Retention mechanisms of white perch (*Morone americana*) and striped bass (*Morone saxatilis*) early-life stages in an estuarine turbidity maximum: an integrative fixed-location and mapping approach

E. W. NORTH[1,*] **AND E. D. HOUDE**[2]

[1]*University of Maryland Center for Environmental Science, Horn Point Laboratory, PO Box 775, Cambridge, MD 21613, USA*

[2]*University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, PO Box 38, Solomons, MD 20688, USA*

ABSTRACT

The small-scale distribution and retention mechanisms of white perch (*Morone americana*) and striped bass (*M. saxatilis*) early-life stages were investigated in the upper Chesapeake Bay estuarine turbidity maximum (ETM). Physical measurements and biological collections were made at fixed-location stations within the ETM during three research cruises in 1998 and two in 1999. Results were compared with mapping surveys of physical properties and organism distributions above, within, and below the ETM. Physical conditions at the fixed stations differed markedly among cruises and between years due to differences in freshwater flow and wind. In each year, striped bass and white perch larval concentrations were highest in waters of salinity 1–4. Larvae were more abundant in the ETM region in 1998, a high-flow year, suggesting that the ETM provides favorable nursery habitat when low salinity waters and the ETM coincide in high freshwater-flow conditions. In 1998, the earliest pelagic life stages of fish larvae (eggs, yolk-sac larvae) and the copepod *Eurytemora affinis*, an important prey of feeding larvae, apparently were retained in deep, landward-flowing water within the salt front and ETM region. Statistical analyses indicated that distributions of white perch and striped bass post-yolk-sac larvae were associated with *E. affinis* distributions and suggested that retention of larval fish could result from tracking prey. Comparing fixed-station and mapping approaches demonstrates the importance of sampling at different spatial scales within the ETM region and suggests that larvae are faced with trade-offs between selecting zones of high retention or high visual-feeding success.

Key words: Chesapeake Bay, estuarine transition zone, estuarine turbidity maximum, larval retention, physical-biological interactions, zooplankton

INTRODUCTION

Estuarine turbidity maximum (ETM) regions are important nursery areas for larval fish, as documented in the St Lawrence River (Dodson *et al.*, 1989; Laprise and Dodson, 1989a; Dauvin and Dodson, 1990; Sirois and Dodson, 2000a; Winkler *et al.*, 2003), the upper Chesapeake Bay (Boynton *et al.*, 1997; North and Houde, 2001, 2003), and potentially the San Francisco Estuary (Jassby *et al.*, 1995; Bennett *et al.*, 2002). ETMs, also referred to as maximum turbidity zones or entrapment zones, are ubiquitous features of coastal plain estuaries (Schubel, 1968) and often occur near the salt front within estuarine transition zones (Sanford *et al.*, 2001). Retention within the ETM region may (1) hold larvae in a zone of increased zooplankton biomass and production (Simenstad *et al.*, 1994; Boynton *et al.*, 1997; Kimmerer *et al.*, 1998; Roman *et al.*, 2001), (2) create a predation refuge because of high turbidity (Chesney, 1989), (3) maintain larvae in optimal temperature or salinity conditions (Strathmann, 1982), and/or (4) prevent them from entering osmotically stressful, high-salinity waters (Winger and Lasier, 1994).

Our objective was to determine how white perch (*Morone americana*) and striped bass (*M. saxatilis*) larvae, which have limited swimming ability, are retained in the upper Chesapeake Bay ETM nursery area where net current flow is down-estuary. In Chesapeake Bay, striped bass and white perch spawn up-estuary of

*Correspondence. e-mail: enorth@hpl.umces.edu

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the salt front (the intersection of the 1.0 isohaline with the bottom) during April and May. The eggs of both species hatch in ~2–3 days at temperatures of 14–20°C; striped bass eggs are buoyant whereas white perch eggs are demersal and adhesive (Mansueti, 1964; Dovel, 1971). Striped bass eggs and the newly-hatched larvae of white perch and striped bass, if drifting passively, potentially could be transported down-estuary at rates of ~7 km day^{-1} during average spring discharge conditions, based on an estimated 8 cm s^{-1} residual down-estuary surface current velocity (North, 2001). The ETM region spans 10–30 km of the upper Bay (Boynton *et al.*, 1997; Sanford *et al.*, 2001). Potentially, early-life stages could be transported in surface waters down-estuary and out of the ETM nursery area in <3 days. Because abundances of white perch and striped bass larvae consistently peak near the ETM (Boynton *et al.*, 1997; North and Houde, 2001, 2003), there must be mechanisms for retention within the region. Understanding how larvae are retained in this dynamic region will help to identify how changing physical conditions could affect the survival of white perch and striped bass larvae.

Passive retention mechanisms of eggs and early-stage larvae may depend on the depth distribution of organisms combined with net residual circulation patterns (Norcross and Shaw, 1984; Miller, 1988). Larval tomcod (*Microgadus tomcod*) used passive up-estuary transport for retention in the St Lawrence River estuary by remaining in deep water (Laprise and Dodson, 1989a, 1990). In the Chesapeake Bay ETM region, deep landward-flowing water down-estuary of the salt front creates a convergence zone near the tip of the salt front (Schubel, 1968) where particles, including fish larvae and their zooplankton prey, could be passively retained. Active retention mechanisms such as diel or tidal vertical migration may become important as larvae develop (Boehlert and Mundy, 1988; Laprise and Dodson, 1989b; Rowe and Epifanio, 1994; Bennett *et al.*, 2002). In the St Lawrence River estuary, larval rainbow smelt (*Osmerus mordax*) are retained within the ETM region by making tidally-timed vertical migrations (Laprise and Dodson, 1989b). Although changes in vertical distribution may appear to be synchronized with current velocities to accomplish transport or retention, vertical migrations actually may be cued by other factors such as temperature, salinity, dissolved oxygen, or predator and prey distributions (Fortier and Leggett, 1983; Breitburg, 1994).

Objectives of our research were to identify the small-scale factors that influence the distribution of white perch and striped bass larvae in the ETM and to determine mechanisms used for retention. Research was designed to address two hypotheses: (1) earliest life stages (eggs and yolk-sac larvae) of white perch and striped bass were retained in deep landward-flowing water and (2) post-yolk-sac larvae made tidally-timed vertical migrations that improved with ontogeny and resulted in retention within the ETM. Changes in larval distributions in relation to light, current velocity, turbidity, salinity and prey distributions were evaluated to determine if larvae maintain their position in deep landward-flowing water, follow high prey concentrations, or undergo diel or tidally-timed vertical migrations. Results of fixed-location and mapping surveys were compared to understand retention mechanisms in the context of the broader ETM nursery area.

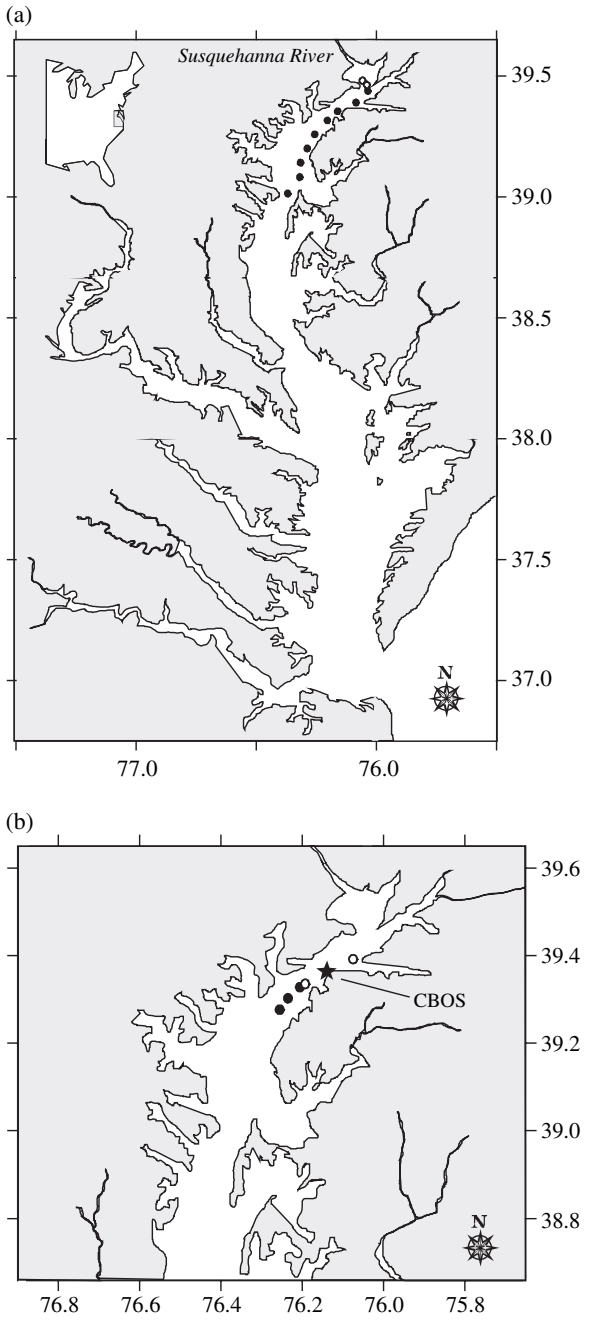
METHODS

Study location and sampling sites

Three research cruises in May 1998 and two in May 1999 were conducted on the 16-m *RV Orion* in the upper Chesapeake Bay (Fig. 1). Each cruise consisted of (1) a CTD survey along the axis of the Bay (Fig. 1a), (2) mapping surveys of ichthyoplankton abundance through the ETM, and (3) a fixed-location sampling station within the ETM to document changes in ichthyoplankton vertical distribution over the tidal cycle (Fig. 1b). Although this paper emphasizes data from the fixed sampling stations, data from the mapping surveys of each cruise are also analyzed. Methods describing the axial CTD and mapping surveys of physical factors, ichthyoplankton, and zooplankton that were conducted up-estuary, within, and down-estuary of the ETM are presented in North and Houde (2001, 2003). Mapping surveys were conducted within an 8-h period at night on 4–5, 12–13, and 22–23 May 1998, and 4–5 and 17–18 May 1999. Methods at the fixed stations are provided herein for research cruises conducted on 3–4, 13–14, and 20–21 May 1998, and 5–6 and 18–19 May 1999.

At the beginning of each cruise, the location of the ETM and salt front were determined in an along-axis survey using a CTD equipped with a 5-cm-pathlength transmissometer to measure temperature, salinity, and turbidity. Information from the axial survey combined with estimated tidal excursions (based on predicted tide current speeds) was used to select the fixed stations so that sampling was conducted in waters with high turbidities near the salt front. During the second cruise in 1999, the 1.0 isohaline was displaced up-estuary from the region of highest turbidity. Consequently, in

Figure 1. Sampling locations in Chesapeake Bay. (a) CTD survey stations. Additional stations in 1999 indicated by open circles. (b) Location of Chesapeake Bay Observing System (CBOS) buoy ('star symbol') and fixed-station locations (1998: solid circles, 1999: open circles).



this cruise sampling was conducted in high turbidities down-estuary of the salt front. At the fixed stations, depth-stratified net collections and CTD casts were made every 1.5 h over a 10- or 12-h period during 1998 cruises and over a 24-h period during 1999.

Physics

Before the cruises, transmissometer voltage was calibrated to nephelometric turbidity units (NTU) units with a Formazin NTU standard. In the field, 100-mL water samples were collected with a pump attached to the CTD frame to calibrate turbidity measurements with total suspended solids (TSS) concentrations. Light intensity (1998 and 1999) and current velocity (only in 1999) also were measured at the fixed stations. A LI-COR LI-100 DataLogger with a LI-190SA Quantum Sensor light meter was used to measure light intensity (μmol photon m^{-2} s^{-1}) at the water surface. Irradiance just below the water surface (I_o) in 1998 was estimated by adjusting measured light intensity for reflectance based on solar declination and zenith angle assuming 4 m s^{-1} wind speeds (Kirk, 1994).

To investigate the potential effect of light levels on larval distributions in 1998, the maximum depth at which visual feeding by fish larvae could occur, termed 'maximum depth of larval visual feeding' (Z_{max}), was estimated. A regression model was constructed to estimate Z_{max} using near-surface irradiance and turbidity from 77 CTD casts in the ETM region of upper Chesapeake Bay in May 2001. Then, the regression model and near-surface turbidity and irradiance from 1998 were used to calculate Z_{max} at fixed stations. The irradiance at Z_{max} was assigned the value of 0.008 μmol photon m^{-2} s^{-1}. The light level at which visual feeding by striped bass larvae appears to cease occurs between 0.008 and 0.030 μmol photon m^{-2} s^{-1} in laboratory experiments: larvae in treatments with light levels ≤0.008 μmol photon m^{-2} s^{-1} consumed 10 times fewer *Artemia* nauplii than those in 0.030 μmol photon m^{-2} s^{-1} treatments (J. Duston, personal communications, Nova Scotia Agricultural College, Truro, N.S., Canada). The non-linear regression model to predict Z_{max} was constructed from turbidity and irradiance profiles in the upper Chesapeake Bay ETM on May 7–14, 2001 during a research cruise on *RV Cape Henlopen*:

$$Z_{max} = 0.6298 \ln I_o - 52.9557 \frac{1}{NTU_s} \quad (\text{adjusted } R^2 = 0.77, N = 77) \qquad (1)$$

where Z_{max} is the depth at which 0.008 μmol photon m^{-2} s^{-1} occurred, NTU_s is near-surface turbidity (NTU) and I_o is near-surface irradiance. The CTD was equipped with a profiling QSP-200L Quantum Scalar Irradiance Sensor and a 5-cm-pathlength transmissometer calibrated to NTU units with a Formazin NTU standard. The regression model was used with 1998 near-surface turbidities and I_o derived

from the LI-COR LI-100 DataLogger to estimate Z_{max} in 1998.

Near-surface (~2.5 m) current velocity measurements were obtained from the Chesapeake Bay Observing System (CBOS) buoy in 1998 (Fig. 1b) and from a 1.2 MHz Broadband Acoustic Doppler Current Profiler (ADCP) in 1999. The ADCP was towed on a catamaran float deployed beside the vessel at constant speed and heading for 10 min along the channel every 1.5 h. Six-minute averages of raw '100% good' data in the bin centered on 2.7 m were used as instantaneous measurements of current velocity at each station. Data from both years were rotated to maximize variance in current velocities in the along-channel direction.

As the CBOS buoy was located 8.1–12.7 km from fixed sampling stations in 1998, CBOS current velocities were adjusted to better match the magnitude and phase of currents near fixed stations. Predicted tides were used to adjust the along-channel current velocity from the near-surface (2.4 m depth) CBOS current meter with the equation:

$$V_{fs} = V_{CBOS} + (P_{fs} - P_{CBOS}) \quad (2)$$

where V_{fs} is the adjusted current velocity at the fixed station, V_{CBOS} is the velocity measured by the CBOS surface current meter, P_{fs} is the predicted current velocity near the fixed station, and P_{CBOS} is the predicted current velocity near the CBOS buoy. Locations of the predicted current velocity estimates were within 2.1 km of fixed stations and within 0.3 km of the CBOS buoy.

Biology

Ichthyoplankton and zooplankton were collected at the fixed stations to determine their vertical distribution and abundance. Collections were made in three depth intervals that varied depending on water depth. Sampling was conducted with a 1-m^2 opening–closing Tucker trawl fitted with 280-μm mesh nets, flow meters, and a temperature-depth recorder. The temperature-depth recorder was not available during the second cruise in 1998 so trawl deployment depths were estimated from trawl wire length and angle measurements. The average depth of the upper Bay channel is approximately 12.5 m; most Tucker-trawl tows were made in 0–3.5, 3.5–7 and 7–11 m depth intervals.

Samples were preserved in ethanol, changed to fresh ethanol within 24 h, and taken to the laboratory for enumeration and identification. When a sample's yolk-sac larvae numbers were >200, or post-yolk-sac larvae numbers were >600, samples were split (up to 1/8) with a plankton splitter and larvae from a fraction of the sample were enumerated. White perch and striped bass post-yolk-sac larvae were identified based on external morphological features (Waldman *et al.*, 1999) and measured with a computer-based digitizing system. Stomachs of 124 white perch larvae from 1998 and 1999 and 75 striped bass larvae from 1998 were excised and contents were identified and enumerated. Only larvae with prey in their guts were included in the gut-contents analysis.

After removal of ichthyoplankton, Tucker-trawl samples were sieved (1-mm mesh) to divide them into large and small zooplankton fractions. The <1 mm fraction was split (up to 1/64) with a plankton splitter and diluted to 200–400 mL. Zooplankton counts from three 1-mL aliquots were averaged and used to determine the concentration of organisms <1 mm (no. m^{-3}) collected in each tow. Copepodites, adult male and female copepods of *Eurytemora affinis*, and *Bosmina longirostris* cladocerans were enumerated. *Eurytemora affinis* and *B. longirostris* distributions were compared with larval fish distributions because they were the most common prey in white perch and striped bass larval stomachs in this and other studies (Beaven and Mihursky, 1980; Setzler-Hamilton *et al.*, 1982; Campfield, 2004; Shoji *et al.*, 2005). Fish larvae of different sizes have different gape limitations, so *E. affinis* copepods were grouped into two size classes: copepodites and adult males (small) and adult females (large). Because some copepods and cladocerans may have been extruded from the 280-μm mesh nets, estimates reported here are considered to be relative concentrations.

Analysis

Results from cruises were mapped with contour plots of physical factors and ichthyoplankton and zooplankton concentrations (Surfer 7.0, Golden Software, Inc., Golden, CO, USA). The gridding method was kriging based on an isotropic linear variogram model. Grid-line geometry was no less than half the average distance between measurements in the X (distance or time) and Y (depth) directions. In the CTD survey contour plots, station locations were expressed as the distance (km) down-estuary from the mouth of the Susquehanna River. In contour plots of the fixed-station results, time (h) starts at the beginning of each station occupation.

Mean salinity of occurrence

Mean salinity of occurrence of each early-life stage was calculated for both fixed-location and mapping survey stations during 1998 and 1999. The mean salinity of water filtered by each net tow was calculated by matching the time and depth intervals of net tows to

salinity data interpolated from CTD casts (Surfer software). Interpolated data were used to eliminate potential bias related to the difference between the time of CTD salinity measurements and net-tow collections (usually ~30 min). Mean salinity of occurrence was determined by averaging net-tow salinities weighted by the concentration of fish eggs and larvae using the equation:

$$S_m = \frac{\sum_{i=1}^{n} s_i c_i}{\sum_{i=1}^{n} c_i} \quad (3)$$

where S_m = mean salinity of occurrence, s_i = salinity of the ith net tow, c_i = egg or larval concentration (no. m^{-3}) in the ith net tow, and n = total number of net tows.

Retention mechanisms

To evaluate potential retention mechanisms, mean depths of occurrence of fish early-life stages and zooplankton were calculated for both fixed-location and mapping survey stations in 1998. Data from 1999 were excluded from this analysis because few larvae were collected during that year. Mean depths of occurrence were determined by averaging net-tow depths (surface = 0 m, middle = 5.75 m, and bottom = 11.0 m) weighted by the concentration of fish eggs and larvae using the equation:

$$D_m = \frac{\sum_{i=1}^{n} d_i c_i}{\sum_{i=1}^{n} c_i} \quad (4)$$

where D_m is the mean depth of occurrence, d_i is the depth of the ith net tow, c_i is the egg or larval concentration in the ith net tow, and n is the total number of net tows. Mapping survey stations at which only a single egg or larva was collected in the entire water column were not included in the calculation of mean depths of occurrence. Potential retention mechanisms were identified with a correlation analysis between mean depths of larval occurrence at fixed stations and the following variables: current velocity, maximum depth of larval visual feeding, potential prey mean depth, and 1.0 isohaline depth (as the upper boundary of the landward-flowing deep water) (SAS Institute Inc, 1997). Pearson correlation analyses were conducted, except for tests with the non-normally distributed variable 'maximum depth of larval visual feeding.' In these cases, nonparametric Spearman correlation coefficients were calculated. In addition to correlation analyses, mean depths of larval occurrence and 1.0 isohaline depths were tested with a one-tailed, paired t-test to determine if the mean depth of larval occurrence was deeper than the mean depth of the 1.0 isohaline (excluding stations up-estuary of the salt front).

Spatial overlap

To quantify spatial overlap between potential prey and fish early-life stages, Schoener overlap indices (Schoener, 1970) were calculated for each cruise in 1998 and then averaged to determine mean overlap. Percent overlap was calculated as:

$$\text{Percent overlap} = 100[1 - 0.5(\sum |p_{ix,t} - p_{jx,t}|)] \quad (5)$$

where $p_{ix,t} = c_{ix,t}/\Sigma\ c_i$, the proportion of the total concentrations of organism i found at depth x and time t, and $p_{jx,t} = c_{jx,t}/\Sigma\ c_j$ the proportion of the total concentrations of organism j found at the same depth x and time t. The Schoener overlap index is a simple yet robust index of niche overlap (Abrams, 1980; Linton *et al.*, 1981; Crowder, 1990) and in our case it quantifies the simplest measure of potential competition or predation: spatial overlap. High overlap values imply greater spatial co-occurrence. Overlap indices were tested for significance using EcoSim (Gotelli and Entsminger, 2003) following the 'RA3' method described in Winemiller and Pianka (1990) and Albrecht and Gotelli (2001).

Multiple regression analyses

Exploratory mixed-model, repeated-measures multiple regression analyses were conducted to determine which physical (salinity, TSS, temperature, depth) or biological (prey concentrations) factors accounted for a significant amount of variability in the depth-specific concentrations of copepod and fish early-life stages. Explanatory variables were limited to those that were likely predictors of organism concentrations based on a descriptive analysis. Metrics for physical factors were the averaged CTD measurements within net-tow depth intervals (salinity, TSS, temperature) and the mid-point depth of the net tows (depth). Salinity and dependent variables (copepod and fish early-life stage concentrations) were $\log_e$-transformed. A mixed-model, repeated-measures design was used to include 'cruise' as a random effect in the model and to account for covariance between samples at adjacent depths using an 'unstructured' covariance matrix (SAS 8.0 PROC MIXED with Kenward–Rogers degrees of freedom method) (SAS Institute Inc, 1997). Models

passed tests for normality (Shapiro–Wilks test) and homogeneity of variance (Pearson correlation tests of |residual| versus predicted values). In addition, all explanatory variables passed multicollinearity tests (tolerance >0.31, condition index <3.4, SAS 8.0 PROC REG, PROC PRINCOMP) (SAS Institute Inc, 1997). The regression analyses were limited to data from 1998 because variances in 1999 data were heterogeneous due to the many zero observations in that year.

Prey concentrations were added to the white perch and striped bass models with respect to larval developmental stage (feeding or not feeding) and larval size. The model for white perch larvae <5 mm included *E. affinis* copepodites and adult males. The models for larvae >5 mm included all *E. affinis* (adult females summed with copepodite and male concentrations). Prey concentrations were $\log_e$-transformed in all models. *Bosmina longirostris* concentrations were not included in the model because no relationship with larval concentrations was observed in descriptive analyses.

Coefficients of determination (R^2) from repeated-measures regression models with both fixed and random effects are unreliable, so are not reported. Instead, *F* statistics (variance ratios) are included in tables of results to indicate the relative amount of variance accounted for by fixed effects. The random effect 'cruise' was not significant in any of the models, so was excluded from tables of results.

RESULTS

Physics

Physical conditions differed markedly between cruises and years (Fig. 2). In 1998, there was above-average freshwater discharge from the Susquehanna River in spring, the salt front was well defined, and high TSS concentrations occurred near the front (Fig. 2a–c). In 1999, a spring with below-average discharge, salinities in the upper Bay were higher, the intersection of the 1.0 isohaline with the bottom had shifted ~15 km up-estuary (Fig. 2d,e), and high TSS concentrations were located down-estuary from the salt front. A detailed description of environmental factors and physical conditions during these cruises is provided by North and Houde (2001).

In 1998, fixed stations were located within the salt front and high turbidity region (Fig. 2a–c), while in 1999 fixed stations were more closely associated with peak turbidities down-estuary of the weakly defined salt front (Fig. 2d,e). Physical conditions over a tidal cycle reflected the differences in the fixed-station location between years. During 1998, the salt front was clearly distinguishable from overlying fresh surface waters as indicated by the advance and retreat of the 1.0 isohaline during flood and ebb tides (Fig. 3a,c,e). In 1999, salinities were higher at the fixed stations (Fig. 4a,b), and during cruise 99-2 the most intense stratification occurred near the 5 isohaline rather than the 1 as in 1998 (Fig. 4b). During both years, elevated TSS concentrations indicated that resuspension events tended to occur when near-surface ebb or flood current velocities were high (Figs 3a,c,e and 4a,b), although there was a notable exception during the second cruise in 1999 at slack tide (Fig. 4b at 12 h). In this case, high TSS concentrations may have resulted because flood tide started near bottom before it occurred near surface, and because high stratification may have trapped resuspension below the pycnocline (Geyer, 1993).

Within years, wind and freshwater discharge events had a strong effect on physical conditions in the ETM region. During the second cruise in 1998, just after a seaward wind event and during a large peak in discharge (North and Houde, 2001), stratification had intensified, and salinity had increased markedly but was confined to the bottom 5 m of the water column (Fig. 3c).

Organism abundance and distribution

The abundance and distribution of white perch and striped bass early-life stages varied between species, life stage, cruise and year. Although striped bass egg abundance (no. m^{-2}) did not differ significantly between years, white perch and striped bass yolk-sac and post-yolk-sac larval abundances were significantly lower in 1999 than in 1998 (Fig. 5). In fact, only one striped bass post-yolk-sac larva and one white perch larva >8 mm were collected in 1999 at the fixed-sampling stations.

Mean salinities of occurrence indicate that white perch and striped bass early-life stages occurred most often in salinities from 1.6 to 2.5 in fixed-station

Figure 2. Contour plots of total suspended solid (TSS) concentrations (mg L^{-1}) and salinity from CTD surveys in 1998 (a–c) and 1999 (d, e). Lines represent salinity, shaded contours represent TSS. CTD cast locations are marked with symbols (▼) at the top of each plot. Arrows indicate the location of fixed-station sampling during each cruise. Figure reproduced from North and Houde (2001) with permission from Estuaries.

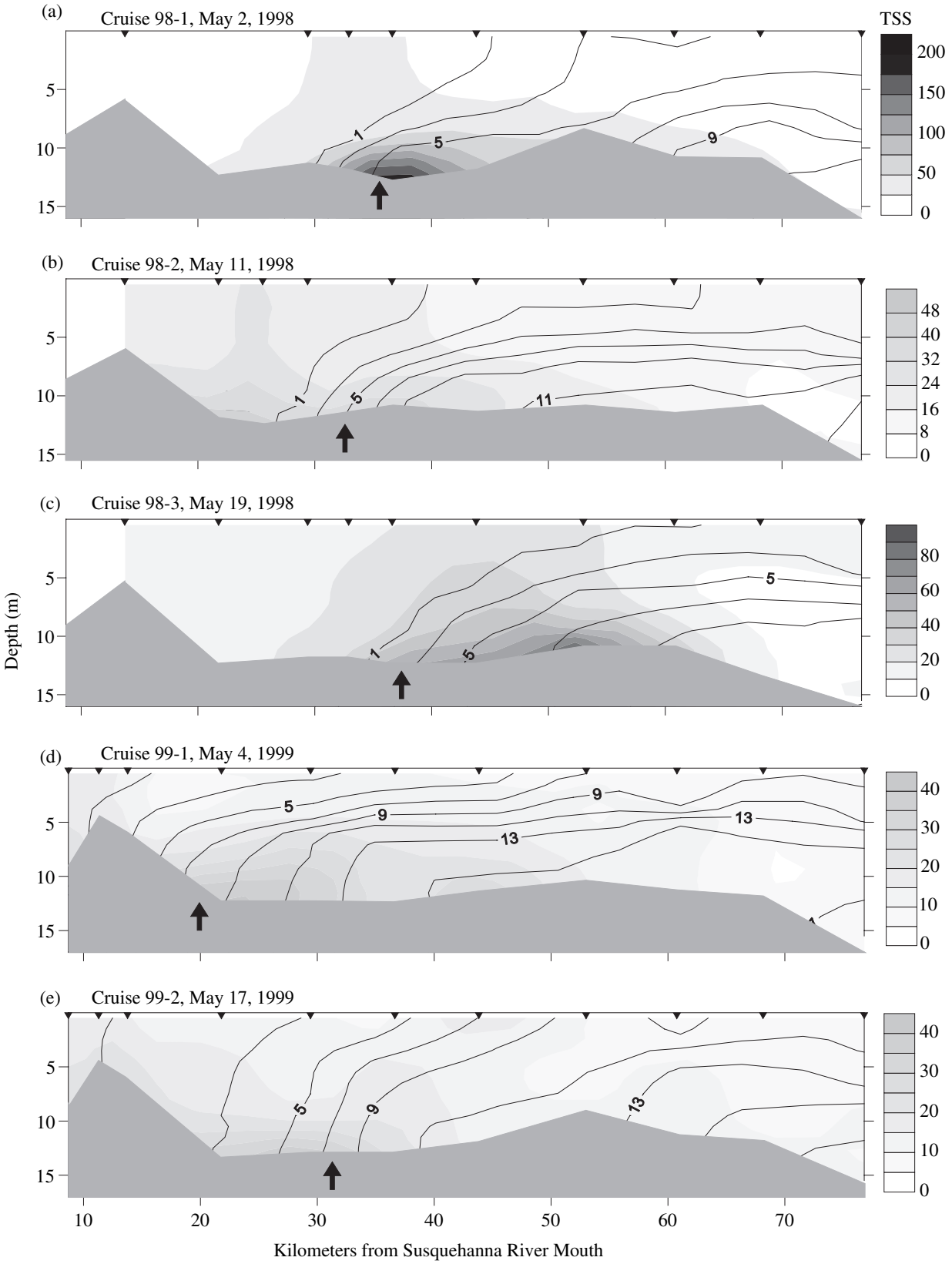
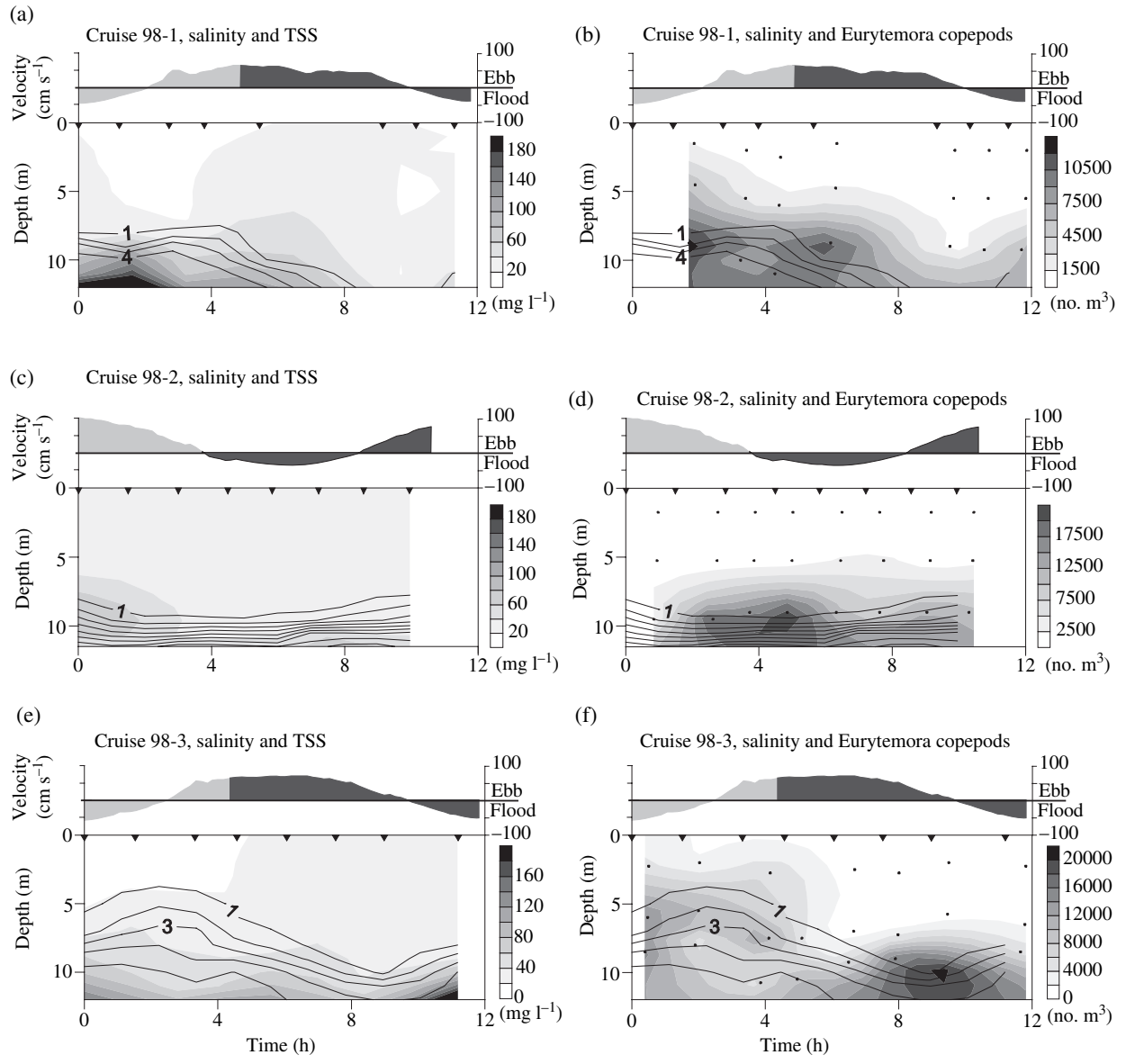

(a)
Cruise 98-1, May 2, 1998
TSS
200
150
100
50
0
1
5
9
(b)
Cruise 98-2, May 11, 1998
48
40
32
24
16
8
0
1
5
11
(c)
Cruise 98-3, May 19, 1998
80
60
40
20
0
1
5
5
(d)
Cruise 99-1, May 4, 1999
40
30
20
10
0
5
9
13
9
13
1
(e)
Cruise 99-2, May 17, 1999
40
30
20
10
0
5
9
13
Depth (m)
5
10
15
10
20
30
40
50
60
70
Kilometers from Susquehanna River Mouth

Figure 3. Fixed-station data. Along-channel current velocity (cm s^{-1}), salinity contour lines, and shaded contours of (a,c,e) total suspended solids concentrations (mg L^{-1}) and (b, d, f) *Eurytemora affinis* copepodite and adult copepod concentrations (no. m^{-3}) from the (a, b) first (c, d) second, and (e, f) third research cruises in 1998. CTD cast times are marked with symbols (▼) at the top of each contour plot. Night indicated by dark gray portion of the current velocity graphs. Black dots in panels (b), (d), and (f) mark the mid-point depths of the net tows.



samples from 1998, but were sampled in higher salinities (2.7–6.6) in 1999 (Table 1). Mean salinities of egg and larvae occurrences in 1998 were similar to those in the 1998 mapping survey samples that had been collected up-estuary, within, and down-estuary of the ETM (compare panels a and b in Table 1). In

Figure 4. Fixed-station data. Along-channel current velocity (cm s^{-1}), salinity contour lines, and (a, b) shaded contours of total suspended solids concentration (mg L^{-1}) and (c, d) shaded contours of white perch yolk-sac larvae concentrations (no. m^{-3}) during the (a, c) first and (b, d) second research cruise in 1999. CTD cast locations are marked with symbols (▼) at the top of each contour plot. Night indicated by dark gray portion of the current velocity graphs. Black dots in panels (c) and (d) mark the mid-point depths of the net tows.

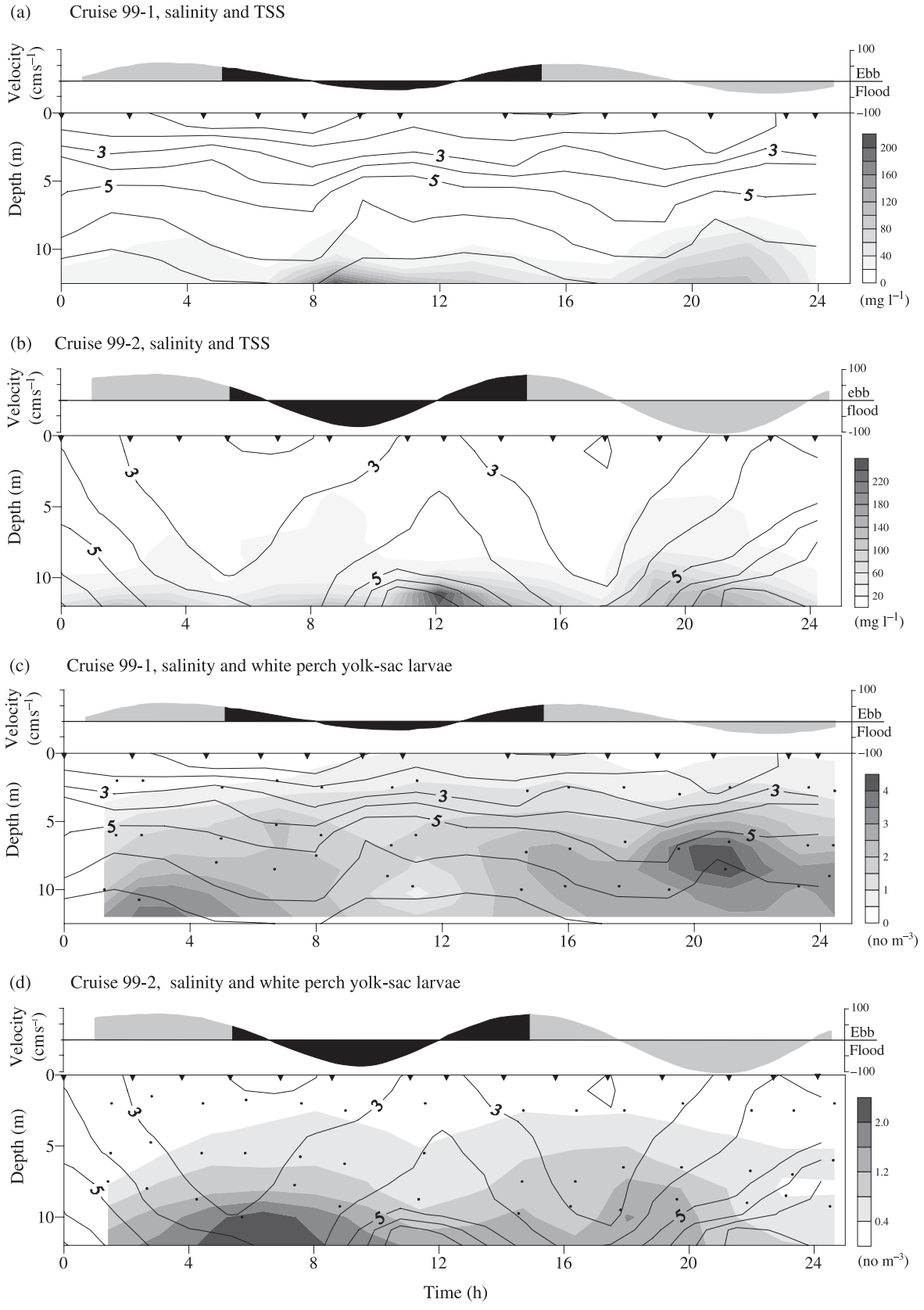
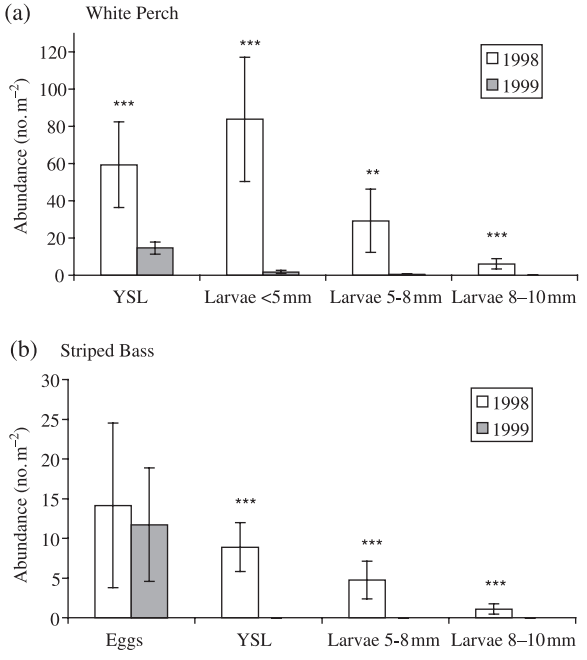

(a) Cruise 99-1, salinity and TSS
Velocity (cms^{-1})
100
Ebb
Flood
−100
Depth (m)
0
5
10
3
5
200
160
120
80
40
0
(mg l^{-1})
0
4
8
12
16
20
24
(b) Cruise 99-2, salinity and TSS
Velocity (cms^{-1})
100
ebb
flood
-100
Depth (m)
220
180
140
100
60
20
(mg l^{-1})
(c) Cruise 99-1, salinity and white perch yolk-sac larvae
Velocity (cms^{-1})
Ebb
Flood
−100
Depth (m)
4
3
2
1
0
(no m^{-3})
(d) Cruise 99-2, salinity and white perch yolk-sac larvae
Velocity (cms^{-1})
Ebb
Flood
−100
Depth (m)
2.0
1.2
0.4
(no m^{-3})
Time (h)

Figure 5. Fixed-station analysis of mean abundance (no. m^{-2}) of early-life stages of (a) white perch and (b) striped bass in 1998 and 1999. Error bars represent ±2 standard errors of the mean. Stars indicate that 1999 mean is significantly different from 1998 mean (**$P < 0.01$, ***$P < 0.001$), based on *t*-tests with unequal variances (equal variances for striped bass eggs).



contrast, mean salinities of egg and larvae occurrences in fixed-station samples in 1999 were 1 to 2 salinity units higher than 1999 mapping survey samples. This indicates that the 1998 fixed-station samples were collected in the salt front where early-life stages were most abundant. In contrast, the fixed stations in 1999 were down-estuary of the location where early-life stages peaked in concentration.

Depth-specific changes in concentrations (no. m^{-3}) of *E. affinis* copepods, fish eggs, yolk-sac larvae and post-yolk-sac larvae occurred over time at the fixed-sampling stations in 1998 (Figs 3, 4, 6 and 7). *Eurytemora affinis* copepods were found in high concentrations at fixed stations, mostly near and below the 1 isohaline (Fig. 3b,d,f). In multiple regression analyses, salinity and tow depth accounted for most of the variability in *E. affinis* copepodite and adult copepod concentrations (Table 2a). Parameter estimates indicated that these *E. affinis* stages mostly occurred in bottom waters in the salt front, a depth distribution that would facilitate passive retention within the ETM region.

Although not illustrated, distributions of striped bass eggs in 1998 were mostly in bottom waters and similar to distributions of white perch yolk-sac larvae (Fig. 6). In contrast, high concentrations of striped bass eggs occurred in both surface and bottom waters in 1999. In the multiple regression analysis, temperature, TSS concentrations, and depth were significant, indicating that egg concentrations in the ETM region were highest in turbid waters in the salt front and increased in abundance as temperatures rose during May 1998 (Table 2b), apparently in response to increased spawning.

Concentrations of white perch and striped bass yolk-sac larvae peaked near bottom during all cruises in 1998 (Fig. 6), but the two species peaked at different times in the tidal cycle, except during cruise 98-2 (coinciding with the high freshwater discharge event). Under non-event conditions (cruises 98-1 and 98-3), striped bass yolk-sac larvae peaked in concentration near the end of flood/beginning of ebb tide whereas white perch yolk-sac larvae peaked in concentration near the end of ebb/beginning of flood tide (Fig. 6a,b,e,f). Mean salinities of occurrence indicated that most yolk-sac larvae of both species occurred within the salt front, but that striped bass (salinity 2.53) were in slightly higher salinities than white perch (1.58) (Table 1a). In multiple regression analyses, tow depth accounted for a significant amount of the variability in white perch yolk-sac larvae concentrations, and TSS concentrations were significant in the model for striped bass yolk-sac larvae. Because high TSS concentrations occurred in bottom waters, white perch and striped bass yolk-sac larvae tended to be located in the water column where conditions were favorable for passive retention within the ETM region (Table 2b,c). Although the mean overlap index between white perch and striped bass yolk-sac larvae was not significant (52%) (Table 3), striped bass yolk-sac larvae had significant overlap with *E. affinis* concentrations (60–69% mean overlap) in all three cruises. White perch yolk-sac and white perch <5 mm larvae also had significant overlap (62%).

In 1999, although in higher salinity waters, white perch yolk-sac larvae during cruise 99-2 had similar distributions to those during cruise 98-1 and 98-3, peaking near bottom at the end of ebb/beginning of flood tide (Fig. 4d). During cruise 99-1, white perch yolk-sac larvae were more broadly distributed through the water column, although at peak abundance in mid- to bottom-depth samples (Fig. 4c).

Calanoid copepodites were the most common prey in guts of white perch and striped bass post-yolk-sac larvae of all size classes. They comprised 55.7%, 82.0%, and 92.0% of prey items in guts of white perch 3.5–5, 5–8, and 8–10 mm in length, respectively, and

Table 1. Mean salinity of occurrence of fish early-life stages from (a) fixed-station sampling within the estuarine turbidity maximum (ETM) and from (b) mapping surveys above, within, and below the ETM. Mean salinity of occurrence was derived from the average salinity of water filtered by each net tow weighted by concentration of fish early-life stages for each year, species, and size class. For fish early-life stages, *N* refers to the number of tows in which eggs or larvae were present.

	1998			1999		
	Mean salinity	Standard error	*N*	Mean salinity	Standard error	*N*
(a) Fixed station						
Net tows (unweighted)	1.13	0.17	69	4.15	0.16	84
White perch						
Yolk-sac larvae	1.58	0.34	68	4.85	0.17	84
Larvae < 5 mm	2.05	0.34	68	5.28	0.07	54
Larvae 5–8 mm	1.95	0.21	65	5.44	0.05	38
Larvae 8–10 mm	2.21	0.10	54	2.69	0.00	1
Striped bass						
Eggs	1.63	0.18	54	3.48	0.13	82
Yolk-sac larvae	2.53	0.15	61	6.57	0.01	3
Larvae 5–8 mm	1.84	0.11	57	5.50	0.00	1
Larvae 8–10 mm	2.05	0.05	48	–	–	0
(b) Mapping survey						
Net tows (unweighted)	2.61	0.47	49	5.88	0.70	34
White perch						
Yolk-sac larvae	1.31	0.58	49	3.37	0.41	34
Larvae < 5 mm	2.59	0.40	45	3.50	0.19	19
Larvae 5–8 mm	3.45	0.33	42	3.83	0.09	12
Larvae 8–10 mm	2.69	0.14	34	1.82	0.01	2
Striped bass						
Eggs	0.21	0.14	40	1.71	0.03	7
Yolk-sac larvae	2.32	0.12	34	3.75	0.03	2
Larvae 5–8 mm	1.46	0.09	32	–	–	0
Larvae 8–10 mm	2.37	0.06	25	–	–	0

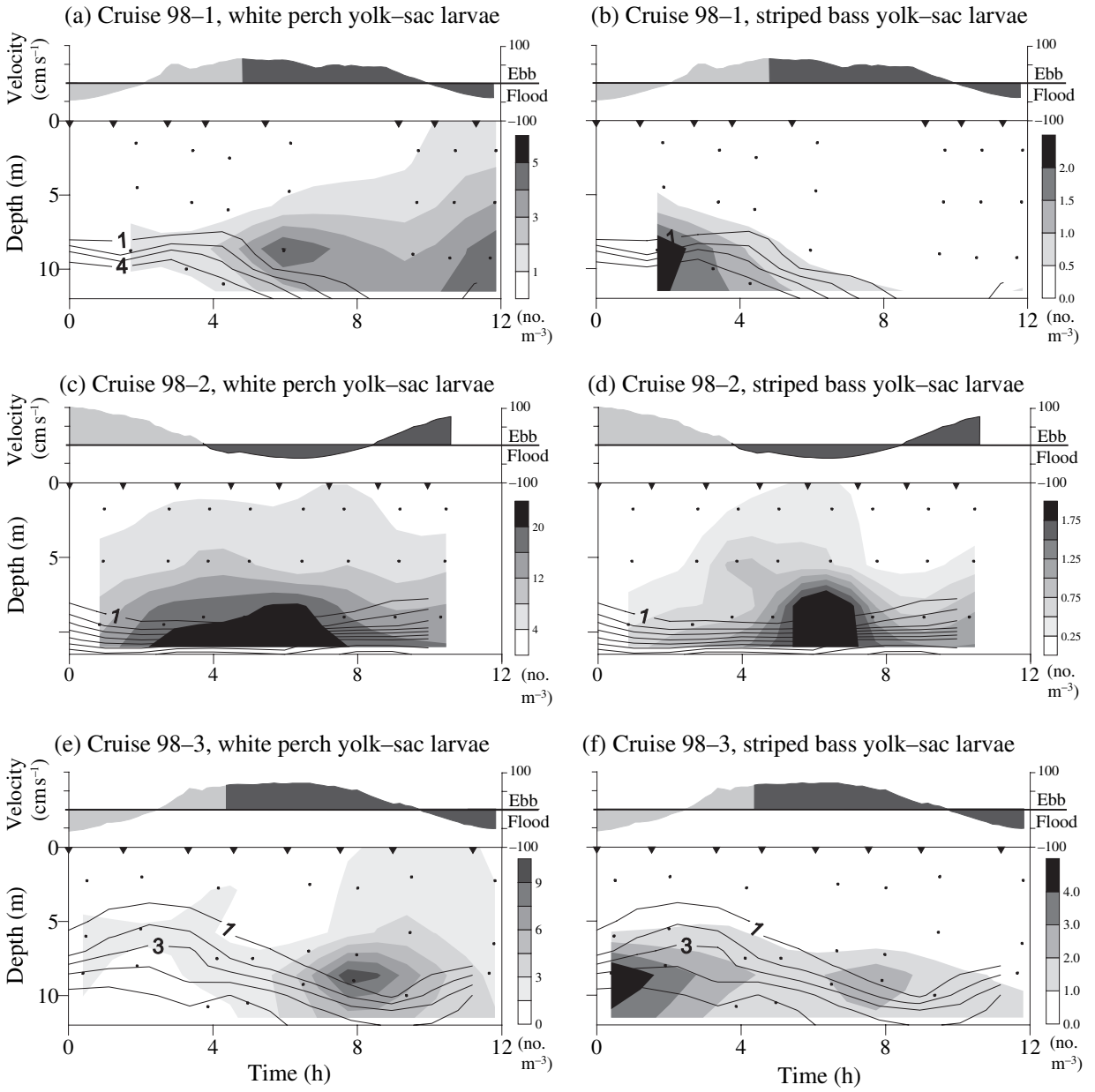
85.4% and 93.5% of prey in 5–8 and 8–10 mm striped bass guts, respectively. Copepodites as small as 250 μm in urosome length were found in the guts, indicating that our net tows with 280-μm net mesh likely underestimated abundance of small copepodites that could be important prey for early-stage fish larvae. The remaining proportion of gut contents was comprised of zooplankters such as *B. longirostris*, copepod nauplii, and rotifers. Most copepodites probably were *E. affinis* because no other calanoid species was identified in larval guts and because *E. affinis* comprised 85% of all calanoid copepodites in the net tows.

In contrast to the spatially distinct distributions of yolk-sac larvae of striped bass and white perch, peak concentrations of 8–10 mm larvae of the two species (1) often were coincident, (2) were not associated with a specific tidal cycle (Fig. 7), and (3) tended to occur where prey concentrations were high (compare Figs 3 and 7). Although not illustrated, the spatial distribution of intermediate size classes, between yolk-sac and 8–10 mm larvae, generally indicated a continuum between these stages. Overlap indices were significant in all three cruises between post-yolk-sac larval stages of white perch and striped bass, for comparisons between species (56–71% mean overlap), and between size classes within each species (68–79% mean overlap) (Table 3). In multiple regression models, *E. affinis* concentrations accounted for most of the variability in concentrations of all sizes of white perch and striped bass post-yolk-sac larvae (Table 2b,c). In addition to *E. affinis* concentrations, tow depth explained a significant amount of variability in concentrations of white perch >5 mm larvae and striped bass 8–10 mm larvae, supporting our observation that concentrations were highest in bottom waters and where high prey concentrations occurred.

Retention mechanisms

Four potential retention mechanisms of *E. affinis* and white perch and striped bass larvae were evaluated in correlation analyses on 1998 data: (1) tidally-timed

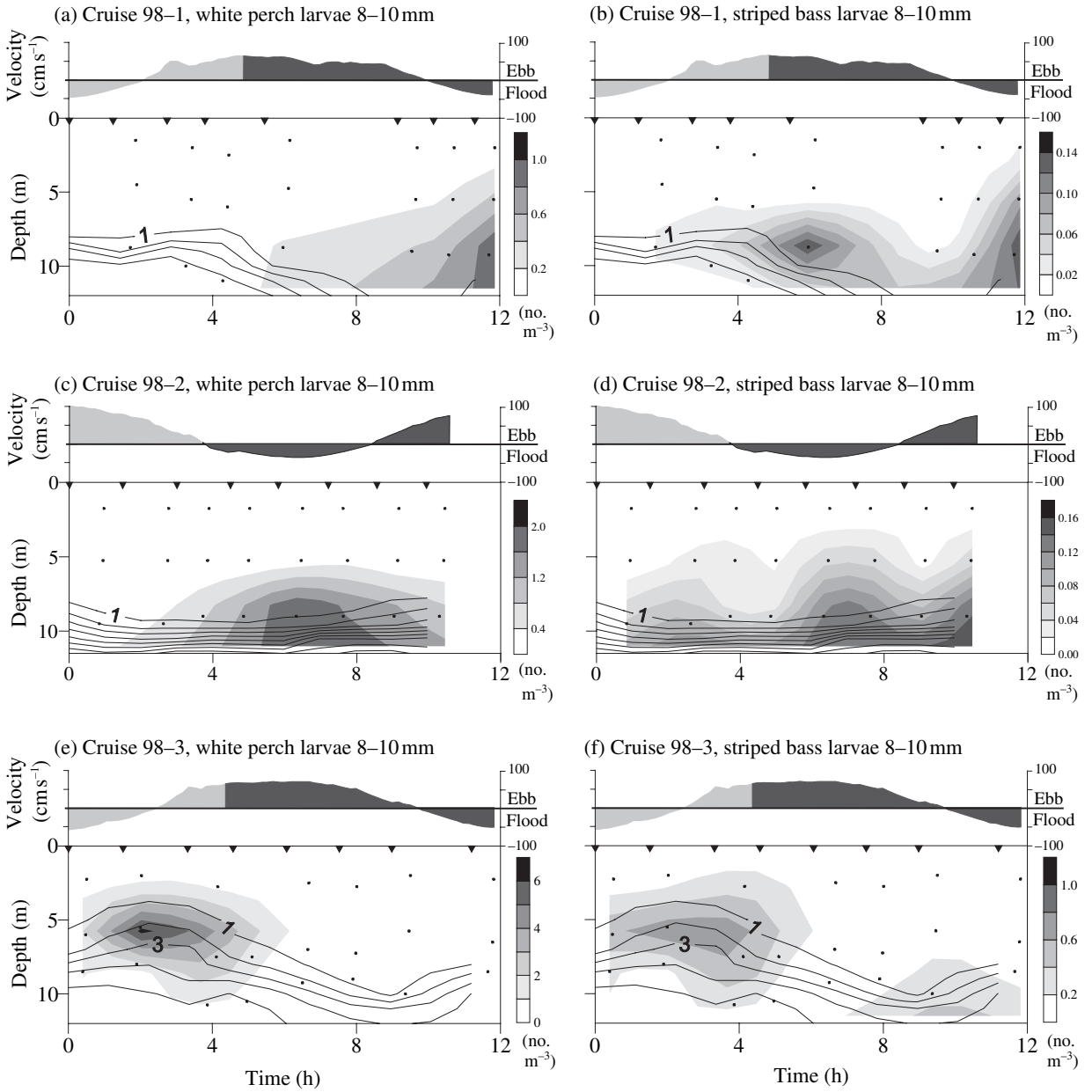
Figure 6. Fixed-station data. Along-channel current velocity (cm s^{-1}), salinity contour lines, and shaded contours of white perch and striped bass yolk-sac larvae concentration (no. m^{-3}) from the (a, b) first, (c, d) second, and (e, f) third research cruises in 1998. CTD cast times are marked with symbols (▼) at the top of each contour plot. Black dots mark the mid-point depth of the net tows. Night indicated by dark gray portion of the current velocity graphs.



vertical migration, (2) diel vertical migration, (3) maintenance in deep, net landward-flowing water, and (4) tracking prey. Deeper mean depth of occurrence during ebb tides and shallower mean depth of occurrence during flood tides would be indicative of tidally-timed vertical migration. There was no evidence to support this mechanism in these time series: mean depths of white perch and striped bass early-life stages, and also of *E. affinis*, were not correlated with current velocity (Table 4, Fig. 8a,c).

A diel vertical migration retention mechanism was not observed. A positive correlation between larval mean depth of occurrence and the maximum depth of larval visual feeding could indicate diel vertical migration. If this mechanism were important, post-yolk-sac larvae would reside in deep, net

Figure 7. Fixed-station data. Along-channel current velocity (cm s^{-1}), salinity contour lines, and shaded contours of 8–10 mm white perch and striped bass larvae concentration (no. m^{-3}) from the (a, b) first, (c, d) second, and (e, f) third research cruises in 1998. CTD cast locations are marked with symbols (▼) at the top of each contour plot. Black dots indicate the mid-point depth of the net tows. Night indicated by dark gray portion of the current velocity graphs.



landward-flowing water during the day (14 h duration in May) and in upper-layer, net down-estuary flowing water during the night (10 h duration in May) (see Fig. 4 for day/night information). In fact, depths of occurrence of white perch <8 mm larvae were negatively correlated with maximum visual feeding depth (Table 4), indicating that mean depths of occurrence were shallower during the day than at night. Mean depths of occurrence of white perch and striped bass larvae often were below the putative maximum depth of larval visual feeding (Fig. 9a–c), except in cruise 98-3 when high concentrations of 8–10 mm larvae did occur at shallower depths (compare Figs 7e, f and 9c).

Maintenance in deep, landward-flowing water down-estuary of the salt front may be an important

Table 2. Multiple regression tables for (a) *Eurytemora affinis*, (b) striped bass and (c) white perch early-life stages from 1998 fixed-station samples. Parameter estimates (Param.) are reported for variables that described a significant ($\alpha = 0.05$) amount of variability in organism concentrations.

Explanatory Variables	Copepodites & adult males			Adult females		
	F	*P*	Param.	*F*	*P*	Param.
(a) *Eurytemora affinis*						
Salinity	15.56	0.0005	0.80 (0.20)	10.19	0.003	0.56 (0.18)
Depth	7.52	0.01	0.16 (0.06)	18.32	0.0001	0.26 (0.06)
TSS Concentration	3.6	0.07	n.s.	0.47	0.50	n.s.

Explanatory Variables	Eggs			Yolk-sac larvae			Larvae 5–8 mm			Larvae 8–10 mm		
	F	*P*	Param.	*F*	*P*	Param.	*F*	*P*	Param.	*F*	*P*	Param.
(b) Striped bass												
Salinity	0.58	0.45	n.s.	4.65	0.04	0.44 (0.20)	0.08	0.78	n.s.	0.32	0.57	n.s.
Depth	8.61	0.006	0.27 (0.09)	3.40	0.07	n.s.	1.18	0.28	n.s.	4.54	0.04	0.16 (0.08)
TSS concentration	8.52	0.007	0.05 (0.02)	2.90	0.10	n.s.	–	–	–	–	–	–
Eurytemora affinis	–	–	–	–	–	–	8.67	0.005	0.52 (0.18)	7.45	0.009	0.45 (0.17)
Temperature	86.64	<.0001	0.91 (0.10)	–	–	–	–	–	–	–	–	–

Explanatory Variables	Yolk-sac larvae			Larvae < 5 mm			Larvae 5–8 mm			Larvae 8–10 mm		
	F	*P*	Param.	*F*	*P*	Param.	*F*	*P*	Param.	*F*	*P*	Param.
(c) White perch												
Salinity	3.01	0.09	n.s.	0.29	0.60	n.s.	2.11	0.16	n.s.	0.09	0.77	n.s.
Depth	25.1	<0.0001	0.29 (0.06)	4.04	0.05	0.10 (0.05)	6.39	0.01	0.22 (0.09)	5.91	0.02	0.21 (0.09)
Eurytemora affinis	–	–	–	45.54	<0.0001	0.87 (0.13)	24.47	<0.0001	1.01 (0.21)	18.96	<0.0001	0.084 (0.19)

Standard errors of the parameter estimates are given in parentheses.
Organism concentrations and salinity were $\log_e$-transformed. Dashes (–) indicate fixed effects that were not included in the model. Sample size (N) = 68 for all models.
TSS, total suspended solids; n.s., not significant.

retention mechanism for *E. affinis* copepodites and adults, striped bass eggs and yolk-sac larvae, and striped bass and white perch post-yolk-sac larvae. At fixed stations, the mean depths of occurrences of these organisms and stages tended to be deeper than the 1 isohaline depths (Table 5). In fact, most were significantly deeper. At mapping survey stations within the salt front, mean depths of white perch and striped bass 8–10 mm larvae were near or below the 1 isohaline depth (Fig. 9d–f).

Post-yolk-sac larvae of white perch and striped bass may have been retained in the ETM region by tracking prey that occurred in deep, net landward-flowing water. In most cases, white perch and striped bass larval mean depths of occurrence were more highly correlated with mean depth of their potential prey (*E. affinis*) than with any other factor (Table 4). The mean depths of occurrence of all stages of white perch larvae were positively correlated with the mean depth of *E. affinis* and the correlation became stronger with increasing larval size. Although striped bass yolk-sac and post-yolk-sac larval mean depths of occurrence were not, or were weakly, correlated with depths of potential prey, the correlations were stronger if data from the second cruise were removed from the analysis (Table 4).

Examination of mapping survey results (Fig. 9d–f) helps to place the fixed-station results in the broader context of the entire ETM nursery area, and suggests that white perch and striped bass post-yolk-sac larvae concentrate in low salinity waters within the ETM region along the face of the salt front. Outside the regions sampled by fixed stations, mean depths of occurrence of post-yolk-sac larvae often were higher in the water column, both up-estuary and down-estuary. At the fixed stations, mean depths of occurrence of white perch post-yolk-sac larvae, 8–10 mm striped bass larvae, and mean depths of *E. affinis* copepodites and adult females were significantly correlated with the 1 isohaline depth (Table 4), as were mean depths

Table 3. Mean percent overlap (Schoener overlap index) between potential prey and fish early-life stages at fixed stations in 1998. Means and standard errors (in parentheses) were calculated from the percent overlap for each cruise in 1998. Overlap indices were tested for significance using EcoSim software (Gotelli and Entsminger, 2003). Shaded overlap indices indicate significant overlap ($\alpha = 0.05$) in all three cruises.

	Prey			Striped bass				White perch			
	Eurytemora affinis copepodites and males	*Eurytemora affinis* adult females	*Bosmina longirostris* cladocera	Eggs	Yolk-sac larvae	Larvae 5–8 mm	Larvae 8–10 mm	Yolk-sac larvae	Larvae <5 mm	Larvae 5–8 mm	Larvae 8–10 mm
Prey											
E. affinis copep/males	100										
E. affinis adult females	75 (5)	100									
B. Longirostris	44 (9)	38 (12)	100								
Striped bass											
Eggs	59 (4)	48 (3)	42 (10)	100							
Yolk-sac larvae	60 (4)	69 (10)	36 (12)	51 (4)	100						
Larvae 5–8 mm	55 (4)	49 (2)	35 (12)	37 (7)	53 (9)	100					
Larvae 8–10 mm	57 (5)	44 (7)	35 (7)	43 (3)	44 (11)	71 (3)	100				
White perch											
Yolk-sac larvae	59 (5)	50 (10)	62 (3)	62 (10)	52 (14)	54 (10)	57 (7)	100			
Larvae <5 mm	61 (14)	48 (14)	43 (3)	46 (13)	46 (13)	56 (0)	63 (2)	62 (3)	100		
Larvae 5–8 mm	48 (13)	39 (14)	35 (11)	35 (14)	42 (15)	66 (8)	60 (2)	50 (9)	73 (10)	100	
Larvae 8–10 mm	53 (9)	45 (11)	40 (10)	39 (8)	43 (11)	71 (10)	69 (6)	56 (11)	68 (6)	79 (3)	100

Table 4. Correlation coefficients (r) for correlation between mean depth of occurrence (by species and stage) and current velocity, maximum depth of larval visual feeding, 1.0 isohaline depth, and mean depth of prey in 1998 at fixed stations.

Mean depth (m)	Current velocity (cm s^{-1})	Maximum depth of visual feeding (m)	1.0 isohaline depth (m)	Mean depth, *Eurytemora affinis* copepodites and males (m)	Mean depth, *Eurytemora affinis* adult females (m)
White perch					
Yolk-sac larvae	n.s.	n.s.	n.s.	0.48*	0.48*
	(n.s.)	(n.s.)	(n.s.)	(0.56*)	(0.66**)
Larvae < 5 mm	n.s.	−0.51*	0.62**	0.78***	0.50*
	(n.s.)	(−0.87***)	(0.66**)	(0.72**)	(n.s.)
Larvae 5–8 mm	n.s.	−0.56**	069***	0.86***	0.67***
	(n.s.)	(−0.71**)	(0.74**)	(0.86***)	(0.79***)
Larvae 8–10 mm	n.s.	n.s.	0.61**	0.84***	0.70***
	(n.s.)	(n.s.)	(0.65**)	(0.80***)	(0.79***)
Striped bass					
Eggs	n.s.	n.s.	n.s.	n.s.	(n.s.)
	(n.s.)	(n.s.)	(n.s.)	(n.s.)	(n.s.)
Yolk-sac larvae	n.s.	n.s.	n.s.	n.s.	n.s.
	(n.s.)	(n.s.)	(n.s.)	(0.58*)	(0.64*)
Larvae 5–8 mm	n.s.	n.s.	n.s.	n.s.	n.s.
	(n.s.)	(n.s.)	(0.59*)	(0.71**)	(0.85***)
Larvae 8–10 mm	n.s.	n.s.	0.52*	0.53*	0.48*
	(n.s.)	(n.s.)	(0.73**)	(0.76**)	(0.81***)
Eurytemora affinis					
Copepodites and males	n.s.	n.s.	0.64**	1.00	0.84***
	(n.s.)	(−0.71**)	(0.67**)	(1.00)	(0.88***)
Adult females	n.s.	n.s.	0.57**	0.84***	1.00
	(n.s.)	(n.s.)	(0.64*)	(0.88***)	(1.00)

Sample sizes were $N = 23$ for white perch larvae, *Eurytemora affinis* copepod and striped bass eggs, $N = 22$ for striped bass larvae. Correlation analysis results excluding data from the second cruise in 1998 (after the high freshwater discharge event) are presented in parentheses ($N = 15$ for white perch larvae, *E. affinis* and striped bass eggs, $N = 14$ for striped bass larvae). Significant Pearson correlation coefficients are reported except for tests with the non-normally distributed variable 'maximum depth of larval visual feeding.' In these cases, significant Spearman correlation coefficients are listed. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and n.s., correlation was not significant ($\alpha = 0.05$).

of striped bass 5–8 mm larvae after data from the second cruise were excluded.

DISCUSSION

Our results indicate that the ETM provides favorable nursery habitat in high freshwater-flow years when low salinity waters and the ETM region coincide. In a high-flow year, the yolk-sac larvae stages of white perch and striped bass, as well as the copepod prey of feeding larvae, were retained in the ETM region by remaining in deep waters within the salt front. High concentrations of feeding larvae were associated with high prey concentrations. Based on analysis of larval distribution data with respect to tidal currents, day–night, depth, salinity and prey concentrations, we suggest that retention of post-yolk-sac larvae resulted from tracking copepod prey that were retained via maintenance in deep waters within the salt front.

Fixed-sampling station results demonstrated that physical conditions strongly influenced the ETM nursery area of striped bass and white perch. These conditions differed markedly between 1998 and 1999, high and low freshwater-discharge years. During 1998 and other years of average or high discharge, the Chesapeake ETM was located near the salt front (Schubel, 1968; Boynton *et al.*, 1997; North and Houde, 2001; Sanford *et al.*, 2001). The low-salinity region near the salt front in Chesapeake Bay was known to be an important nursery habitat for white perch and striped bass larvae (Dovel, 1971; Boynton *et al.*, 1997; North and Houde, 2001, 2003). In 1998, when larvae were abundant, most white perch and striped bass early-life stages were found within the salt front and

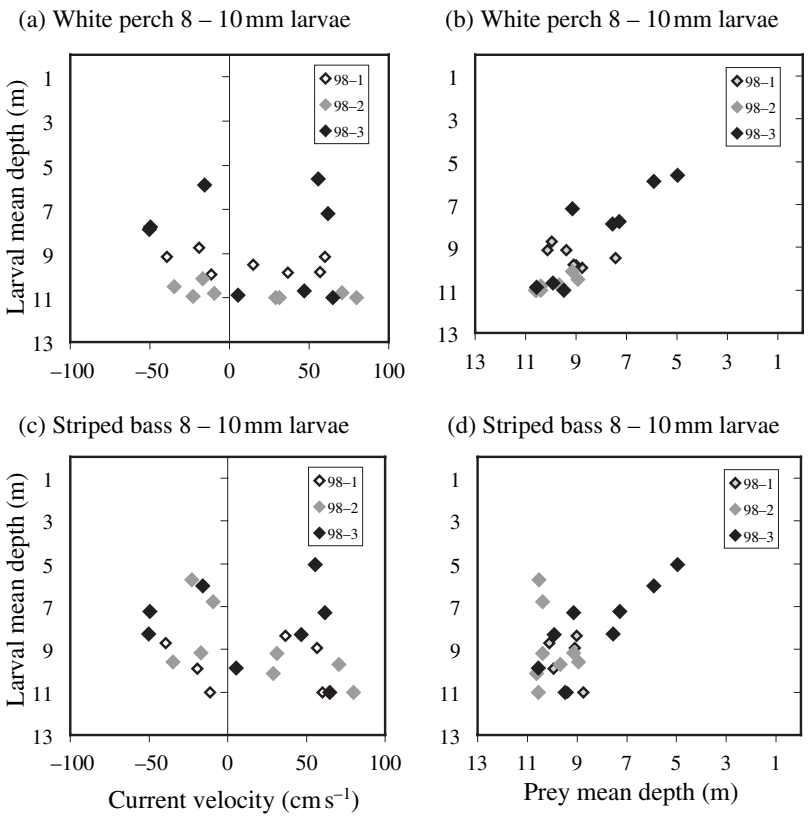


Figure 8. Mean depths of white perch and striped bass 8–10 mm larvae occurrences (m) in relation to (a, c) current velocity (cm s^{-1}) and (b, d) mean depth of prey (m). Prey are *Eurytemora affinis* copepodites and adult males. Data are from research cruises in 1998 (98-1, 98-2, 98-3). Cruises are represented by different symbols. Negative current velocity is up-estuary (i.e. flood tide).

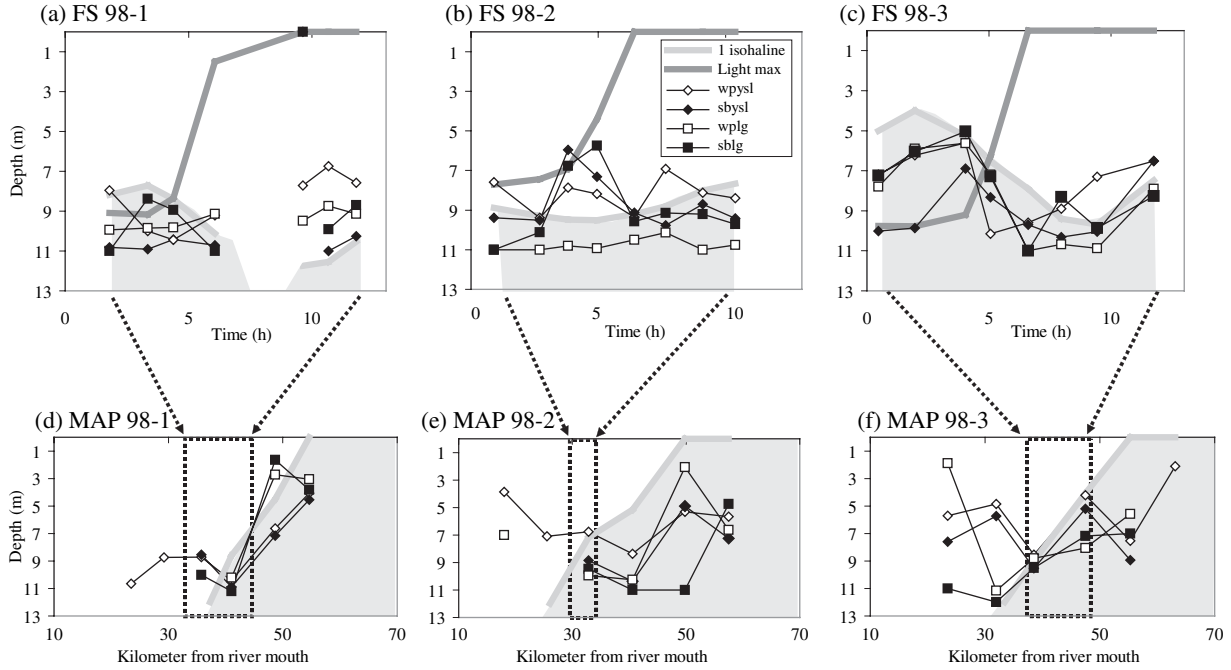
ETM (mean salinities of occurrence ranged from 1 to 3.5). These results, coupled with the high prey concentrations (*E. affinis*) in the upper estuary during high flow years (Kimmel and Roman, 2004), underscore the conclusion that the ETM region is an important larval nursery area during years of high freshwater flow.

In years of low freshwater flow, characteristics of the ETM nursery potentially can have negative consequences for fish early-stage retention and survival. In 1999, the high mean salinities (2–5) of larval occurrence (Table 1) at the fixed stations resulted because the ETM was located down-estuary of the salt front, and down-estuary of low-salinity areas where larvae were more abundant. In 1999, some early-stage white perch larvae did occur in the ETM region, indicating that they may have been trapped in the relatively high-salinity ETM convergence zone. But, the virtual absence of striped bass larvae and large white perch larvae (8–10 mm) at both fixed-location and mapping-survey stations in 1999 (North and Houde, 2001, 2003) suggests that (1) the weak convergence zone could have allowed substantial loss of early-life stages down-estuary, (2) high salinities in the ETM region could have caused larval mortality due to osmotic stress (Winger and Lasier, 1994), and/or (3) higher salinities in 1999 may have reduced the sinking rate of eggs and yolk-sac larvae, thus increasing buoyancy and potential for loss.

The effect of episodic wind and discharge events on physical conditions within the ETM region was notable. In 1998, a seaward wind event followed by a high freshwater-discharge event compressed the salt front (Fig. 3c) where high concentrations of *E. affinis* and fish early-life stages occurred (Figs 3d, 6c,d and 7c,d). Episodic events could influence retention and survival of fish larvae by promoting loss from the ETM nursery area due to enhanced down-estuary transport of fresh waters on top of the salt front (North *et al.*, 2005), and by creating osmotically stressful conditions due to rapidly increasing salinities within the salt front.

A conceptual diagram of an ETM region in a high flow year (Fig. 10) characterizes three zones where differences in residual current velocity, salinity, turbidity and light penetration have important implications for larval fish. Zone A is up-estuary of the salt front; Zone B is in the convergence zone at the salt front where light penetration is limited; and Zone C is down-estuary of the convergence zone where light regularly penetrates into low salinity waters. Most of the fixed-station sampling in 1998 was conducted in Zone B.

Figure 9. (a–c) Fixed-station data (FS). Mean depths of occurrence (m) of white perch (wpysl) and striped bass (sbysl) yolk-sac larvae and white perch (wplg) and striped bass (sblg) 8–10 mm larvae during fixed-station sampling for three research cruises in 1998 (98-1, 98-2, 98-3). Also depicted are 1.0 isohaline depth, and the estimated maximum depth of larval visual feeding (light max). Night occurs when maximum depth of larval visual feeding is zero. Shaded area represents salinities >1 (d,e,f) Mapping data (MAP). Mean depths of occurrence (m) of white perch (wpysl) and striped bass (sbysl) yolk-sac larvae, and white perch (wplg) and striped bass (sblg) 8–10 mm larvae from three research cruises in May 1998 (98-1, 98-2, 98-3). Shaded area represents salinities >1. Dashed boxes represent the region of the salt front in which fixed-station sampling occurred based on displacement calculations and 1 isohaline depth. Mapping surveys were conducted at night.



Zone A may be an important nursery habitat in estuaries where discharge rates, and subsequent down-estuary transport, are not as strong as discharge rates in upper Chesapeake Bay. Although mapping surveys of the ETM region have identified Zone B as a primary nursery area in upper Chesapeake Bay (Boynton *et al.*, 1997; North and Houde, 2003), Zone A also may be important for these larval fishes in other estuarine systems. High abundances of white perch and striped bass larvae were found within and up to 12 km up-estuary of the salt front in the Patuxent River (Campfield, 2004), a tidal tributary whose mean springtime freshwater discharge (14.7 $m^3 s^{-1}$) is two orders of magnitude smaller than the Susquehanna River which supplies the upper Chesapeake Bay (1889.8 $m^3 s^{-1}$, data from United States Geological Survey, http://waterdata.usgs.gov/nwis/sw). Physical trapping mechanisms in Zone B may be an important characteristic of larval fish nursery areas in systems with high freshwater flow rates like the upper Chesapeake Bay.

Results from our fixed-station sampling in Zone B indicate that *E. affinis* copepods were retained by maintenance in deep, low-salinity water immediately down-estuary of the salt front during high freshwater flow conditions. Mean depths of occurrence of *E. affinis*, the most important prey of larval white perch and striped bass in the upper Chesapeake ETM region (this study; Shoji *et al.*, 2005), were significantly deeper than the 1.0 isohaline (Table 5). Roman *et al.* (2001) also found that high concentrations of zooplankton, notably *E. affinis*, likely resulted from physical processes associated with the convergence zone near the salt front in upper Chesapeake Bay.

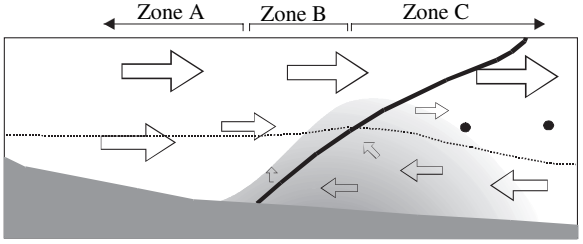
Transport to the ETM region probably occurs in the egg (striped bass) and yolk-sac larvae (white perch) stages (North and Houde, 2003), but retention in the ETM region appears to commence with the yolk-sac larvae stage for striped bass and the post-yolk-sac larvae <5 mm for white perch. Mean depths of these stages were significantly deeper than the 1 isohaline and results of regression analyses indicated that these stages were in a position to be passively retained in the ETM. The regression analysis also showed that *E. affinis* male and copepodite concentrations explained most of the variability in concentrations of white

Table 5. Mean difference between the depth of the 1 isohaline and the mean depth of organism occurrences at 1998 fixed stations.

	Data from all 1998 cruises	Data from 1998 cruises excluding 98-2
White Perch		
Yolk-sac larvae	−0.04 (0.37)	0.35 (0.54)
Larvae < 5 mm	**1.02**** (0.31)	0.67 (0.45)
Larvae 5–8 mm	**1.29***** (0.24)	**1.07**** (0.34)
Larvae 8–10 mm	**1.43***** (0.26)	**1.13**** (0.37)
Striped bass		
Eggs	0.88 (0.67)	0.41 (1.06)
Yolk-sac larvae	**1.09*** (0.46)	**1.89**** (0.54)
Larvae 5–8 mm	0.01 (0.55)	**1.07*** (0.46)
Larvae 8–10 mm	0.54 (0.38)	0.84 (0.40)
Eurytemora affinis		
Copepodites & males	**0.97***** (0.21)	**0.84*** (0.29)
Adult females	**1.43***** (0.28)	**1.68***** (0.39)

Standard errors of the mean are given in parentheses. Stations up-estuary of the salt front were excluded from this analysis. Positive numbers indicate that mean depths of organism occurrence were deeper than the 1 isohaline depths. Bold numbers with stars indicate significant one-tailed paired *t*-test results, testing the hypothesis that the mean depth of organism occurrence was deeper than the 1 isohaline depth (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Tests were conducted on data from all cruises in 1998 ($N = 21$), and on data excluding cruise 98-2 during the high discharge event ($N = 13$).

Figure 10. Conceptualization of physical conditions in an estuarine turbidity maximum nursery area within the estuarine transition zone during high freshwater flow conditions. Arrows indicate hypothetical residual current velocity and dots mark null zones where net transport is neither up- nor down-estuary. Maximum depth of larval visual feeding (dashed line) and 1 isohaline depth (solid line) are depicted. Zones indicate areas of similar physical conditions. Shaded area represents region of high turbidity.



perch post-yolk-sac larvae <5 mm. It may be that these <5 mm larvae were (1) passively retained in the same area as their prey, (2) actively tracking high prey concentrations, or (3) undergoing a transition from passive retention to active tracking. In yet another alternative, first-feeding larvae may have survived only where prey concentrations were high, resulting in a close association between peak prey and first-feeding larvae concentrations.

Distributions of white perch and striped bass post-yolk-sac larvae converged with ontogeny and growth within the ETM region, at least to the length of 10 mm, suggesting a similar retention mechanism for these species at this stage. The spatial distributions of white perch and striped bass post-yolk-sac larvae (8–10 mm) were reasonably coherent (Fig. 7) and had significant overlap indices in all three 1998 cruises (Table 3). The increase in spatial coherence with development may result from enhanced swimming abilities and suggests potential for competition between the two species within the ETM region if prey concentrations were limiting for growth or survival.

Retention of white perch and striped bass post-yolk-sac larvae in the upper Chesapeake ETM region may result from tracking *E. affinis* prey that use maintenance in deep waters as a retention mechanism. Copepods, notably *E. affinis*, are important prey for white perch and striped bass larvae based on analysis of gut contents (this study; Beaven and Mihursky, 1980; Limburg *et al.*, 1997; Campfield, 2004; Shoji *et al.*, 2005). The consistent and strong positive correlations between mean depths of occurrence of feeding larvae and *E. affinis*, and the significant effect of *E. affinis* concentrations in the regression models for feeding larvae suggest that active tracking by larvae is a mechanism for retention in the ETM region. This proposed mechanism differs from the retention mechanism in the San Francisco Estuary where striped bass larvae undertake tidally-timed or reverse diel vertical migrations (Bennett *et al.*, 2002).

Although striped bass larval behavior may appear to differ between estuaries, the underlying retention mechanism could be the same, i.e. tracking high prey concentrations. Although a consistent behavioral pattern is not clearly evident, *E. affinis* makes tidally-timed vertical migrations in the Conwy Estuary, North Wales (Hough and Naylor, 1991, 1992), in the Columbia River estuary (Simenstad *et al.*, 1994; Morgan *et al.*, 1997) and in the San Francisco Estuary during day (Kimmerer *et al.*, 1998), but it remains in deep waters of the upper Chesapeake Bay (Roman *et al.*, 2001). If the fundamental cue driving larval vertical migratory behavior is high prey concentrations, then the plasticity in larval fish behavior observed in San Francisco Estuary (Bennett *et al.*, 2002) may stem from plasticity in prey behavior, or differences in prey types that use dissimilar retention

mechanisms. In the St Lawrence estuary, Atlantic herring (*Clupea harengus harengus*) larvae appear to track high prey concentrations: the semidiurnal migrations and average depth of larval occurrence were closely related to larval prey distributions (Fortier and Leggett, 1983). Tracking high prey concentrations may be a fundamental behavior that offers a simple explanation for striped bass larval adaptation and survival in estuarine systems with very different physical conditions such as the San Francisco Estuary and Chesapeake Bay.

Both striped bass and white perch post-yolk-sac larvae occurred in high numbers in the convergent Zone B where turbidities were high and light levels in deep waters potentially dropped below the threshold for larval visual feeding. High turbidities in the ETM region appear to promote growth of rainbow smelt larvae, potentially by reducing energetic costs associated with predator avoidance (Sirois and Dodson, 2000b). Light levels also influence the feeding and growth of fish larvae (Blaxter, 1986; Chesney, 1989). Chesney (1989), and McHugh and Heidinger (1977) found that striped bass larvae have the ability to feed in the dark. In fact, Chesney demonstrated that some striped bass larvae survived and grew when held in total darkness for 25 days, although larvae in treatments with light had much higher growth rates. The ability to feed in darkness, perhaps using mechano- or chemo-sensory cues, may allow larvae to take advantage of high prey concentrations in Zone B.

Chesney's (1989) observations that light strongly enhanced larval growth suggest that ETM Zone C (Fig. 10) may be an important area for larval feeding and growth. During fixed-station sampling in 98-3, peak concentrations of striped bass and white perch post-yolk-sac larvae (8–10 mm) were found in Zone C, where the maximum depth of larval visual feeding was deeper than the 1 isohaline depth (Fig. 9c). During mapping surveys, the mean depths of occurrence of post-yolk-sac larvae were shallower down-estuary of fixed stations (Fig. 9d–f), suggesting that larvae down-estuary of the tip of the salt front were in a position to feed visually during the day. There may be a trade-off between potentials for high growth and low retention within Zone C. For example, larvae in well-lit waters in this zone (Fig. 10) may be at greater risk of advective loss from the ETM area when discharge and seaward wind events enhance down-estuary transport in surface waters (North *et al.*, 2005). Vertical migration in this region may allow larvae to optimize both feeding success and retention.

Our results suggest that the spatial scale of sampling can lead to major differences in conclusions about the relative importance of prey types. When sampling was conducted on small spatial scales, e.g. at fixed stations within the ETM region, there was no apparent relationship between concentrations of fish larvae and the cladoceran *B. longirostris* whereas the relationship between *E. affinis* and feeding fish larvae was significant. When sampling was conducted on large spatial scales in mapping surveys, both *B. longirostris* and *E. affinis* explained a significant amount of the variability in concentrations of both white perch and striped bass post-yolk-sac larvae (North and Houde, 2003). Although fixed-station results underscore the importance of *E. affinis* copepods for fish larvae in Zone B, mapping survey results support the conclusion that both *E. affinis* and *B. longirostris* are ubiquitous components of temperate ETM communities and are important prey for larval fish. Both are important prey of rainbow smelt and tomcod larvae in the St Lawrence River ETM (Sirois and Dodson, 2000b; Winkler *et al.*, 2003) and of striped bass and white perch in the Potomac, Hudson, and Patuxent River estuaries (Beaven and Mihursky, 1980; Setzler-Hamilton *et al.*, 1982; Limburg *et al.*, 1997; Campfield, 2004).

When our mapping and fixed-station studies were integrated, results suggested that *E. affinis* and white perch and striped bass larvae appeared to concentrate in low-salinity waters along the face of the salt front in Zones B and C (Fig. 10). Changes in the 1 isohaline depth over time at the 98-3 fixed station were predominantly caused by tidal advection (North, 2001). If *E. affinis* and white perch and striped bass larvae track low salinity waters, then apparent changes in their vertical distribution during tide stages at a fixed location within the salt front (e.g. Fig. 9c) could result from tidal advection of the sloping front past the fixed station, not tidal vertical migratory behavior. Because the scope of inference of our fixed station samples was limited to 1 yr and to a small area within the ETM region, it remains possible that white perch and striped bass post-yolk-sac larvae may vertically migrate in Zone A or C. Larval herring and smelt make tidally-timed vertical migrations in the St Lawrence River estuary (Fortier and Leggett, 1982, 1983; Laprise and Dodson, 1989b). and striped bass, yellowfin goby (*Acanthogobius flavimanus*), and longfin smelt (*Spirinchus thaleichthys*) made tidally-timed, or reverse-diel, vertical migrations in the San Francisco Estuary (Bennett, 1998; Bennett *et al.*, 2002). Differences between our observations in Chesapeake Bay and results of other studies may indicate (1) actual behavioral differences between populations and species of copepods and fish larvae, (2) differences in sampling zone within the broader salt front and ETM region,

and/or (3) differences in organism responses to physical conditions in estuaries with freshwater flow regimes and current velocities that differ from those in upper Chesapeake Bay.

The complexity in interpreting larval distributions underscores the importance of understanding the implications of sampling in a tidally dynamic feature like the ETM. The extent of tidal excursion and the locations of fixed-sampling stations can limit the scope of inference about populations that are distributed throughout this complex physical feature. Although complex, tradeoffs between utilization of zones of visual feeding (Zone C) and high retention (Zone B) may have important implications for larval growth and survival, and warrant further investigation. Integrating information on interactions between physical conditions, fish larvae and their prey at both small (e.g. fixed station) and large (e.g. mapping survey) scales is a useful approach to develop a comprehensive understanding of factors that affect fish recruitment in estuaries.

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REFERENCES

Abrams, P. (1980) Some comments on measuring niche overlap. *Ecology* **61:**44–49.

Albrecht, M. and Gotelli, N.J. (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia* **126:**134–141.

Beaven, M. and Mihursky, J. (1980) *Food and Feeding Habits of Larval Striped Bass: An Analysis of Larval Striped Bass Stomachs from 1976 Potomac Estuary collections*. Final Report submitted to Maryland Power Plant Siting Program. Solomons, Maryland: UMCES[CBL] Ref. No. 79–45.

Bennett, W.A. (1998) Vertical migration and retention of native and exotic larval fish within the entrapment zone of a tidally dominated estuary. In: *Report of the 1994 Entrapment Zone Study*. W. Kimmerer (ed.) Interagency Ecological Program for the San Francisco Bay/Delta Estuary Technical Report 56, Romberg Tiburon Center, Tiburon, CA. pp. 113–136.

Bennett, W.A., Kimmerer, W.J. and Burau, J.R. (2002) Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low salinity zone. *Limnol. Oceanogr.* **47:**1496–1507.

Blaxter, J.H.S. (1986) Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.* **115:**98–114.

Boehlert, G.W. and Mundy, B.C. (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Symp.* **3:**51–67.

Boynton, W.R., Boicourt, W., Brant, S. *et al.* (1997) *Interactions between physics and biology in the estuarine turbidity maximum (ETM) of Chesapeake Bay, USA*. ICES CM 1997/S 11, ICES, Copenhagen. 38 pp.

Breitburg, D.L. (1994) Behavioral response of fish larvae to low dissolved oxygen concentrations in a stratified water column. *Mar. Biol.* **120:**615–625.

Campfield, P.A. (2004) *Ichthyoplankton Community Structure and Feeding Ecology in the Patuxent River Estuarine Transition Zone*. Masters Thesis, College Park: University of Maryland at College Park, 177 pp.

Chesney, E.J. Jr. (1989) Estimating the food requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. *Mar. Ecol. Prog. Ser.* **53:**191–200.

Crowder, L.B. (1990) Community ecology. In: *Methods for Fish Biology*. C.B. Schreck & P.B. Moyle (eds) Bethesda: American Fisheries Society, pp. 609–634.

Dauvin, J.-C. and Dodson, J.J. (1990) Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary. *Mar. Ecol. Prog. Ser.* **60:**1–12.

Dodson, J.J., Dauvin, J.-C., Ingram, R.G. and d'Anglejan, B. (1989) Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplanktonic fauna of the middle St. Lawrence estuary. *Estuaries* **12:**66–81.

Dovel, W.L. (1971) *Fish Eggs and Larvae of the Upper Chesapeake Bay*. Solomons, MD, USA: University of Maryland, NRI Special Report No. 4, UMCES[CBL] Ref. no. 71–88, 71 pp.

Fortier, L. and Leggett, W.C. (1982) Fickian transport and the dispersal of fish larvae in estuaries. *Can. J. Fish. Aquat. Sci.* **39:**1150–1163.

Fortier, L. and Leggett, W.C. (1983) Vertical migrations and transport of larval fish in a partially mixed estuary. *Can. J. Fish. Aquat. Sci.* **40:**1543–1555.

Geyer, W.R. (1993) The importance of suppression of turbulence by stratification on the estuarine turbidity maximum. *Estuaries* **16:**113–125.

Gotelli, N.J. and Entsminger, G.L. (2003) *EcoSim: Null Models Software for Ecology. Version 7*. Burlington, Vermont: Acquired Intelligence Inc. and Kesey-Bear. http://garyentsminger.com/ecosim/index.htm.

Hough, A.R. and Naylor, E. (1991) Field studies on retention of the planktonic copepod *Eurytemora affinis* in a mixed estuary. *Mar. Ecol. Prog. Ser.* **76:**115–122.

Hough, A.R. and Naylor, E. (1992) Endogenous rhythms of circatidal swimming activity in the estuarine copepod *Eurytemora affinis* (Poppe). *J. Exp. Mar. Biol. Ecol.* **161:**27–32.

Jassby, A.D., Kimmerer, W.J., Monismith, S.G. *et al.* (1995) Isohaline position as a habitat indicator for estuarine populations. *Ecol. Appl.* **5:**272–289.

Kimmel, D.G. and Roman, M.R. (2004) Long-term trends in mesozooplankton abundance and community composition in the Chesapeake Bay USA: influence of freshwater input. *Mar. Ecol. Prog. Ser.* **267:**71–88.

Kimmerer, W.J., Burau, J.R. and Bennett, W.A. (1998) Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnol. Oceanogr.* **43:**1697–1709.

Kirk, J.T.O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*, 2nd edn. Cambridge: Cambridge University Press, 509 pp.

Laprise, R. and Dodson, J.J. (1989a) Ontogenetic changes in the longitudinal distribution of two species of larval fish in a turbid well-mixed estuary. *J. Fish Biol.* **35:**39–47.

Laprise, R. and Dodson, J.J. (1989b) Ontogeny and the importance of tidal vertical migrations in the retention of larval smelt *Osmerus mordax* in a well-mixed estuary. *Mar. Ecol. Prog. Ser.* **55:**101–111.

Laprise, R. and Dodson, J.J. (1990) The mechanism of retention of pelagic tomcod, *Microgadus tomcod*, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary. *Environ. Biol. Fish.* **29:**293–302.

Limburg, K.E., Pace, M.L. and Fischer, D. (1997) Consumption, selectivity, and use of zooplankton by larval striped bass and white perch in a seasonally pulsed estuary. *Trans. Am. Fish. Soc.* **126:**607–621.

Linton, L.R., Davies, R.W. and Wrona, F.J. (1981) Resource utilization indices: an assessment. *J. Anim. Ecol.* **50:**283–292.

Mansueti, R.J. (1964) Eggs, larvae, and young of the white perch, *Roccus americanus*, with comments on its ecology in the estuary. *Chesapeake Sci.* **5:**3–45.

McHugh, J.J. and Heidinger, R.C. (1977) Effects of light on feeding and egestion time of striped bass fry. *Prog. Fish-Cult.* **39:**33–34.

Miller, J.M. (1988) Physical processes and the mechanisms of coastal migration of immature marine fishes. *Am. Fish. Soc. Symp.* **3:**68–76.

Morgan, C.A., Cordell, J.R. and Simenstad, C.A. (1997) Sink or swim? Copepod population maintenance in the Columbia River estuarine turbidity-maxima region. *Mar. Biol.* **129:**309–317.

Norcross, B.L. and Shaw, R.F. (1984) Oceanic and estuarine transport of fish eggs and larvae: a review. *Trans. Am. Fish. Soc.* **113:**153–165.

North, E.W. (2001) *Transport and Retention of Fish Early-life Stages in Chesapeake Bay: Mechanisms and Implications for Recruitment*. PhD Dissertation. College Park: University of Maryland at College Park, 305 pp.

North, E.W. and Houde, E.D. (2001) Retention of white perch and striped bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries* **24:**756–769.

North, E.W. and Houde, E.D. (2003) Linking ETM physics, zooplankton prey, and fish early-life histories to white perch (*Morone americana*) and striped bass (*M. saxatilis*) recruitment success. *Mar. Ecol. Prog. Ser.* **260:**219–236.

North, E.W., Hood, R.R., Chao, S.-Y. and Sanford, L.P. (2005) The influence of episodic events on transport of striped bass eggs to an estuarine nursery area. *Estuaries* **28:**106–121.

Roman, M.R., Holliday, D.V. and Sanford, L.P. (2001) Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. *Mar. Ecol. Prog. Ser.* **213:**215–227.

Rowe, P.M. and Epifanio, C.E. (1994) Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Mar. Ecol. Prog. Ser.* **110:**105–114.

Sanford, L.P., Suttles, S.E. and Halka, J.P. (2001) Reconsidering the physics of the Chesapeake Bay Estuarine Turbidity Maximum. *Estuaries* **24:**655–669.

SAS Institute Inc (1997) *SAS/STAT®* Software: Changes and Enhancements Through Release 6.12. Cary, NC: SAS Institute Inc., 1167 pp.

Schoener, T.W. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51:**408–418.

Schubel, J.R. (1968) Turbidity maximum of the northern Chesapeake Bay. *Science* **161:**1013–1015.

Setzler-Hamilton, E.M., Jones, P.W., Drewry, G.E. *et al.* (1982) *A Comparison of Larval Feeding Habits Among Striped Bass, White Perch and Clupeidae in the Potomac Estuary*. Final Report to Maryland Department of Natural Resources. Solomons, MD, USA: UMCES[CBL] Ref. No. 81–87, 328 pp.

Shoji, J., North, E.W. and Houde, E.D. (2005) The feeding ecology of white perch *Morone americana* (Pisces) larvae in the Chesapeake Bay estuarine turbidity maximum: the influence of physical conditions and prey concentrations. *J. Fish Biol.* **66:**1328–1341.

Simenstad, C.A., Morgan, C.A., Cordell, J.R. and Baross, J.A. (1994) Flux, passive retention, and active residence of zooplankton in Columbia River estuarine turbidity maxima. In: *Changes in Fluxes in Estuaries: Implications from Science to Management*. K.R. Dyer & R.J. Orth (eds) Fredensborg, Denmark: Olsen and Olsen, pp. 473–482.

Sirois, P. and Dodson, J.J. (2000a) Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*. *Mar. Ecol. Prog. Ser.* **203:**233–245.

Sirois, P. and Dodson, J.J. (2000b) Influence of turbidity, food density and parasites on the ingestion and growth of larval rainbow smelt *Osmerus mordax* in an estuarine turbidity maximum. *Mar. Ecol. Prog. Ser.* **193:**167–179.

Strathmann, R.R. (1982) Selection for retention or export of larvae in estuaries. In: *Estuarine Comparisons*. V.S. Kennedy (ed.) New York: Academic Press, pp. 521–536.

Waldman, J.R., Young, J.R., Lindsay, B.P., Schmidt, R.E. and Andreyko, H. (1999) A comparison of alternative approaches to discriminate larvae of striped bass and white perch. *N. Am. J. Fish. Manage.* **19:**470–481.

Winemiller, K.O. and Pianka, R.R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Mono.* **60:**27–55.

Winger, P.V. and Lasier, P.J. (1994) Effects of salinity on striped bass eggs and larvae from the Savannah River, Georgia. *Trans. Am. Fish. Soc.* **123:**904–912.

Winkler, G., Dodson, J.J., Bertrand, N., Thivierge, D. and Vincent, W.F. (2003) Trophic coupling across the St. Lawrence River estuarine transition zone. *Mar. Ecol. Prog. Ser.* **251:**59–73.