ABSTRACT

Title of Document: THE INFLUENCE OF EPISODIC RIVER FLOW EVENTS ON STRIPED BASS (*MORONE SAXATILIS*) SPAWNING IN CHESAPEAKE BAY, USA

Ginger Lee Jahn, Master of Science, 2010

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The upper Chesapeake Bay is an important and dynamic nursery habitat for striped bass (*Morone saxatilis*) eggs and larvae. The hypothesis that pulses in flow cause temperature changes that cue striped bass spawning was evaluated with field surveys and historical data analyses. Water temperatures in April and May were negatively correlated with river flow (1956-2002), suggesting that water temperatures decrease during flow events and then increase as flow diminishes, potentially providing a cue for spawning. Survey data from the upper bay in 2007 and 2008 were analyzed in conjunction with historical data on striped bass eggs in tributaries of Chesapeake Bay. Results suggest that increasing water temperatures are the dominant cue for striped bass spawning. Temperature increases after pulsed flow events may cue striped bass spawning and may result in more favorable prey abundances and

better larval survival compared to years when spawning is cued by water temperature increases alone.

THE INFLUENCE OF EPISODIC RIVER FLOW EVENTS ON STRIPED BASS (*MORONE SAXATILIS*) SPAWNING IN CHESAPEAKE BAY, USA

By

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Thesis submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of Master of Science
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Dedication

I dedicate this to my parents. Thank you for always being there for me and encouraging me to pursue my dreams.

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Introduction

The objective of this research program is to understand how pulses in river flow affect striped bass (*Morone saxatilis*) early life stages in the upper Chesapeake Bay. Striped bass is a commercially and recreationally important anadromous fish found along the east coast of North America from northern Florida to Canada (Setzler-Hamilton and Hall, 1991). Most striped bass (up to 90%) are spawned in the tributaries of Chesapeake Bay (Berggren and Lieberman, 1978). Spawning occurs up-estuary of the salt front in April and May, when water temperatures are between 12 and 23˚C (Setzler-Hamilton *et al*., 1981; Uphoff, 1989).

Striped bass larvae can occur in high concentrations in the estuarine turbidity maximum (ETM) of the upper Chesapeake Bay (North and Houde 2003). An ETM is a region where higher turbidity and suspended sediment concentrations occur than those found up- and down-estuary (Schubel, 1968). ETMs are located at the heads of many coastal plain estuaries such as the Chesapeake Bay (Schubel, 1968). In the upper Chesapeake Bay, the ETM is usually located between the head of the bay and Tolchester (Fig. 1) in a region dominated by the influence of freshwater flow from the Susquehanna River (Schubel, 1968). The exact position of the ETM tends to be associated with the location of the salt front which is controlled by river flow, but may be up or down estuary depending on other physical conditions (Boynton *et al*., 1997, Sanford *et al*. 2001). The ETM is created by sediment resuspension and particle trapping that result from tidal scour, tidal asymmetries, and estuarine circulation (Sanford *et al*., 2001).

The ETM acts as an important nursery area for the early life stages of striped bass (North and Houde, 2001). The ETM may provide striped bass larvae a refuge from predation by visual predators (Chesney, 1989). Also, striped bass larvae in the ETM are located in a region of favorable salinities for survival (Winger and Lasier, 1994). Within the ETM, larvae may be retained in an area of concentrated zooplankton prey (Boynton *et al*., 1997; Kimmerer *et al*., 1998; Roman *et al.*, 2001; North and Houde, 2003). The distribution of the copepod *Eurytemora affinis*, a common prey of striped bass larvae, in Chesapeake Bay is likely controlled by the same advective processes in the ETM region that trap the suspended sediments which characterize ETMs (Roman *et al*., 2001).

In upper Chesapeake Bay, larval striped bass feeding success and growth rates were highest in years when they were most associated with the ETM (Martino *et al.*, 2007; Martino, 2008). High growth rates and feeding success during early life may enhance juvenile recruitment: growth rates (G) in striped bass larvae were inversely correlated with mortality rates (Z) and the ratio of these two rates (G:Z) was positively correlated with the juvenile recruitment index for the upper Chesapeake Bay, the Potomac River, and the Choptank River (Rutherford *et al*., 1997).

ETM regions and the organisms found within them, such as zooplankton and larval fish, can be influenced by river flow. Above average river flow leads to higher sediment loading (Sanford *et al*., 2001), increased inputs of detritus and organic matter (Turner and Chadwick, 1972), high concentrations of *Eurytemora affinis* in the upper estuary (Kimmerer, 2002; Kimmel and Roman, 2004), enhanced concentrations of zooplankton and ichthyoplankton in the ETM (North and Houde, 2006; Martino *et* *al*., 2007), and may promote higher survival of striped bass larvae (North and Houde 2001; Martino *et al*., 2007; Martino, 2008). There were significant positive correlations between mean freshwater flow in April and May and striped bass young-of-the-year abundances (1986-2002) in the upper Chesapeake Bay (North and Houde, 2001; North *et al*., 2005). In the Sacramento-San Joaquin Estuary, striped bass year class strength was positively correlated with river flow in the first summer of life (Stevens, 1977); however this relationship broke down in later years (Kimmerer *et al*., 2001). However, in the Roanoke River, high juvenile striped bass abundance indices were associated with low to moderate discharge (Rulifson and Manooch III, 1990). Also, in the Hudson River Estuary, there was no significant relationship between river flow and larval striped bass abundance or the juvenile striped bass index (Pace *et al*., 1993).

Episodic river flow events influence circulation patterns and striped bass egg transport in ETM region. Numerical modeling and field observations in the upper Chesapeake Bay showed that short-term pulses can result in non-linear responses in the salt front and ETM (North *et al*., 2004). High flow events result in down-estuary movement of the salt front, but there can be a lag in the movement of the turbidity maximum (North *et al*., 2004). When striped bass eggs were added to the numerical model, egg transport to the ETM nursery area was lower during pulse flow events than during steady state conditions, but higher immediately after the event when the salt front rebounded up-estuary (North *et al*., 2005). The model result suggested that the optimum time for striped bass egg transport to the ETM nursery area is just after a pulse in river flow. During 1986-2002 there was a positive correlation between the number of pulses in freshwater flow in April and May and striped bass young-of-the-year abundances in upper Chesapeake Bay (North *et al*., 2005), suggesting that pulsed events influence survival to the juvenile stage. If striped bass spawn just after pulses in flow, eggs may encounter favorable transport conditions to the ETM region which could promote survival.

In several different systems, peaks in striped bass egg abundances often occurred when water temperatures were increasing rapidly (Virginia portion of Chesapeake Bay: Grant and Olney, 1991, Olney *et al*., 1991; Miramichi River, Gulf of St. Lawrence: Robichaud-LeBlanc, *et al*., 1996; Potomac River and Upper Chesapeake Bay: Rutherford and Houde, 1995; Patuxent River: Secor and Houde, 1995; Savannah River: Van Den Avyle and Maynard, 1994). The literature suggests that increases in water temperature occur following peaks in river flow (Fig. 2) (Rutherford et al., 1997). This implies that increasing water temperatures following pulses in river flow could act as a cue for striped bass to spawn when egg transport to the ETM is optimal.

An understanding of the spawning dynamics and recruitment variability of striped bass and the potential dependence on river flow conditions has important management implications. In Chesapeake Bay, striped bass have experienced large stock fluctuations. The striped bass fishery crashed in the late 1970s and early 1980s leading to a moratorium in Maryland and Delaware in the mid-late 1980s (Setzler-Hamilton and Hall, 1991). This action combined with several years of good environmental conditions led to the recovery of the population and a reopening of the fishery (Richards and Rago, 1999). Previous research suggests that episodic river flow events and associated temperature changes could act as cues for striped bass spawning in the Chesapeake Bay. These events also may create enhanced retention conditions in the ETM, which could influence the survival of striped bass early life stages. In years of above average river flow the striped bass nursery area may be larger than in other years, increasing the survival of larvae (Secor *et al*., 1996). Therefore, changes in flow due to natural inter-annual variability, or anthropogenic factors such as dams, development, or climate change could influence larval survival and impact striped bass populations.

The objective of this research is to examine the variability in timing of striped bass spawning in relation to episodic river flow events. The research is guided by the hypothesis that striped bass spawn in response to increasing water temperatures that occur after high river flow events. Analyses presented here include correlations of historical river flow and water temperature, graphical and statistical analyses of data from field collections in the upper Chesapeake Bay in 2007 and 2008, and graphical and statistical analyses of data from fourteen historical surveys in tributaries of the Chesapeake Bay.

Methods

River Flow and Temperature

Historical data was collected to characterize river flow and temperature conditions during the striped bass spawning season, determine whether temperatures vary in relation to pulses in flow, and establish a definition for a pulse in river flow for use in analyses of striped bass spawning. Historical river flow (i.e., daily discharge rates, $m^3 s^{-1}$) for the Susquehanna River at Conowingo Dam (1968-2009), the Potomac River near Washington, D.C. Little Falls Dam and Pump Station (1930-2009), the Patuxent River near Bowie, MD (1978-2009), and the Nanticoke River near Bridgeville DE (1943-2009) (Fig. 1) were downloaded from the United States Geological Survey (http://waterdata.usgs.gov/nwis/rt). River flow and water temperature at Holtwood Dam on the Susquehanna River from 1956 to 2002 was also retrieved (courtesy PPL Corporation and Normandeau Associates).

Statistical analyses were conducted on detrended data. River flow and water temperatures were detrended for April and May of each year to eliminate the seasonal trend of decreasing river flow and increasing water temperature. The data were detrended by fitting a linear regression to each year and subtracting the values predicted by the regression from the actual values. A Spearman correlation analysis was conducted with detrended river flow from April and May in the upper Chesapeake Bay, Nanticoke River, Patuxent River and Potomac River to determine the degree of similarity between these river systems using SAS v. 9.2 (SAS Institute Inc. 2009).

Additional analyses were focused on data from the Susquehanna River and upper Chesapeake Bay where field collections of striped bass eggs were conducted. Detrended river flow and water temperature data at Holtwood Dam for April and May were examined with a cross correlation analysis to find the temporal lag that resulted in the highest correlation between flow and water temperature. In addition, a Spearman correlation analysis was conducted with the lagged data to determine if temperature changes were significantly associated with changes in flow. The effects of episodic pulses in river flow on water temperatures and the number and frequency of pulses from 1990-2002 were examined graphically to characterize these occurrences in recent years. Based on this examination a definition for a pulse in flow was determined.

Field Collections

Research cruises were conducted to collect striped bass eggs and larvae before and after pulses in river flow in the upper Chesapeake Bay and to examine how physical conditions change in relation to pulses in river flow. Striped bass early life stages were collected in April and May of 2007 and 2008 during research cruises that were part of the Bio-physical Interactions in the Turbidity Maximum (BITMAX-II) program. A combination of large-boat and small-boat surveys was conducted. Two week-long cruises were completed each year during the striped bass spawning season in the upper Chesapeake Bay in and around the ETM region aboard the 44.5 meter *R/V Hugh R. Sharp*. On each cruise, two transects of stations in the channel along the axis of the upper Bay were sampled. CTD casts and plankton collections were made to examine physical conditions and collect zooplankton and early life stages of fish.

At six stations, a 0.25-m^2 opening MOCNESS equipped with three 200 micrometer mesh nets was used to sample three depths: below the pycnocline, in the pycnocline, and above the pycnocline. The flow meter attached to the MOCNESS frame was used to calculate the volume of water filtered by each net. At seven axial stations, a 1-m^2 mouth opening Tucker trawl was equipped with two 280 micrometer mesh nets and was used to sample two depths: from near bottom to the pycnocline and from the pycnocline to the surface. The volume of water filtered by each net was calculated from revolutions of a General Oceanics flow meter inside the mouth of each net.

One-day, small-boat "rapid response" cruises were conducted to survey physical and biological conditions along the axis of the upper Bay before and after pulses in flow. In April and May 2007, four "rapid response" cruises were conducted in the upper Chesapeake Bay, in and around the ETM region, aboard the 7.6 meter *R/V Terrapin*. On each cruise, CTD casts and bongo net tows were conducted at seven to eleven axial stations to collect zooplankton and early life stages of fish. The CTD was equipped with a transmissometer, and temperature and conductivity sensors. A paired 60 cm diameter bongo net with 280 micrometer mesh nets and General Oceanics flow meters was fished from near bottom to the surface to collect striped bass eggs and larvae from the entire water column. Because the width of the mouth openings of the bongo net (60 cm) was similar to the MOCNESS (63 cm), the catching efficency of the two nets were assumed to be similar. The four rapid response and two large-boat cruises in 2007 bracketed a pulse in river flow.

In April and May 2008, three rapid response cruises were conducted, two aboard the *R/V Terrapin* and one aboard the 19.8 meter *R/V Aquarius* (weather conditions prevented additional cruises). The same boat and equipment was used during the 2008 “rapid response” cruises as in 2007. During the third “rapid response” cruise on the *R/V Aquarius*, CTD casts and Tucker trawl tows were made at seven axial stations to sample zooplankton and early life stages of fish. The CTD was equipped with temperature and conductivity sensors. A 1 m^2 Tucker trawl with 280 micrometer mesh nets sampled two depths, from near bottom to the pycnocline and from the pycnocline to the surface. In 2008, the three rapid response and two large-boat cruises bracketed two of three pulses that occurred during April and May. CTD data from all cruises were processed with SBE Data Processing v. 7.12 (Sea-Bird Electronics, Inc., 2007) and SAS v. 9.2 software and plotted with Surfer v. 8.05 (Golden Software Inc., 2004) to describe physical conditions in the upper Chesapeake Bay during the research cruises.

To determine if striped bass spawn in response to high river flow events, eggs and larvae collected during cruises were enumerated, staged, and measured. To summarize egg data from each cruise with a single value, an index of egg abundance (A) was calculated as:

$$A = \frac{\sum_{i=1}^{N} C}{N}$$

where C is the number of eggs per cubic meter (concentration) at each station and N is the number of stations.

The spawn dates of surviving larvae were estimated and compared to the timing of pulses in river flow. Concentrations of larvae in each sample (number per cubic meter) were calculated. Striped bass larvae were measured to the nearest 0.1

mm using Image J and results from each cruise were summarized in length-frequency plots. Spawning date was estimated for each one millimeter age class less than 8 mm using an average egg stage duration of two days (Setzler-Hamilton and Hall, 1991) and an age-at-length key developed by averaging the two keys (1992 and 1993) from Kellogg (1996). Larvae > 8 mm in length were not included in the analysis because bongo nets did not appear to capture larvae > 8 mm with equal efficiency as a 2 m^2 Tucker trawl in a net calibration study (Houde *et al.* 1988, Fig. 15).

Historical Data

In addition to field collections, historical striped bass egg abundances were examined to determine if peaks in striped bass spawning occurred after pulses in flow in the upper Chesapeake Bay and tributaries of Chesapeake Bay. Egg abundance data were retrieved for the Potomac River 1974-1977 (courtesy Walter Boynton), the Potomac River 1987-1989 and the Upper Bay 1988-1989 (courtesy Edward Rutherford), the Patuxent River 1991 (courtesy David Secor), the Nanticoke River 1992-1993 (Kellogg, 1996), and the Upper Bay 1998-1999 (courtesy Elizabeth North). Data were available to calculate the striped bass egg abundance index for 14 years in the four systems (Table 1).

River flow data were available for the 14 years in the four systems, and temperature data were available for all cruise dates. Historical daily river flow values were downloaded for the Potomac River near Washington, D.C. Little Falls Dam and Pump Station (1930-2009), the Patuxent River near Bowie, MD (1978-2009), and the Nanticoke River near Bridgeville DE (1943-2009) (Figs. 1 and 3). Daily temperature data were only available for four of the historical datasets (Potomac 1989, Patuxent

1991, and Upper Bay 1998-1999). For the other 10 datasets, temperatures measured at the station farthest up-estuary on the cruises were used to estimate the temperatures experienced by spawning striped bass.

The flow data were detrended and pulses in flow were identified. A pulse in flow was defined as the date of the peak in flow of any event that was in the highest 10% of detrended daily flow data for April and May within a year and river system. The data were detrended so that the higher-than-average flows that tend to occur early in the season did not affect pulse classification. This definition of a pulse resulted in identifying as many as five and as few as one pulses in each spawning season. Visual inspection of the data indicated that this definition was satisfactory because it takes into account the within-season variability that the fish experience as opposed to a definition based on between-season variability. It also tends to include most of the high flows while minimizing what appears to be small scale noise. An additional pulse definition was applied to the data to examine the influence of the definition on the results of the analysis. The pulse criteria were taken from North et al. (2005) and defined as a flow event that lasted at least two days and was greater than twice the average flow in the river system in April and May of that year. In years with multiple close peaks in flow, separate pulses were defined as those where flow values between peaks were substantially lower than twice the average flow for more than 3 days.

A statistical analysis was conducted to determine if the number of pulses in flow accounts for a significant amount of the variability in striped bass juvenile recruitment. North *et al*. (2005) found a significant correlation between the striped bass young-of-the-year index in the upper bay with average river flow in March-May and with the number of pulses in flow in April and May for the years 1986-2002. In addition, they found that average river flow and the number of pulses described a significant amount of variability in the striped bass young-of-the-year index in a regression analysis. This suggests that river flow conditions during the egg and larval stages of striped bass may have an effect on survival to the juvenile stage. To determine if this relationship is still significant, these correlation and regression analyses were repeated in SAS (v. 9.2) with data from 1986-2008.

Data analysis and statistics

The hypothesis that striped bass spawn in response to increasing water temperatures after high river flow events was tested. Using two definitions of a pulse in flow (described above), the dates of the peaks in flow of individual pulse events were recorded. The cruise prior to a peak in flow was classified as 'pre-pulse' and the cruise immediately after was classified as 'post-pulse'. Any post-pulse cruises that occurred more than five days after the pulse were not included in the analysis based on the timing of the response of temperature to flow and on egg-stage duration. Temperature in the upper Chesapeake Bay lagged behind river flow by one day, indicating that temperatures began to increase one day after the pulse. We assumed that spawning in response to the pulse could be expected to occur two to three days after the peak in flow, and the egg stage lasts approximately another two days (Setzler-Hamilton and Hall, 1991). Therefore, cruises were classified as 'post-pulse' if they occurred within a 5-day window after the peak in flow. Any pulse that did not have a cruise before or after it was eliminated from the analysis. The two egg abundance datasets ('pre-pulse' and 'post-pulse') were compared in SAS (v. 9.2) with a nonparametric Wilcoxon signed-rank test to determine if significantly more eggs were present after a pulse than before the pulse.

Results

River Flow and Temperature

River flow in the Chesapeake Bay in April and May was highly variable and differed markedly between the river systems of interest: the Susquehanna, Potomac, Patuxent, and Nanticoke Rivers. The river flow minimum, maximum, mean, and standard deviation for these systems were 148, 13224, 1749, and 1361 $m^3 s^{-1}$, respectively, in the Susquehanna River (1968-2009); 65, 8778, 494, and 489 $m^3 s^{-1}$ in the Potomac River (1930-2009); 2.8, 237.9, 13.9, and 14.2 $m^3 s^{-1}$ in the Patuxent River (1978-2009); and 0.8, 32.0, 3.5, and 2.2 $m^3 s^{-1}$ in the Nanticoke River (1943-2009). Historic river flow at Conowingo Dam had a significant negative correlation during the striped bass spawning season (ρ= -0.41, $p<0.0001$, n=2379), in accord with the expectation that river flow decreases during the spring in this region.

River flow in April and May in each river system was detrended and correlated across systems to determine the degree of similarity between river systems. Results of a Spearman rank-order correlation analysis showed a very high degree of association between river flow at Conowingo Dam and Holtwood Dam (ρ=0.96, $p<0.0001$, n=2126) and significant, though lower, correlations between all other river systems (Table 2). Daily water temperature data were available for Holtwood Dam but not Conowingo Dam. Variations in water temperature were assumed to be similar between these two dams because of the high correlation between river flow at these two locations. The average water temperature in April and May 1956-2002 at Holtwood Dam was 14.35˚C with a standard deviation of 4.80˚C. Historic water temperature at Holtwood Dam had a significant positive correlation during April and May (ρ= 0.84, $p<0.0001$, n=2858) as expected.

A cross-correlation analysis was conducted with detrended flow and temperature data from Holtwood Dam to determine if pulsed events influence water temperature in the upper Chesapeake Bay. Results of the cross correlation analysis indicate that changes in detrended water temperature lag behind changes in river flow by one day, and that detrended river flow lagged by one day is significantly correlated with detrended water temperature (ρ=-0.50, $p<0.0001$, n=2793). The negative value of the correlation coefficient indicates that increasing flow is associated with decreasing water temperatures, and vice versa, during pulse events in the striped bass spawning season. A visual examination of river flow and water temperature data at Holtwood Dam from 1990-2002 confirms that water temperatures tend to decrease during a peak in flow and increase following a peak in flow (e.g., Fig. 4).

The magnitude and variation in pulsed events (when detrended discharge rates exceed 90th percentile values) differed between river systems (Fig. 5). The 90th percentile values in the Susquehanna River were larger in magnitude and had greater interannual variability than the other systems. The minimum, maximum, and standard deviation of the 90th percentile values for flow were 323, 2776, and 509 $m^3 s^{-1}$, respectively, in the Susquehanna River; 21, 1106, and 226 $m^3 s^{-1}$ in the Potomac River; 1.6, 27.2, and 6.6 $m^3 s^{-1}$ in the Patuxent River; and 0.1, 5.3, and 0.9 $m^3 s^{-1}$ in the Nanticoke River. The magnitude and variability of the 90th percentile decreased as total flow decreased in the systems, from the Susquehanna River, to the Potomac

River, to the Patuxent River and finally to the lowest pulse event magnitude and variability in the Nanticoke River.

Field Collections

Field collections were conducted to determine if striped bass spawn before or after pulses in river flow in the upper Chesapeake Bay and to examine how physical conditions change in relation to pulses in river flow. In 2007, one pulse in flow occurred in the upper Chesapeake Bay on April 22 (Fig. 6). The pulse was associated with an initial decrease in water temperature, followed by an increase in water temperature (Fig. 7). One axial survey was completed before the pulse and six were completed after the pulse (Fig. 6).

Salinity, turbidity and water temperatures in the striped bass spawning and nursery area varied within and between the cruises (Fig. 8). Water temperatures increased on average through the season, and lower temperatures were generally found at greater depths and at down-estuary locations. The locations of peak turbidities occurred in the region between river kilometers 30 and 40 for all cruises except on May 22, when it moved up estuary approximately 10 kilometers (Fig. 8E). The salt front (the intersection of the 1 salinity isohaline with the bottom) location varied from around river kilometer 15 to around river kilometer 35. On May 8, 2007 the salt front was located farthest up-estuary (Fig. 8D), which could have been due to a down-estuary wind event (North *et al*., 2004).

The pulse in flow on April 22 affected the physical characteristics of the upper bay by forcing the salt front down estuary to near the turbidity peak, which was followed by movement of the salt front up-estuary on the following two cruises (Fig.

8). The salt front was most associated with the turbidity peak following the pulse in flow and again approximately one month later (Fig. 8).

Striped bass eggs were collected on all seven axial surveys in 2007 (Table 3, Fig. 9), although only one egg was present on the first cruise on April 12 when water temperatures were still below favorable conditions (~12˚C) for striped bass spawning (Setzler-Hamilton and Hall, 1991). The highest striped bass egg concentrations occurred on the second survey (April 25, 2007), just after the pulse in flow, and were located in the region of the ETM (Fig. 9B). The following cruise (May 4, 2007) also had relatively high egg concentrations located in the region of the ETM and the salt front (Fig. 9C). The stations with the highest egg concentrations collected during the two cruises following the pulse were located just down-estuary of the salt front and within five kilometers of highest turbidity values (Fig. 9B and C). The highest striped bass egg abundance index followed the single pulse in flow that occurred in 2007 (Fig. 10).

Larval lengths show the expected progression toward larger sizes through the season (Fig. 11). The ranges in length on each survey were from four to ten millimeters (Fig. 11B), suggesting that spawning had occurred over many days. Spawning dates estimated from mean egg-stage duration and age-length keys (Setzler-Hamilton and Hall, 1991; Kellogg, 1996) indicate that most surviving larvae were spawned from April 25 to May 28, 2007 (Fig. 12). Based on this larval length analysis, it appeared that most of the surviving larvae were spawned in early to mid-May, at least one week after the pulse in river flow, but still during increasing water temperatures.

In 2008, three pulses in flow occurred in the upper Chesapeake Bay (April 4, May 13 and May 19), and cruises were completed before and after the second and third pulses (Fig. 13), but not before the first pulse. The temperature gauge at Havre de Grace was inoperable during a portion of the spawning season so additional data were used from Tolchester (http://www.ndbc.noaa.gov), a site down-estuary of the ETM region (Fig. 1). Water temperatures at Tolchester were similar to Havre de Grace temperatures, but Tolchester seemed to be flashier, probably because measurements were taken near the sea surface as opposed to measurements at a depth of one meter as at Havre de Grace. The three pulses were associated with decreases in temperature followed by increases at Tolchester, but only the first and third pulses were associated with a subsequent increase in temperature at Havre de Grace (Fig. 14).

Salinity, turbidity and water temperatures in the striped bass spawning and nursery area varied between the five cruises completed in the upper bay in 2008 (Fig. 15). Water temperatures increased on average through the season, and lower temperatures were generally found at greater depths and down-estuary (Fig. 15). During the last cruise (June 5, 2008) turbidity data were not collected, but during the first four cruises the highest turbidities were located between river kilometers 15 and 35. The only axial survey that had a well defined ETM was the first cruise (April 17, 2008) which occurred after the first pulse in flow (April 4) (Fig. 15A). The location of the salt front varied from around river kilometer 15 to around river kilometer 30. After the second pulse in flow on (May 13), the salt front was down-estuary of its pre-pulse position (compare panels B and C of Fig. 15), and then following the third pulse the salt front was farther down estuary (compare panels C and D of Fig. 15). After the second pulse (May 13) the turbidity peak was located down-estuary of its initial position (Fig. 15C), and following the third pulse it rebounded farther up-estuary than prior to the pulses (Fig. 15D). However, these pulses were relatively small and it is possible that the changes may have been influenced by wind (North *et al.*, 2004). The salt front was most associated with the turbidity peak following the first pulse in flow (Fig. 15A).

Striped bass eggs occurred on all seven axial surveys in 2008 (Table 4, Fig. 16). The highest striped bass egg concentrations occurred on the first cruise (April 20, 2008) up-estuary of the ETM (Fig. 16A). Two stations located up-estuary of the salt front and turbidity peak during the first cruise (following the first pulse in flow) had striped bass egg abundances five and eleven times greater than any other station sampled in 2008 (Fig. 16A). The egg abundance index was highest after the first pulse in flow (Fig. 16). However, no sample was collected prior to the first pulse, so it is not known if this index represents an increase or decrease compared to pre-pulse conditions. Following the second pulse, the egg abundance index increased and occurred during the beginning of the third pulse (Fig. 17). Egg abundance index values were minimal after the third pulse.

Larval lengths did not show a clear progression toward larger sizes through the season (Fig. 18). The ranges in length on each cruise were from four to six millimeters, suggesting that spawning occurred over several days prior to each cruise. Spawning date estimates suggest that surviving larvae were spawned from April 11 to May 27, 2008 (Fig. 19). Based on this analysis, it appeared that most surviving larvae originated from eggs spawned in mid- to late-April, after the first pulse in river flow and before the second and third pulses, but still during generally increasing water temperatures (Fig. 19) and during the time when peak egg concentrations were found (Fig. 17).

Historical Data

The abundances of striped bass eggs varied greatly between and within systems and years (Fig. 20, 21, 22). Maximum abundance indices (eggs m^{-3} $station^{-1}$) were generally higher after the year 1988, and were highest in the Nanticoke River followed by the upper bay. The timing of occurrence of striped bass eggs tended to be later in the upper bay than in the other tributaries (compare Fig. 20 with Figs. 21 and 22), although cruises were rarely conducted before striped bass spawning had begun so it is difficult to determine and compare the start date of spawning between systems. The cruises conducted earliest in the season suggest that striped bass spawning appears to begin from late March (*e.g.* Fig. 21C) to mid April (*e.g.* Fig. 20B). In nineteen percent of the years (three out of 16), eggs were found when the temperatures at the farthest up-estuary station were below the minimum reported favorable temperature for spawning (12˚C) (Setzler-Hamilton and Hall, 1991) (Fig. 20E, 21A, 22B). The peak in egg abundance also occurs later in the upper bay than in the other tributaries. Average date of peak egg abundance was May 9 with a standard deviation of 13 days in the upper bay compared to April 20 with a standard deviation of seven days in the other tributaries. Even when the upper bay data from 1998 and 1999 was removed to avoid biasing due to the lack of cruises in April, the average peak egg abundance date was May 3 with a standard deviation of 13 days.

Historical egg abundance index data were plotted with flow and water temperature records for the Upper Bay 1988-1989 and 1998-1999 (Fig. 23), the Potomac River 1974-1977 and 1987-1989 (Fig. 24), the Patuxent River 1991 (Fig. 25), and the Nanticoke River 1992-1993 (Fig. 26). The highest egg abundance index values for each year generally were related to rising temperatures and did not always occur after pulses in flow. In the Upper Bay the highest striped egg abundance index within each year occurred during increasing water temperatures in 1988, 1998, 2007, and 2008 (Fig. 10, 17, and 23). During 1999 (Fig. 23D) water temperature had begun to decrease on the day of the cruise, but the eggs collected had probably been spawned prior to that day during increasing water temperature. In 1989 (Fig. 23B), striped bass could have spawned during decreasing temperatures, but daily temperature data were not available so this cannot be confirmed. In the Potomac River daily temperature data were available only for 1989 and the peak in striped bass egg abundance index occurred during a period of increasing water temperature (Fig. 24G). If we assume that the temperature changes during the period between measurements taken on cruises were linear, then the within-year peaks in the striped bass egg abundance index in the Potomac River occurred during increasing water temperature in 1974, 1975, and 1976 (Fig. 24A, 24B, 24C). The Potomac River data collected in 1977, 1987, and 1988 did not have a cruise prior to the egg peak so water temperatures are not known (Fig. 24D, 24E, 24F). In the Patuxent River in 1991, the peak in striped bass egg abundance occurred as water temperature was peaking (Fig. 25). Again, assuming a linear change in temperature between cruises, the peak in egg abundance in the Nanticoke River in 1992 occurred during increasing water temperature (Fig. 26A), but in 1993 it occurred during a very small decrease that had been preceded by an increase (Fig. 26B).

A statistical analysis was conducted to test the hypothesis that post-pulse egg abundance indices were significantly higher than pre-pulse egg abundances. Using the 90^{th} percentile definition of a pulse, there were 38 pulses in the sixteen years and systems. For each pulse, the egg abundance from the cruise prior to the pulse was classified as 'pre-pulse' and the egg abundance that occurred within five days after the pulse was classified as 'post-pulse'. If no survey was conducted either before or within five days after a pulse, the pulse was excluded from the analysis. A total of 19 pairs of pre- and post-pulse egg abundance indices were available for the analyses. Eight (42%) of the pairs of data used in the analyses supported the hypothesis based on a comparison of pre- and post-pulse egg abundances (Table 5). Because the egg abundance data were not normally distributed, a Wilcoxon signed-rank test was used to test the hypothesis. The Wilcoxon signed-rank test indicated that there was no significant difference between the pre- and post-pulse egg abundances ($p=0.16$, $n=19$) (Fig. 27).

The definition of the pulse influenced the outcome of the hypothesis test. The above analysis was repeated with a pulse defined as a flow event that lasted at least two days and was greater than twice the average flow in the river system in April and May of that year (North *et al*., 2005). Using this definition, there were one or more pulses in flow in 13 out of the 16 years of data, indicating that large pulses in flow are a relatively consistent characteristic of the hydrograph of these systems during striped bass spawning season. There were a total of 19 pulses in the sixteen years and systems. When the pulses that lacked surveys either before or within five days after the pulse were excluded, there were 11 usable pairs of pre- and post-pulse egg abundance indices to test the hypothesis. Seven of the pairs (64%) supported the hypothesis based on a comparison of pre- and post-pulse egg abundances (Table 6). A one-tailed Wilcoxon signed-rank test indicated that post-pulse egg abundance indices were significantly higher than pre-pulse egg abundance indices ($p=0.02$, $n=11$) (Fig. 28).

Average flow and the number of pulse events account for a significant amount of variability in an index of striped bass juvenile recruitment. Using data from 1986-2002, North *et al*. (2005) found significant correlations between the striped bass young-of-the-year index and average river flow in March-May ($r = 0.72$, $p = 0.0011$) and between the striped bass young-of-the-year index and number of pulses in April and May ($r = 0.67$, $p = 0.0031$). There was no correlation between the average river flow and the number of pulses ($r = 0.30$, $p = 0.23$). When including data from 1986-2008, the correlations between striped bass young of the year index and average flow ($r = 0.66$, $p = 0.0006$) and number of pulses ($r = 0.55$, $p = 0.0061$) were significant, but weaker, and there was still no correlation between average river flow and number of pulses ($r = 0.24$, $p = 0.27$). Using data from 1986-2002 in a regression analysis, the average river flow in March-May and number of pulses in April and May described a significant amount of variability in striped bass young-of-the-year index (adjusted $R^2 = 0.71$, $n = 17$, $p < 0.0001$) (North *et al.*, 2005). When data from 1986-2008 were included, the regression was also significant, though weaker (adjusted $R^2 = 0.56$, $n = 23$, $p = 0.0001$).

Discussion

This study provides an improved understanding of the relationship between river flow and dynamic features of temperature during the striped bass spawning season in Chesapeake Bay and their potential effects on striped bass spawning. After removing seasonal trends, water temperatures in upper Chesapeake Bay were significantly negatively correlated with river flow and tended to decrease during and increase following pulses in river flow. The highest striped bass egg abundances found each year were usually associated with increasing water temperatures, confirming observations in previous studies (Grant and Olney, 1991; Olney *et al*., 1991; Robichaud-LeBlanc, *et al*., 1996; Rutherford and Houde, 1995; Secor and Houde, 1995; Van Den Avyle and Maynard, 1994). The hypothesis that higher egg abundances are found after pulses in flow was rejected when pulses were defined using 90th percentile flow values. In contrast, the hypothesis was supported when pulses were defined using twice the average flow for each season. This finding suggests that spawning could be cued by pulses in flow if the pulses are of sufficient magnitude and duration.

Analysis of flow and temperature data indicated that episodic river flow events usually result in a decrease in water temperature followed by an increase in water temperature in the Susquehanna River. This flow-temperature phenomenon also has been found in other river systems. For example, in the Hurunui River, North Canterbury, New Zealand, Hockey *et al*. (1982) found that during summer (December to March) from 1957-1979 water temperature was negatively correlated with discharge and positively correlated with maximum daily air temperature. Stream temperature was also found to be inversely proportional to stream flow in the Western United States and Canada (Gibbons and Salo, 1973). In my study there was no consistent minimum size of pulse required to affect water temperature. In some cases relatively small increases in flow that did not meet either definition for a pulse had a clear effect on temperature (*e.g.* Fig. 23C, April 30, 1998 and Fig. 23D, May 17, 1999), and in some cases pulses that met the 90th percentile criterion did not appear to affect water temperature (*e.g.* Fig. 23D, April 28, 1999), although this outcome was less common. These differences may be due to variability in the temperature conditions that occur during rainfall events, which are usually associated with cold temperature anomalies (Miller *et al*., 2006).

While river flow can influence water temperature, river flow only accounted for 50% of the variability in water temperature at Holtwood Dam so it may be unreasonable to expect pulses in flow to provide a consistent cue for striped bass spawning. The results of the hypothesis tests and river flow analyses indicate that large pulses that are at least twice the seasonal average may be necessary to provide a cue for spawning, and these pulses only occurred in 81% of the spawning seasons examined. During years with few or temporally widespread pulses, water temperatures in the Susquehanna River sometimes increased independent of flow, likely attributable to changes in air temperature and solar radiation (Hockey *et al*., 1982; Gibbons and Salo, 1973). Water temperature data was available before and after the peak in egg abundance in 13 of the 16 years studied. Of those years, 85% (11 out of 13) of the egg abundance peaks occurred either during or within two days of rising water temperatures (Fig. 10, 17, 23, 24, 25, 26). Regardless of how pulses were defined, increasing temperatures related to either decreasing flow after a pulse or simply to air temperature changes appear to be the most consistent cue for striped bass spawning.

Fishes in general have been found to cue their spawning response to many seasonal, lunar, diel and environmental cues. Many flood plain fishes spawn in response to water level changes. For example, in the rice-fish farming system of Malaysia, the catfish, *Clarias macrocephalus*, spawns in response to the seasonal rise in water level due to increased irrigation and rainfall (Ali, 1993), and in the floodplains of southeastern Australia spawning of golden perch (*Macquaria ambigua*) and silver perch (*Bidyanus bidyanus*) has been linked to flooding (Humphries *et al.*, 1999). Two grouper species (*Epinephelus guttatus* and *E. striatus*) from the West Indies were found to aggregate and spawn within four days of the full moon during January and February (Colin *et al*., 1987). Cubera snappers (*Lutjanus cyanopterus*) on the Belize Barrier Reef aggregated for spawning during the time of rising water temperatures between March and September; with most spawning occurring shortly after the full moon (3-8 days), and within 40 minutes of sunset (Heyman *et al*., 2005). Different species of salmon appear to cue their spawning migration to environmental variables such as river flow and temperature and biological variables such as sex and body size (Quinn, 2005). The thermal conditions of their spawning site may also have an effect; spawning tends to occur earlier in the season at higher latitudes and cooler temperatures, resulting in similar larval emergence times between latitudes (Quinn, 2005). Proximally, female salmon spawn in response to courting, once her redd is adequately prepared (Quinn, 2005). In laboratory studies, Atlantic silversides

(*Menidia menidia*) spawned in response to change from darkness to light (sunrise) and decreases in current velocities (slack tide) (Middaugh and Takita, 1983). Further studies on two additional species of silversides, *M. beryllina* and *M. peninsulae*, found that *M. peninsulae* also spawned in response to a combination of diel light cycle and current velocities, but *M. beryllina* cued its spawning to the light cycle alone. Our results support the observation of other researchers that striped bass spawn when temperatures are rising (Grant and Olney, 1991; Olney *et al*., 1991; Robichaud-LeBlanc, *et al*., 1996; Rutherford and Houde, 1995; Secor and Houde, 1995; Van den Avyle and Maynard, 1994). Additionally, there is weaker evidence that suggests spawning by striped bass may be cued to large pulses in flow.

In addition to water temperature, the timing of spawning also may be affected by the behavior and sexual condition of adult striped bass which in turn may be influenced by the environmental conditions that they experience prior to spawning. The migration of striped bass to upstream spawning grounds appeared to be cued by increasing temperatures in their down-estuary locations, rather than by a temperature threshold in the Miramichi River (Douglas *et al*., 2009). Once on the spawning grounds, striped bass females tended to remain in the freshwater spawning region. In the Choptank River males commonly moved between freshwater and brackish water (Hocutt *et al*., 1990). In both the Roanoke and Miramichi Rivers, striped bass females remained on the spawning grounds for less time than males, probably leaving once they were spent, while some males stayed on the spawning grounds until all females had left (Carmichael *et al*., 1998; Douglas *et al*., 2009).

The environmental conditions experienced by striped bass prior to spawning may influence whether they are ready to spawn. In the Santee-Cooper Reservoir, South Carolina, 25% of striped bass females on the spawning grounds were not ripe by mid-April, even though favorable spawning temperatures were reached by the beginning of April (Scruggs 1957), suggesting that even when favorable spawning temperatures are reached, all females may not be physiologically ready to spawn. Based on hatchery experiments, changes in temperature prior to spawning influence fecundity (Clark *et al*., 2005), oocyte growth (Blythe et al., 1994a), and notably the timing of spawning. When striped bass broodstock were held on shortened (six and nine month) seasonal temperature and photoperiod cycles to induce early spawning, ovulation occurred in fewer females than those held on a yearly cycle (Blythe *et al*., 1994b). The shortened cycles probably did not allow sufficient time for recovery and growth of new oocytes, which takes at least six months (typically September through March) (Blythe *et al*., 1994a). It is therefore possible that in some years, pulses, particularly those early in the season, may not cue intensive spawning because all females are not physiologically ready to spawn. Also, pulses late in the season may not cue intensive spawning because by that time most females have spawned and left the spawning grounds. In summary, the timing of a pulse, its strength, and adult condition act in concert to determine whether spawning may occur in response to a pulse in flow.

While rising temperatures rather than pulses in flow may be the primary cue for striped bass spawning, the pulses may still play a role in controlling larval survival. In an updated regression analysis of recruitment success of striped bass in relation to freshwater flow, following the approach of North *et al*. (2005), 56% of the variation in juvenile striped bass abundance was accounted for by mean spring flow and the number of pulse events when flow rates were at least twice the mean flow. Larval survival may be enhanced after pulses in flow due to changes in prey distributions and concentrations. There is evidence that temporal and spatial overlap between striped bass larvae and their prey is highest during high flow years and that prey abundances could peak after pulses in flow. In the upper Chesapeake Bay, prey levels were highest during average and above average river flow years, and spatial overlap of striped bass feeding-stage larvae with their prey was highest in above average flow years, likely due to hydrologic conditions that concentrated prey and larvae (Martino, 2008). In the Hudson river, high abundances of *Bosmina freyi* prey led to higher consumption rates by striped bass larvae (Limburg *et al*., 1997), and temporal overlap of feeding-stage larvae with a zooplankton (*Bosmina*) bloom could have improved survival to the juvenile stage in both the Husdon River and upper Chesapeake Bay (Limburg *et al.*, 1999; Martino, 2008). But, these relationships are still poorly understood. In the Potomac River (1987-1989) and the upper Chesapeake Bay (1988-1989), the concentration of striped bass larval prey during a cohort's first 20 days post-hatch was either significantly negatively correlated with river flow or non-significant (Rutherford, 1992), suggesting that highest prey abundances may occur during low flows after a pulse. If zooplankton prey abundances are positively influenced by pulses in flow, then the feeding conditions after pulses in flow may enhance larval survival.

Examination of flow records and abundances of striped bass prey indicate that prey concentrations may increase after pulses in flow in the Potomac River and upper Chesapeake Bay. There were two large pulses in flow in 1987, 1988, and 1989 in the Potomac River (Fig. 29). In 1987 and 1988, striped bass zooplankton prey concentrations were high approximately 18 and 12 days after a pulse in flow (Fig. 30) (Rutherford, 1992). If the striped bass had spawned a few days after the pulse in flow, their feeding-stage larvae would have occurred just before and during these high abundances of prey because striped bass begin feeding approximately 7 to 12 days after eggs are spawned (Rutherford and Houde, 1995). In 1989, the highest peaks in copepod and copepodite abundance occurred prior to the pulses in flow, but abundances did increase ten days following a pulse (Fig. 30). In the upper Chesapeake Bay there was one pulse in flow in 1988 and two pulses in flow in 1989 (Fig. 31). In 1988, peaks in copepod, copepodite, and nauplii abundance did not occur after the pulse in flow, but the final survey in that year was only 10 days after the pulse, too early for striped bass larvae spawned in response to the pulse to have reached feeding stage (Fig. 32) (Rutherford, 1992). In 1989, there was a peak in copepod, copepodite, and nauplii abundances approximately 20 days after the first pulse in flow and abundances increased again following the second pulse in flow (the survey was conducted approximately fourteen days after the pulse) (Fig. 32). Overall, peaks in prey concentrations appeared to follow pulses in flow in 2 out of 3 years in the Potomac River and in 1 out of 2 years in the upper Chesapeake Bay, but in some cases insufficient sampling makes these estimates uncertain.

This brief visual analysis suggests that pulses in river flow may stimulate production of striped bass prey species at times that would result in high abundances of prey overlapping temporally with striped bass feeding stage larvae whose eggs were spawned in response to rising water temperatures after a pulse (Fig. 33), thereby creating a 'match' from Cushing's match/mismatch hypothesis (Fig. 34) (Cushing, 1967; Cushing 1969; Cushing and Dickson, 1976; Cushing 1990). The match/mismatch hypothesis has been supported for various species and locations (*e.g.* Brander and Hurley, 1992; de la Fontaine *et al.*, 1984; Ellertsen et al., 1989; Fortier and Gagné, 1990; Fortier *et al*., 1992). In Lake Marion, South Carolina, Chick and Van den Avyle (1999) suggested that transport of larvae into the lake habitat rather than retention in river and transition zones may promote the feeding success of striped bass larvae by providing a better match with higher prey concentrations. During a drought in the San Francisco Bay there were dramatic declines in striped bass zooplankton prey, and it was suggested that larval growth may have been limited by prey availability (Bennett *et al*., 1995). In upper Chesapeake Bay, Martino (2008) found higher prey abundances in average and above average river flow years and stronger spatial overlap of striped bass larvae with their prey in years of above average river flow, leading to higher survival to the juvenile stage. My observations suggest it may also apply to striped bass larvae in the Chesapeake Bay on shorter time scales. Pulses in river flow may provide a cue that increases the probability of a temporal and spatial match between feeding stage striped bass and high prey concentrations.

It is important to note that the effect of river flow on striped bass prey may change the spatial distribution of prey in addition to promoting temporal peaks in concentrations. In the Potomac River and Upper Chesapeake Bay, highest zooplankton concentrations were found in the years of highest striped bass growth rates, growth/mortality ratios, and recruitment indices (Rutherford and Houde, 1995). Martino (2008) found that in years of high river flow, the location of striped bass feeding stage larvae overlapped with that of their prey better than in lower flow years, but his analysis did not examine short term changes in flow within the season (pulses), only the April and May mean flow for the year. Results of my study indicate that pulsed events may cue striped bass spawning in some years and, when combined with results of previous studies, suggest that years with pulsed events could have more favorable prey distributions that promote larval growth and survival compared to years when spawning is cued by water temperature increases alone.

Wind also affects the region in which striped bass spawn. Down-estuary wind events tend to cause the salt front to move up-estuary and vice versa (North *et al.*, 2004), which could act to concentrate striped bass larvae and their prey. Wind increases turbulence, which also can raise the encounter rates between larval fish and their prey (MacKenzie and Leggett, 1991). These wind effects could promote more successful feeding in striped bass larvae; however, wind events during April and May in the upper Chesapeake Bay did not account for a significant amount of variability in striped bass juvenile recruitment (1986-2002) (North *et al.*, 2005), suggesting that other factors (*i.e.* river flow and pulses in flow) are more important for determining survival.

It should be noted that the analyses presented herein were constrained by a lack of data on daily water temperature and temporal resolution of collections of striped bass eggs, larvae, and larval prey. Improved temporal resolution of egg abundances (i.e. more frequent cruises in each year) and new technologies (i.e. towed digital visual recognition systems) may improve our abilities to detect and understand the cues that influence striped bass spawning.

Despite limitations of the data used in this study, results indicate that if anthropogenic climate change affects river flow conditions in the Chesapeake Bay, there are implications for survival of striped bass early-life stages and subsequent juvenile recruitment. Climate change models vary in their predictions of the result of increasing atmospheric CO_2 on environmental conditions in the Chesapeake Bay watershed. The most uncertain variable is how climate change will affect river flow, but it is expected that average flow will increase, particularly in the winter and spring (Najjar *et al.*, 2010). These model predictions are for changes in relatively long-term averages (monthly-yearly); the potential effects on small scale episodic events are even less well understood. Precipitation intensity is expected to increase, potentially causes stronger pulses in river flow (Najjar *et al*., 2010). If climate change markedly alters the characteristics of the hydrograph in the tributaries, then the relationships between juvenile survival and mean flow (North and Houde 2001; Martino, 2008), mean water temperature (Martino, 2008) and pulses in flow (North *et al*., 2005) will likely change. On the surface it would appear that increased pulses would favor striped bass recruitment; however, pulses in flow often were followed by initial decreases in water temperatures, and when decreases are large or rapid there may be lethal or sub-lethal effects on eggs and larvae already present in the water column (Dey, 1981; Rutherford *et al*., 1997). The compounding factor of increasing water temperatures induced by climate change also will directly and indirectly influence larval growth rates and will likely have much larger scale physical and trophic effects (Najjar *et al*., 2010) that will complicate our understanding of the consequences of climate change on striped bass populations in the Chesapeake Bay and along the mid-Atlantic coast. Recognizing these links between small scale (episodic) changes in river flow, water temperature, and striped bass spawning may be an important factor in understanding the effects of climate change on striped bass recruitment in the future.

Tables

Table 1: Sources of data on striped bass egg abundance. Data were retrieved for four systems in fourteen years and used in the historical analysis to determine whether striped bass spawn in response to pulses in river flow.

System	**Year**	**Data Source**	**Citation**
Upper Bay	1988	Edward Rutherford	Rutherford, 1992
Upper Bay	1989	Edward Rutherford	Rutherford, 1992
Upper Bay	1998	Elizabeth North	North, 2001
Upper Bay	1999	Elizabeth North	North, 2001
Potomac	1974	Walter Boynton	Setzler-Hamilton *et al*., 1980
Potomac	1975	Walter Boynton	Setzler-Hamilton *et al*., 1980
Potomac	1976	Walter Boynton	Setzler-Hamilton *et al*., 1980
Potomac	1977	Walter Boynton	Setzler-Hamilton *et al*., 1980
Potomac	1987	Edward Rutherford	Rutherford, 1992
Potomac	1988	Edward Rutherford	Rutherford, 1992
Potomac	1989	Edward Rutherford	Rutherford, 1992
Patuxent	1991	David Secor	Secor *et al*., 1994
Nanticoke	1992	Kellogg, 1996	Kellogg, 1996
Nanticoke	1993	Kellogg, 1996	Kellogg, 1996

Table 2: Results of Spearman correlation analysis between detrended river flow in April and May in different river systems of the Chesapeake Bay. The Susquehanna River was measured at Holtwood Dam (1956-2002) and Conowingo Dam (1968-2009), the Potomac River was measured near Washington, D.C. at Little Falls Dam and Pump Station (1930-2009), the Patuxent River was measured near Bowie, MD (1978-2009), and the Nanticoke River was measured near Bridgeville, DE (1943-2009) (Fig. 1). The three values in each section are the Spearman correlation coefficient (*rho*), the p-value, and the number of data points in the analysis. All correlations were significant at the $\alpha = 0.05$ level.

	Holtwood Flow	Conowingo Flow	Potomac Flow	Patuxent Flow	Nanticoke Flow
Holtwood Flow	1 2858	0.96 <0.0001 2126	0.62 <0.0001 2858	0.39 <0.0001 1517	0.37 <0.0001 2858
Conowingo Flow		1 2571	0.57 <0.0001 2571	0.37 <0.0001 1961	0.37 <0.0001 2571
Potomac Flow			1 4889	0.54 <0.0001 1961	0.45 <0.0001 4096
Patuxent Flow				1 1961	0.55 <0.0001 1961
Nanticoke Flow					1 4096

Table 3: Station information and egg concentrations from collections in the upper Chesapeake Bay during April and May in 2007. Six cruises were conducted and are labeled according to the vessel (BM: *R/V Hugh R. Sharp*, RR: *R/V Terrapin*), year (07) and cruise number (last two digits). UTC is Coordinated Universal Time; EST is North American Eastern Standard Time.

Cruise	Date	Station	Time (UTC)	Time (EST)	Latitude	Longitude	Egg Concentration (eggs m^{-3})
BM0702	4/12/2007	68	14:20	10:20	39.21	-76.26	0.0000
BM0702	4/12/2007	70	15:47	11:47	39.31	-76.22	0.0067
BM0702	4/12/2007	72	17:59	13:59	39.37	-76.11	0.0000
BM0702	4/12/2007	74	19:29	15:29	39.44	-76.02	0.0000
RR0701	4/25/2007	1	10:54	06:54	39.21	-76.25	0.0174
RR0701	4/25/2007	2	12:29	08:29	39.26	-76.24	3.4021
RR0701	4/25/2007	3	14:00	09:40	39.31	-76.22	4.6980
RR0701	4/25/2007	4	15:23	11:23	39.33	-76.19	1.9176
RR0701	4/25/2007	5	17:17	13:17	39.35	-76.17	1.4867
RR0701	4/25/2007	6	18:25	14:24	39.38	-76.12	1.5215
RR0701	4/25/2007	7	19:08	15:08	39.40	-76.05	0.0164
RR0702	5/4/2007	1	10:48	06:48	39.21	-76.25	0.0000
RR0702	5/4/2007	2	12:04	08:04	39.26	-76.24	0.1013
RR0702	5/4/2007	3	13:20	09:20	39.31	-76.22	0.7332
RR0702	5/4/2007	4	14:12	10:12	39.35	-76.17	3.8787
RR0702	5/4/2007	5	15:19	11:19	39.36	-76.15	0.4838
RR0702	5/4/2007	6	16:04	12:04	39.38	-76.12	1.7771
RR0702	5/4/2007	7	17:14	13:14	39.40	-76.05	0.1795
RR0702	5/4/2007	8	18:09	14:09	39.44	-76.02	0.0180
RR0702	5/4/2007	9	18:51	14:51	39.47	-76.06	0.0000
BM0703	5/9/2007	20	10:36	06:36	39.44	-76.02	0.0220
BM0703	5/9/2007	22	11:40	07:40	39.38	-76.12	0.1212
BM0703	5/9/2007	24	12:58	08:58	39.31	-76.22	0.0966
BM0703	5/9/2007	26	14:32	10:32	39.21	-76.25	0.0000
RR0703	5/22/2007	1	09:40	05:40	39.21	-76.26	0.0000
RR0703	5/22/2007	2	10:44	06:44	39.26	-76.24	0.0000
RR0703	5/22/2007	3	11:36	07:36	39.31	-76.22	0.1122
RR0703	5/22/2007	4	12:20	08:20	39.35	-76.17	0.2931
RR0703	5/22/2007	5	13:12	09:12	39.36	-76.15	0.5596
RR0703	5/22/2007	6	14:03	10:03	39.37	-76.12	1.1889
RR0703	5/22/2007	7	14:54	10:54	39.40	-76.05	0.4103
RR0703	5/22/2007	8	15:43	11:43	39.44	-76.02	0.2630
RR0703	5/22/2007	9	16:16	12:16	39.47	-76.06	0.0000
RR0703	5/22/2007	10	17:06	13:06	39.51	-76.09	0.0000
RR0704	5/30/2007	1	09:40	05:40	39.26	-76.24	0.0000
RR0704	5/30/2007	2	10:44	06:44	39.31	-76.22	0.0147
RR0704	5/30/2007	3	11:26	07:26	39.35	-76.17	0.1788
RR0704	5/30/2007	4	12:35	08:35	39.36	-76.15	0.0884
RR0704	5/30/2007	5	13:20	09:20	39.37	-76.12	0.2088
RR0704	5/30/2007	6	14:17	10:17	39.40	-76.05	0.1437
RR0704	5/30/2007	7	14:55	10:55	39.44	-76.02	0.0000
RR0704	5/30/2007	9	16:58	12:58	39.47	-76.06	0.0000
RR0704	5/30/2007	10	17:40	13:40	39.51	-76.09	0.0000

Table 4: Station information and egg concentrations from collections in the upper Chesapeake Bay during April and May in 2008. Five cruises were conducted and are labeled according to the vessel (BM: *R/V Hugh R. Sharp*, RR: *R/V Terrapin*, MEN: *R/V Aquarius*), year (08) (except for MEN0706) and cruise number (last two digits). UTC is Coordinated Universal Time; EST is North American Eastern Standard Time.

Cruise	Date	Station	Time (UTC)	Time (EST)	Latitude	Longitude	Egg Concentration (eggs m^{-3})
BM0802	4/20/2008	71	11:00	07:00	39.44	-76.02	33.9714
BM0802	4/20/2008	73	12:16	08:16	39.38	-76.12	15.4796
BM0802	4/20/2008	75	13:39	09:39	39.31	-76.22	0.9833
BM0802	4/20/2008	77	15:00	11:00	39.21	-76.26	0.0755
RR0801	5/1/2008	1	09:45	05:45	39.26	-76.24	0.0000
RR0801	5/1/2008	2	10:52	06:52	39.31	-76.22	0.0000
RR0801	5/1/2008	3	11:35	07:35	39.35	-76.17	0.0000
RR0801	5/1/2008	4	12:14	08:14	39.37	-76.12	0.0000
RR0801	5/1/2008	5	12:58	08:58	39.40	-76.05	0.0000
RR0801	5/1/2008	6	13:49	09:49	39.42	-76.04	0.0000
RR0801	5/1/2008	7	14:23	10:23	39.43	-76.03	0.0556
RR0801	5/1/2008	8	15:06	11:06	39.47	-76.06	0.0000
RR0801	5/1/2008	9	15:46	11:46	39.51	-76.09	0.0000
BM0803	5/19/2008	67	11:28	07:28	39.44	-76.02	2.0417
BM0803	5/19/2008	68	12:20	08:20	39.40	-76.05	0.2252
BM0803	5/19/2008	69	13:09	09:09	39.38	-76.11	0.1606
BM0803	5/19/2008	70	13:57	09:57	39.35	-76.17	0.0993
BM0803	5/19/2008	71	14:40	10:40	39.31	-76.22	0.0000
BM0803	5/19/2008	72	15:26	11:26	39.26	-76.24	0.0000
BM0803	5/19/2008	73	16:24	12:24	39.21	-76.26	0.0000
RR0802	5/29/2008	1	09:40	05:40	39.26	-76.24	0.0000
RR0802	5/29/2008	2	10:52	06:52	39.31	-76.22	0.0131
RR0802	5/29/2008	3	11:28	07:28	39.35	-76.17	0.0000
RR0802	5/29/2008	4	12:17	08:17	39.36	-76.15	0.0000
RR0802	5/29/2008	5	13:06	09:06	39.38	-76.12	0.0386
RR0802	5/29/2008	6	13:47	09:47	39.40	-76.05	0.1539
RR0802	5/29/2008	7	14:22	10:22	39.44	-76.02	0.0131
RR0802	5/29/2008	8	14:55	10:55	39.47	-76.06	0.0000
RR0802	5/29/2008	9	15:31	11:31	39.51	-76.09	0.0000
MEN0706	6/5/2008	8	13:39	9:39	39.21	-76.26	0.0000
MEN0706	6/5/2008	9	14:34	10:34	39.26	-76.24	0.0023
MEN0706	6/5/2008	10	15:05	11:05	39.31	-76.22	0.0082
MEN0706	6/5/2008	12	18:14	14:14	39.35	-76.17	0.0272
MEN0706	6/5/2008	13	18:55	14:55	39.38	-76.12	0.0224
MEN0706	6/5/2008	14	19:32	15:32	39.40	-76.06	0.0000

Table 5: Dates of pulses in flow in each year and system and the associated cruise dates and egg abundances when pulses were defined using 90^{th} percentile values. There were a total of 19 pulses in flow that had data collected before the pulse and within five days after the pulse. The hypothesis that post-pulse egg abundances were higher than pre-pulse egg abundances was supported for eight of the 19 pulses. Whether the expected decrease in water temperature was followed by an increase in water temperature is also noted. If daily water temperature data were not available, no data ('n.d.') is noted.

System	Peak Flow Date	Pre-Pulse Cruise	Pre-Pulse Egg Abundance Index	Post-Pulse Cruise	Post-Pulse Egg Abundance Index	Support Hypothesis?	Expected Temperature Changes?
Conowingo	5/21/1988	5/17/1988	0.1609	5/24/1988	0.1495	no	n.d.
Conowingo	5/13/1989	5/11/1989	1.9982	5/15/1989	0.1181	no	n.d.
Conowingo	5/18/1989	5/15/1989	0.1181	5/23/1989	1.3631	yes	n.d.
Conowingo	4/22/2007	4/12/2007	0.0017	4/25/2007	1.3103	yes	yes
Conowingo	5/13/2008	5/1/2008	0.0078	5/17/2008	0.0857	yes	no
Potomac	4/6/1974	4/2/1974	0.0000	4/9/1974	0.0112	yes	n.d.
Potomac	4/27/1975	4/21/1975	0.1564	4/28/1975	0.4241	yes	n.d.
Potomac	4/2/1976	3/30/1976	0.0162	4/5/1976	0.0007	no	n.d.
Potomac	4/9/1988	4/7/1988	0.6905	4/14/1988	0.5264	no	n.d.
Potomac	5/8/1988	5/5/1988	0.1122	5/12/1988	0.0496	no	n.d.
Potomac	5/8/1989	5/6/1989	0.0326	5/9/1989	0.1963	yes	no
Potomac	5/12/1989	5/9/1989	0.1963	5/16/1989	0.0094	no	no
Potomac	5/18/1989	5/16/1989	0.0094	5/20/1989	1.9143	yes	yes
Patuxent	4/16/1991	4/15/1991	0.0263	4/18/1991	5.8575	yes	yes
Patuxent	5/7/1991	5/6/1991	1.0577	5/9/1991	0.3672	no	yes
Patuxent	5/18/1991	5/17/1991	0.0000	5/21/1991	0.0000	no	yes
Nanticoke	5/9/1992	5/7/1992	0.0437	5/11/1992	0.0352	no	n.d.
Nanticoke	4/17/1993	4/15/1993	7.0688	4/20/1993	1.1434	no	n.d.
Nanticoke	4/22/1993	4/20/1993	1.1434	4/24/1993	0.4498	no	n.d.

Table 6: Dates of pulses in flow in each year and system and the associated cruise dates and egg abundances when pulses were defined using twice average flow values. There were a total of 11 pulses in flow that had data collected before the pulse and within five days after the pulse. The hypothesis that post-pulse egg abundances were higher than pre-pulse egg abundances was supported for seven of the 11 pulses. Whether the expected decrease in water temperature was followed by an increase in water temperature is also noted. If daily water temperature data were not available, no data ('n.d.') is noted.

System	Peak Flow Date	Pre-Pulse Cruise	Pre-Pulse Egg Abundance Index	Post-Pulse Cruise	Post-Pulse Egg Abundance Index	Support Hypothesis?	Expected Temperature Changes?
Upper Bay	5/21/1988	5/17/1988	0.1609	5/24/1988	0.1495	no	n.d.
Upper Bay	5/18/1989	5/15/1989	0.1181	5/23/1989	1.3631	yes	n.d.
Upper Bay	4/22/2007	4/12/2007	0.0017	4/25/2007	1.3103	yes	yes
Potomac	4/6/1974	4/2/1974	0.0000	4/9/1974	0.0112	yes	n.d.
Potomac	4/27/1975	4/21/1975	0.1564	4/28/1975	0.4241	yes	n.d.
Potomac	4/2/1976	3/30/1976	0.0162	4/5/1976	0.0007	no	n.d.
Potomac	5/8/1988	5/5/1988	0.1122	5/12/1988	0.0496	no	n.d.
Potomac	5/8/1989	5/6/1989	0.0326	5/9/1989	0.1963	yes	no
Potomac	5/18/1989	5/16/1989	0.0094	5/20/1989	1.9143	yes	yes
Patuxent	4/16/1991	4/15/1991	0.0263	4/18/1991	5.8575	yes	yes
Nanticoke	5/9/1992	5/7/1992	0.0437	5/11/1992	0.0352	no	n.d.

Figures

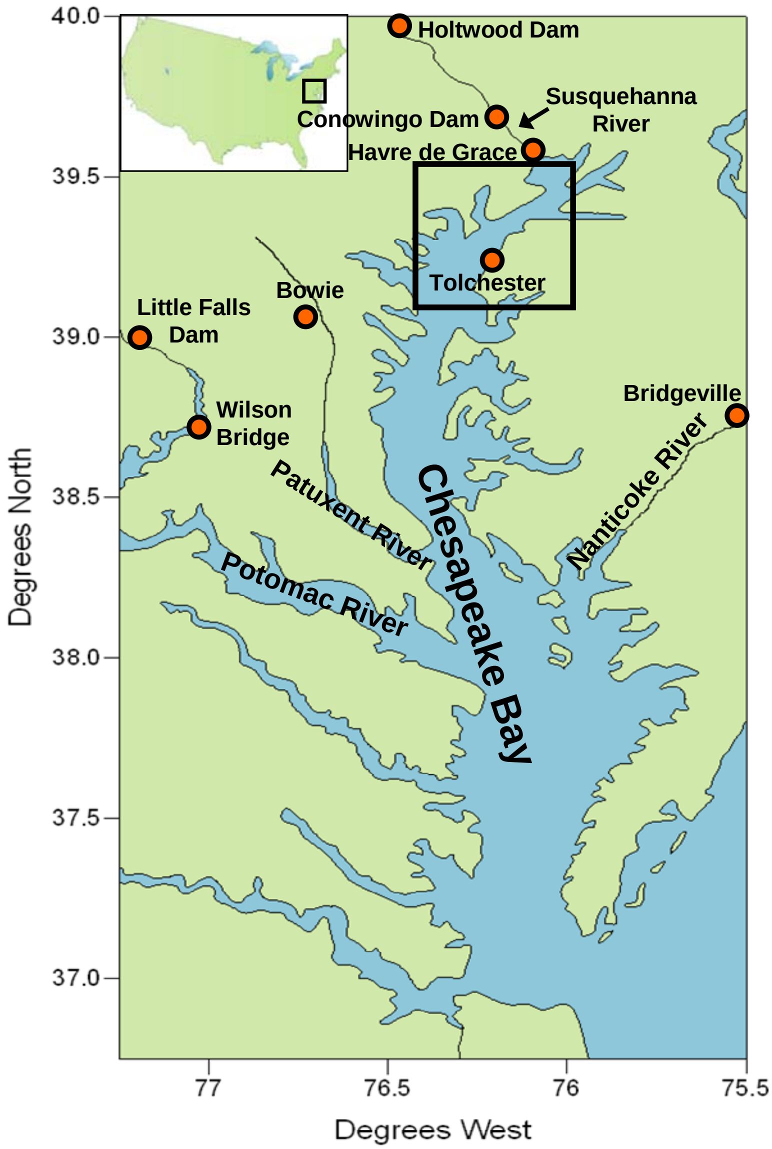


Figure 1: Map of Chesapeake Bay which is located on the east coast of the United States (black box in inset). The estuarine turbidity maximum is typically located just up-bay of Tolchester (large black box). The locations of historical water flow and water temperature measurements are indicated (Holtwood Dam, Conowingo Dam, Havre de Grace, Tolchester, Little Falls Dam, Wilson Bridge, Bowie, MD, and Bridgeville, DE).

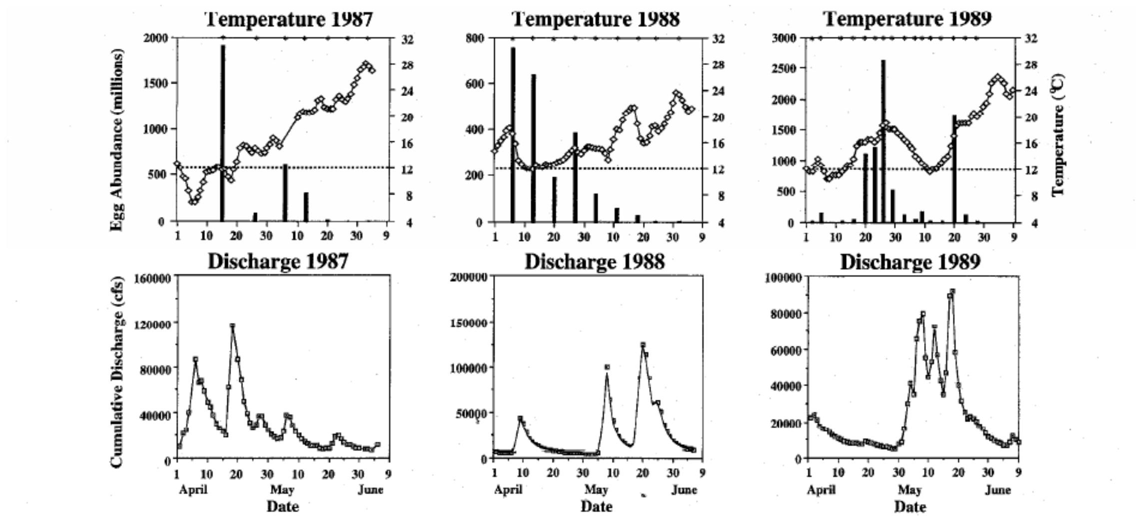


Figure 2: Top panels: Water temperature measured at Wilson Bridge (lines) and estimated total river egg abundance (bars) for the Potomac River. Bottom Panels: River discharge measured at Little Falls Dam on the Potomac River. Note that water temperatures drop during and increase following peaks in river discharge. Figure reproduced from Rutherford *et al*., 1997.

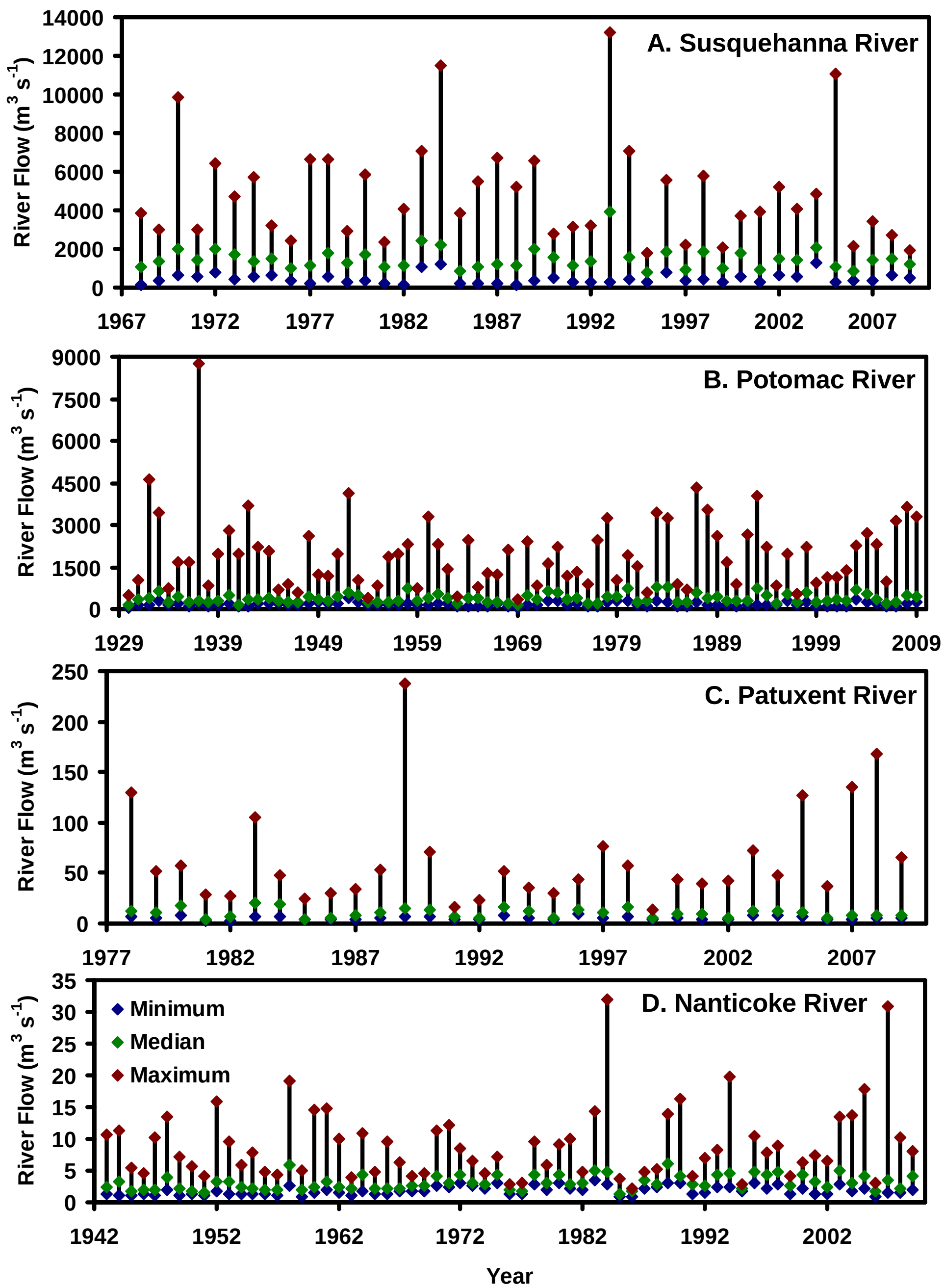


Figure 3: Maximum (red diamond), median (green diamond), and minimum (blue diamond) daily flow values in April and May during each year for A) Susquehanna, B) Potomac, C) Patuxent, and D) Nanticoke Rivers. Note the difference in scale and time between systems. Historical river flow data for each river system were downloaded from the United States Geological Survey (http://waterdata.usgs.gov/nwis/rt).

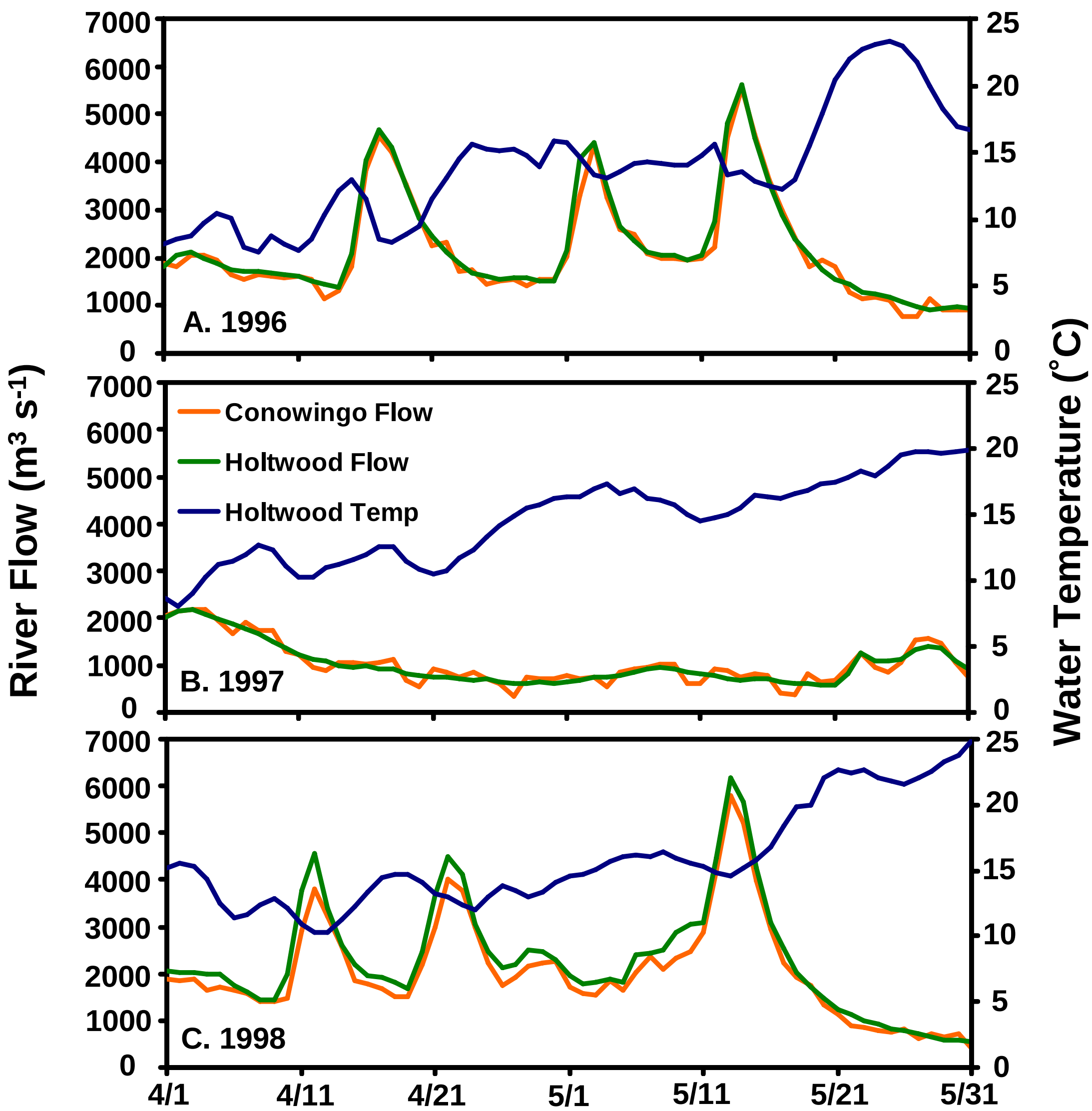


Figure 4: Conowingo and Holtwood daily discharge and Holtwood water temperature measured during April and May 1996 (top panel), 1997 (middle panel), and 1998 (bottom panel) (http://waterdata.usgs.gov/nwis/sw, Holtwood temperature and flow data courtesy of PPL Corporation and Normandeau Associates). Note that temperature declines are followed by increases in temperature during pulses in river flow.

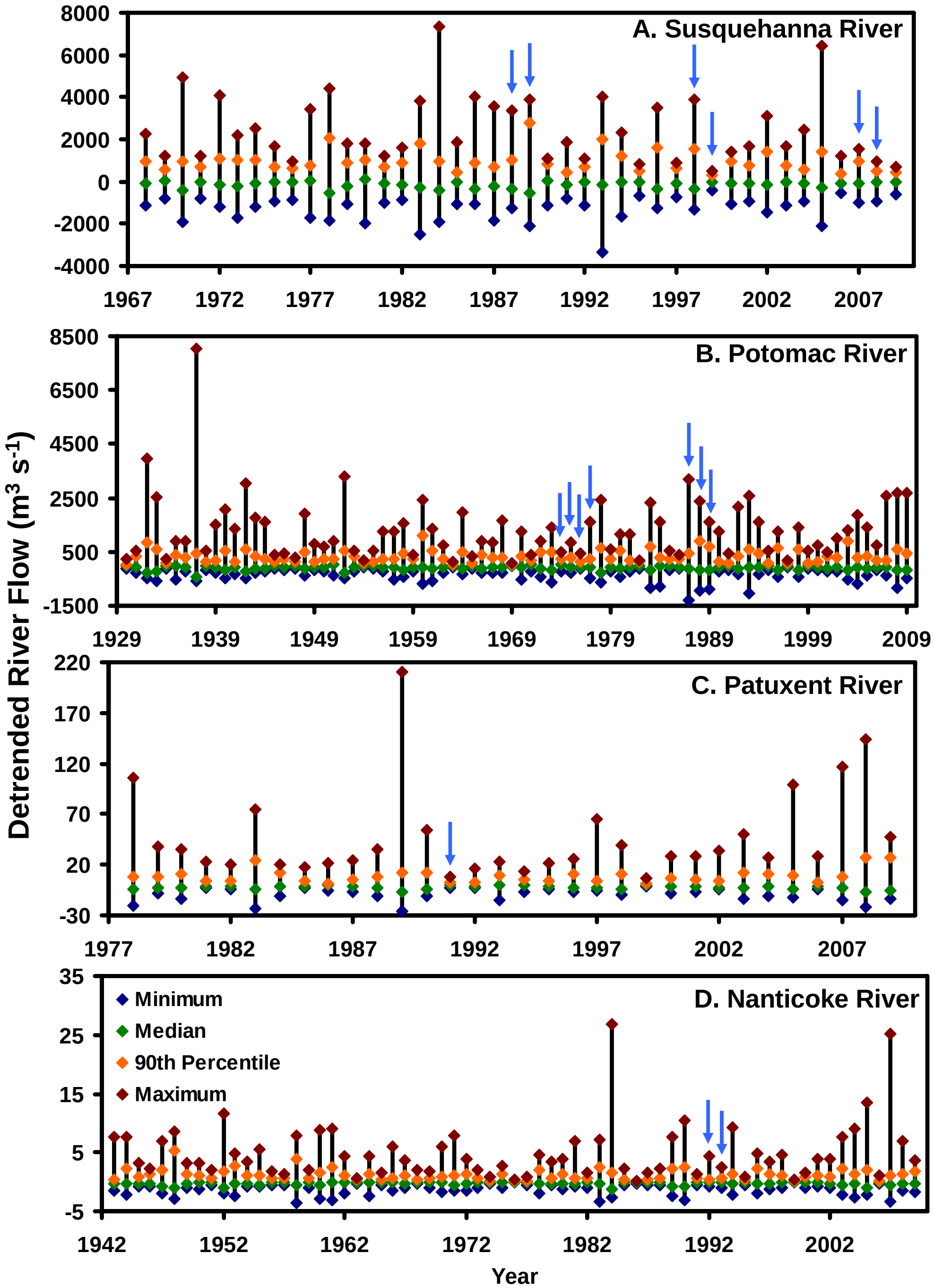


Figure 5: Maximum (red diamond), median (green diamond), minimum (blue diamond), and 90th percentile (orange diamond) of daily flow values in April and May during each year after the time series was detrended for A) Susquehanna, B) Potomac, C) Patuxent, and D) Nanticoke Rivers. Note the difference in scale and time between systems. Blue arrows indicate years and systems that striped bass egg abundance data were collected and used in analyses presented herein.

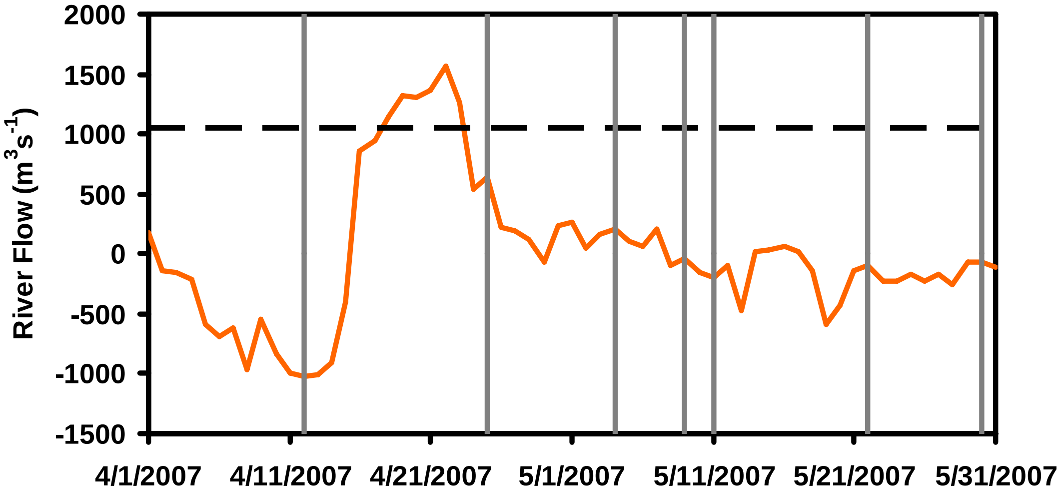


Figure 6: Detrended Susquehanna River flow at Conowingo Dam (orange line) during the striped bass spawning season. Pulses in river flow were defined as the peak in flow of daily flow values that exceeded the 90th percentile of the detrended flow values(dashed line). Based on this definition, one pulse in flow occurred on April 22 during the striped bass spawning season in 2007. Research cruises were conducted in the upper bay both before and after the pulse in flow (gray bars).

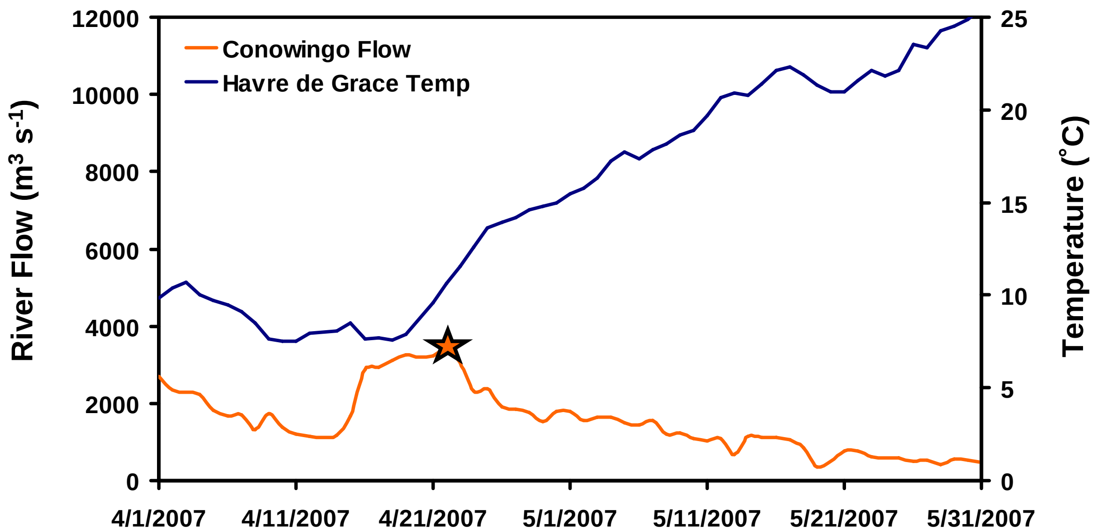


Figure 7: Water temperature (blue line) was measured at Havre de Grace and river flow (orange line) was measured at Conowingo Dam during April and May of 2007. Water temperature decreased during the pulse in river flow that occurred on April 22 (orange star) and increased following the pulse.

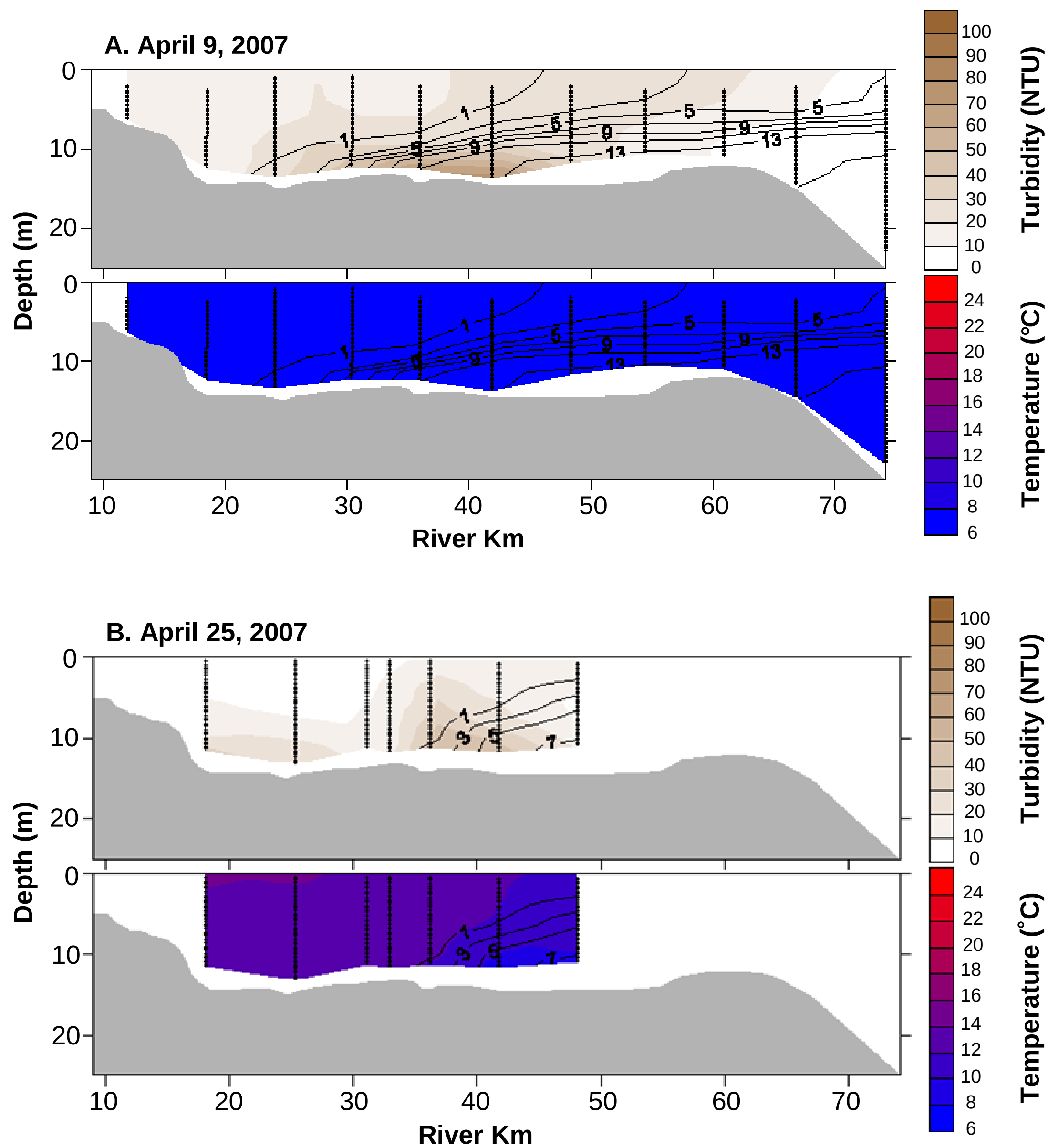
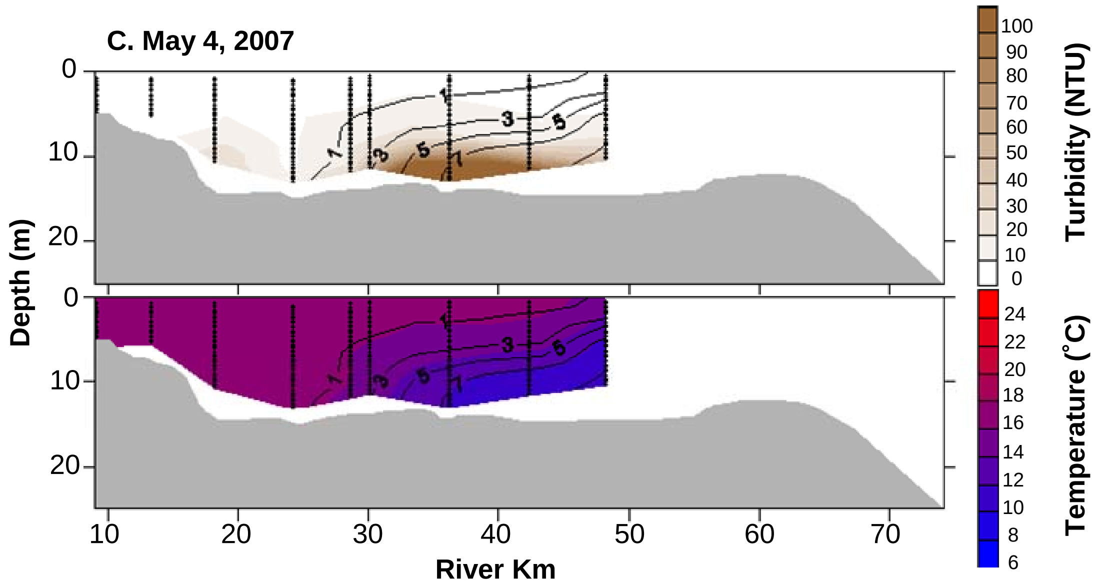
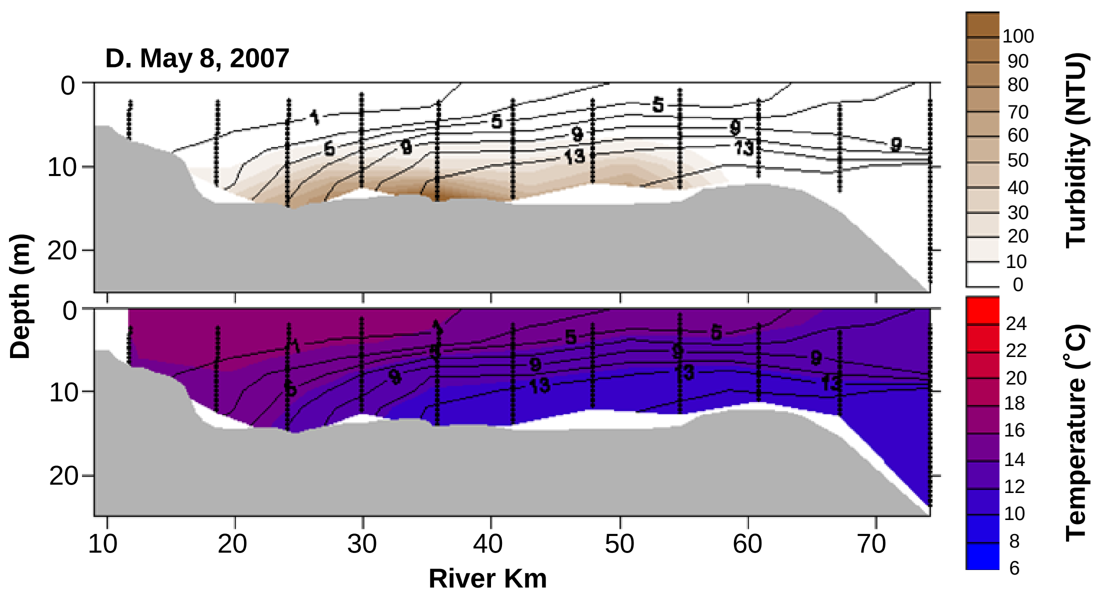


Figure 8: Turbidity (brown shaded contours), temperature (red to blue shaded contours), and salinity (line contours on both plots) were measured in the upper Chesapeake Bay during research cruises on A) April 9, B) April 25, C) May 4, D) May 8, E) May 22, and F) May 30 of 2007. A pulse in river flow occurred on April 22, between the first (panel A) and second (panel B) cruises.





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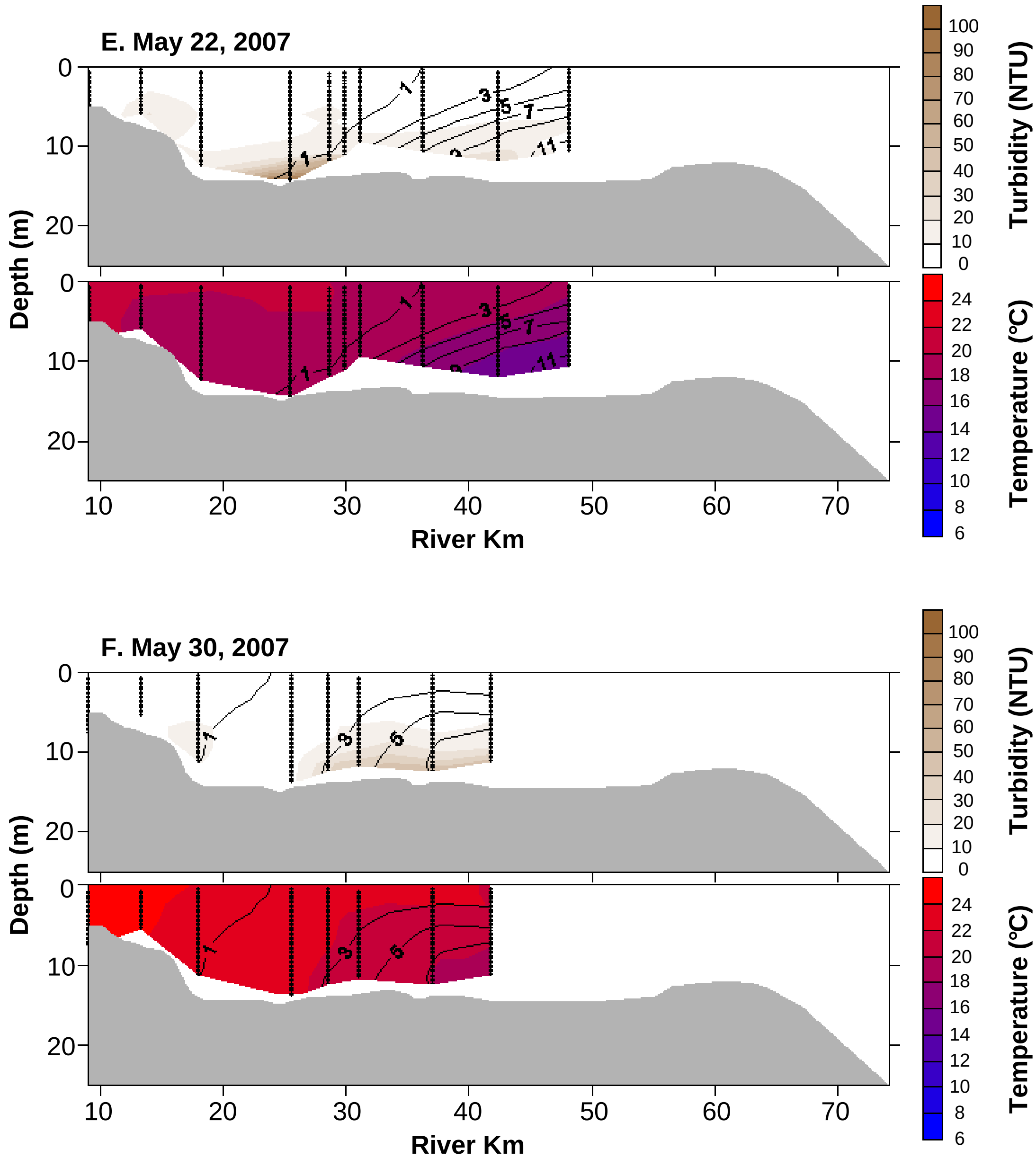

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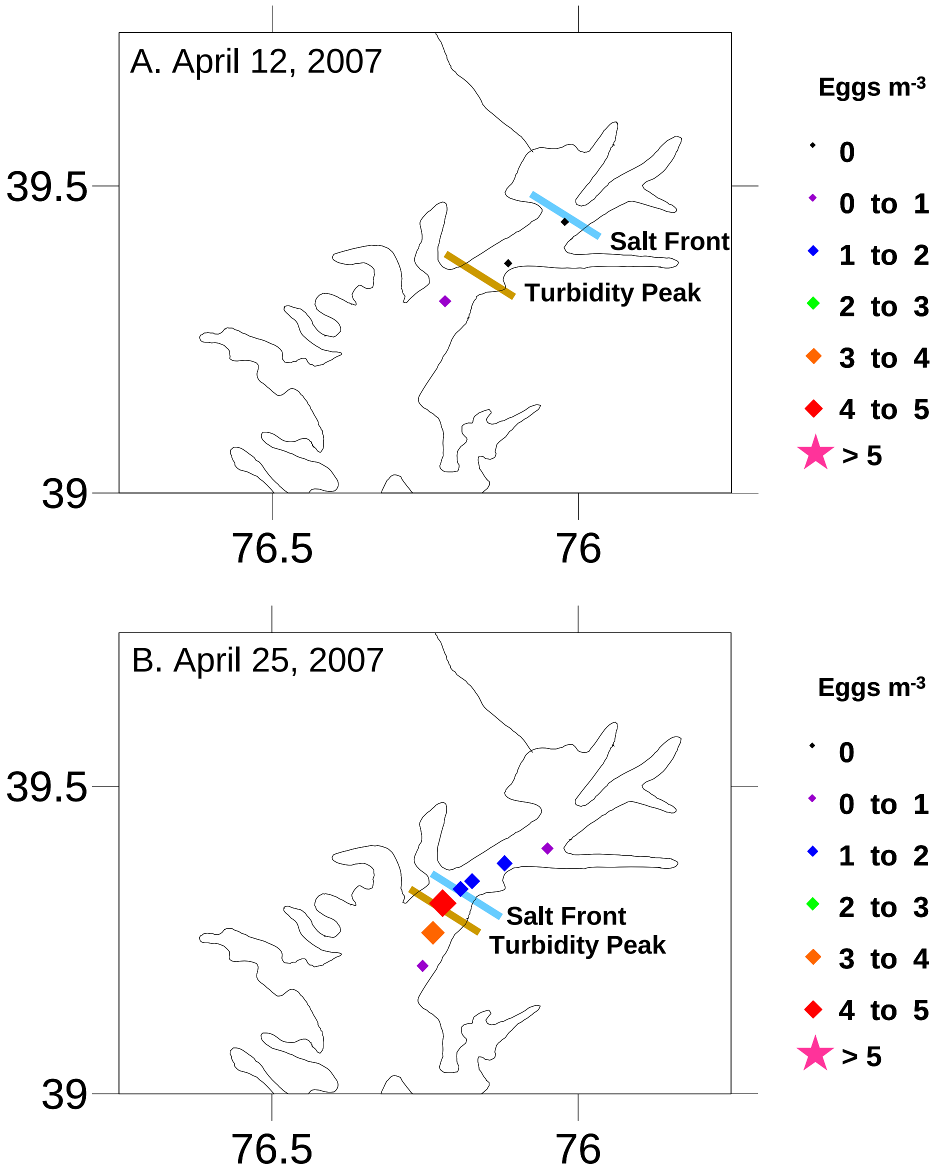
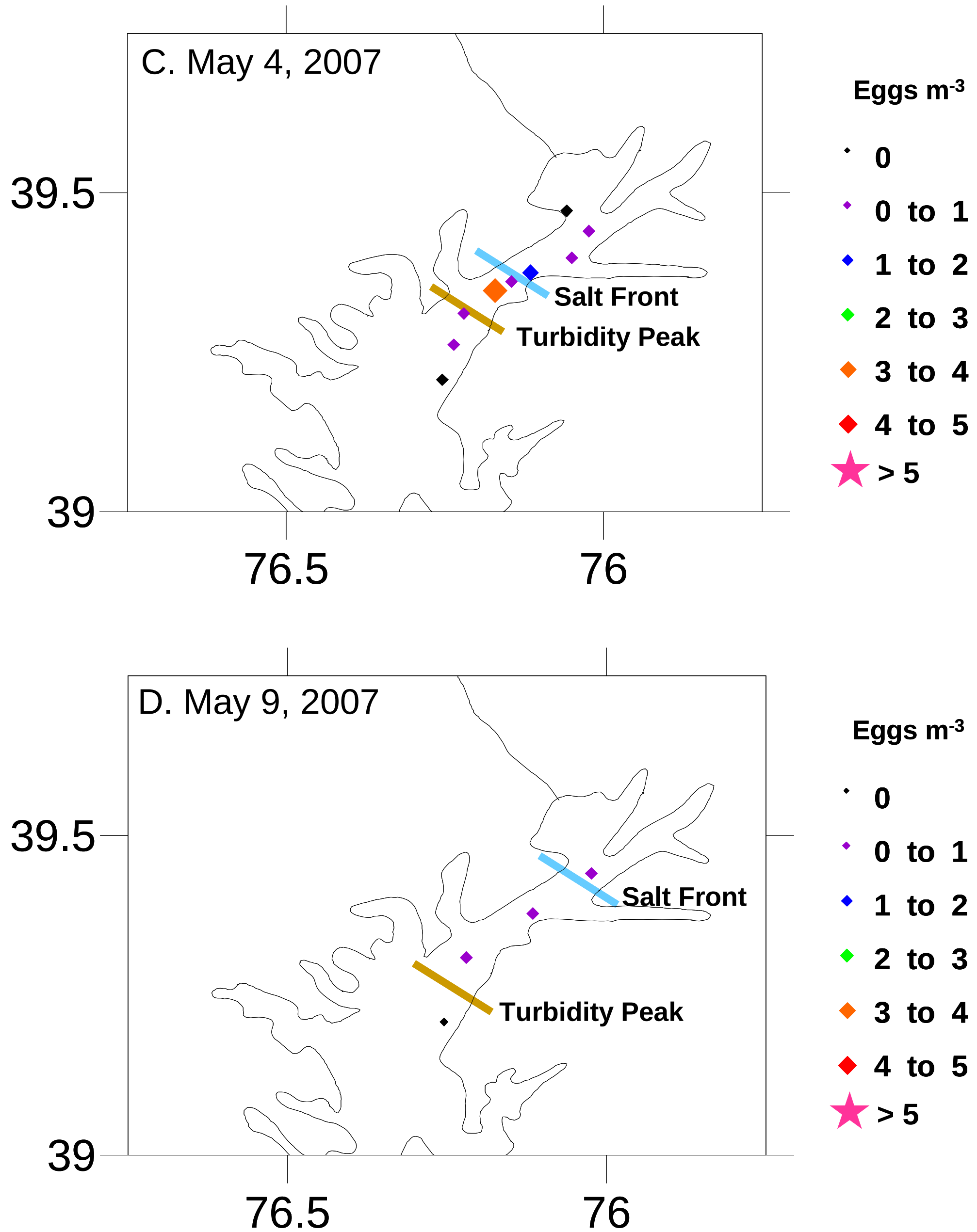


Figure 9: Striped bass egg concentrations (diamonds) collected at stations in the upper Chesapeake Bay on A) April 12, B) April 25, C) May 4, D) May 9, E) May 11, F) May 22, and G) May 30 in 2007. The size and color of the symbols for egg concentrations reflect the magnitude of egg concentrations (scale to the left of each panel). The locations of the salt front (the intersection of the 1 isohaline with bottom) and peak turbidities are indicated. A pulse in river flow occurred on April 22, 2007, between the first (panel A) and second (panel B) cruises.



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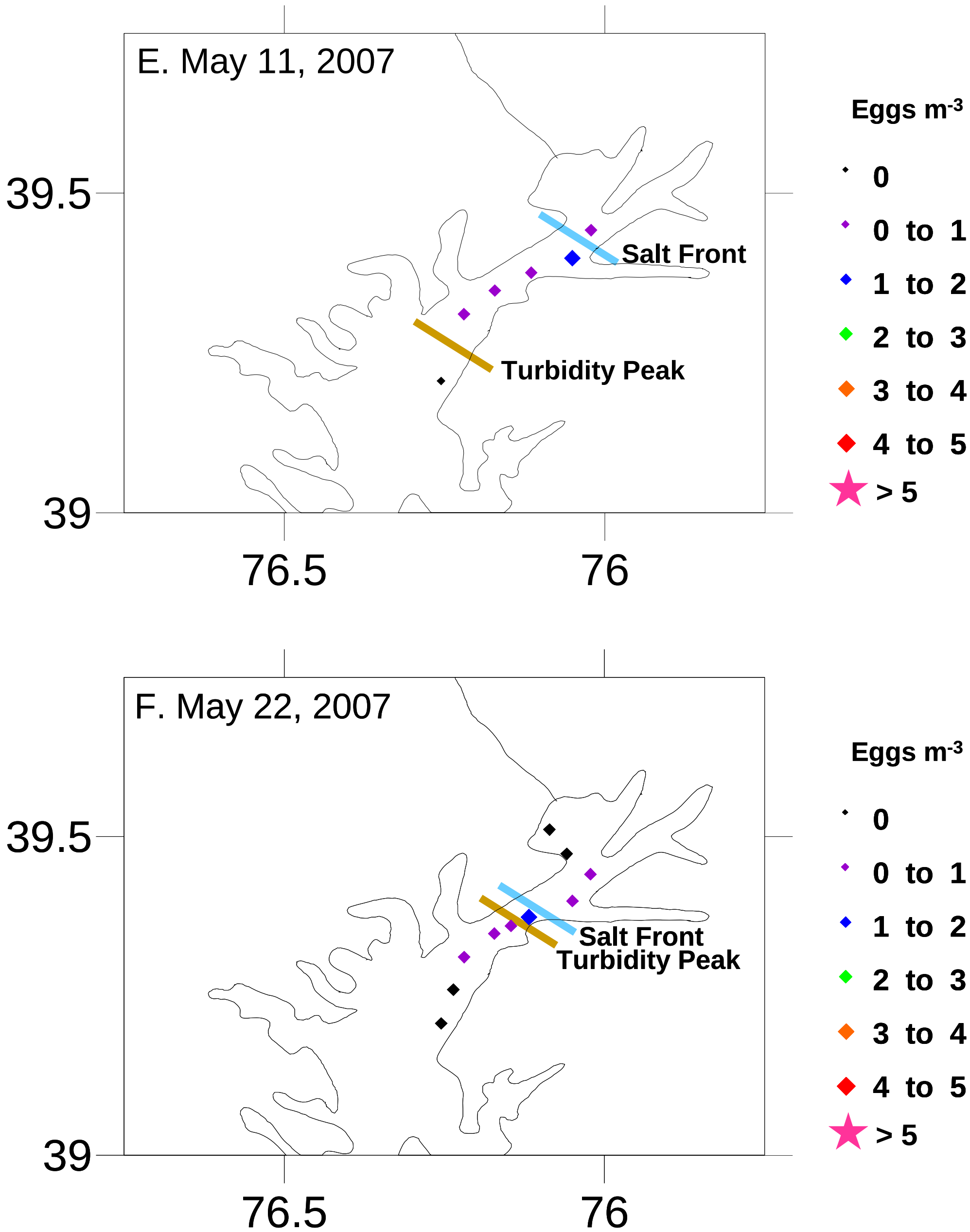

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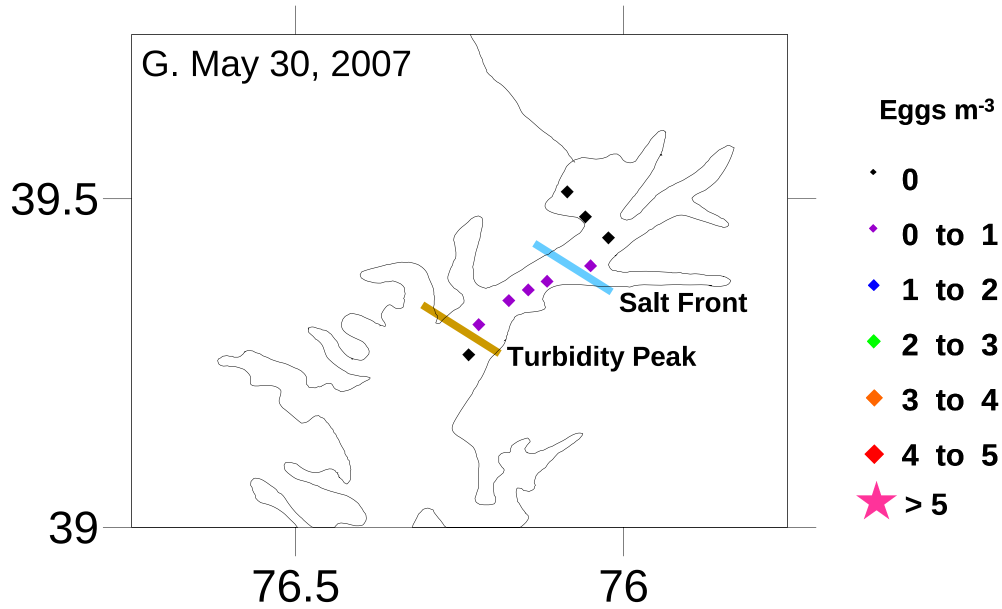

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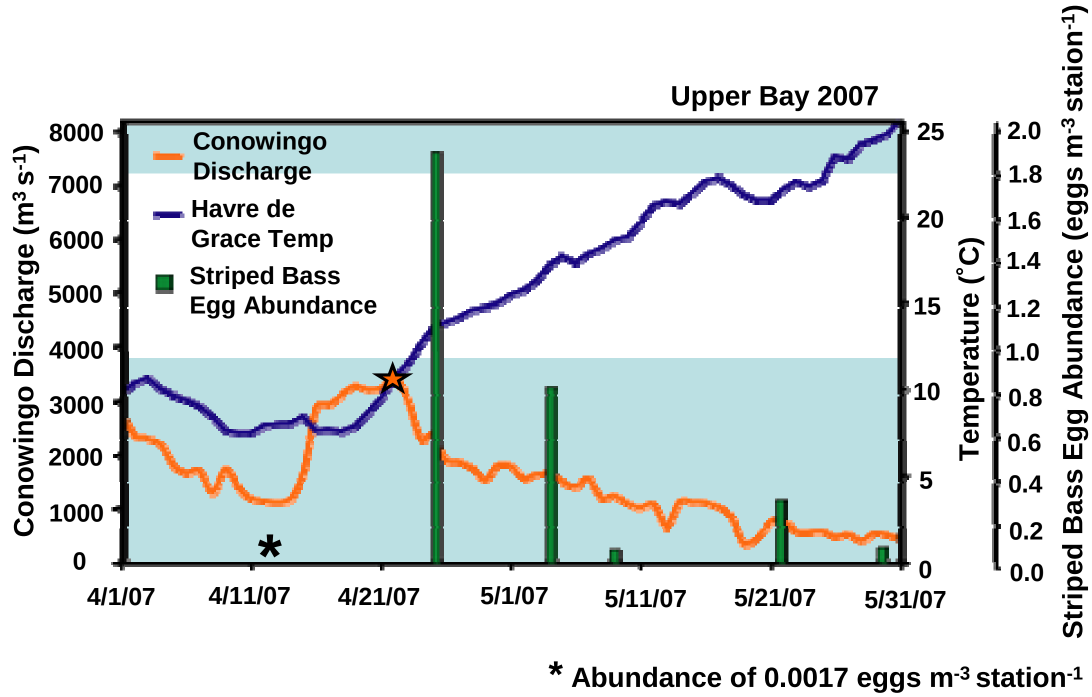


Figure 10: River flow at Conowingo Dam (orange line and left chart axis), water temperature at Havre de Grace (blue line and right chart axis), and striped bass egg abundance index (green bars and far right axis). Striped bass egg abundance index (green bars) increased following a pulse in river flow (orange star) during rising water temperatures. Note that the asterisk indicates that very few eggs were collected and the abundance index value is not visible. The light blue shading indicates water temperatures outside the favorable range for striped bass spawning which occurred prior to the pulse in flow.

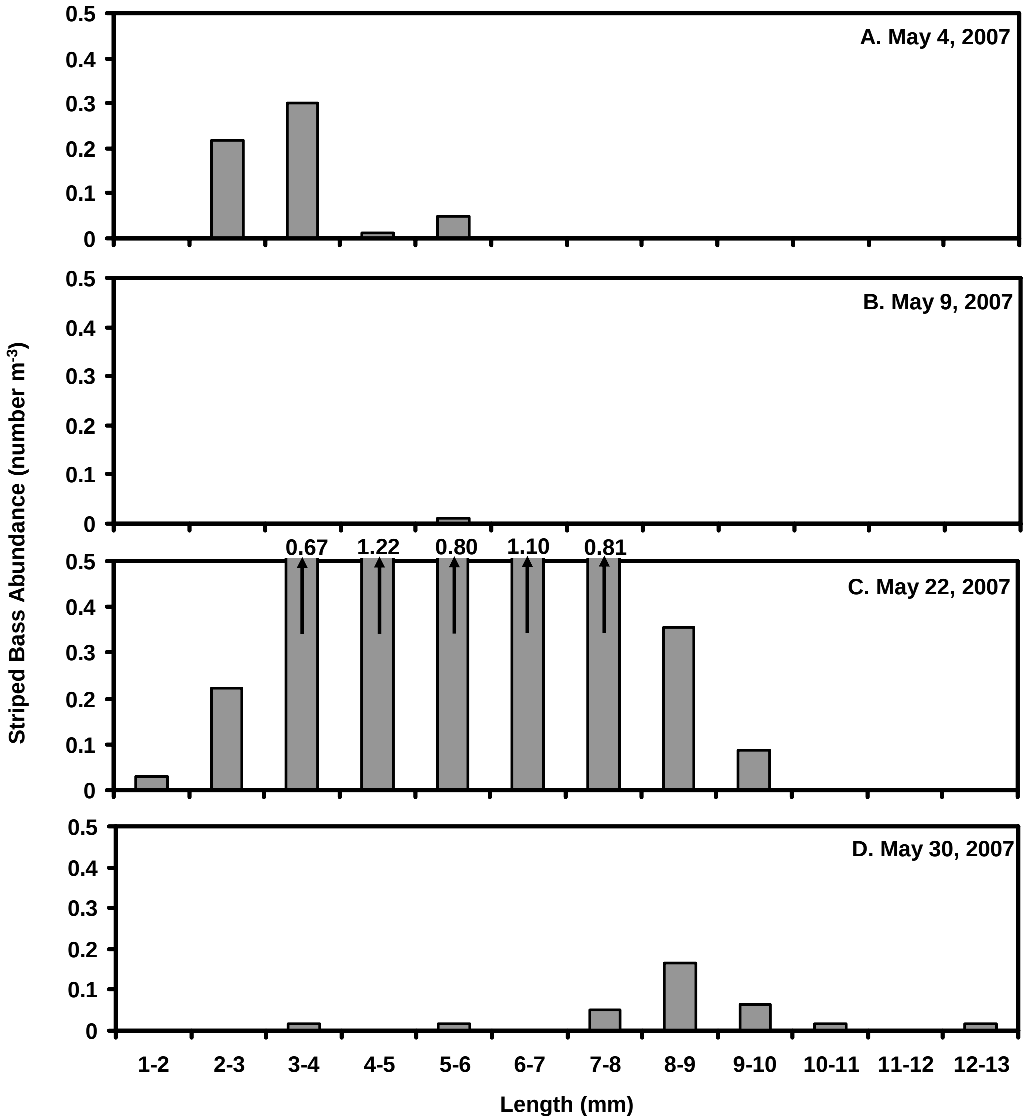


Figure 11: Concentrations by length class of striped bass larvae caught in the upper Chesapeake Bay during research cruises on A) May 4, B) May 9, C) May 22, and D) May 30 in 2007. Cruises on April 12 and April 25, 2007 did not capture any striped bass larvae. The arrows on the May 22 panel indicate abundances beyond the top of the graph as indicated.

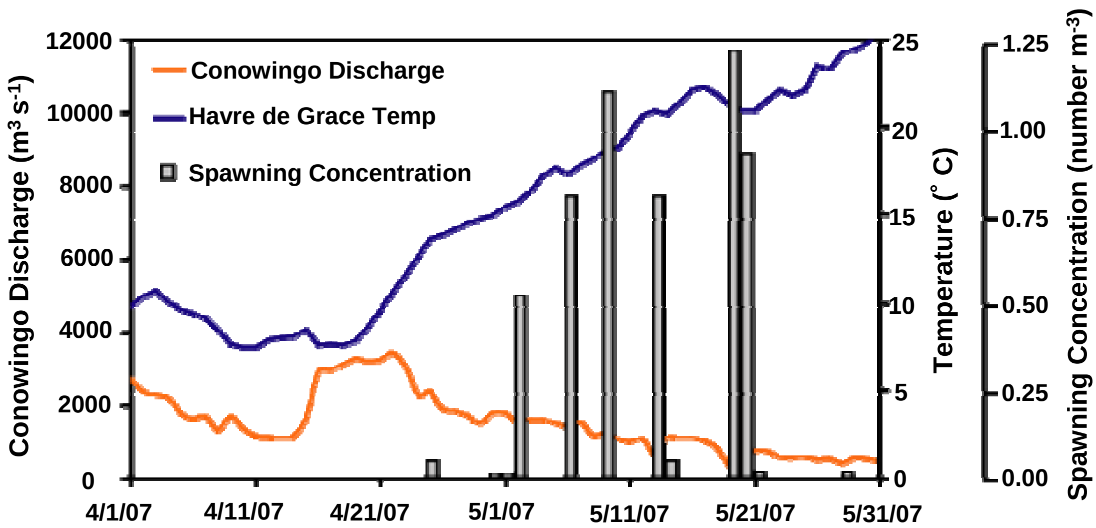


Figure 12: River flow at Conowingo Dam (orange line), water temperature at Havre de Grace (blue line), and estimated concentrations of striped bass larvae spawned on each date (gray bars) in 2007. Spawning date was estimated using the average length-at-age equation from Kellogg (1996) and an average egg stage duration of two days (Setzler-Hamilton and Hall, 1991).

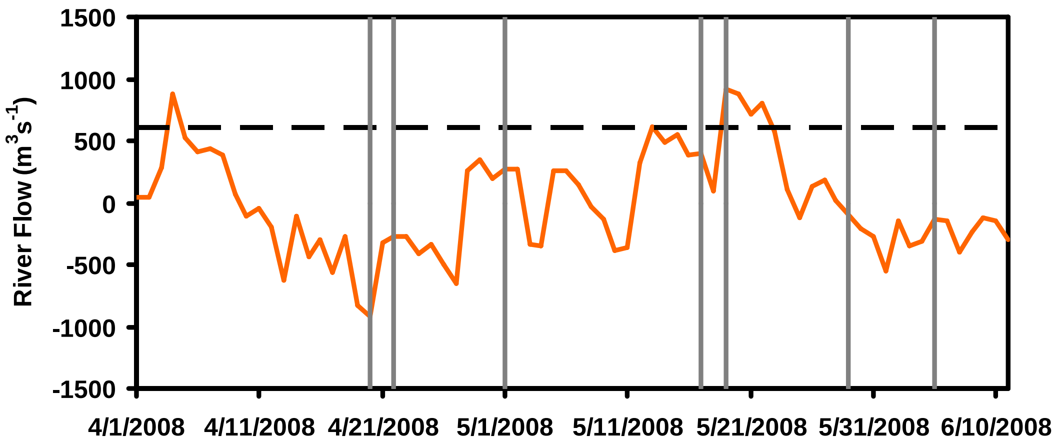


Figure 13: Detrended Susquehanna River flow at Conowingo Dam (orange line) during the striped bass spawning season. Pulses in river flow were defined as the peak in flow of daily flow values that exceeded the 90th percentile of the detrended flow values (dashed line). Based on this definition, pulses in flow occurred on April 4, May 13, and May 19 during the striped bass spawning season in 2008. Research cruises were conducted in the upper bay after the first pulse and before and after the second and third pulses (gray bars).

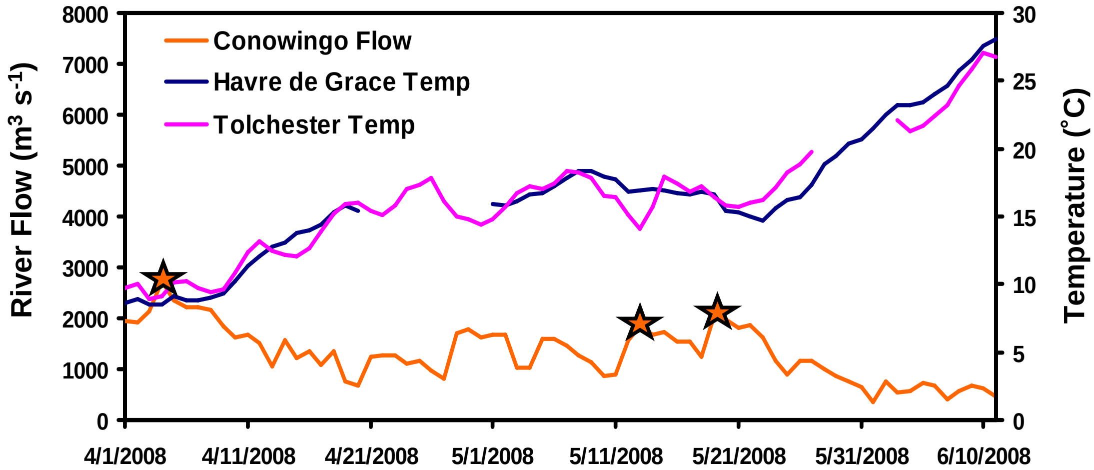


Figure 14: Water temperature was measured at Havre de Grace (blue line) and Tolchester (pink line) and river flow (orange line) was measured at Conowingo Dam during April and May of 2008. During 2008, the three pulses in flow (April 4, May 13, and May 19 (orange stars)) at Conowingo Dam (orange line) were associated with water temperature changes at both Havre de Grace (blue line) and Tolchester (pink line), although water temperatures at Havre de Grace did not increase after the second pulse in flow as they did at Tolchester.

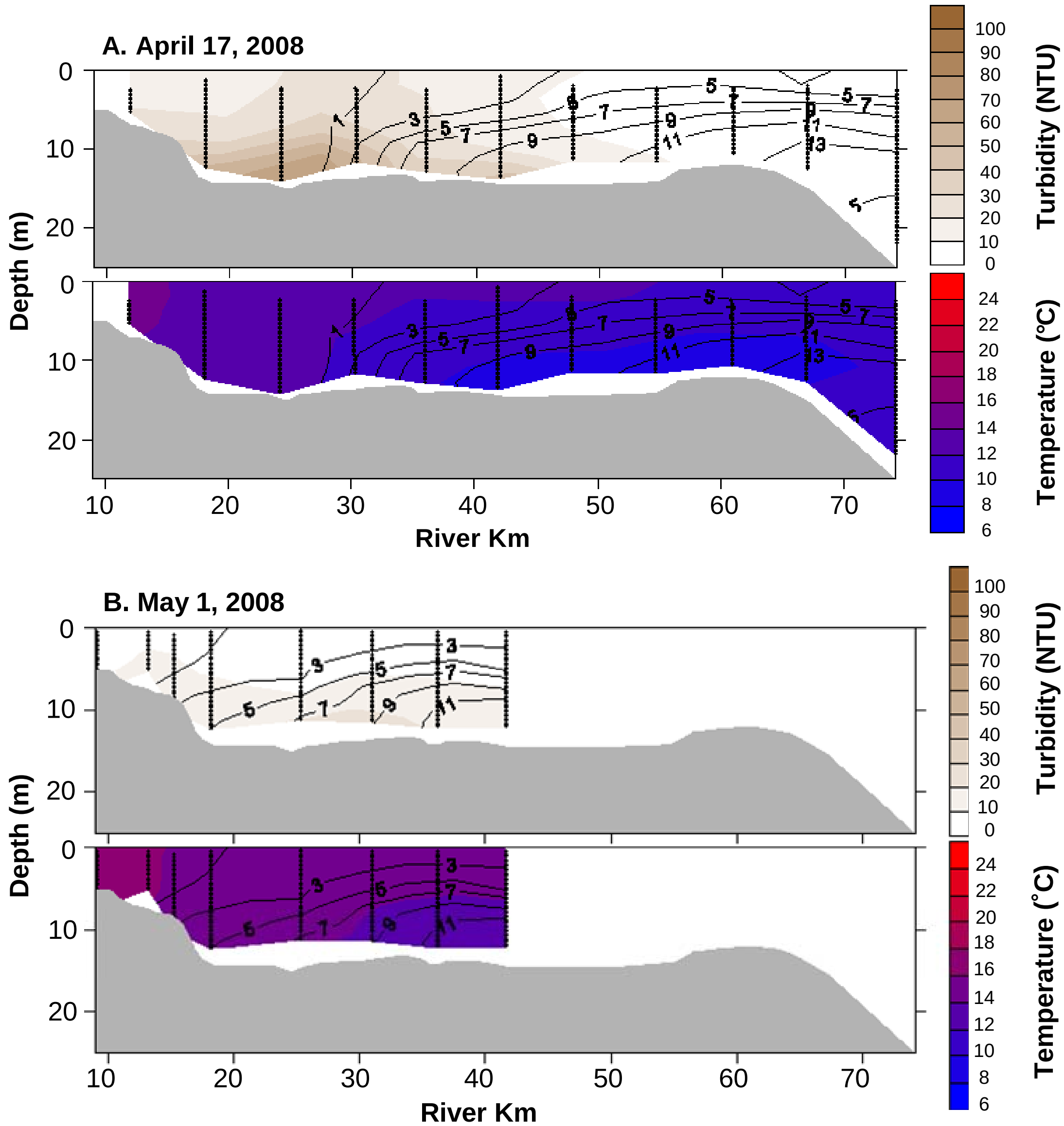
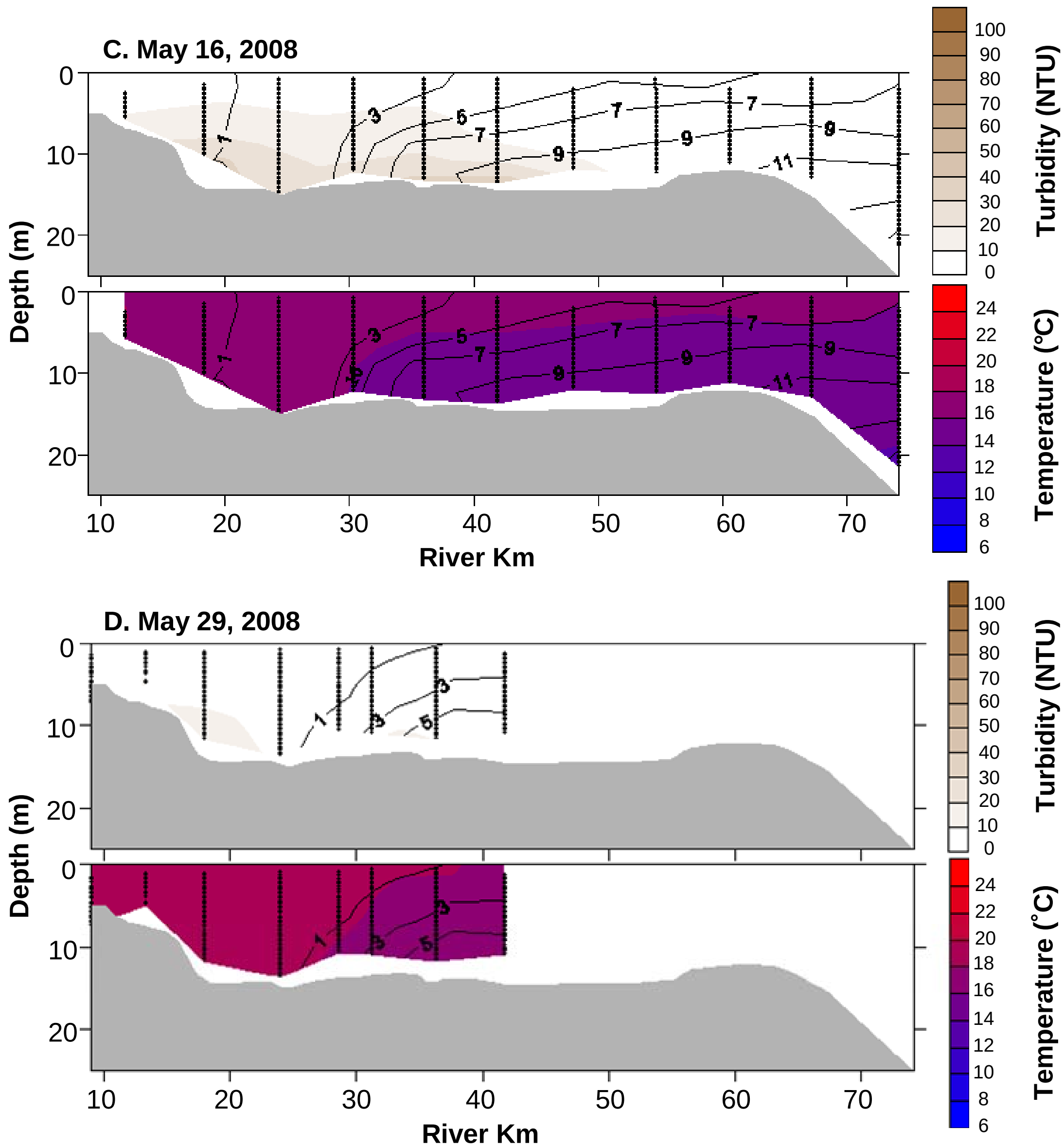


Figure 15: Turbidity (brown shaded contours), temperature (red to blue shaded contours), and salinity (contours on both plots) were measured in the upper Chesapeake Bay during four research cruises on A) April 17, B) May 1, C) May 16, and D) May 29 of 2008. During a research cruise on June 5, 2008 only temperature and salinity were measured. Pulses in river flow occurred on April 4, May 13, and May 19, before the first cruise, between the second (panel B) and third (panel C) cruises, and between the third (panel C) and fourth (panel D) cruises.



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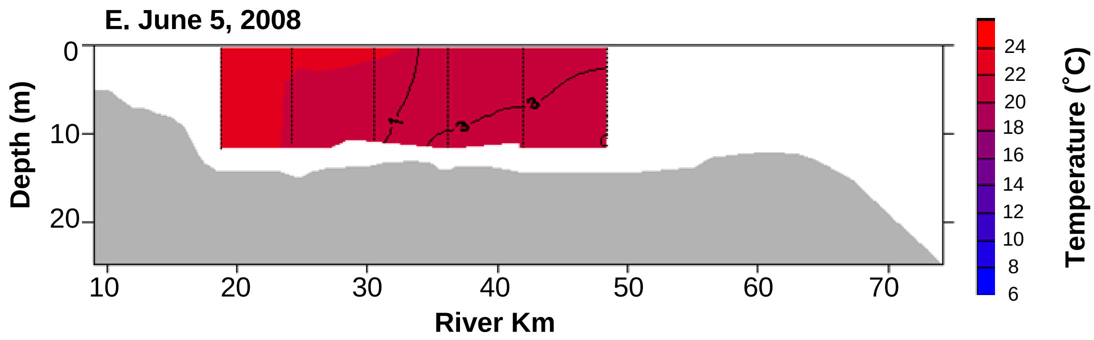

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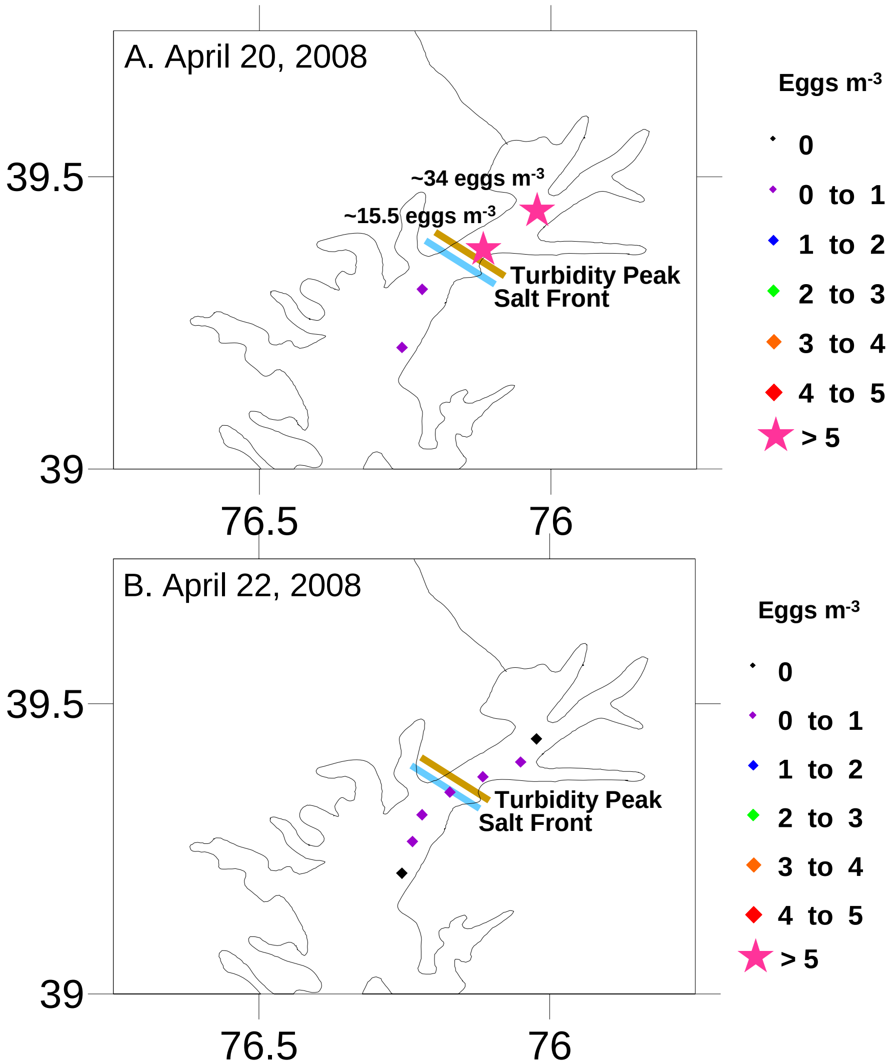
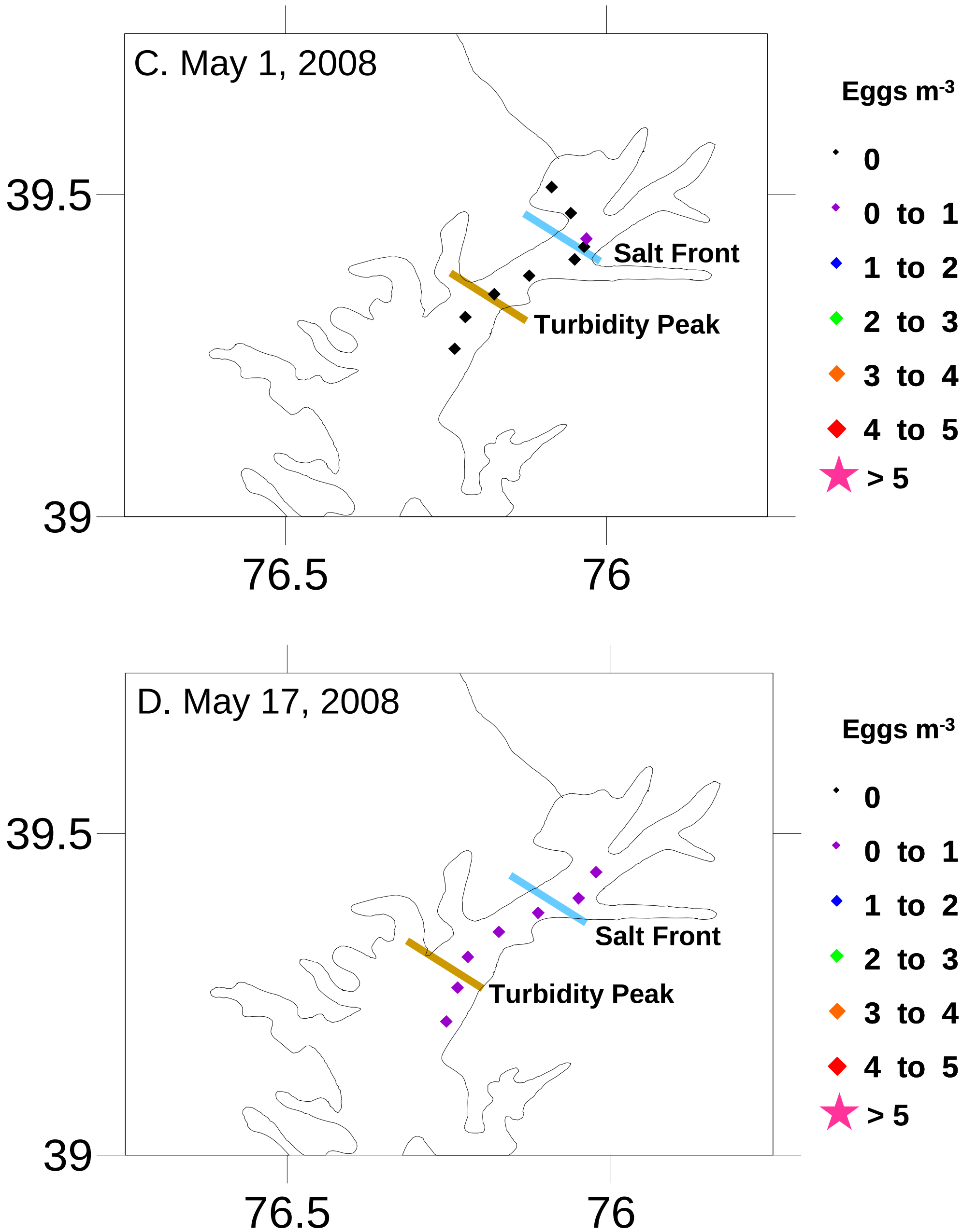


Figure 16: Striped bass egg concentrations (diamonds) collected at stations in the upper Chesapeake Bay on A) April 20, B) April 22, C) May 1, D) May 17, E) May 19, F) May 29, and G) June 5, in 2008. The size and color of the symbols for egg concentrations reflect the magnitude of egg concentrations (scale to the left of each panel). The locations of the salt front (the intersection of the 1 isohaline with bottom) and peak turbidities are indicated. Turbidity was not measured during the cruise on June 5, 2008 (panel G). Pulses in river flow occurred on April 4, May 13, and May 19, before the first cruise (panel A), between the third (panel C) and fourth (panel D) cruises, and on the day of the fifth (panel E) cruise.



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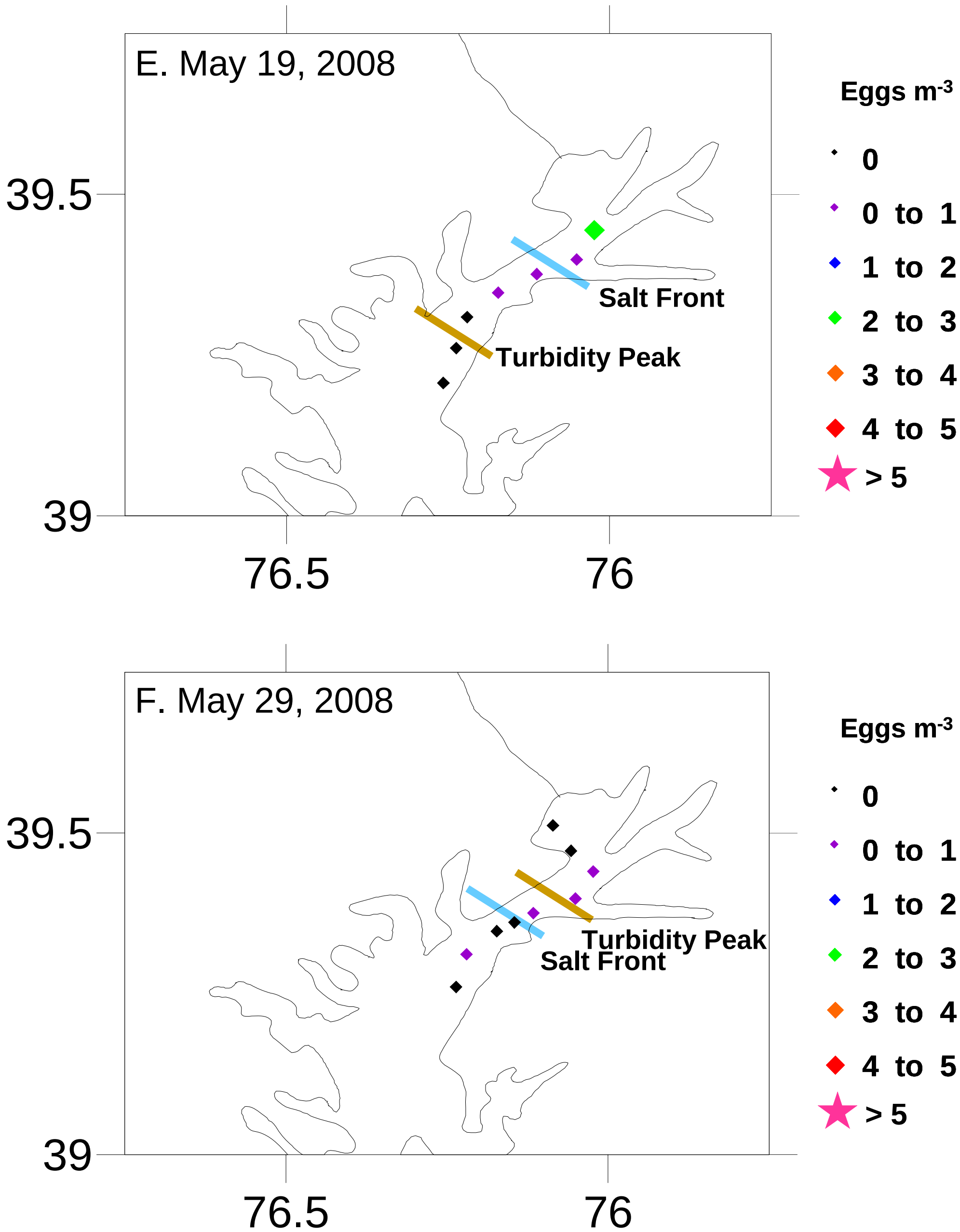

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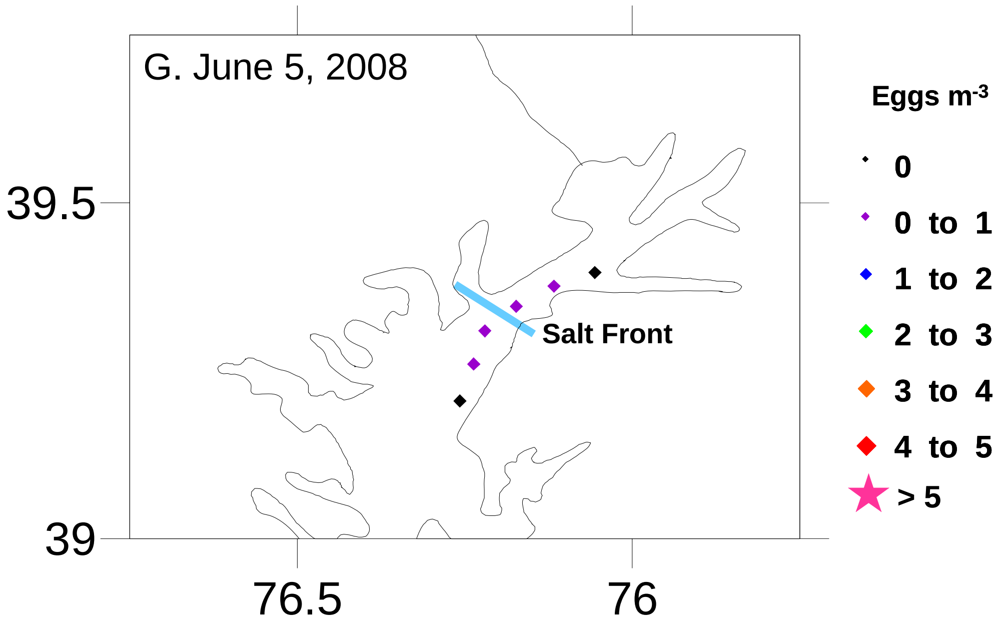

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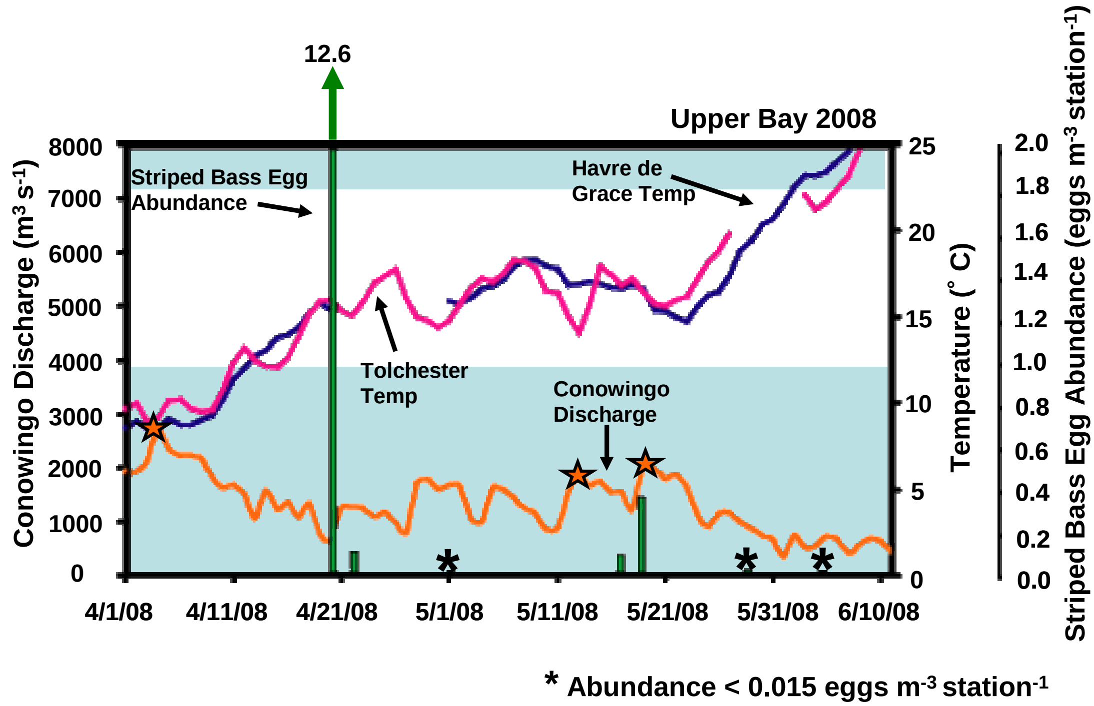


Figure 17: River flow at Conowingo Dam (orange line and left chart axis), water temperature at Havre de Grace (blue line and right chart axis) and Tolchester (pink line and right chart axis), and striped bass egg abundance index (green bars and far right axis). Striped bass egg abundance index (green bars) was highest during rising water temperatures at Havre de Grace (blue line) and Tolchester (pink line) that followed a pulse in flow at Conowingo Dam (orange star), but no cruise was conducted prior to the pulse to determine pre-pulse conditions. Note that the asterisk indicates that very few eggs were collected and the abundance index value is not visible. The light blue shading indicates water temperatures outside the favorable range for striped bass spawning which occurred prior to the pulse in flow.

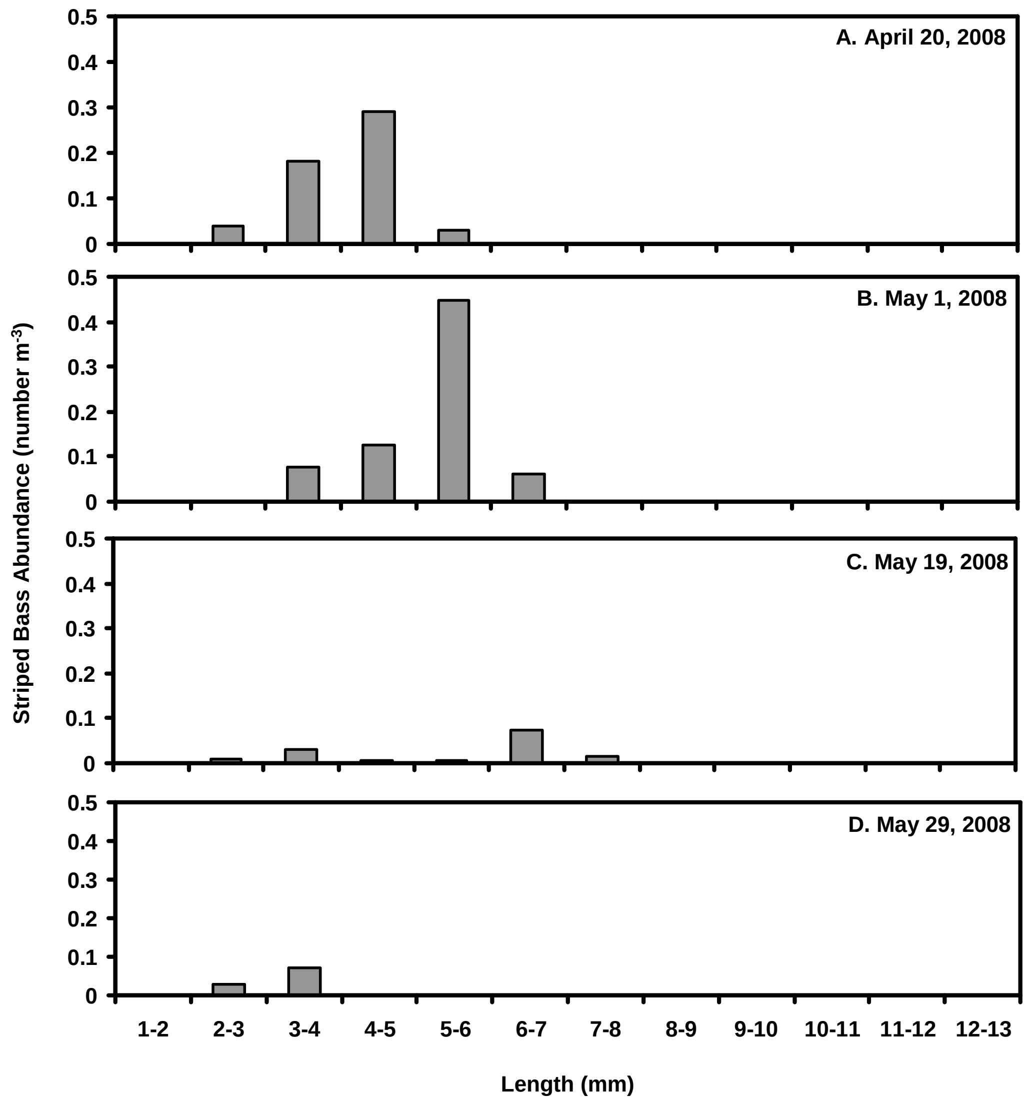


Figure 18: Concentrations by length class of striped bass larvae caught in the upper Chesapeake Bay during research cruises on A) April 20, B) May 1, C) May 19, and D) May 29 in 2008.

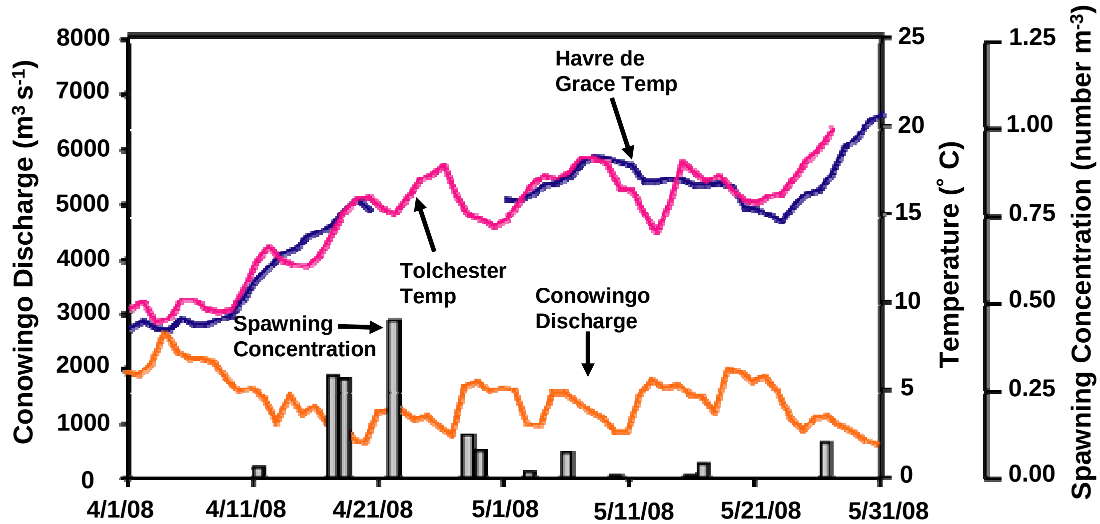


Figure 19: River flow at Conowingo Dam (orange line), water temperature at Havre de Grace (blue line), water temperature at Tolchester (pink line), and estimated concentrations of striped bass larvae spawned on each date (gray bars) in 2008. Spawning date was estimated using the average length-at-age equation from Kellogg, 1996 and an average egg stage duration of two days (Setzler-Hamilton and Hall, 1991).

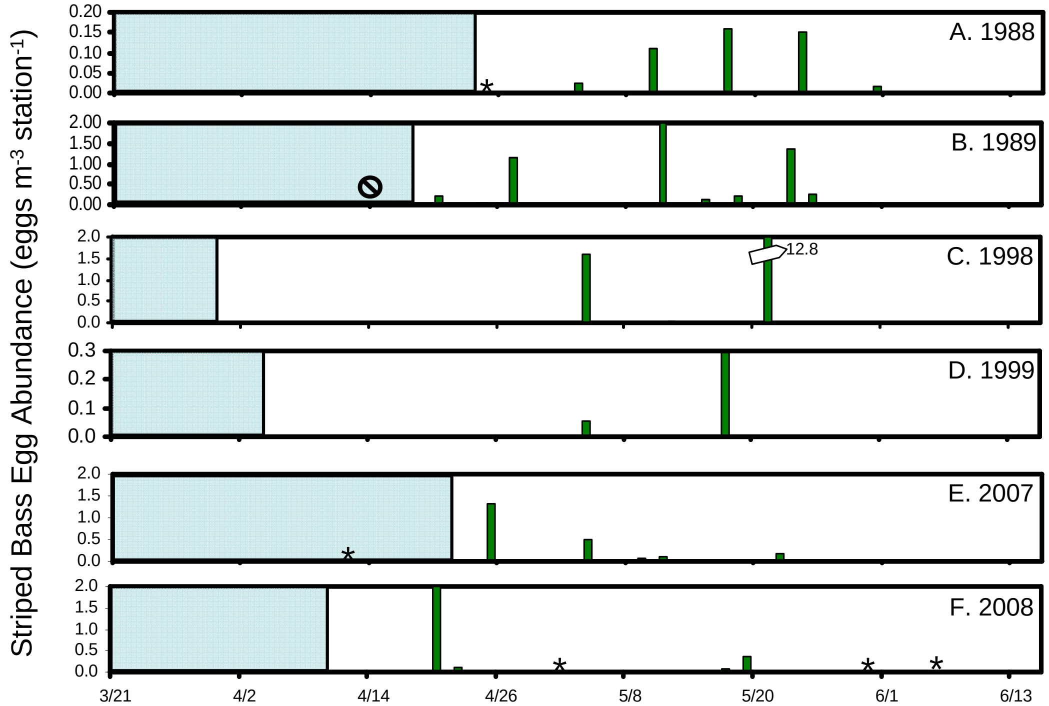


Figure 20: Striped bass egg abundance index in the upper Chesapeake Bay for A) 1988, B) 1989, C) 1998, D) 1999, E) 2007, and F) 2008. The blue boxes indicate temperatures below 12˚C, the reported minimum favorable temperature for spawning (Setzler-Hamilton *et al*., 1981). The asterisks indicate egg abundances too small to appear on the graph. The slashed-circle symbol indicates cruises during which no eggs were collected, and the white break on the bar indicates egg abundances above the upper limit of the graph.

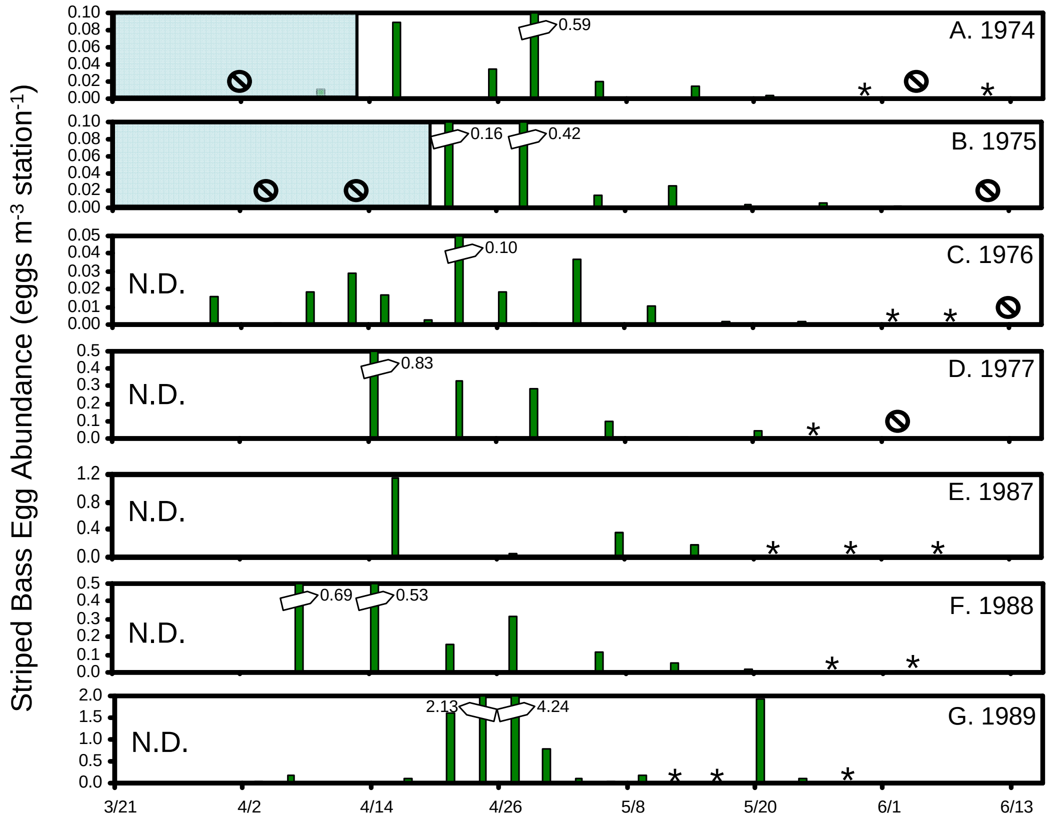


Figure 21: Striped bass egg abundance index in the Potomac River for A) 1974, B) 1975, C) 1976, D) 1977, E) 1987, F) 1988, and G) 1989. The blue boxes indicate temperatures below 12˚C, the reported minimum favorable temperature for spawning (Setzler-Hamilton *et al*., 1981); N.D. indicates that temperature data was not available. The asterisks indicate egg abundances too small to appear on the graph. The slashed-circle symbol indicates cruises during which no eggs were collected, and the white breaks on the bar indicate egg abundances above the upper limit of the graph.

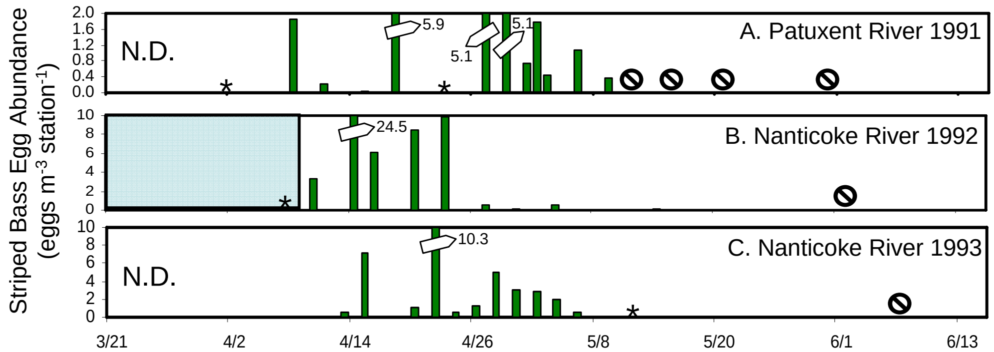


Figure 22: Striped bass egg abundance index in the Patuxent River for A) 1991, and the Nanticoke River for B) 1992, and C) 1993. The blue boxes indicate temperatures below 12˚C, the minimum reported favorable temperature for spawning (Setzler-Hamilton *et al*., 1981); N.D. indicates that temperature data was not available. The asterisks indicate egg abundances too small to appear on the graph. The slashed-circle symbol indicates cruises during which no eggs were collected, and the white breaks on the bar indicate egg abundances above the upper limit of the graph.

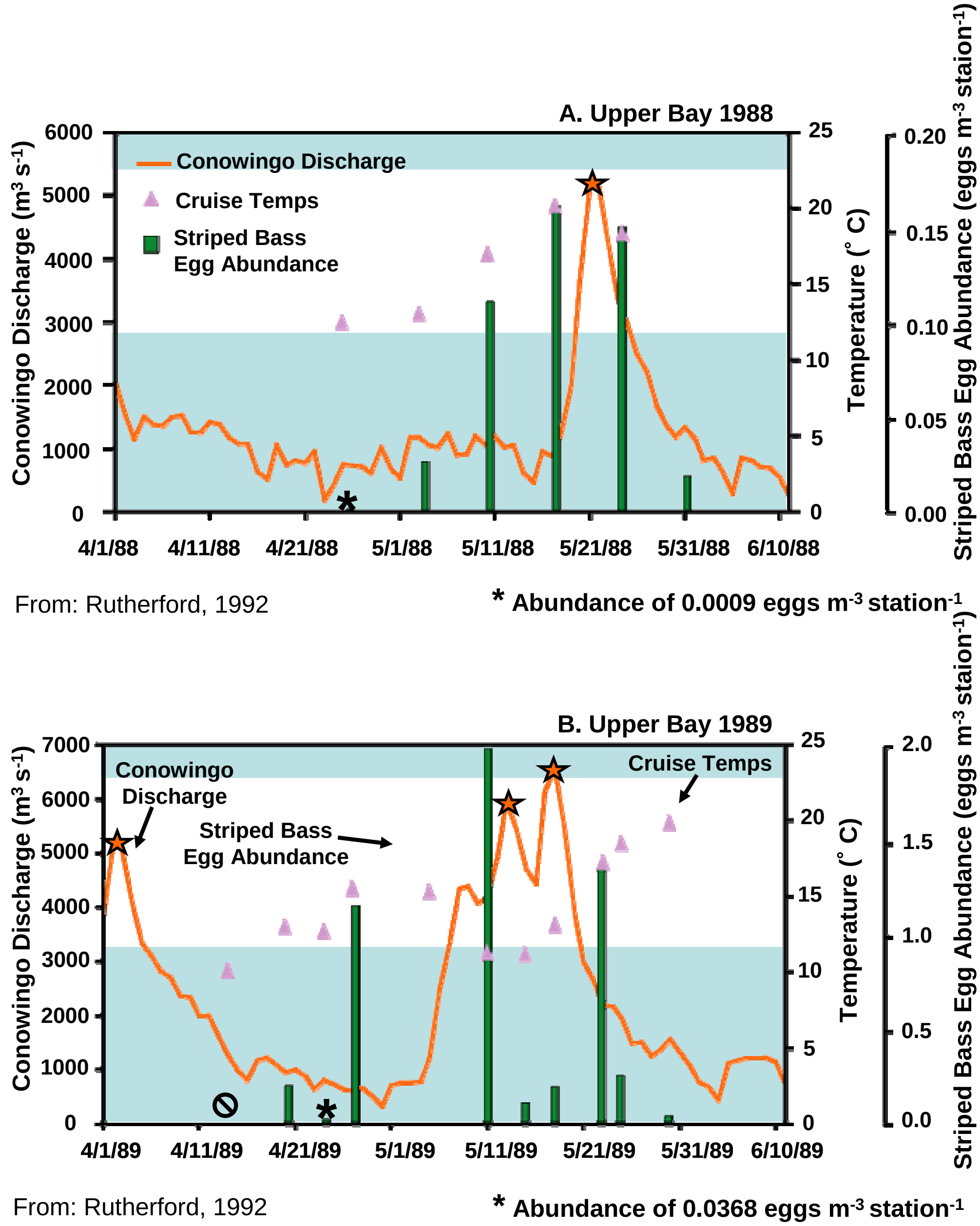
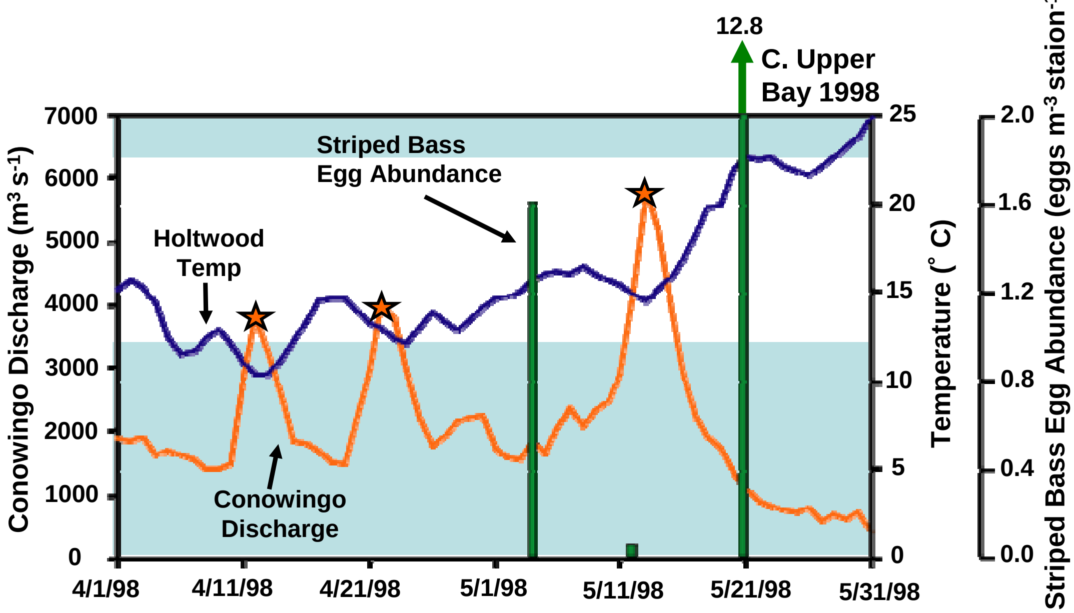
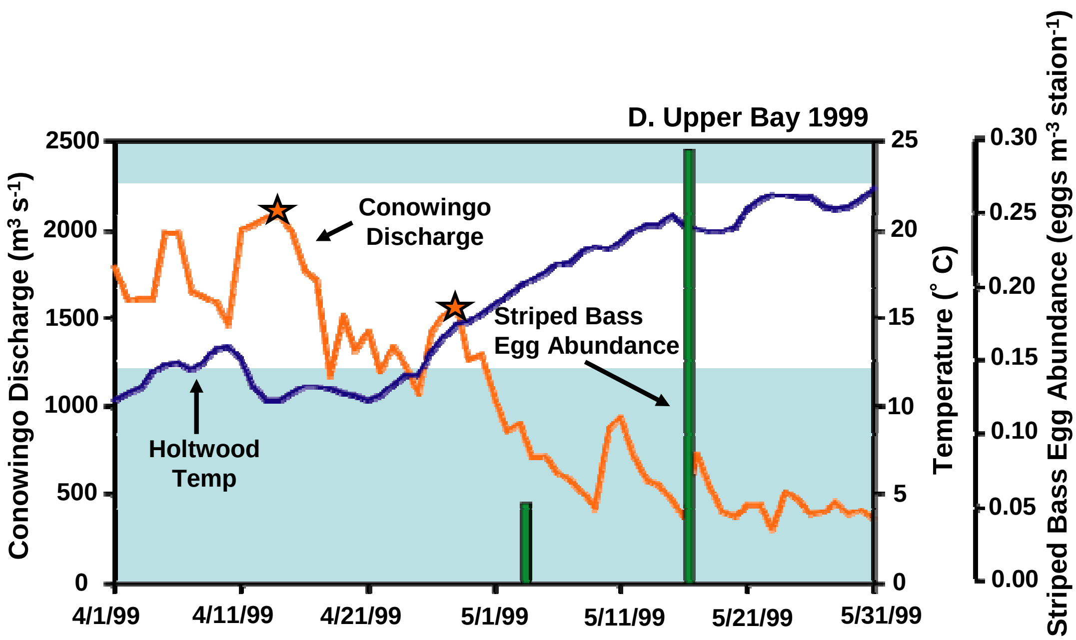


Figure 23: River discharge (orange line), daily water temperatures (blue line), cruise temperatures (purple triangles), and striped bass egg abundance index (green bars) in the upper bay during A) 1988, B)1989, C) 1998, and D) 1999. The orange stars indicate pulses in river flow, the asterisks indicate egg abundances too small to appear on the graph, the slashed-circle symbol indicates cruises during which no eggs were collected, and the light blue shading indicates water temperatures outside the favorable range for striped bass spawning.



From: North, 2001



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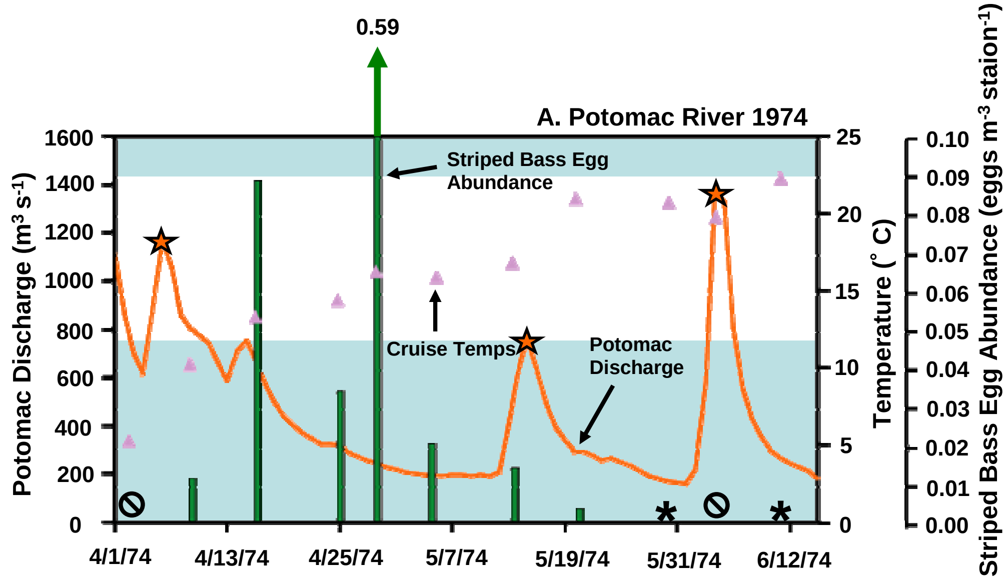
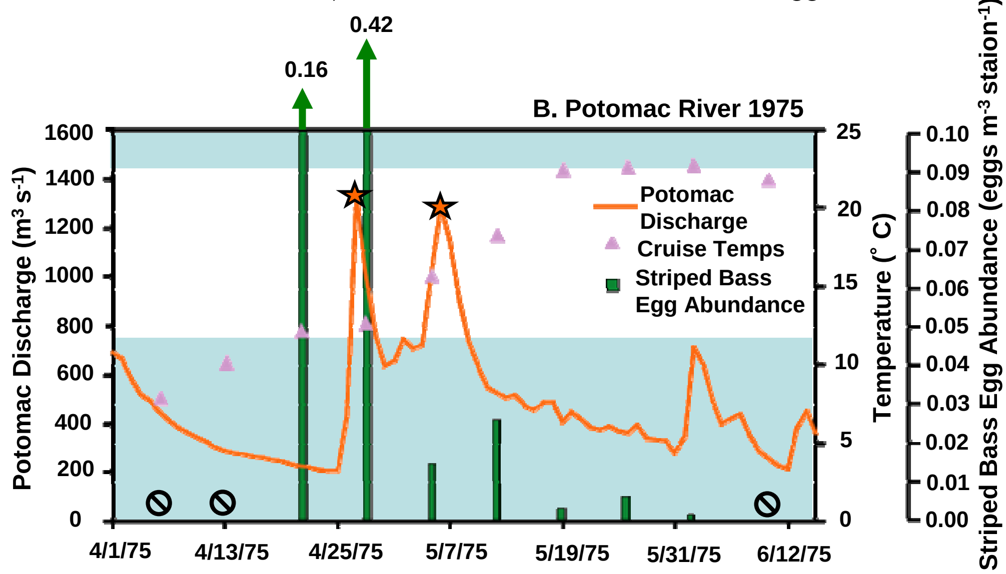
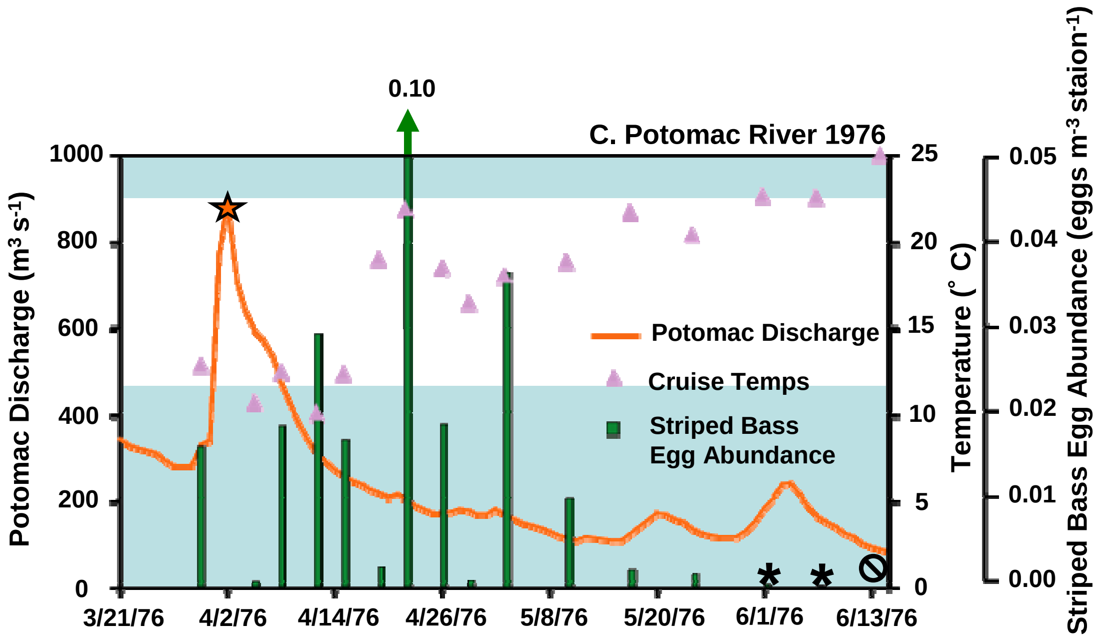


From: Setzler-Hamilton *et al.*, 1980

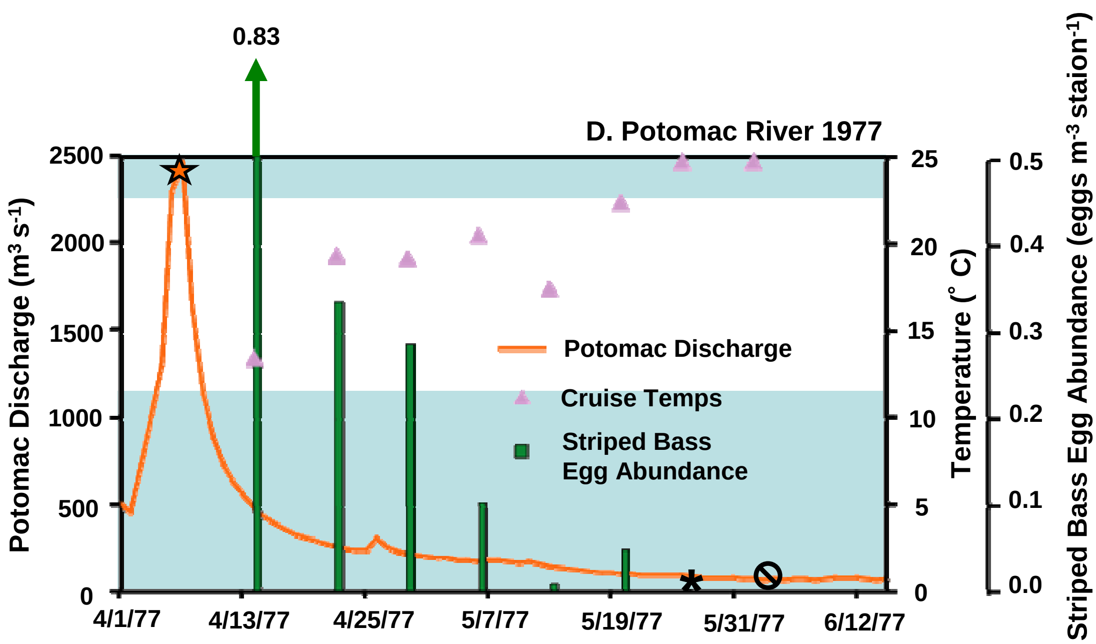


From: Setzler-Hamilton *et al.*, 1980

Figure 24: River discharge (orange line), daily water temperatures (blue line), cruise temperatures (purple triangles), and striped bass egg abundance index (green bars) in the Potomac River during 1974-1977 and 1987-1989. The orange stars indicate pulses in river flow, the asterisks indicate egg abundances too small to appear on the graph, the slashed-circle symbol indicates cruises during which no eggs were collected, and the light blue shading indicates water temperatures outside the favorable range for striped bass spawning.

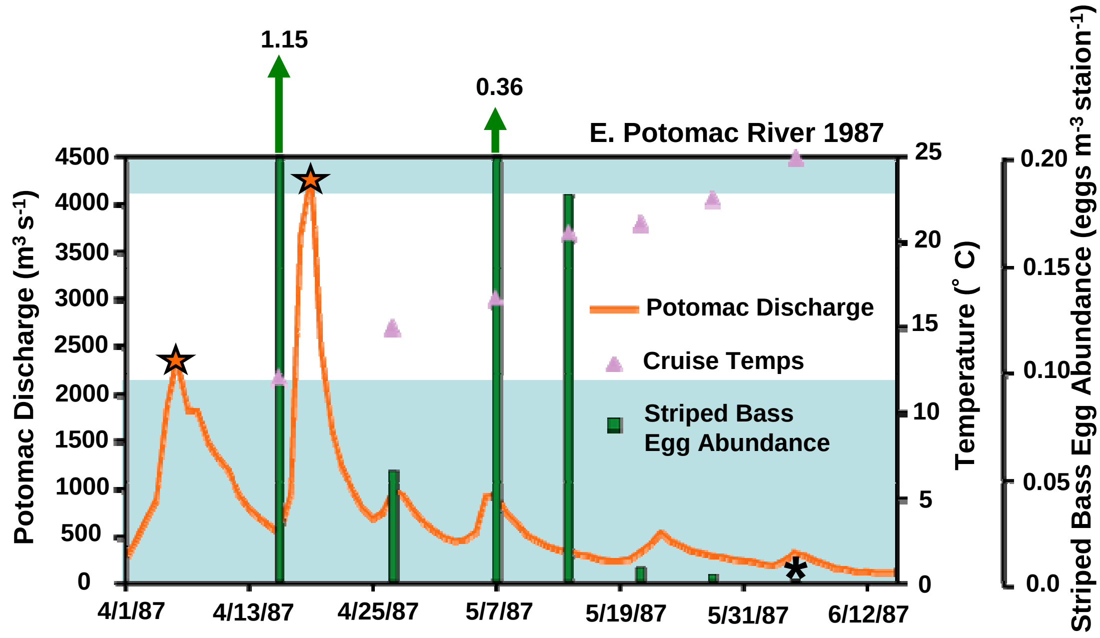


From: Setzler-Hamilton *et al*., 1980 *** Abundance < 0.0005 eggs m^{-3} station^{-1}**



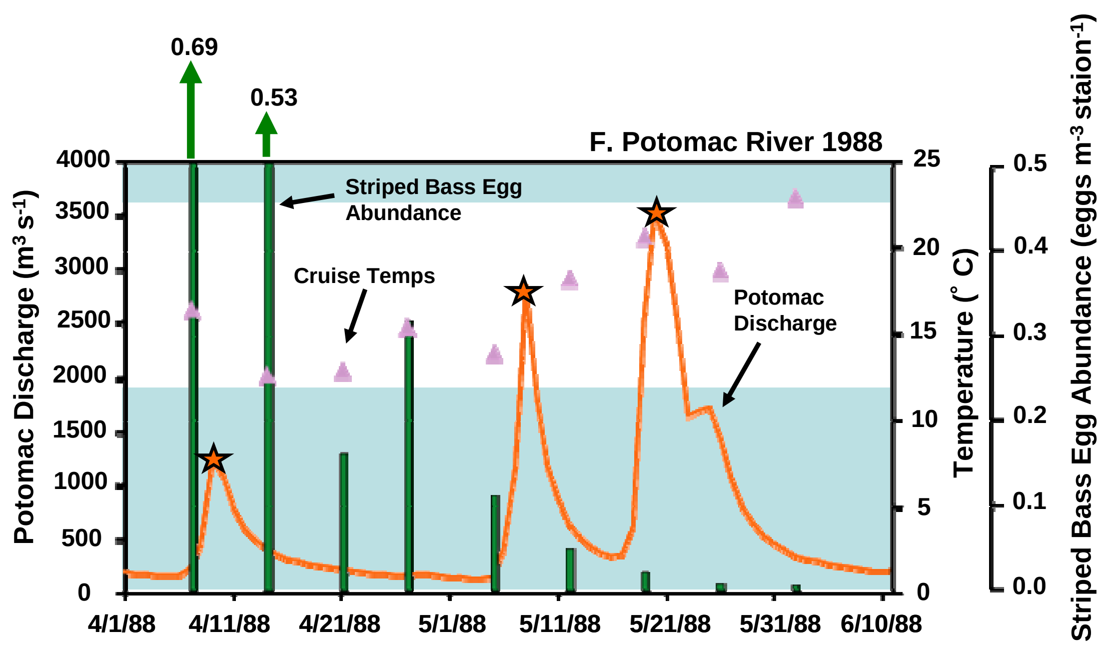
From: Setzler-Hamilton *et al*., 1980 *** Abundance 0. 0010 eggs m^{-3} station^{-1}**

Figure 24: Continued.



From: Rutherford, 1992

* Abundance 0. 0006 eggs m^{-3} station^{-1}



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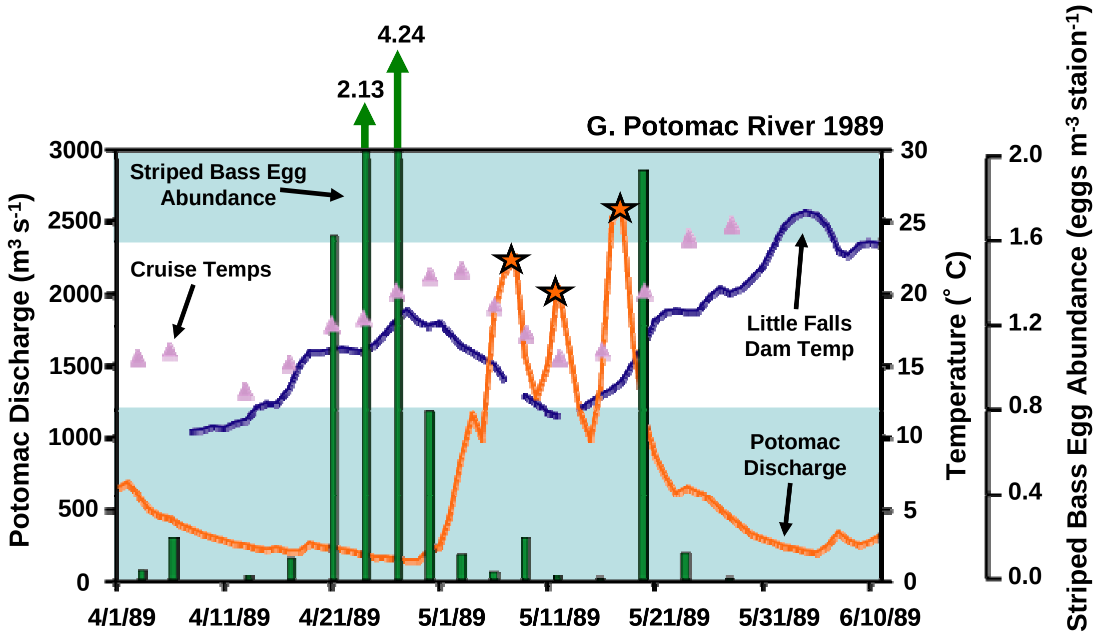

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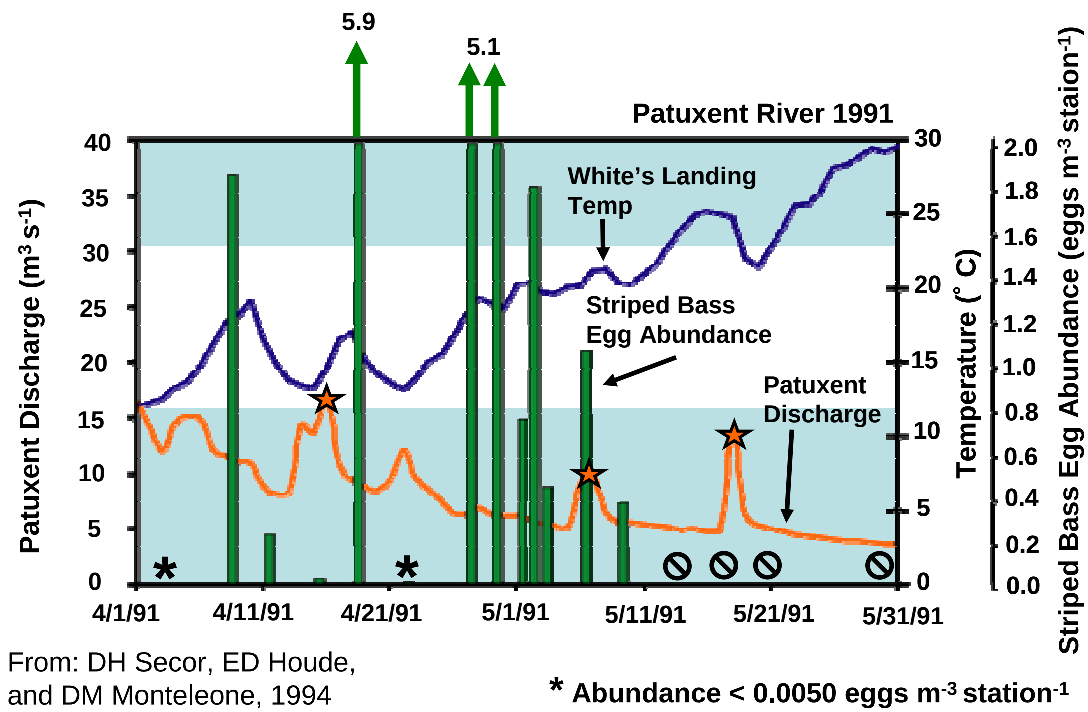
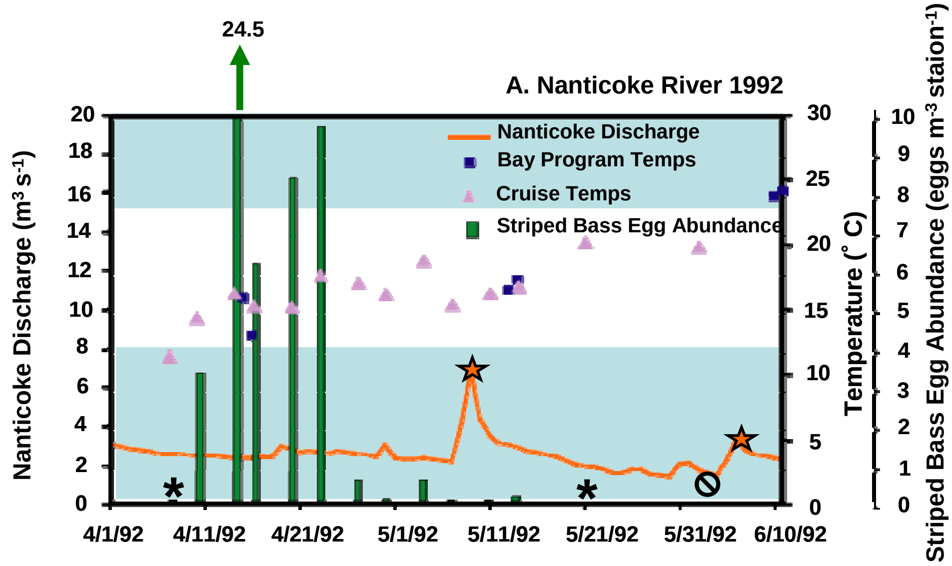
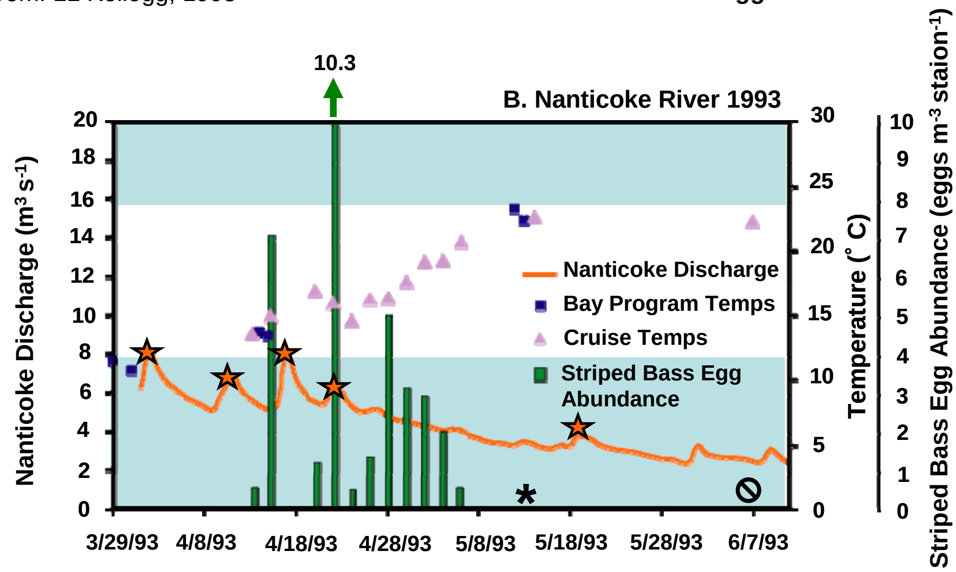


Figure 25: River discharge (orange line), daily water temperatures (blue line), and striped bass egg abundance index (green bars) in the Patuxent River during 1991. The orange stars indicate pulses in river flow, the asterisks indicate egg abundances too small to appear on the graph, the slashed-circle symbol indicates cruises during which no eggs were collected, and the light blue shading indicates water temperatures outside the favorable range for striped bass spawning.



From: LL Kellogg, 1995

* Abundance <0.0300 eggs m^{-3} station^{-1}



From: LL Kellogg, 1995

* Abundance 0. 0158 eggs m^{-3} station^{-1}

Figure 26: River flow (orange line), cruise temperatures (purple triangles), Chesapeake Bay program temperatures (blue boxes), and striped bass egg abundance index (green bars) in the Nanticoke River during A) 1992 and B) 1993. The orange stars indicate pulses in river flow, the asterisks indicate egg abundances too small to appear on the graph, the slashed-circle symbol indicates cruises during which no eggs were collected, and the light blue shading indicates water temperatures outside the favorable range for striped bass spawning.

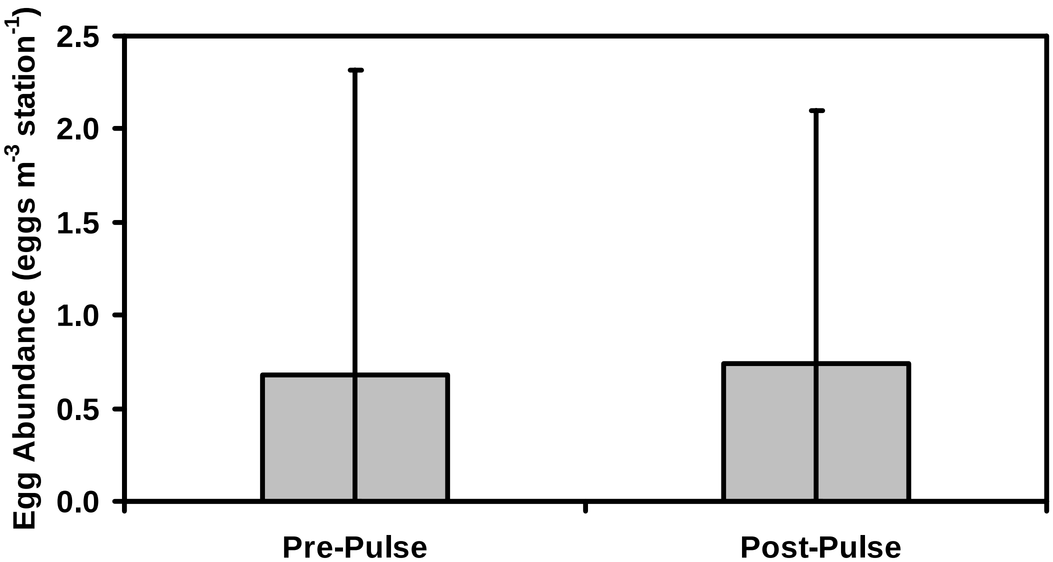


Figure 27: Average pre- and post- pulse egg abundance indices. A pulse was defined as the date of the peak in flow of any event that was in the highest 90% of detrended daily flow data for April and May within the year and river system. Error bars represent one standard deviation of the mean. Based on a Wilcoxon signed-rank test, there was no significant difference between the pre- and post-pulse egg abundance indices ($p=0.16$, $n=19$).

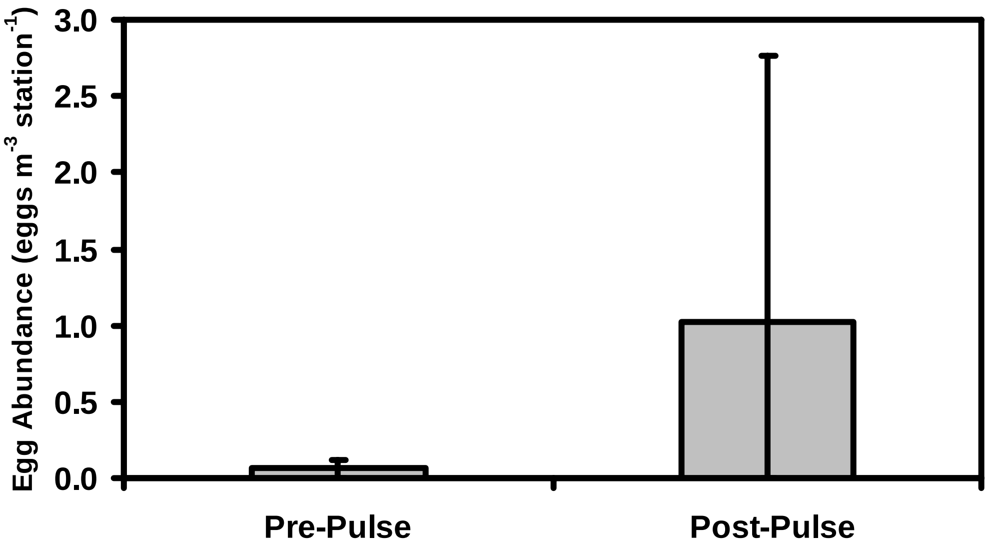


Figure 28: Average pre- and post- pulse egg abundance indices. Here, a pulse was defined as an event lasting at least two days and exceeding twice the average flow for April and May within the year and river system. Error bars represent one standard deviation of the mean. Based on a Wilcoxon signed-rank test, there was a significant difference between the pre- and post-pulse egg abundance indices ($p=0.02$, $n=11$).

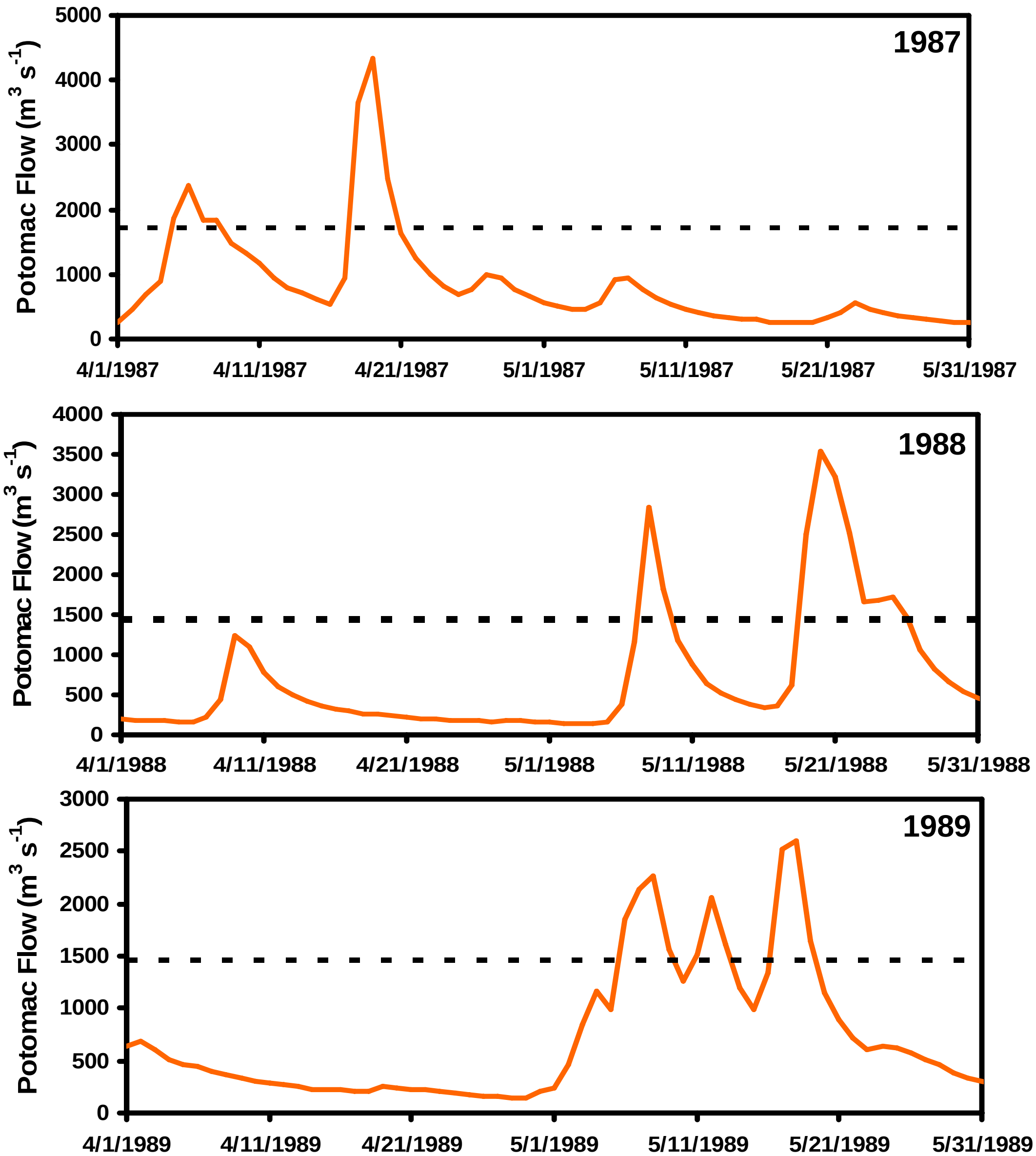


Figure 29: Potomac River flow (1987-1989) at Little Falls Dam (orange line). Pulses were defined as twice mean flow for April and May (dashed line). In years with multiple close peaks (as in 1989), separate pulses were defined as those where flow values were notably lower than twice the average flow for more than three days.

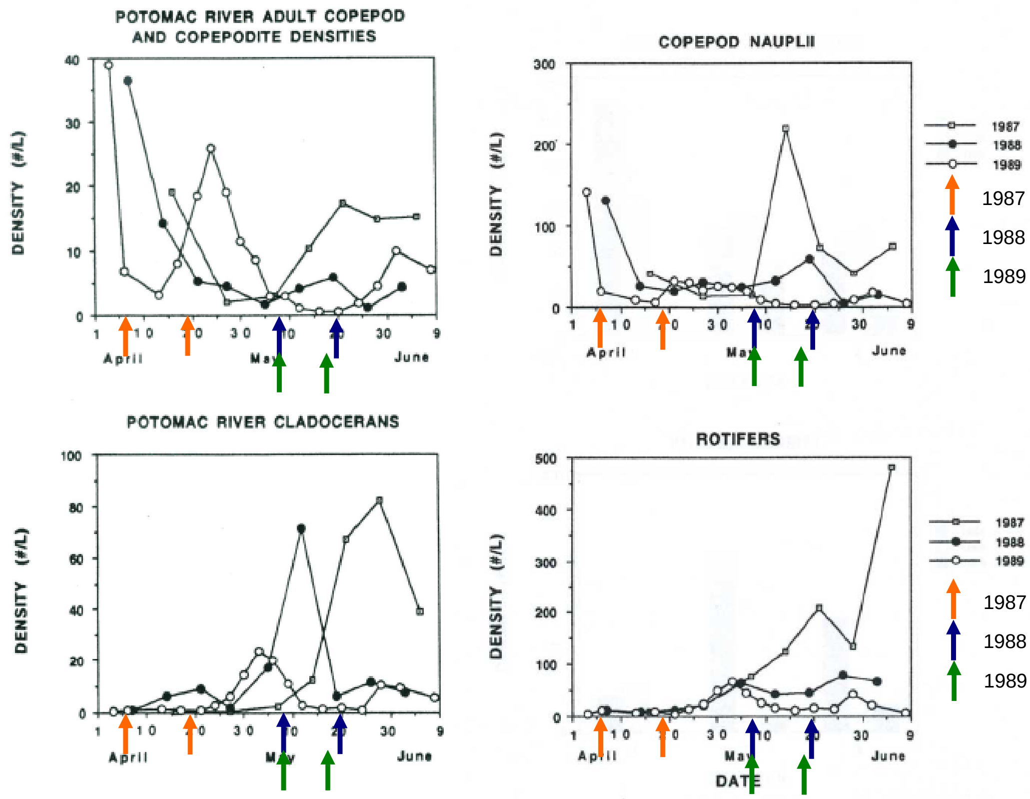


Figure 30: Concentrations of striped bass larval prey (adult copepods, copepodites, copepod nauplii, cladocerans, and rotifers) in the Potomac River 1987-1989. Figure reproduced from Rutherford, 1992. Pulses in flow are indicated by orange (1987), blue (1988) and green (1989) arrows.

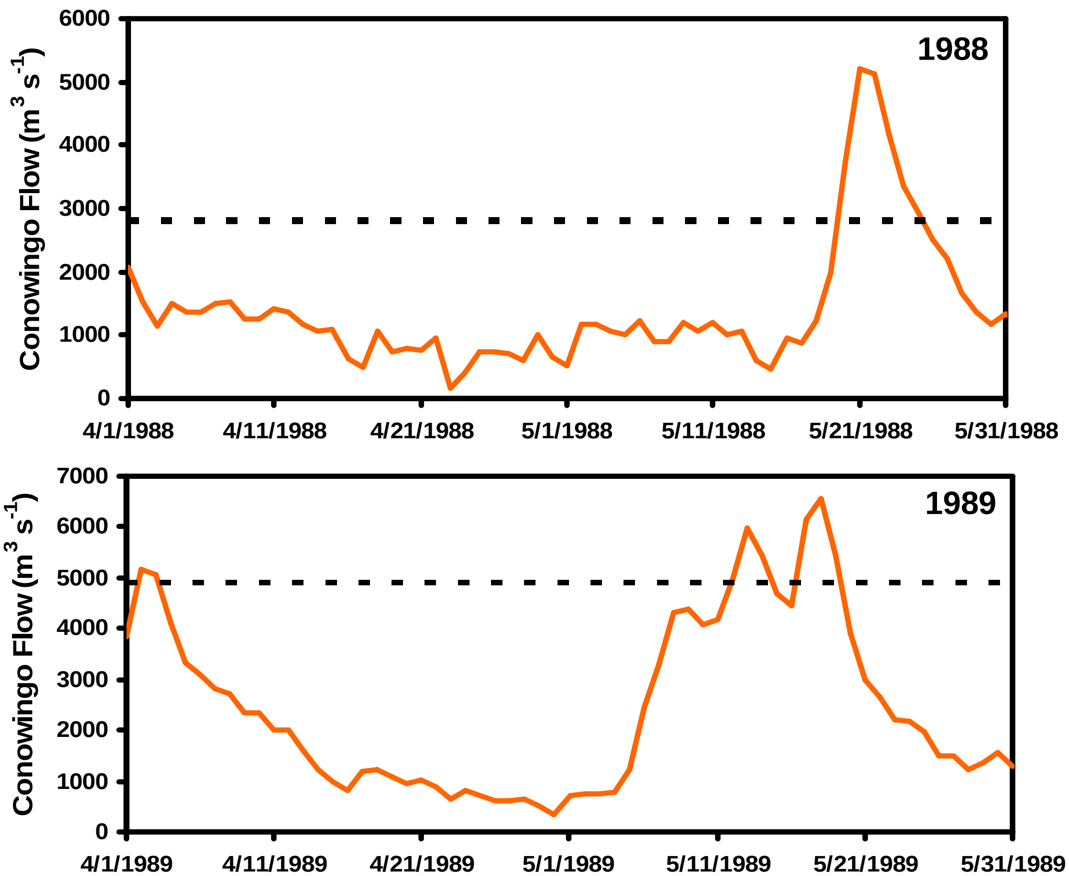


Figure 31: Susquehanna River flow (1988-1989) at Conowingo Dam (orange line). Pulses were defined as twice mean flow for April and May (dashed line). In years with multiple close peaks (as in 1989), separate pulses were defined as those where flow values were notably lower than twice the average flow for more than three days.

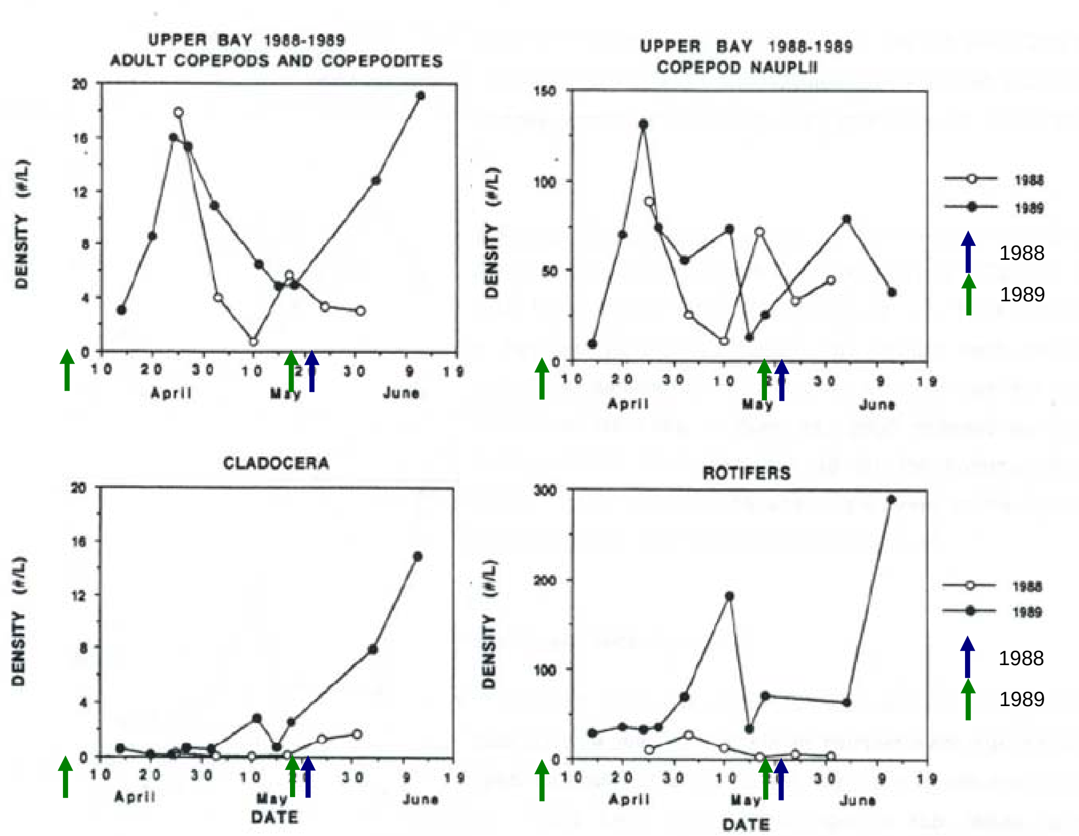


Figure 32: Concentrations of striped bass larval prey (adult copepods, copepodites, copepod nauplii, cladocerans, and rotifers) in the Susquehanna River 1988-1989. Figure reproduced from Rutherford, 1992. Pulses in flow are indicated by blue (1988) and green (1989) arrows. Note that the pulse on the left edge of the graph occurred on April 2, 1989.

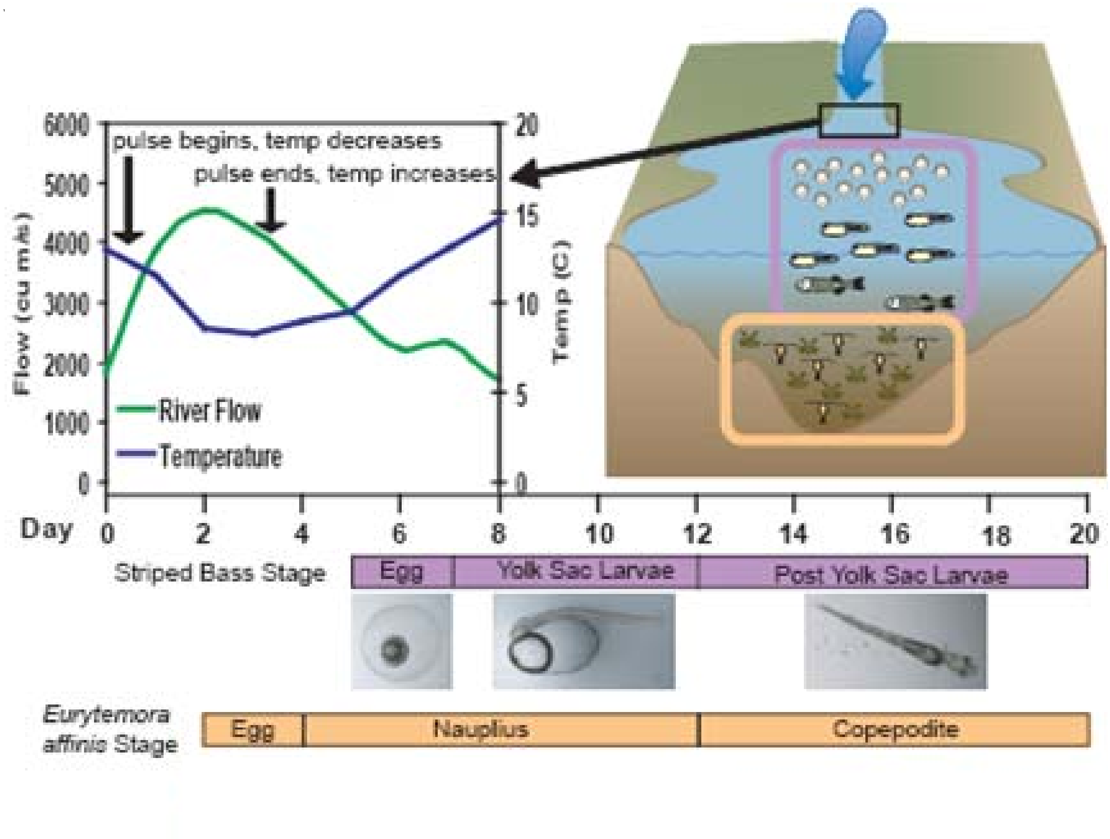


Figure 33: A pulse in river flow may stimulate production in striped bass prey such as the copepod *E. affinis*. As the pulse diminishes, the increasing water temperature may act as a cue for striped bass spawning, resulting in a match between *E. affinis* copepodites and the first feeding stage of striped bass larvae. The upper left and lower panels show physical (upper left) and fish/copepod life stages (lower panel) from the beginning of an increase in flow (day 0) to 20 days after the initiation of the pulse. The timing of life stages is based upon Devreker *et al*. (2007). The upper right panel presents an idealized schematic of the location of the physical measurements and organisms.

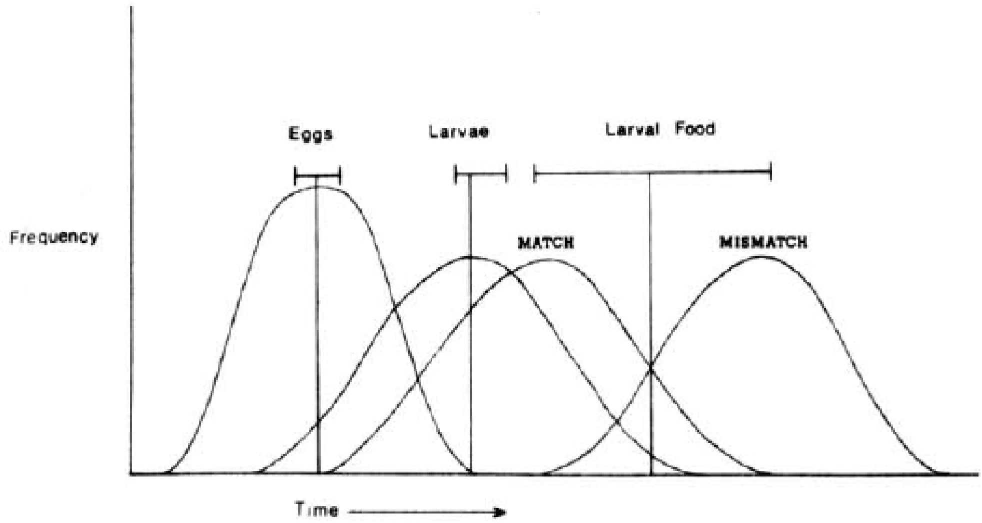


Figure 34: According to Cushing's match/mismatch hypothesis, spawning occurs at a fixed time (note the short horizontal range bar), but production of larval prey varies (note the longer horizontal range bar), resulting in either a match, in which larval prey and larvae occur at the same time, or a mismatch, in which larval prey and larvae occur at different times. In the case of striped bass larvae in Chesapeake Bay, a pulse in river flow could cue both striped bass spawning and larval prey production. Figure reproduced from Cushing, 1990.

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