Time, space, food and physics: the temporal and spatial distribution of anadromous fish larvae in an estuarine turbidity maximum (ETM)

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ABSTRACT

Physical and biological characteristics of the Chesapeake Bay estuarine turbidity maximum (ETM) region may influence larval retention, survival, and recruitment of anadromous white perch (Morone americana) and striped bass (M. saxatilis). This hypothesis was evaluated in spatially explicit surveys of the physical and biological properties of the upper Chesapeake Bay estuary. Five cruises, three in May 1998 and two in May 1999, were conducted. Gradients in depth-specific patterns of larval abundance and zooplankton prey were determined and related to salinity, turbidity and temperature. Physical conditions in the upper estuary, including the location of the ETM and salt front, differed between cruises and years, but the spatial patterns in distributions of larvae and potential prey were consistent. Most striped bass eggs (96%) and white perch yolk-sac larvae (69%) were located up-estuary of the salt front (1 PSU isohaline). Virtually all postlarval striped bass (93%) and most white perch (73%) were located within 10 km of highest turbidity measurements, in the region where Eurytemora affinis copepods, potential prey of larvae > 5 mm, peaked in abundance. A statistical analysis suggested that physical parameters, especially total suspended solids concentrations and salinity, explain more of the variability in larval distributions than do prey concentrations. Total abundance of larvae was lower in 1999, a low freshwater flow year, than in 1998, a high flow year. Juvenile abundances of white perch (1977-99) and striped bass (1968-99) were positively correlated with spring freshwater flow. Results confirmed the importance of the ETM region as a nursery area for anadromous fish and indicated that annual changes in freshwater flow may control larval survival and recruitment by modifying the physical characteristics of the ETM region.

INTRODUCTION

Estuarine turbidity maximums, characterized by elevated turbidity and suspended sediment concentrations compared to those up- and down-estuary, are found in coastal plain estuaries throughout the world (Schubel 1968). The ETM region is an important nursery area for larval fish in the St. Lawrence River estuary (Dodson et al. 1989, Dauvin and Dodson 1990, Sirois and Dodson 2000) and San Francisco Bay/Delta (Jassby et al. 1995). Retention within the ETM region may place larvae in a zone of increased zooplankton biomass and production (Simenstad et al. 1994; Boynton et al. 1997), create a predation refuge due to high turbidity (Chesney 1989), maintain larvae in optimal temperature or salinity conditions (Strathmann 1982), and/or keep them from entering osmotically stressful, high salinity waters (Winger and Lasier 1994).

The goal of this research is to determine how physical and biological properties of the Chesapeake Bay estuarine turbidity maximum (ETM) region influence larval retention, survival, and recruitment of anadromous white perch (Morone americana) and striped bass (M. saxatilis). Elevated abundance of white perch larvae, striped bass larvae, and their potential prey were reported in and near the upper Chesapeake Bay ETM (Boynton et al 1997, Roman et al 1997). Boynton et al. (1997) suggested that the

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ETM region could be an important nursery area for larval fish where biological conditions structured by the physics of the region could enhance recruitment potential.

Variations in life history strategies and behaviors may affect larval use of the ETM region as a nursery area. Spawning by white perch and striped bass peaks in April and May in the headwaters of Chesapeake Bay and its tributaries (Mansueti 1964; Dove1 1971). White perch spawn demersal eggs that adhere to the substrate in tidal fresh and brackish waters. Depending upon temperature, yolk-sac larvae hatch at a length of -2.6 mm in about 2 days. Larvae absorb the yolk-sac, develop a gas bladder, and begin feeding on rotifers, copepod nauplii and small copepodites 3 to 5 days post hatch at a length of -3.8 mm (Mansueti 1964, Setzler-Hamilton et al 1982). Diets shift to larger copepodites, Bosmina logirostris cladocerans, and Eurvtemora affinis copepods with development (Setzler-Hamilton et al 1982).

In contrast, striped bass spawn pelagic eggs in tidal freshwater up-estuary of the salt front (Dove1 1971; Secor and Houde 1995) where the slightly-heavy eggs (specific gravity=1 .0005) are suspended by currents greater than 0.3 m s^{-1} (Albrecht 1964). Striped bass larvae hatch in about 2 days at a larger size (-3.1 mm) than white perch and do not develop a gas bladder and absorb their yolk-sac until they are >5 days old and >5 mm in length (Mansueti 1958, 1964; Doroshev 1970). Striped bass larvae begin feeding on rotifers, copepodites, and Bosmina before shifting toward adult copepods (including Eurvtemora) and larger cladocerans as they grow (Setzler-Hamilton et al 1982).

Since the net flow of water is down-estuary, larval fish that use the ETM region as a nursery area must have mechanisms of dispersal to the ETM and retention within it. Larvae of white perch and striped bass that are spawned in the freshwater reaches of the upper Chesapeake Bay could be retained in the ETM region by the convergence zone associated with the landward margin of the salt intrusion, the area in which the ETM occurs (Schubel 1968). Alternatively, larvae could use tidally-timed vertical migration for retention by moving up into surface waters during flood and down into bottom waters during ebb tide (Laprise and Dodson 1989; Dauvin and Dodson 1990; Rowe and Epifanio 1994; Bennett 1998).

Although the ETM is a well-established feature of the upper Chesapeake Bay, its location and intensity are variable. The ETM ranges from 10 - 30 km in extent and is generally associated with the tip of the 1 PSU isohaline, but can be displaced from it by as much as 10 km due to tidal excursion (Boynton et al 1997). The longitudinal position of the ETM varies among hours, days, seasons, and years depending upon tidal excursion, wind forcing, and the amount of freshwater flow (Sanford et al. submitted; Boynton et al. 1997). Since the location and extent of the ETM nursery area and larval retention mechanisms are implicitly linked to the variable physics of the region, seasonal and annual changes in ETM properties may have consequences for larval survival and recruitment.

Using results from field research conducted in 1998 and 1999, combined with environmental monitoring and juvenile fish survey data, we sought to 1) relate the spatial and temporal patterns in the distribution and abundance of white perch and striped bass larvae to physical and biological characteristics of the ETM region, and 2) link variability in these factors to larval survival and recruitment success.

METHODS

Five research cruises were conduced in the upper Chesapeake Bay (Fig. la) on the 52-ft RV Orion during the spawning seasons of striped bass and white perch. Three cruises were in May 1998 (2-5, 1 1-14, and 19-22 May, referred to as 98-1, 98-2, 98-3, respectively) and two were in May 1999 (4-6 and 17-

19 May, referred to as 99-l and 99-Z). Each cruise consisted of 1) a CTD survey along the axis of the Bay, 2) net tows to map gradients in ichthyoplankton distribution (Fig. **lb),** and 3) a fixed-station occupation within the ETM to document changes in ichthyoplankton abundance over the tidal cycle. Although limited sampling was conducted outside the channel, only results of the gradient mapping in the shipping channel are presented here.

The location of the ETM and **landward** margin of salt intrusion (defined as the intersection of the 1 PSU isohaline with bottom) were determined in the axial CTD survey using a **Seabird** CTD equipped with a **SeaTech** 5-cm pathlength transrnissometer to measure temperature, salinity, and turbidity. Water samples (100 ml) were collected with a pump attached to the CTD **frame** to calibrate turbidity **(NTU)** measurements with total suspended solids (TSS) concentrations. Based on results of the axial survey, six gradient-mapping stations were designated; one within the ETM, and 2 up-estuary and 3 down-estuary from the ETM station at intervals equal to one-half the tidal excursion (first cruise) or two-thirds the tidal excursion (remaining cruises) at the ETM location (Fig. lb).

Sampling at the gradient mapping stations was conducted from up-estuary to down-estuary at night and was completed in 7 to 8 hours (Fig. lb). At each station, physical measurements and depth-stratified collections of ichthyoplankton and zooplankton were conducted. Zooplankton samples (50 L) were collected by a pump at depth intervals that corresponded to ichthyoplankton tows: 3.5 - 0 **m**, 7 - 3.5 **m**, and near bottom - 7 m depth. After filtering pumped water onto a 35 micron sieve, zooplankton was preserved in 5% formalin. In the laboratory adult female *Eurytemora **affinis*** **copepods** and *Bosmina **longirostris*** cladocerans were enumerated.

Ichthyoplankton was collected in depth-stratified tows of a Tucker trawl in two or three depth intervals depending on water depth. The **1-m^2** opening-closing Tucker trawl was fitted with **280-µm** mesh nets, a flow meter,. and a temperature-depth recorder. Because the average depth of the upper Bay channel was about 12 m, most Tucker-trawl tows were made in 0 - 3 .5 **m**, 3.5 - 7 **m** and 7 - 11 m depth intervals. Ichthyoplankton samples were preserved in ethanol and taken to the laboratory for enumeration and identification. White perch and striped bass postlarvae (post yolk-sac larvae) were identified using criteria based on external morphological features (Waldman et al. 1999) and then measured.

Freshwater discharge, water level, wind, and water temperature monitoring data were used to identify large-scale environmental forcing events that produced physical conditions observed during the cruises (Fig lb). Since nearly all **freshwater** input to the upper Bay is from the Susquehanna River (Schubel and Pritchard **1986),** daily mean discharge data **(U**. S. Geological Survey) for the Susquehanna River at the Conowingo Dam in Maryland was used to index **freshwater** input.

Results **from** cruises were mapped with contour plots of physical parameters and ichthyoplankton and zooplankton concentrations (Surfer software). In these plots, station locations were expressed as "kilometers from river mouth", the distance from the mouth of the Susquehanna River (Fig. lb). To explore possible relationships between the distribution of larvae and their potential prey, Pearson correlation coefficients were calculated between concentrations of **5-8mm** and **8-10mm** larvae and zooplantkon. Mean abundances of white perch yolk-sac larvae and postlarvae were tested for differences between years by **ANOVA** (SAS 6.12 PROC MIXED) with cruise designated as a random effect after log, transformation.

An exploratory statistical analysis was conduced to determine whether temperature, salinity, TSS, or prey concentrations accounted for a significant amount of variability in the distribution patterns of larvae by size class. The model included quadratic and interaction terms of the physical parameters, Eurytemora and Bosmina concentrations for feeding larvae, 'cruise' as a random effect, and the categorical variables tow and year (when both 1998 and 1999 data were used). All explanatory variables were centered and examined for multicollinearity (SAS 6.12 PROC PRINCOMP, PROC REG). Based on these results, Temperature' and Temperature x Salinity terms were dropped from the model. A repeated measures analysis was conducted on log, or square root transformed larval concentration data (SAS 6.12 PROC MIXED). The analysis of postlarval concentrations was limited to data from 1998 because of serious heterogeneity of variance problems related to high numbers of zero observations in 1999.

To explore possible relationships between river flow and juvenile recruitment, Pearson correlation coefficients were calculated between spring Susquehanna River discharge rates and indices of white perch and striped bass young-of-the-year (YOY) abundance in the upper Chesapeake Bay. Spring Susquehanna River flow rates were means of the daily discharge data from March through May. The white perch (1977-99) and striped bass (1968-99) YOY abundance indices in the upper Bay were obtained from the summer Striped Bass Juvenile Index Seine Survey (Maryland Department of Natural Resources). Although correlation analyses were conducted on the entire time series of juvenile abundance (1968-99), comparison of the relationship between freshwater flow and white perch and striped bass abundances was confined to the 1989-99 period because the striped bass spawning population had collapsed during the late 1970s to mid 1980s.

RESULTS

Physics. Freshwater flows to the upper Bay differed in spring 1998 and 1999. When compared to the 30-yr mean Susquehanna monthly discharge, discharge values in 1998 were generally above average while those from 1999 were below average (Fig. 2a). In fact, May 1999 was the driest May in the past 30 years.

Discharge in May 1998 was distinguished by a large peak that occurred during the second research cruise (Fig. 2b). During this event, water temperature at the CBOS northern Bay buoy declined by about 1 °C on average (Fig. lb). The peak in flow was preceded by strong northern winds that caused a decrease in water level in the upper Bay. After the wind-forcing and high freshwater-flow events, discharge declined steadily prior to the third research cruise. The most significant feature of environmental conditions in May 1999 was the very low discharge rate (Fig 2b).

Salinity and turbidity profiles from the gradient-mapping surveys reflect the differences in environmental conditions between cruises and years. During the first research cruise in 1998 (98-1), the salt front was located near km 30 (Fig. 3a). Eight days later (98-2 cruise), during the peak in discharge, the pycnocline had intensified and the salt front had moved up-estuary (Fig. 3b). Salinity in the lower layer increased substantially as indicated by the location of the intersection of the 5 PSU isohaline with bottom, which had shifted more than 15 km up-estuary between the first and second cruise. By the third research cruise (98-3), after the peak in freshwater discharge, the salt front had moved down-estuary and stratification had weakened (Fig. 3c). During each survey in 1998, maximum turbidity was located near the foot of the salt front.

In 1999, turbidity in the upper Bay was generally lower than in 1998 while salinity was higher (Fig. 3d and e). Stratification near the salt front was less intense and the intersections of the 1 PSU isohalines with the bottom were about 15 km further up-estuary than those in 1998. Temperature in the upper Bay in 1999 was generally lower than in 1998, but was > 12 °C where salinity was <11 PSU in 1998 and

1999. The salinity structure on **4-5** May cruise was more stratified than on **17-** 18 May, perhaps due to north winds just prior to the first cruise.

White perch and striped bass. The spatial distribution of fish early-life stages along the axis of the upper Chesapeake Bay varied by year, cruise, species, and stage of development. For example, comparison of the distribution of white perch and striped bass larvae during the first 1998 cruise (98-l) indicates differences in distribution of white perch and striped bass larvae, and between stages of development within species (Fig. 4). Both white perch yolk-sac larvae and striped bass eggs, the earliest life stages collected, were located in bottom waters up-estuary of the salt front, although the distribution pattern of white perch yolk-sac larvae was broader and extended into the salt front. Although postlarvae of both species were found in the ETM region, later-stage (5-10 mm) white perch larvae were located near surface and down-estuary of distribution of later-stage striped bass larvae (5-10 mm), which were located in bottom waters at the tip of the salt front. Comparison of the distribution of 5-8 mm larvae reveals differences between cruises (compare Fig. 4g with Fig. 6a) and between years (compare Fig. 4b with Fig. 6e).

Despite these variations, there were consistent patterns in the distribution of yolk-sac and postlarvae in relation to physical conditions. The relationship between the distribution of early-life stages and the ETM region is summarized in plots of abundance (number under 1 m^2) by life stage relative to the location of maximum turbidity, the center of the ETM (Figure 5). Relationships between the concentration of early-life stages (numbers per m^3) and physical parameters are summarized in Table 1. The ETM region is defined as +/- 10 km from maximum turbidity.

White perch yolk-sac larvae were most abundant up-estuary of and within the ETM region except during the second 1998 cruise (Fig. 5a). Most yolk-sac larvae were found in waters of salinity <5 PSU (87%) and in mid-depth and bottom waters (76%) (Table 1). In contrast to yolk-sac larvae, white perch postlarvae were more prevalent and concentrated near and within the ETM (Fig. 5b-d). Like yolk-sac larvae, substantial numbers of postlarvae were only found down-estuary of the ETM region during the second 1998 cruise. Peak concentrations of postlarvae varied with respect to depth of peak occurrence, with larvae < 5mm in mid-depth and bottom waters and later-stage larvae near surface. Despite differences between cruises and years, 73% of white perch postlarvae were located within 10 km of maximum turbidity (Table 1).

Striped bass eggs were located up-estuary of maximum turbidity values (Fig. 5e). Peak concentration of eggs among cruises ranged from near-surface to near-bottom. Overall, 96% of striped bass eggs were collected up-estuary of the salt front in <1 PSU salinity (Table 1). In 1998, striped bass yolk-sac and postlarvae were concentrated within and just above the tip of the salt front. Most were in mid-depth and bottom waters with one exception: 5-8mm larvae were most concentrated in surface waters during the second 1998 cruise (Fig. 6a). Nearly all striped bass yolk-sac larvae (94%) and postlarvae (93%) were collected within 10 km of maximum turbidity (Fig. 5f-h, Table 1).

Striped bass larvae were approximately one-tenth as abundant as white perch larvae (Fig. 7). The abundances of white perch and striped bass yolk-sac and postlarvae (number under 1 m^2) were lower in 1999 than in 1998. The difference in mean abundance of white perch yolk-sac larvae between 1998 and 1999 was not significant (ANOVA, $F = 2.31$, $P < 0.2255$) but the difference in mean abundance of postlarvae between years was significant (ANOVA, $F = 15.56$, $P < 0.0005$). Similar statistical analyses were not conducted for striped bass larvae because only 2 yolk-sac larvae and no postlarvae were collected in 1999. Striped bass eggs were present in 1999 (mean 0.60 eggs/m^3 +/- 0.34 standard error), but fewer in number than in 1998 (mean 11.7 eggs/m^3 +/- 6.5 standard error).

Zooplankton. Like fish early-life stages, the distribution of Eurytemora adult females and Bosmina varied between cruises and years in relation to physical conditions. For example, comparison of contour plots of zooplankton concentrations (numbers per L) between the 98-2 and 99-l cruises demonstrates a shift in distribution that coincides with the change in salt front and ETM location (Fig. 6c,d,f,g). During both years, most Bosmina (79%) were located in salinity <1 PSU and most Eurytemora 74%) were in salinity >1 PSU (Table 1). Eurvtemora abundance peaked within the ETM region (Fig. 8a) while Bosmina abundance tended to decline from up-estuary to down-estuary, except during the second 1998 cruise (Fig. 8b).

Eurytemora and Bosmina were more broadly distributed than postlarvae of fish (5-8mm, 8-10mm). These zooplankton are potential prey of the larvae (compare Fig. 8 with Fig. 5). In general, the distribution of both white perch and striped bass larvae overlapped considerably with high concentrations of their potential prey in 1998 and 1999. For example, during the second 1998 cruise, 5-8mm (Fig. 6a) and 8-10mm (Fig. 6b) striped bass larvae were located where both Eurvtemora (Fig. 6c) and Bosmina (Fig. 6d) concentrations were high, although not highest. On the first 1999 cruise, 5-8 mm white perch larvae (Fig. 6e) were located coincident with highest concentrations of both Eurvtemora (Fig. 6f) and Bosmina (Fig. 6g).

There was a significant correlation between 8-10mm striped bass concentrations and Eurvtemora concentrations in 1998 ($r = 0.40$, $n = 49$, $P < 0.004$), but not between 5-8mm larvae and Eurvtemora ($r = 0.17$, $n = 49$, $P < 0.256$) nor between Bosmina and either larval size class (5-8mm: $r = 0.10$, $n = 49$, $P < 0.489$; 8-10mm: $r = -0.10$, $n = 49$, $P < 0.491$). The correlations of both size classes of white perch larvae with Eurvtemora concentrations were significant (5-8mm: $r = 0.35$, $n = 83$, $P < 0.001$; 8-10mm: $r = 0.36$, $n = 83$, $P < 0.001$), but not with Bosmina concentrations in 1998 and 1999 (5-8mm: $r = 0.05$, $n = 83$, $P < 0.651$; 8-10mm: $r = 0.12$, $n = 83$, $P < 0.289$).

Statistical model. The preceding descriptive analysis suggests that both physical and biological factors could influence the distribution of early life stages of white perch and striped bass. An exploratory repeated measures analysis was conduced to determine whether temperature, salinity, TSS, or prey concentrations described a significant amount of variability in the distribution of larvae by size class. Results of the analysis are summarized in Table 2. Salinity, TSS and/or their interaction are important factors that explain variability in the distribution of white perch larvae. Depth is also important for white perch yolk-sac and postlarvae < 5mm. In contrast, TSS and its interactions with salinity and temperature were highly significant for all stages of striped bass larvae. Eurvtemora concentration was a significant factor in only the model for striped bass 8 – 10 mm postlarvae; Bosmina concentration was not a significant factor in any model. Preliminary results indicated physical parameters accounted for more variability than did zooplankton variables in explaining fish larvae distributions.

YOY recruitment. The abundances of YOY white perch and striped bass were lower in 1999, a low freshwater flow year, than in 1998, a high flow year (Fig. 9). The correlation analysis between YOY abundance and spring Susquehanna discharge indicates that this relationship also holds in other years. The correlation between white perch YOY and freshwater discharge was not significant for the 1989-1999 period ($r = 0.55$, $n = 11$, $P < 0.083$) (Fig. 9), but was significant when the entire 1977-1999 period was considered ($r = 0.47$, $n = 23$, $P < 0.025$). In contrast, there was a stronger and significant correlation ($r = 0.80$, $n = 11$, $P < 0.003$) between freshwater discharge and striped bass YOY abundance from 1989-99 (Fig. 9). Despite the striped bass stock collapse in the late 1970s and early 1980s, spring freshwater discharge and YOY abundance remained significantly correlated ($r = 0.41$, $n = 32$, $P < 0.021$) for the entire 19681999 period.

DISCUSSION

Results of field research indicate that the ETM region is an important white perch and striped bass nursery area where larvae are retained in a region of elevated prey concentrations. Changes in physical conditions that structured the ETM between cruises and years influenced the distribution of larvae and their potential prey. The observation that physical parameters appear to account for more variability in fish larvae distribution than biological parameters may be related to the spatial scale on which these factors were examined and to the timing of sample collection (i.e. night). At smaller spatial scales within the ETM region, prey concentration may have more influence on larval distribution pattern than physical factors, especially during daylight when feeding larvae may track high prey concentrations.

Although both striped bass and white perch postlarvae were found in greatest numbers in and near the ETM, the location of their peak abundances did not always coincide. The spatial distributions of striped bass postlarvae concentration and abundance were more strongly associated with bottom waters at the tip of the salt front than were white perch larvae. Furthermore, the exploratory statistical analyses indicated that physical parameters associated with the ETM (parameters containing TSS) better explained the variability in striped bass distribution than that of white perch. This suggests that striped bass larvae may use the convergence zone at the tip of the salt front for retention within the ETM. The broader distribution of white perch postlarvae within the ETM region and location of peak concentrations of later-stage larvae in both surface and bottom waters may indicate that white perch larvae use tidally-timed vertical migration for maintenance within the ETM region.

Differences in the patterns of distribution of white perch and striped bass larvae may be related to the developmental stage at which transport to, and aggregation within, the ETM region occurs. Striped bass eggs generally are spawned in freshwaters and transported down-estuary, hatching near or within the salt front. Dispersal of eggs to the salt front may be necessary for striped bass survival since larvae can suffer 99-100% mortality in low hardness water of 0‰ (Winger and Lasier 1994). In contrast, white perch hatch from demersal eggs in tidal freshwater, swim up or are mixed upward into the water column for transport down-estuary as yolk-sac larvae, and accumulate in the ETM region as postlarvae. Transport down-estuary during the yolk-sac stage and early development of a swimbladder may allow white perch larvae to quickly develop tidally-timed vertical migrations for retention once in the ETM region.

Episodic events within years may influence larval survival by altering conditions favorable for retention. During the 1998 spawning season, the wind and fleshwater-flow event prior to and during the second research cruise (98-2) significantly affected location of the salt front, ETM, and larval distributions. Down-estuary current, enhanced by discharge or wind forcing, could swiftly transport eggs and early-stage larvae out of the ETM region into areas of low prey abundance, high predation potential and osmotically stressful high salinity. Mortality is highly probable for striped bass larvae down-estuary of the ETM as Secor et al. (1995) inferred in a mark-recapture study. No larvae released below the salt front in the Patuxent River were recaptured, while larvae released above it were retained and recaptured near, or upstream of, their release site.

In addition to episodic events, annual differences in levels of freshwater flow dramatically altered the character of the salt front and ETM in Chesapeake Bay. Results from 1998 are consistent with other findings (Schubel 1968; Boynton et al. 1997; Sanford et al. submitted) that indicate the upper Chesapeake Bay ETM was associated with the salt front and maintained by gravitational circulation with tidal asymmetry. In 1999, the ETM appeared to be fixed near shoaling topography down-estuary of the salt-front that was displaced up-estuary compared to those in 1998. The 1999 ETM may have resulted from gravitational circulation just down-estuary of a topographic high (Burau et al. 1998). The low TSS concentrations within and near the ETM in 1999 may have been due to decreased suspended sediment input during low runoff conditions as well as a weaker convergence zone.

The decline in abundance of white perch and striped bass postlarvae between 1998 and 1999 and the positive correlation between river flow and YOY abundance suggests that annual variation in freshwater input may influence adult spawning behavior and larval survival. For striped bass, low flow velocities and lower temperatures coupled with unusually high salinities could have resulted in decreased adult spawning in 1999, leading to the decline in egg abundance. The close association of striped bass larvae with the ETM and salt front in 1998 and their virtual absence in 1999 despite the presence of eggs suggests that larval striped bass survival may be strongly connected to physics of the ETM convergence zone during high-flow years. In contrast, white perch larval survival may not be as closely linked. White perch larvae were broadly distributed in the ETM region in both 1998 and 1999, and YOY abundance was only weakly, although positively, related to river flow. White perch larvae may be less dependent than striped bass on convergence-zone structure if they use tidally-timed vertical migration to assure retention rather than remaining near bottom down-estuary of the salt front. Although there was no significant difference in yolk-sac abundance between years, the decrease in freshwater habitat volume in 1999 may have influenced white perch spawning and egg survival.

Variability in freshwater flow may govern survival and recruitment of white perch and striped bass larvae by controlling retention of early-life stages in the estuarine turbidity maximum (ETM) region, by insuring overlap of preferred larval temperature/salinity zones with the area of highest prey production and greatest predation refuge in the ETM (North and Houde, submitted), and by controlling ETM productivity through delivery of organic material to the detritus-based food web (Turner and Chadwick 1972, Boynton et al 1976). Both white perch and striped bass survival and recruitment may be influenced by flow-induced changes in ETM characteristics that affect postlarval growth and predation mortality rates. In addition, striped bass survival and recruitment may also depend upon early-stage retention in the ETM controlled by flow-induced changes in convergence zone strength.

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Table 1. Percent eggs, larvae by size-class, and zooplankton collected during cruises in 1998 and 1999 in relation to physical parameters or depth intervals. YSL=yolk-sac larvae.

	White Perch					Striped Bass						
Percent	YSL	Postlarvae < 5 mm	Postlarvae 5 - 8 mm	Postlarvae 8 - 10 mm	All Postlarvae	Eggs	YSL	Postlarvae 5 - 8 mm	Postlarvae 8 - 10 mm	All Postlarvae	Bosmina	Eurytemora
within 10 km of maxturbidity	46.6	68.5	79.0	86.9	73.2	18.8	94.2	95.0	85.5	93.1	45.6	75.5
in salinity <1 PSU	68.9	35.2	26.2	25.4	31.7	96.0	31.6	57.6	35.5	53.0	79.2	26.4
in salinity >1 and <5 PSU	18.0	51.5	53.9	66.6	53.4	3.3	65.3	39.7	57.5	43.4	17.1	40.3
in bottom waters	51.1	61.1	42.2	55.6	54.8	33.6	71.9	43.8	73.1	49.8	22.3	55.9
in bot & mid-depth waters	75.7	85.2	69.7	73.0	79.4	71.5	88.5	59.7	85.3	65.0	53.3	84.8
in temperature >15 and <20 C°	**65.5**	**59.4**	**73.9**	**85.3**	**65.9**	13.3	69.6	93.3	80.0	90.6	47.3	51.0

Table 2. Results of repeated measures analysis for larvae by size class. Model includes physical (salinity, temperature, total suspended solids (TSS)) and biological parameters (Eurytemora and Bosmina concentrations).

	Salinity	$Salinity^2$	Temp	TSS	TSS^2	TSS x Salinity	TSS x Temp	Depth	Year	Eury.	Bos.	r	N	Outliers Removed
White Perch														
Yolk-sac larvae	*			*				**				-0.17	83	0
Larvae <5mm						*		*				0.09	48	1
Larvae 5 - 8 mm	**	*										0.42	47	2
Larvae 8 -10 mm	*					*						0.33	46	3
Striped Bass														
Yolk-sac larvae	*			***		***	***					0.48	82	1
Larvae 5 - 8 mm		**		***	*	**	***					0.32	48	1
Larvae 8 -10 mm				**		*	**			*		0.35	49	0

Key

= parameter not included in model

* = significant, $P < 0.05$

** = significant, $P < 0.001$

*** = significant, $P < 0.0001$

r = Pearson correlation coefficient of the absolute value of the model residuals versus predicited values.

N= the number of data points used to fit each model

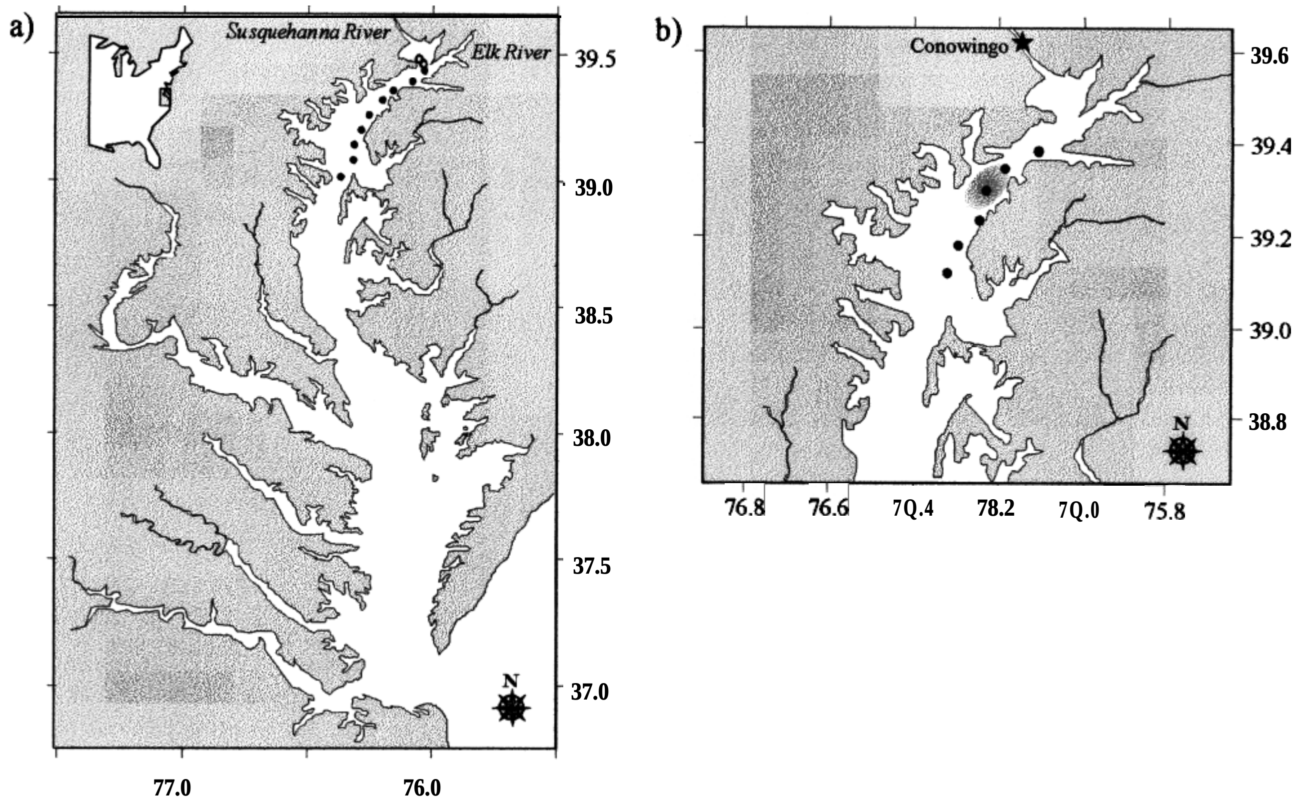

Figure 1. Chesapeake Bay, USA. a) Axial CTD survey stations. b) An example of gradient mapping stations in the 19-22 May 1998 research cruise. Shaded area represents the ETM. Conowingo is location of freshwater discharge measurements. Latitudes in decimal fractions.

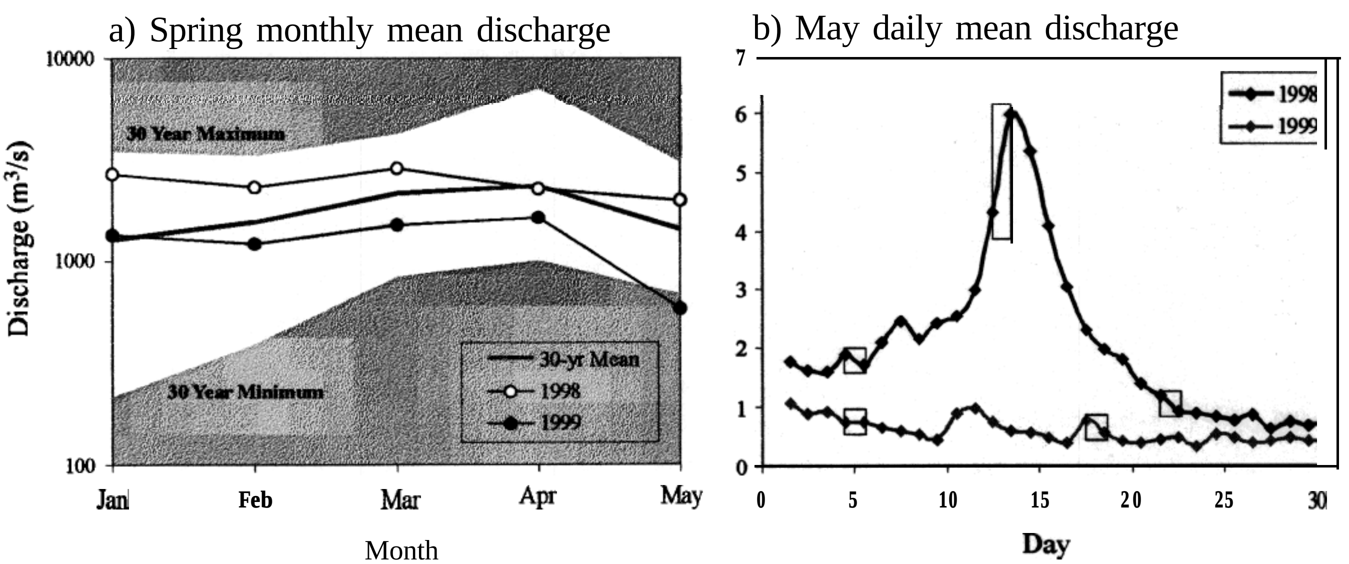

Figure 2. a) Thirty-year mean monthly Susquehanna River discharge at Conowingo (19681998) on a logarithmic scale. Also depicted are 30-year maximum and minimum, and 1998 and 1999 mean monthly discharge values. b) Daily Susquehanna River Discharge in May 1998 and 1999. Boxes indicate time of gradient mapping cruises.

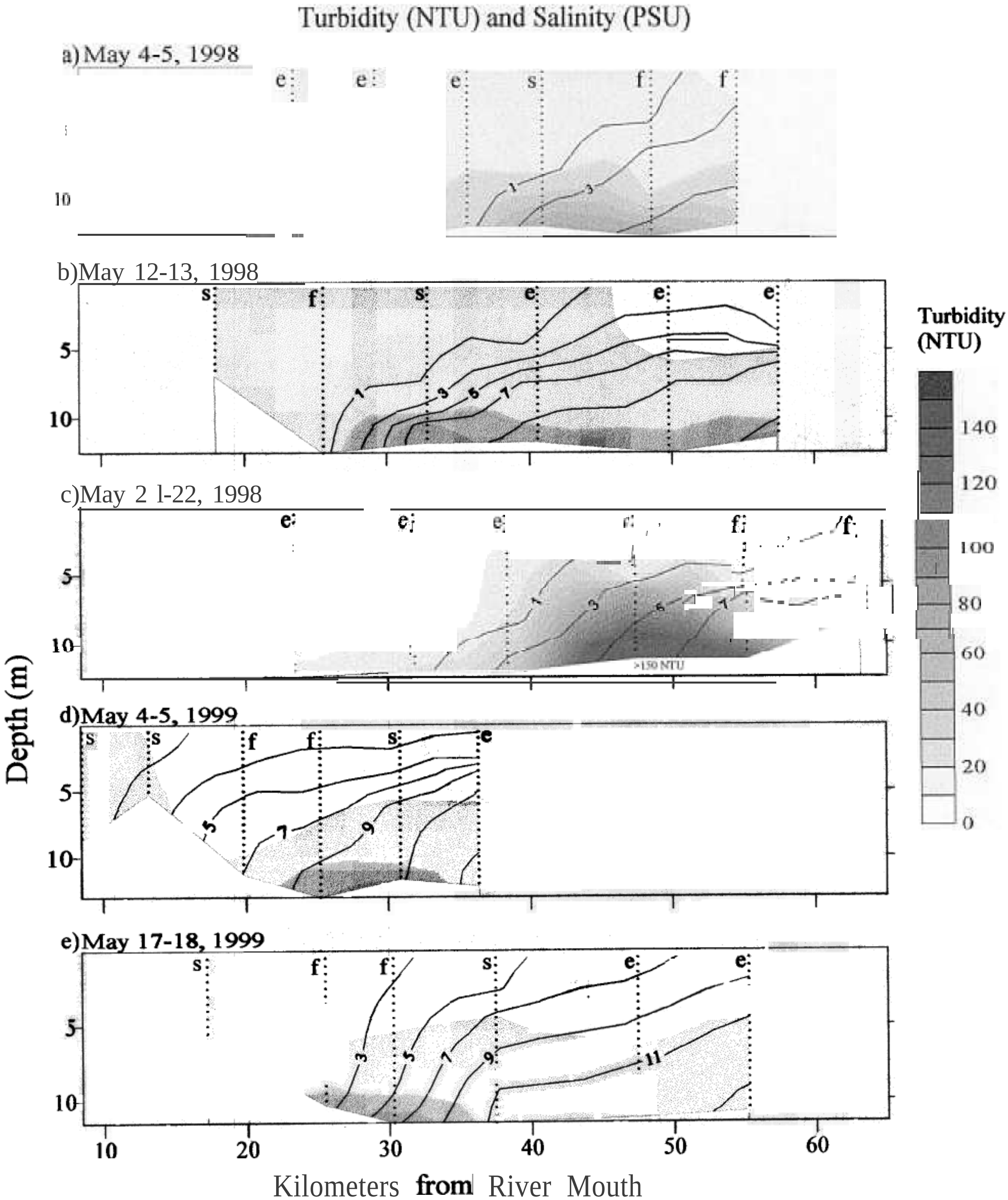

Fig. 3. Contour plots of turbidity (NTU) and salinity (PSU) contour lines from the gradient mapping surveys of the five research cruises. The upper left corner of each panel indicates the date of each survey. The location of each CTD cast is marked by a letter which represents the stage of the predicted tide (e = ebb, s = slack, f = flood).

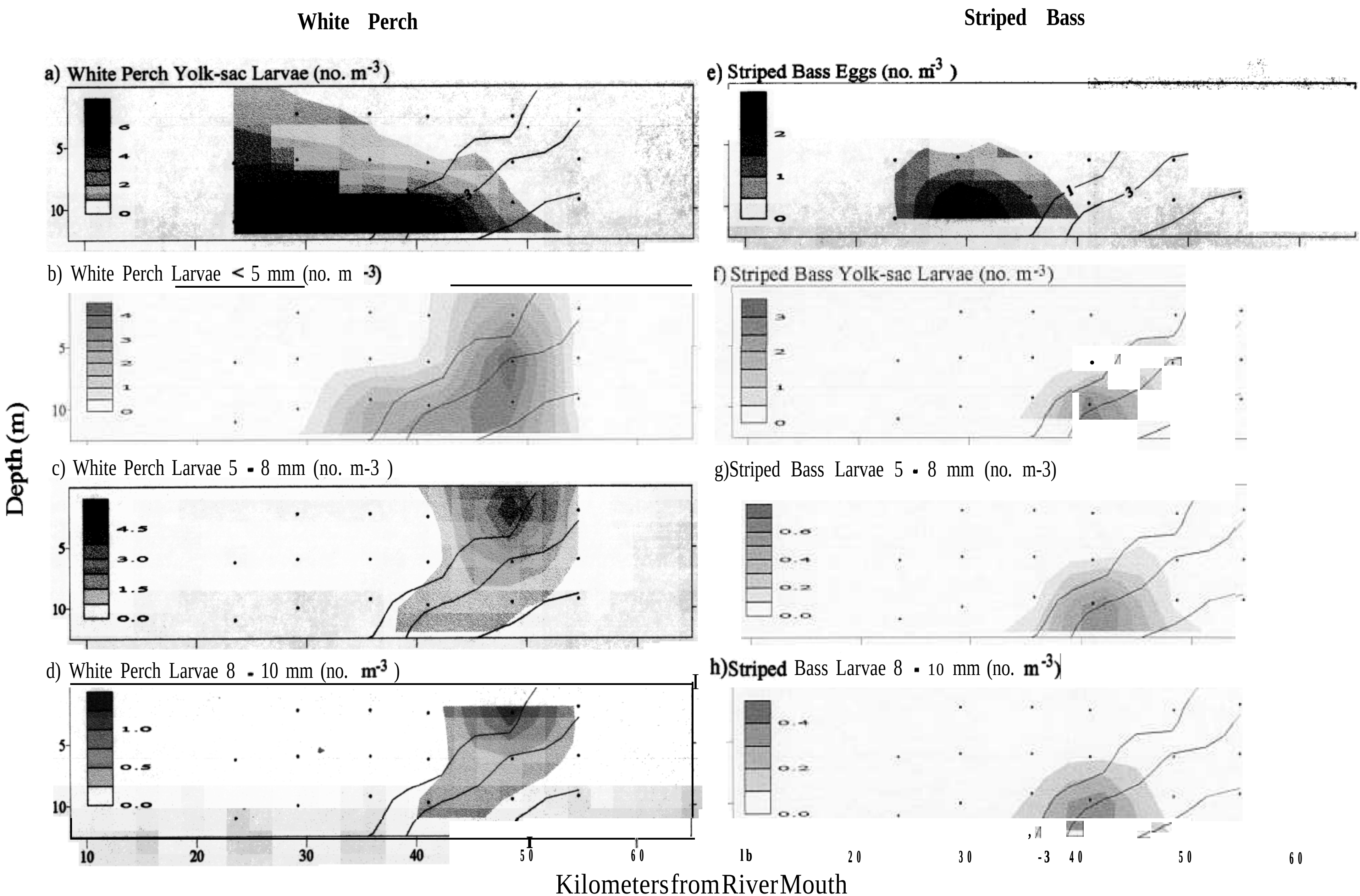

Fig. 4. Contour plots of white perch and striped bass early life stages (no. m^{-3}) with salinity (PSU) contour lines from 4-5 May 1998 gradient mapping survey of ichthyoplankton abundances. Black dots indicate the midpoints of ichthyoplankton tow-depth intervals.

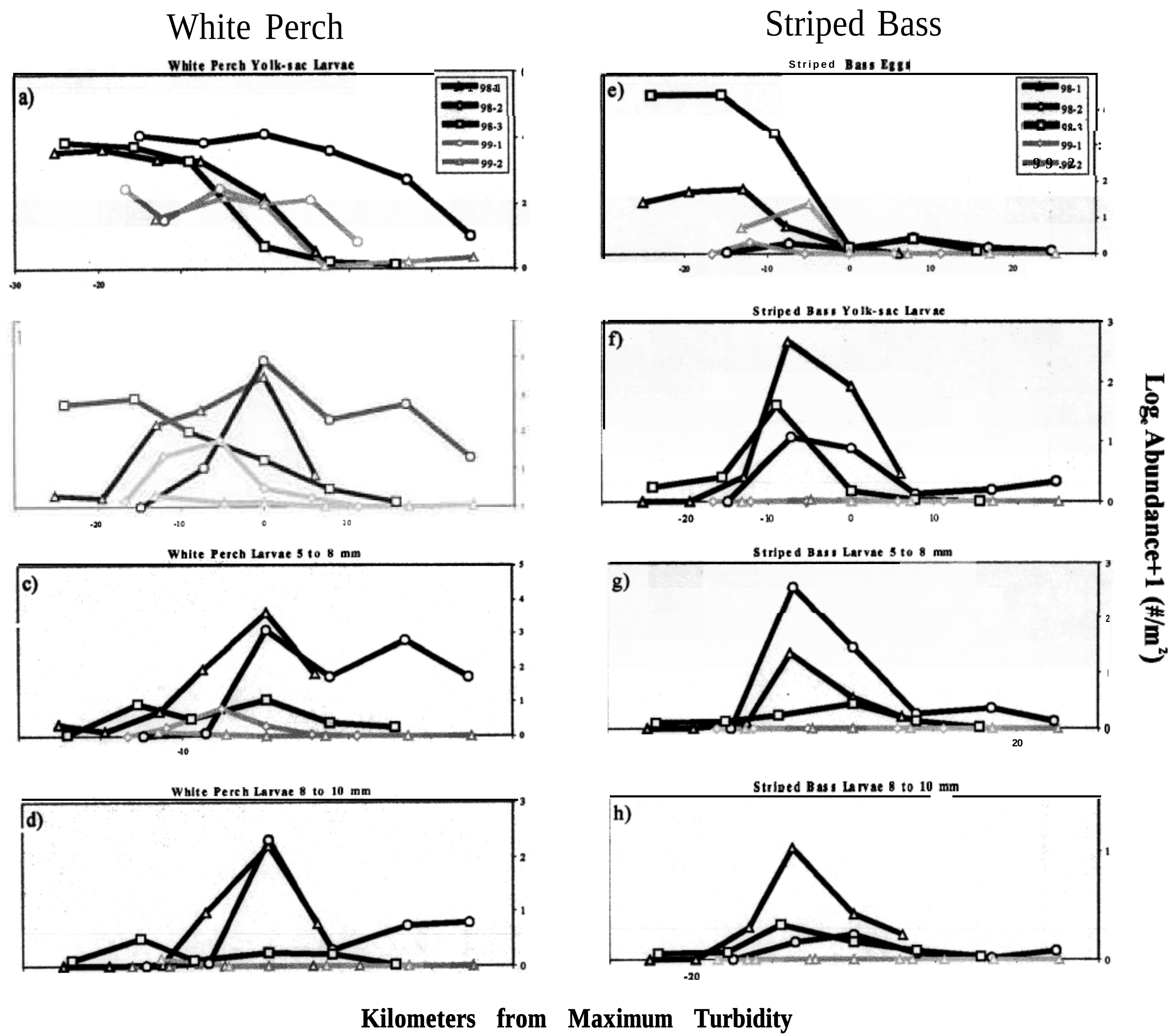

Fig. 5. White perch and striped bass abundance (number under 1 m^2) by early-life stage versus distance from maximum turbidity (NTU) measurements for each cruise in 1998 (98-1, 98-2, 98-3) and 1999 (99-1, 99-2).

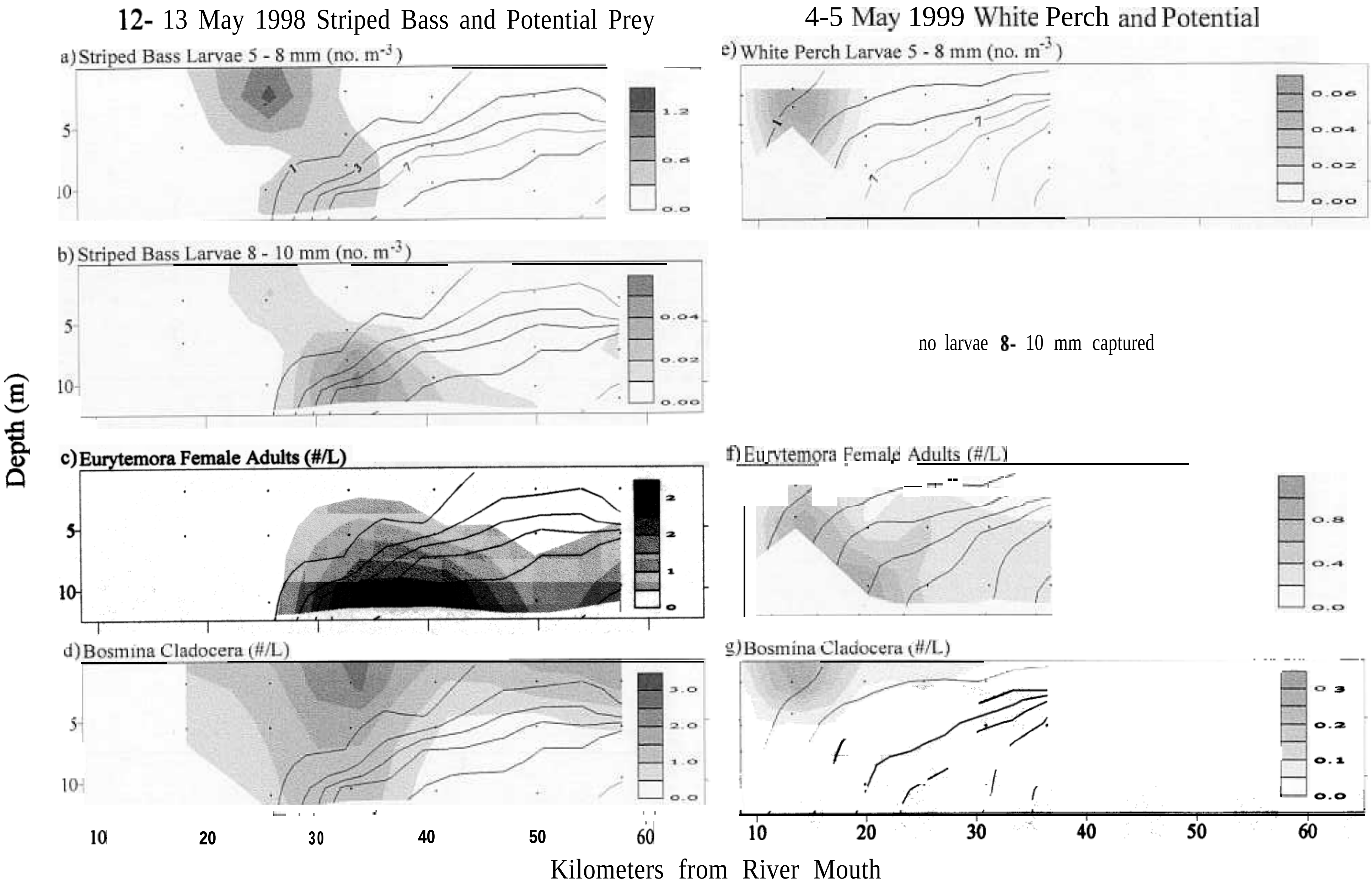

Fig. 6. a-d) Contour plots of striped bass, Eurytemora and Bosmina concentrations (no. m-3) and salinity (PSU) contour lines 12-13 May cruise. e-g) Contour plots of white perch, Eurytemora and Bosmina concentrations (no. m-3) and salinity (PSU) contour lines 4-5 May 1999 cruise. The upper left corner of each panel contains species and size-class information. Black dots indicate the midpoints of the depth intervals of ichthyoplankton tow or zooplankton collections.

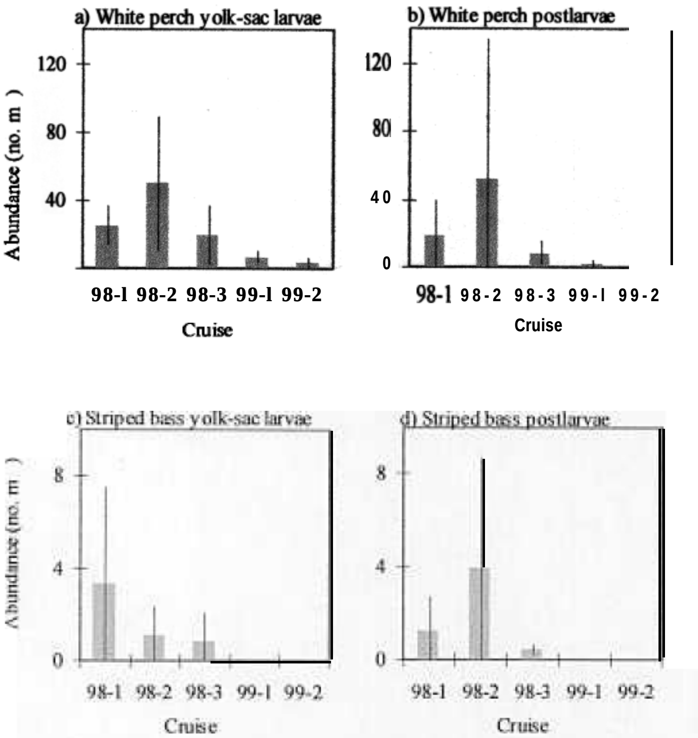

Figure 7. Abundance (no. m^{-2}) of white perch a) yolk-sac larvae and b) postlarvae, and striped bass c) yolk-sac larvae and d) postlarve during each cruise in 1998 (98-1, 98-2, 98-3) and 1999 (99-1, 99-2). Error bars indicate +/- 2 standard errors of the mean.

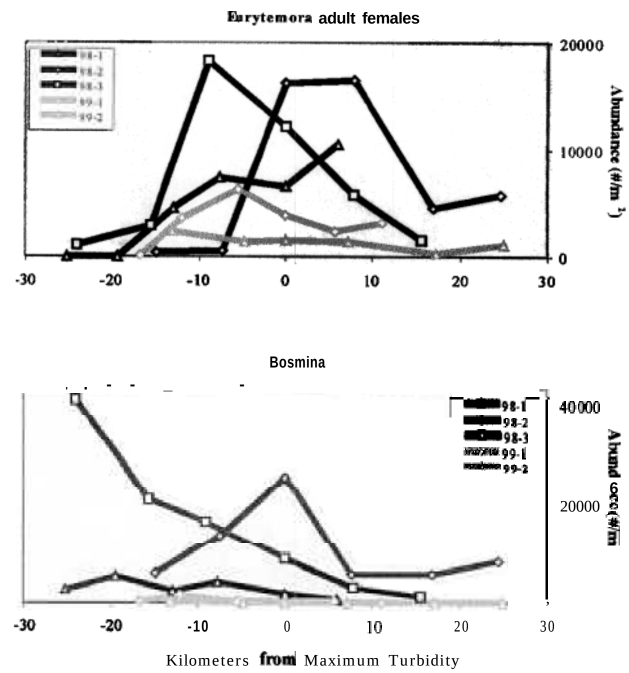

Fig. 8. Eurytemora and Bosmina abundance (number under 1 m^2) by early-life stage relative to distance from maximum turbidity (NTU) measurements for each cruise in 1998 (98-1, 98-2, 98-3) and 1999 (99-1, 99-2).

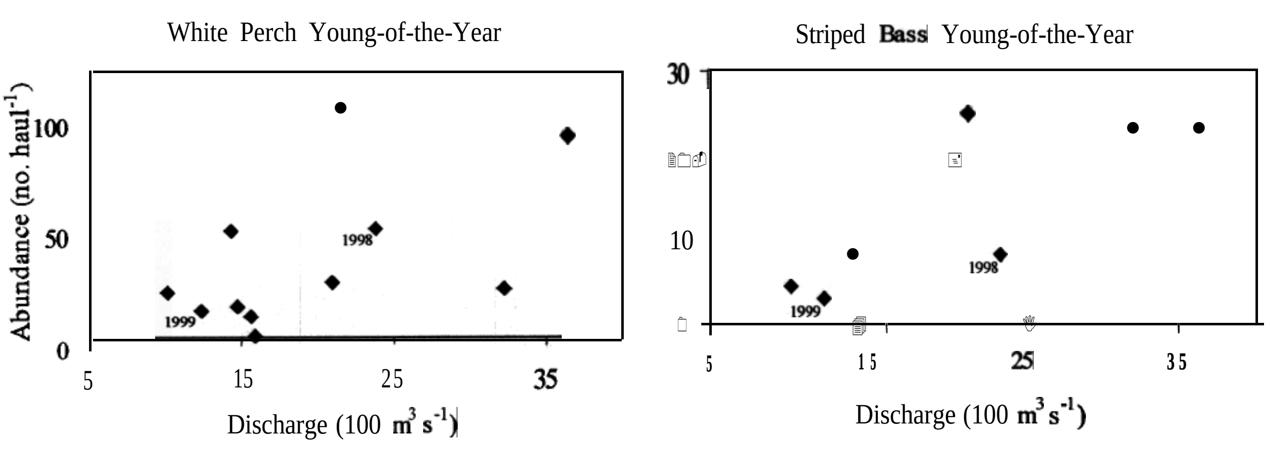

Figure 9. Abundance of young-of-the-year (no. haul-‘) white perch and striped bass from 1989-99 in the upper Chesapeake Bay in relation to spring Susquehanna River discharge (100 $m^3 s^{-1}$). Abundance data are from the Striped Bass Juvenile Index Seine Survey (Maryland Department of Natural Resources).