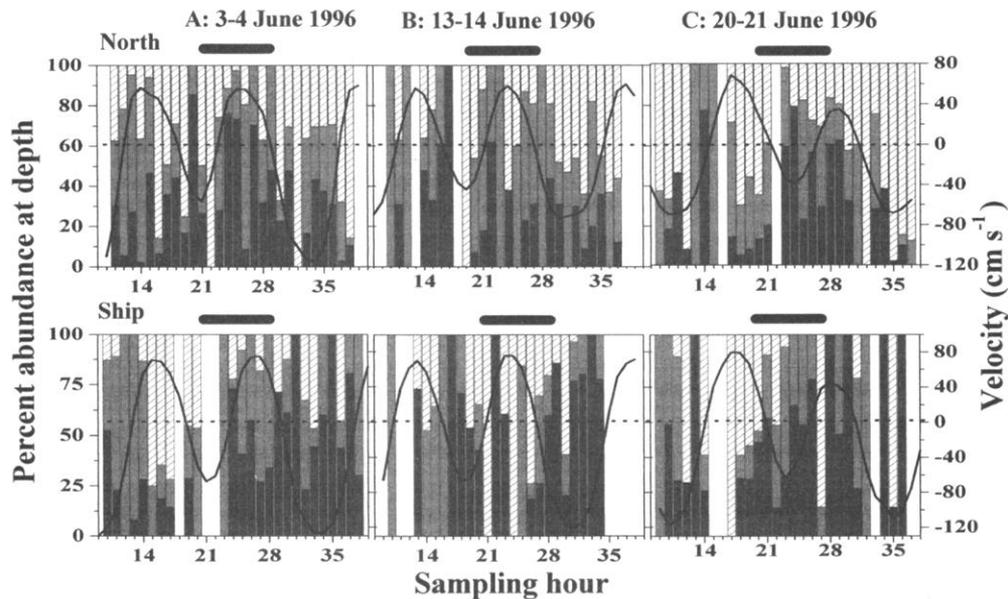


Fig. 7. Examples of percent of total abundance for longfin smelt in near surface, middepth, and near-bottom samples during cruises in 1996, with water-column mean tidal velocity from the nearest ADCP station. Legend is the same as in Fig. 6.

variable catch and expression of migration behavior within years and locations may have been influenced in part by our sampling methods. While the Lagrangian sampling design employed in 1994–1995 generally avoids problems with aliasing of organism movements (Kimmerer et al. 1998), we adopted a Eulerian design in 1996 (see *Methods*) to obviate several logistical problems in previous years. However, because we adhered to an hourly sampling routine and use of mean depth of abundance in the water column to estimate vertical position, observed patterns of migratory behavior are unambiguous. Avoidance of sampling gear by larger postlarval and juvenile fishes probably influenced the catch of larger size classes and species, especially postlarval and juvenile longfin smelt, which were poorly represented in our 1995 catch even though they were abundant in our sampling locations (R. Baxter, California Department of Fish and Game, pers. comm.). Nonetheless, this bias probably had a minor influence on distributional patterns among depths because overall fish catch was similar between day and night and often greater during day sampling. Finally, in 1996, irregular bottom topography at the ship channel site and unanticipated collection of sediment in some samples damaged many smaller larvae, precluding measurement and in some cases identification to species. This could have influenced our estimates of mean depth of abundance for striped bass, thus obscuring a relationship with tidal velocity at the ship channel site. Longfin smelt were generally larger and more robust, thus experienced less damage and provided a more accurate estimate of vertical distribution. If we assume longfin smelt (in 1995) and unidentified larvae (in the ship channel, 1996) were in concordance with respect to the behavioral response of other species within years and locations, this raises the probability that tidal vertical migration is a persistent but not fixed behavioral strategy.

Given that our results indicate behavioral responses can be plastic, questions remain concerning the nature of the plasticity, the cues and incentives (proximate and ultimate causes, respectively, Morgan 1995) for this behavior, as well as the degree of retention provided to young fishes. The apparent behavioral plasticity observed may occur at the level of the individual phenotype or as a population level polymorphism undergoing rapid selection (Cousyn et al. 2001); however, determining its origin is beyond the scope of this study. Overall, native and exotic species with developed swim bladders had similar migration behavior in different environmental conditions and generally appeared to change mean depth of abundance at or near slack tides. This suggests that fishes responded to a common stimulus, or cue, related to the velocity field. Motions that are most detectable by pelagic organisms occur at the scale of organism size (Okubo 1988), which for larval fishes is centimeters. Differences in centimeter-scale turbulence have been observed near our sampling locations in the northern San Francisco Estuary (Stacey et al. 1999). These small-scale motions could provide a way for organisms to distinguish ebb from flood tides and, therefore, provide the necessary cues for vertical migration. Because similar behavior persists in zooplankton sampled during our study that is similarly related to the velocity field (Table 3, Kimmerer et al. 1998, 2002),

zooplankton may also be able to use ebb-flood asymmetries in turbulence as cues for migration.

Although it remains uncertain whether the vertical migration behaviors shown in this study are sufficient to overcome seaward advection, young fishes may benefit by greater cooccurrence with zooplankton prey in the LSZ than elsewhere. Zooplankton and young fishes cooccur in peak abundance in the LSZ (Kimmerer et al. 1998, 2002), such that improved feeding success may be an ultimate incentive for young fishes to migrate vertically. However, due to low levels of primary and microbial production reported for the LSZ (Hollibaugh and Wong 1996; Kimmerer et al. 1998), the incentive for zooplankton to maintain position remains uncertain (Kimmerer et al. 2002). In situations where the LSZ spreads from channels over productive shallow bays, horizontal rather than vertical movements may improve feeding success and retention. Investigations are currently underway to examine this possibility and will shed further light on the value of these shallow regions as important nursery habitat.

Our results have implications for the study of LSZ habitats in a wide variety of estuaries. Although adherence to a strategy of vertical migration appears to be a prominent feature of young fish behavior under a wide range of hydrological conditions, such behavior does not appear to be fixed, or under the control of a tidal endogenous rhythm (Forward 1988; Forward et al. 1998). Rather, polymorphic cohorts may undergo rapid selection for successful strategies, or individual fishes may retain the ability to switch strategies under consistent exogenous cues including tidal velocity and light (Boehlert and Mundy 1988; Neilson and Perry 1990). Although evidence for position maintenance strategies can be intermittent among sites (Forward et al. 1998), or slightly modified (from a semidiel to diel pattern, Stephenson and Power 1989), rarely have fish larvae been observed to adopt distinct strategies potentially switching or undergoing selection for tidal versus diel cues. Such plasticity in response would have been missed without conducting investigations under different hydrological regimes and LSZ positions. Given the traditional interest in the mechanisms underlying vertical distributions (Boehlert and Mundy 1988; Neilson and Perry 1990) and the likely significance of LSZs as essential nursery habitat in estuaries (Miller et al. 1985; Jassby et al. 1995), our results support a growing body of work indicating that fishes can employ a surprising array of strategies to locate or be retained in optimal habitats (Jones et al. 1999; Swearer et al. 1999).

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