Order Number 9207758

Factors affecting survival of early life stages of striped bass

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The College of William and Mary, 1991

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FACTORS AFFECTING SURVIVAL OF EARLY LIFE STAGES OF STRIPED BASS

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

By

John Clarke McGovern

1991

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

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Approved, 6 August 1991

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ACKNOWLEDGMENTS

Just as a carpenter is only as good as his tools, a student's performance will reflect the capabilities of his instructors. I have been very fortunate in having a very knowledgeable committee who were more than willing spend time with me and critique various aspects of my study. I am very grateful to them for their help and friendship throughout all stages of this research. I thank my committee chairman, John E. Olney, for his help over the years and also for his keen sense of what is important in science. I also thank Charles A. Wenner for his assistance not only with this project but also for getting me through my masters research and encouraging me to go on for a Ph.D. George C. Grant also provided much advice and helpful criticism during the sampling and writing phases of this research. I also thank James A. Colvocoresses and Peter A. VanVeld for their constructive review of this manuscript.

I thank those individuals who spent many hours in the field, both day and night to help me collect data. Patricia A. Crewe spent more than her share of time in the field helping me collect biological data during the 1988 and 1989 spawning seasons. Louis B. Daniels III toured the Pamunkey

River at night during the 1989 spawning season to help collect fish predators of striped bass eggs and larvae. The computerized environmental station which measured a vast array of physical data during both spawning seasons could not have been engineered without the assistance of Buddy Matthews and John Posenau. The fine art of otolith analysis of juveniles was taught to me by Lisa Kline and Louis Daniels. Patrice Mason, Eugene Burreson and Elizabeth McGovern assisted me with Scanning Electron Microscopy. Other individuals whose assistance is much appreciated include John D. Field, Martin R. Cavaluzzi, Carole C. Baldwin, Kathryn D. Kavanaugh, Elizabeth Maddox, Tim Shannon, and Steve Snyder.

Finally, I thank my family, in particular, my wife Beth and mother, Margaret, for their help and support during my years as a graduate student.

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ABSTRACT

Field surveys in the Pamunkey River, Virginia, indicated that numerous fish and invertebrate predators varied in their spatiotemporal coincidence with eggs and larvae of striped bass, Morone saxatilis, on spawning grounds. In 1986 laboratory experiments, the cyclopoid copepod Acanthocyclops vernalis was observed to attack and kill striped bass larvae. In addition, juveniles or adults of satinfin shiner, spottail shiner, tessellated darter, white perch, striped bass, bluegill, pumpkinseed, channel catfish, and white catfish ate yolk-sac larvae under laboratory conditions. Consumption of larvae by spottail shiners and satinfin shiners increased with increasing prey density to a maximum observed ingestion of 150 and 81 larvae per predator per hour, respectively. In contrast to these laboratory results, neither eggs nor larvae of striped bass were positively identified in the guts of field-collected fishes, although various fish species consumed many eggs of the white perch.

In 1988 laboratory presentations, bay anchovy, and Atlantic menhaden tested positive as potential predators. Consumption of striped bass larvae by bay anchovy increased at higher prey densities to a maximum of 42 larvae/h at prey

densities of 1,650/m^3. Examination of 229 stomachs of bay anchovy collected during peak spawning in 1988 and 1989 provided direct evidence of predation on striped bass eggs and larvae.

The relationship between patterns of survival inferred from the back-calculation of juvenile birthdates were compared with data sets describing predator and prey fields, egg production, food abundance, and changing environmental conditions during the 1988 and 1989 spawning seasons. The physical factors pH, rainfall, dissolved oxygen, and water temperature were measured at 30-minute intervals and observations of predator, prey, egg and larval densities were recorded weekly or semi-weekly.

In 1988, a year of average recruitment, only 11% of the juveniles aged (n=78) were born during the week of peak spawning when over 48% of the eggs were produced. In 1989, a year of high recruitment, the temporal distribution of juvenile hatchdates more closely followed the distribution of eggs with 30% of the juveniles (n=96) born during the week of peak spawning when 40% of the eggs were spawned. Potential fish predators were collected in greater numbers during peak spawning in 1988 (61/100m^3) than during the same period of time in 1989 (12/100m^3). Water temperatures were lower during peak spawning in 1988 (16°C) than during 1989 (19°C). Also, prey items for first-feeding larvae decreased the week following peak spawning in 1988 from an average number of 194

to 74 individuals/l. Lower water temperatures and reduced food densities in 1988 may have produced a combined effect of prolonging developmental stages of striped bass eggs and larvae, thereby making them more susceptible to elevated predator densities.

FACTORS AFFECTING SURVIVAL OF EARLY LIFE STAGES OF STRIPED BASS

INTRODUCTION

The striped bass, Morone saxatilis (Walbaum) is an anadromous fish of extreme commercial and recreational importance along the east coast of the United States. After a severe population decline during the 1970's and early 1980's, the size of the spawning stock in Virginia has increased over the past few years (Olney et al. 1991). Olney et al. (1991) concluded that an increase in abundance of the spawning stock during the period 1980-1989 was partly due to successful management and two years of good recruitment.

Variability in annual recruitment due to the caprices of survival rates of eggs and larvae is believed to be the cause of fluctuations in the size of population of many species of fishes (Cushing 1974, Steele et al. 1980, Houde 1987). Various abiotic and biotic factors, including lethal environmental conditions, starvation, and predation, have been suggested as possible mechanisms which may affect survival rates of fish eggs and larvae thereby controlling recruitment. It is possible that any one of these aforementioned factors could act alone in controlling survival of striped bass early life stages, however, a more probable explanation would invoke complex interrelationships between egg production, larval nutrition, predation and environmental variables. Such interactions are poorly

understood and difficult to quantify (Rothschild 1986).

Several abiotic factors including water temperature, salinity, pH, dissolved oxygen, and toxic contaminants are believed to be important in regulating survival of striped bass eggs and larvae (Setzler et al. 1980, Hall et al. 1984, 1987a). Uphoff (1989) concluded that density-independent environmental variables such as water temperature, rainfall and river flow directly or indirectly affected the survival of early life and the subsequent success of year-classes of striped bass in the Choptank River, Maryland. Although results from in-situ and on-site field studies indicated that low pH in eastern shore rivers and contaminants in the Potomac River may have reduced survival, Hall et al. (1984, 1986, 1987a, 1987b) were unable to isolate a single abiotic factor as a cause for striped bass mortality. Coutant (1987) hypothesized that high water temperatures and low dissolved oxygen in summer habitats of Cherokee Reservoir, TN and the Chesapeake Bay may be responsible for the decline of striped bass observed in these areas. He suggested that gonadal development in stressed fishes may be compromised by using energy reserves for increased metabolic demand.

Starvation has long been considered to be an important source of larval mortality (Hjort 1914). Cushing's (1975) match-mismatch hypothesis suggested that temporal asynchrony of seasonal plankton blooms and spawning contributed to recruitment variability. In a shipboard experiment, Lasker

(1975, 1978) introduced a spatial component to Cushing's (1975) hypothesis by showing that survival of nothern anchovy, Engraulis mordax, was linked to predictable periods of food patchiness and ocean stability. However, relatively small, undeveloped larvae such as the northern anchovy may more susceptible to starvation than larvae that hatch at larger sizes like those of striped bass (Rice et al. 1987b; Miller et al. 1988). Larvae that are large and well developed at hatching may be more resistant to starvation as they have greater energy reserves than smaller, less developed larvae. In addition, food may not be a limiting factor for larvae in well-mixed estuarine habitats. In laboratory studies of the feeding behavior of striped bass, Chesney (1989) found that first-feeding larvae required microzooplanktonic food items such as copepod nauplii and cladocera in densities greater than 50/l. Microzooplankton densities in estuarine waters usually range from 50 to 100 per liter and can exceed 200 per liter (Houde 1978; Hunter 1984). During spring, in the tidal-freshwater portions of the Potomac River, Setzler-Hamilton et al. (1981) reported microzooplankton densities ranging from 25 to 310 l^{-1} in 1976 and 1 to 1,311 l^{-1} in 1977. The lower limits of these microzooplankton densities, however, were below threshold feeding requirements (Chesney 1989) and Setzler-Hamilton et al. (1987) have reported starving larvae in the Potomac. In the open ocean where structure of the water column may

influence the availability of food for larvae, the average density of food items is usually much lower, ranging from 13 to 40 per liter (Hunter 1984).

Striped bass larvae are extremely voracious, raptorial feeders that prey on taxa such as cladocera and calanoid copepods (Setzler-Hamilton et al. 1981; Ruliffson 1984). This species has been found to be highly resistant to food deprivation under laboratory conditions (Martin et al. 1985). Chesney (1989) provided evidence that striped bass larvae could feed, grow and survive under varying adverse conditions of low-light, complete darkness and high turbulence-turbidity situations. Although some evidence of poor nutritional condition was determined for larvae collected by Setzler-Hamilton et al. (1987) in the Potomac and Choptank Rivers, most studies (Daniel 1976; Rogers and Westin 1977, 1981; Beaven and Mihursky 1980; Martin and Malloy 1980; Martin and Setzler-Hamilton 1981; Martin et al. 1985; Setzler-Hamilton et al. 1987) have indicated that starvation alone was not a significant mortality factor for striped bass.

Predation is now believed to constitute the largest component of early life mortality of fishes (Bailey and Houde 1987, Houde 1987), however, few data are available on the potential for predation on striped bass early life stages. Recent mortality estimates averaging 68% d^{-1} on the Pamunkey River, VA (Olney et al. 1991) indicated that

predation on striped bass eggs might be very high and other studies (Dendy 1978, Smith and Kernehan 1981, Monteleone and Houde 1989) have suggested predation on striped bass yolk sac larvae by hydroids, copepods and fishes. However, a detailed knowledge of the predator field to which eggs and larvae are subjected as well as estimates of predation rates are required to better understand the role of predators in survival of early developmental stages of striped bass.

The interactive effects of abiotic and biotic factors can have a pronounced effect on recruitment. As factors such as temperature, pH and food abundance vary, so will growth and metabolic rates of fish larvae (Ware 1982). These physical and biological conditions may increase the risk of larvae to predation by reducing swimming speed and the capability of larvae to escape (Frank and Legget 1982; Rice et al. 1987a). Because the risk of predation is size-dependent (Post and Prankevicius 1987), reduced growth rates of larvae due to poor nutritional condition, low water temperature and or other stressful environmental conditions may cause them to be susceptible to predators. In addition, slower growing larvae may be more vulnerable to predators which are gape-limited (Werner and Gilliam 1984). Similarly, depressed water temperatures, toxic contaminants or pH extremes may prolong the development of eggs thereby increasing the risk of predation to these early life stages.

The overall goal of this study was to examine the

interactive effects of predation, starvation and environmental variables on survival of striped bass early life stages. This dissertation consists of two chapters. The first chapter attempts to fill the current void in the literature on predation studies concerning the early life history stages of striped bass and has been published in Transactions of the American Fisheries Society (McGovern and Olney 1988). This component of the research was designed to (1) identify potential vertebrate and invertebrate predators present on the striped bass spawning grounds, (2) document acceptability of striped bass larvae as prey items in the laboratory, (3) establish consumption rates of yolk-sac larvae by two fish predators under laboratory conditions, and (4) examine stomach contents of potential fish predators collected on the spawning grounds. Chapter 2 incorporated these data on predation to accomplish the overall goal of examining the effects of contrasting biotic and abiotic factors on survival of early life stages of striped bass in the Pamunkey River during 1988 and 1989 and gain insight into the mechanisms of recruitment. Patterns of survival inferred from the back-calculation of juvenile birthdates were compared to data sets describing predator and prey fields, food abundance and changing environmental conditions. Additional goals that were not addressed in Chapter 1 are: (1) test bay anchovy (Anchoa mitchilli) and Atlantic menhaden (Brevoortia tyrannus) as potential

predators of striped bass yolk-sac larvae, (2) measure predation rates of bay anchovy and Acanthocyclops vernalis, and (3) examine stomach contents of bay anchovy collected during peak spawning of striped bass.

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Potential Predation by Fish and Invertebrates on Early Life Stages of Striped Bass in the Pamunkey River, Virginia

A precipitous decline in landings of striped bass Morone saxatilis on the east coast during the last decade and concurrent decreases in young-of-the-year abundance, especially in the Chesapeake Bay have prompted research and regulatory attempts to identify causes of the decline and to control further stock depletion (Goodyear 1985). Although many factors affect striped bass abundance (Setzler et al. 1980), evidence suggests that principal variations in survival occur within the pelagic egg and larval stages (Chadwick et al. 1977; Polgar 1977; Ulanowicz and Polgar 1980; Whipple et al. 1981). Investigations have included attempts to isolate mortality sources through studies of larval starvation (Martin et al. 1985) and of toxic effects of heavy metals and pesticides on larval (Mehrle et al. 1982; Hall et al. 1987a, 1987b). The cumulative evidence is inadequate to identify causes of the decline in striped bass stocks, although preliminary results (Hall et al. 1984, 1985, 1987a) indicate that toxic contaminants on the spawning grounds, particularly in areas exhibiting episodic depression in pH, may reduce survival of eggs and larvae.

Though predation is believed to affect abundance of larval fish (Hunter 1981; Bailey and Houde 1987), the potential effects of

predators on survival of striped bass eggs and larvae have been largely neglected. As a result, probable linkages between predation mortality, nutritional deficiency, and sublethal toxic effects on larval growth are unknown. Although it is likely that both fish and invertebrate species are predators on early life history stages, few studies have documented such interactions. Setzler et al. (1980) speculated that adult and juvenile white perch Morone americana may consume large numbers of striped bass larvae, though direct evidence was not presented. Smith and Kernehan (1981) found the free-living copepod Cyclops bicuspidatus thomasi (=Diacyclops thomasi [Kiefer 1978]) attached to larval striped bass and white perch in the Chesapeake and Delaware Canal. Most larvae had damage that was extensive enough to be fatal. Although Smith and Kernehan (1981) considered the significance of predation to be minimal, they indicated that the actual incidence of predation may have been higher than observed. Reports of predation on striped bass larvae by freshwater sessile polyps (e.g. Craspedacusta sowerbyi; Dendy 1978) are the only additional data available.

In our study, we attempted to (1) determine kinds and relative abundances of potential fish and invertebrate predators of striped bass larvae through field surveys during striped bass spawning periods, (2) document acceptability of striped bass yolk-sac larvae as a prey item through laboratory presentations to fish and invertebrates, (3) establish preliminary estimates of consumption of yolk-sac larvae under laboratory conditions of various prey

densities, and (4) examine stomach contents of target fish predators collected on the spawning grounds.

METHODS

Midwater and bottom trawls and oblique plankton tows were used in surveys of fish, ichthyoplankton, and zooplankton along a 38-km section of the Pamunkey River, from station P-30 at river kilometer (km) 50 (West Point) to station P-53 at km 88 (Pamunkey Indian Reservation near Lestor Manor). This portion of the river brackets the striped bass spawning grounds and was divided into 5-km strata from which stations were randomly selected before each cruise. Plankton surveys to estimate striped bass egg production were conducted twice weekly between 2 April and 14 May 1985 until striped bass spawning activity ceased. In addition, plankton surveys to examine egg distribution with depth were conducted on 23-24 April 1987. Two cruises (15 and 19 April) were selected from among the 1985 samples for identification of zooplankton taxa.

Plankton samples (18 collections) at each station consisted of stepped oblique tows of a 60-cm bongo sampler, equipped with 333-µm-mesh nets. Both nets were metered for volumetric estimates and catches were combined before preservation with 5-8% buffered formalin. Infrequent zooplankton taxa were initially sorted from whole plankton samples, while abundant taxa were sorted from successive aliquots and reported as individuals per cubic meter of water filtered. Calculations of striped bass egg production followed the methods of Houde (1977).

Potential fish predators were collected at 18 stations during 23 April-14 May 1985 by bottom and midwater deployment of a 4.8-m shrimp trawl (24-collections) and a 1.5 X 1.5 square Cobb trawl (23 collections), respectively. Upon capture, specimens were immediately preserved with 5-8% buffered formalin for later identification, enumeration, measurement (standard length), and gut content analysis. Trawl collections were nonquantitative and species occurrence is reported as percent composition of the catch.

In April and May 1986, experimental animals were collected by bottom trawls and plankton tows. A 7.6-m beach seine (at station P-52, km 86) and electroshock (at station P-47, km 78) were used to capture nearshore fishes. Individuals were immediately transported to a field laboratory on the Pamunkey River and acclimated in aerated, static tanks containing 42-525 L of filtered river water.

Individuals of 14 fish species and 4 invertebrate taxa were presented with striped bass larvae in initial experiments designed to test the acceptability of yolk-sac larvae as prey items. We were limited by the availability of fish predators in good condition and, therefore, unable to test various sizes of some species with sufficient replication. Single fishes were acclimated in 3-L or 10-L clear-glass, globe-shaped vessels for 1 h after a 48-h starvation period. Twenty striped bass yolk-sac larvae (hatchery reared) were then introduced into experimental chambers for a 1-h test period during daylight hours. At the completion of each test, the predator was removed and contents of chamber filtered through a 110-μm mesh plankton sieve and preserved in 70%

alcohol for enumeration of surviving prey. Potential invertebrate predators were starved for 12 h after capture. Four individuals of an invertebrate taxon were then placed in a 150-mL watch glass with 10 yolk-sac larvae and observed continuously for 15 min. Observations of attack behavior of the cyclopoid copepod Acanthocyclops vernalis were recorded by a video camera with a 55-mm f/28 lens. Predator-prey interactions were viewed on a monitor and viewed with a video cassette recorder. This system permitted observation of predatory behavior in slow motion. Scanning electron microscopy was used to examine A. vernalis mouthparts and damaged areas on attacked larvae in an effort to determine if wound size matched measured distances between copepod maxillae.

Consumption rates by satinfin shiner Notropis analostanus and spottail shiner N. hudsonius were determined at five prey densities (20, 100, 333, 1,650, and 3,300 larvae/m^3) in 50-L opaque plastic cylinders, with five replicates per density treatment. Test species were acclimated in aerated test chambers for the final 12 h of a 48-h of starvation and tested for 1 h. At the completion of each test, protocol was as described above. Consumption data are reported as number of yolk-sac larvae consumed per predator hour.

To estimate counting error during preparation of prey densities, 8 replicates of 100 larvae were counted, filtered through a 110-µm sieve, and preserved. Postexperimental counting error was estimated by placing 10 replicates of 20 larvae in 50-L test chambers for 1 h (the length of consumption rate experiments). Contents of the vessels were then filtered and preserved.

RESULTS

Potential Fish and Invertebrate Predators on the Spawning Grounds

Striped bass spawning activity in spring 1985 was observed along a 33-km segment of the river from just above West Point, Virginia (km 55), to the Pamunkey Indian Reservation near Lestor Manor (km 88). Egg production estimates based on seven ichthyoplankton surveys (73 samples) indicated that peak spawning activity (>90% of the total egg production) occurred along a 13-km river segment between stations P-39 and P-47 (km 65 and 78, respectively). Severe spring drought in 1985 altered salinity distribution patterns along the lower portion of the river and resulted in absence or reduction of spawning activity between West Point and the vicinity of Sweet Hall marsh. Striped bass eggs are rarely collected in salinities greater than 0.3 0/00 (Setzler et al. 1980; Table 1). During the 1985 sampling period (2 April-14 May), density estimates (numbers/m^3) at positive stations (where eggs occurred) ranged from 0.2 to 2,187.8 eggs and 0.1 to 3.7 larvae. During the 2-d sampling period in 1987 spawning season, egg densities at positive stations ranged from 0.5 to 8.4/^{3} and abundances were not correlated (r^2 = 0.34) with station depth (Figure 1).

Midwater and bottom trawls captures 18 species comprising 6,163 specimens (Table 2). The bay anchovy Anchoa mitchilli and Atlantic menhaden Brevoortia tyrannus were the most abundant species, comprising 58 and 27% of the total catch, respectively. Both species were ubiquitous, occurring in all sampled strata form

stations P-30 (km 50) to P-53 (km 88). Relative abundance of bay anchovies (adults and juveniles) and menhaden (postlarvae and juveniles) varied with increasing distance from the Pamunkey River mouth with percent composition decreasing for bay anchovies and increasing for menhaden. The hogchoker Trinectes maculatus and white catfish Ictalurus catus, though less abundant over the area sampled, were also collected over most of the stations; an additional six species were less common or widespread (Table 2). Beach seining at station P-52 (km 87) April-May 1986 contributed six additional species (satinfin shiner, yellow perch Perca flavescens, tessellated darter Etheostoma olmstedi, pumpkinseed Lepomis gibbosus, bluegill L. macrochirus, and Atlantic needlefish Strongylura marina). Data for the distribution of these species along the 37-km transect are lacking in this study because seine collections were made at only one station (P-52). However, unpublished data (J. Colvocoresses, Virginia Institute of Marine Science, personal communication) indicate that their distribution extends downriver from P-52 within the boundaries of freshwater habitat. In addition, electroshock sampling revealed that several of these species (yellow perch, pumpkinseed, and bluegill) were very abundant within the area of maximum egg production (station P-47).

Habitat preferences and vertical distribution patterns of fishes were suggested by availability to seine and by casual observation. Young centrarchids (Lepomis spp.), yellow perch, and Atlantic needlefish, as well as young and adults of tessellated

darter and satinfin shiner, were captured by seine in shallow and vegetated nearshore zones. These species did not appear in bottom or midwater trawls (with the exception of tessellated darter) along the axis of the deepest portion of the river. Young Atlantic needlefish appeared only in late May after striped bass spawning has ceased and were observed floating motionless in nearshore surface waters. The satinfin shiner was common to very abundant in large nearshore schools throughout the striped bass spawning period (1-27 April 1985). Lepomis spp. and yellow perch juveniles were taken infrequently. Tessellated darters were commonly collected by seine, although they were not as abundant as satinfin shiners.

Fourteen taxa of invertebrates were identified in zooplankton collections. Density ranges of selected species thought to be potential predators of striped bass eggs and larvae are presented in Table 1. Zooplankton taxa were dominated by calanoid copepods, primarily Eurytemora affinis and the cladoceran Bosmina sp. Taxa considered most likely predators of striped bass larvae were cyclopoid copepods (A. vernalis and Mesocyclops edax), the gammarid amphipod Gammarus unifasciatus, the cladoceran Leptodora kindti, water mites (Acarina), insect larvae, and the mysid Neomysis americana.

As with fishes, zooplankton abundance varied along the 37-km transect (Table 1). Peak abundance of calanoid copepods (primarily E. affinis) was observed in the lower portion of the study area and densities decreased with decreasing salinity. Certain taxa (cladocerans, cyclopoids) were found predominantly in less-saline

to fresh water, with peak abundances of these species occurring within areas of maximum striped bass egg and larval abundance. Other taxa (G. unifasciatus, isopods and insect larvae) were consistently collected over all stations, though in low abundance in stations where they co-occurred with early life stages of striped bass.

Laboratory Studies on Predation

Juveniles or adults of nine species of resident Pamunkey River fishes fed on striped bass larvae in laboratory trials (Table 3). These included adult and juvenile satinfin shiner, adult spottail shiner, juvenile white and channel catfish Ictalurus punctatus, adult tessellated darter, juvenile bluegill, juvenile and adult pumpkinseed, adult white perch, and juvenile striped bass. In addition, yellow perch and Atlantic silverside may have taken larvae in initial experiments, but counts of one larva (Table 3) were outside our limits of counting error (see following section). Three species (American eel Anguilla rostrata, hogchoker and Atlantic needlefish) did not accept yolk-sac larvae in laboratory presentations. American eel elvers and hogchokers were hardy and kept living in aquaria for 3-5 weeks, but we could not induce them to feed on yolk-sac larvae despite multiple attempts. We were unable to maintain bay anchovy and menhaden after capture. Juvenile sciaenids, Atlantic croaker Micropogonias undulatus and spot Leiostomus xanthurus, were easily maintained in the laboratory when kept in saline water (1-5%) but we were unable to acclimate

these species to ambient Pamunkey River water.

Of the four invertebrate taxa tested (watermites, Leptodora kindti, Gammarus unifasciatus, and A. vernalis), only the cyclopoid copepod A. vernalis showed any predatory behavior towards striped bass larvae. With the use of a low-light video system, we were able to film and repeatedly observe the attack behavior of A. vernalis in slow motion. After detecting the prey, the copepod oriented itself to the moving larva, rapidly attacked, then fled. An attacked larva reacted by violent thrashing. Occasionally, the copepod grasped a larva but could not remain in contact due to the nature of the prey's reaction. After a larva had been immobilized by one or more attacks, copepods were observed grasp and feed on the dead or dying prey. Scanning electron microscopy of attacked striped bass larvae showed large wounds in various regions of the integument (Figure 2A). Closer examination of one such wound revealed a jagged, roughly torn hole about 100-µm in diameter, with loose skin hanging from the body (Figure 2B). No damage of this nature was observed in any control larvae. Examination of the mouthparts of A. vernalis (Figure 2C) indicated that the distance between maxillae corresponded to the diameter of the striped bass wound.

Consumption rate experiments

Adult satinfin shiners and spottail shiners were selected for use in consumption experiments because of their abundance and availability as well as their hardiness and appetite in the

laboratory. Counting errors during preparation of test densities of striped bass larvae ranged from 1 to 6%. In most tests (63%), larvae were either counted correctly or with a 1% error; in three tests the counting error ranged from 3 to 6 %. Counting errors during filtration and enumeration were slightly higher; however 90% of tests either were counted correctly or had errors less than 5%.

Consumption of yolk-sac larvae by satinfin shiners and spottail shiners increased with increasing prey density to maximums of 81 and 150 larvae per predator per hour, respectively (Table 4). These estimates were considered to be the lower limits because we did not maintain test densities during the test period by continuous addition of larvae. Consumption rates were higher and variability in consumption rate was much lower for replicates of spottail shiner than those of satinfin shiner. At prey densities simulating ambient Pamunkey River conditions (20-100 larvae/m^3), consumption by satinfin shiners and spottail shiners ranged from 0 to 100%.

Gut content analysis

Examination of 235 stomachs of 14 species of fishes collected in the Pamunkey River provided no evidence of predation on striped bass eggs or larvae. Of these, six species readily accepted striped bass larvae in the laboratory (Table 3). Not all specimens examined, however, were taken at times when striped bass eggs or larvae or both were abundant. Fish eggs were found in stomachs of satinfin shiner, white catfish, channel catfish, bay anchovy, and

white perch, but most eggs were those of white perch. However, several unidentifiable larger eggs (>3.0 mm diameter) occurred in the guts of white and channel catfish (Table 5). Eleven invertebrate taxa were identified (Table 5), with amphipods, ostracods, cladocerans, and copepods constituting the most abundant dietary items. Amphipods, polychaetes, and insect larvae were the principal Prey of the primarily benthic feeders (sciaenids, hogchoker, and channel catfish) and were absent or rare in stomachs of water column foragers such as the menhaden and bay anchovy. Planktivory (cladocerans and copepods as significant prey items) was evident in the diets of tessellated darter, white catfish, and satinfin shiner.

DISCUSSION

Our findings, together with those of previous investigators (Dendy 1978; Kohler and Ney 1980; Smith and Kernehan 1981), implicate six fish families (clupeids, cyprinids, ictalurids, percids, centrarchids, and moronids), representing 10 species (blueback herring, satinfin shiner, spottail shiner, white catfish, channel catfish, tessellated darter, bluegill, pumpkinseed, white perch, and striped bass), and at least two invertebrate species (A. vernalis and the hydra Craspedacusta sowerbyi) as potential predators of early life stages of striped bass. Additional taxa should be considered as potential predators on the basis of their abundance on the spawning grounds and our knowledge of their feeding behavior, although documentation of the acceptability of striped bass larvae as a prey item is lacking. These include bay anchovy (Engraulidae), Atlantic menhaden and other clupeids, other percids including yellow perch, inland silverside Menidia beryllina, other cyclopoid species, and insect larvae. Neomysis americana was not abundant on the spawning grounds and not considered a potential predator.

Details of the distribution, abundance, and natural history of these potential fish predators are lacking, but available data suggests that some are common and abundant inhabitants of striped bass spawning grounds. Our data on midwater and bottom trawl catches from the Pamunkey River agree with previous surveys of tidal freshwater rivers in Virginia (Massman et al. 1962).

Although Alosa spp. larvae were abundant in our plankton samples, juvenile alosids (reported to be predators of white bass larvae by Kohler and Ney 1980) generally peak in abundance during midsummer. Although few data are available on small-scale distribution patterns of these potential nearshore predators, our data indicated that eggs were randomly distributed with depth, some occurring as shallow as 2 m. Thus, cyprinid, percid, and centrarchid species limited to nearshore habitats may have the opportunity to feed on early life stages of striped bass.

At least six cyclopoid copepod species are abundant on striped bass spawning grounds in the Chesapeake Bay region and may be predators of striped bass larvae. Burbidge (1972) found A. vernalis and Eucyclops agilis in the James River, although E. agilis occurred above areas of normal striped bass spawning activity. Eucyclops agilis has also been reported from upper Chesapeake Bay (Grant and Berkowitz 1979). Diacyclops thomasi was collected in the Chesapeake and Delaware Canal (Smith and Kernehan 1981). Mesocyclops edax, and abundant copepod in the Pamunkey River (Wass 1972) has been included in a list of predators of larval fish in Lake Erie (Davis 1959). In addition, Wass (1972) lists Halicyclops fosteri and Mesocyclops leukardti (=M. americana Dussart 1984) as Pamunkey River inhabitants.

Direct evidence of natural predation by fishes on striped bass eggs and larvae was lacking, but our data, together with published accounts, revealed generalized feeding habits or planktivory by some species implicated as potential predators (Tables 3, 5). As

a result, the likelihood of predation by these species on striped bass early life stages would presumably increase during periods of peak spawning and larval abundance. Our examination of stomach contents of field-collected fishes indicated that satinfin shiner, tessellated darter, white catfish, and channel catfish fed on a wide variety of prey items. Furthermore, unidentified eggs within the size range of those of striped bass were recorded in the stomachs of ictalurids and white perch. Bluegill and pumpkinseed prey on a wide variety of organisms including small fish and fish eggs (Bailey and Harrison 1948; Seaburg and Moyle 1964; Goodson 1965; Keast and Webb 1966; Scott and Crossman 1973). White catfish have been found with insect larvae and fish in their stomachs, but they also consume other items including fish eggs (Steven 1959; Goodson 1965). Satinfin shiners have been described briefly as feeding principally on insects (Lee et al. 1980) but our results do not confirm these findings. Although bottom feeding is more characteristic of channel catfish, food is also taken at the surface, especially by younger fish (Scott and Crossman 1973), and R. Rulifson (East Carolina University, personal communication) has identified remains of Morone sp. in ictalurid stomachs from the Roanoke River, North Carolina.

Cannibalism and predation by moronid larvae or juveniles have been suggested as important sources of mortality of striped bass. For example, Boyton et al. (1981) found that larval fish replaced insect larvae as the dominant food item of juvenile striped bass (25-100 mm standard length) in some areas of the Potomac River,

Maryland, suggesting that slow-growing or late-spawned striped bass larvae might be cannibalized. Our observations of predation on yolk-sac larvae by 29-d old striped bass (15-18 mm standard length) suggest that cannibalism could occur within the duration of a normal spawning season.

Given the abundance of juvenile bay anchovies in midchannel areas of the Pamunkey River (Table 2, 3) and considering their laboratory predation rates on larval sea bream Archosargus rhomboidalis reported by Dowd (1986), bay anchovy may be a key predator on fish eggs and larvae, including striped bass, in tidal freshwater systems. Finally, we are not aware of feeding studies of young yellow perch or Atlantic silverside and our limited data on menhaden indicated high selectivity for cladocerans. Consequently, we cannot comment on the potential of these three species as predators of striped bass early life stages.

The lack of field confirmation of laboratory results may be due to inadequate sample size, absence of natural predation, absence of temporal and spatial coincidence of potential predators and prey, egg and larval densities below threshold values necessary for successful prey encounter, or rapid digestion of soft-bodied prey. Rapid digestion rates (estimated to be 30 min) and regurgitation of sea bream larvae by juvenile bay anchovy have been recently observed in laboratory experiments (Dowd 1986). On the other hand, lack of consumption in laboratory preparations (Table 3) is difficult to evaluate and does not necessarily imply that striped bass larvae can be excluded as an acceptable prey item of

the fish we tested. Restricted movement in experimental chambers, starvation, and handling may have produced stress that biased our observations.

Finally, the abundance of the cyclopoid copepod A. vernalis (10-651 individuals/m^3) on the spawning grounds suggests that a high probability of predatory encounter is likely in patches with high densities of striped bass larvae. Small-scale aggregations (centimeters to meters) of eggs or larvae are not presently known to exist in the environment of larval striped bass, although density data from replicate plankton tows filtering large volumes can be quite variable (Conte et al. 1979). The application of automated sampling techniques (Ortner et al. 1981) to measure scales of patchiness in tidal freshwater systems may be useful in assessing the relative importance of cyclopoid predation to survival of striped bass larvae (Smith and Kernehan 1981).

Table 1.- Density ranges (number/m^3) of striped bass eggs and larvae and potential predators collected at nine stations on the Pamunkey River, 15 and 19 April 1985, and average temperature and salinity at each station. Plus signs (+) indicate values less than 0.1. Blanks indicate organisms were not taken at that station.

Organism and measurement	Station P-31	P-34	P-37	P-40
		Densities		
Striped bass eggs			+	+-1.6
Striped bass larvae		+		0-3.8
Calanoid copepods	2,562.7-6,349.4	1,421.3-11,672.7	1,180.5-3,110.4	3,054.8-4,614.4
Cyclopoid copepods				
Acanthocyclops vernalis			0-27.0	0-55.0
Mesocyclops edax			0-18.0	
Clacocerans		+	0-43.7	+-655.1
Leptodora kindti				
Amphipods	2.2-32.1	1.3-1.5	0.1-183.5	4.9-626.6
Mysids				
Neomysis americana	108.0-130.9	0.6-3.4	23.2-174.7	+-27.8
Water mites	+	+-0.5	+	+
Insect larvae	+	+	+-0.4	0-10
		Water characteristics		
Average temperature (C)	16.2	16.3	16.2	16.2
Average salinity (0/00)	7.7	5.5	3.8	1.4

Table 1.- Extended

Organism and measurement	Station P-43	P-46	P-49	P-52	P-55
			Densities		
Striped bass eggs	0.2-3.6	0-21.2	1.3-6.2	+-0.2	+
Striped bass larvae	0.2-0.4	2.1-2.2	0.6-0.7	+-0.9	
Calanoid copepods	275.1-742.2	211.2-589.9	32.3-2,512.3	22.6-975.9	6.2-61.2
Cyclopoid copepods					
Acanthocyclops vernalis	19.9-21.5	115.5-136.9	58.5-650.7	97.3-224.0	9.4-49.6
Mesocyclops edax	0-5.0	1.9-7.3	5.7-128.4	27.2-28.0	1.6-8.0
Clacocerans	11.7-171.3	160.7-685.9	756.9-1,691.5	355.1-752.2	67.3-217.2
Leptodora kindti		0-16.5	17.8-58.0	0-30.5	12.9-18.6
Amphipods	16.6-108.6	7.2-59.0	10.0-49.7	10.5-125.4	0.5-1.8
Mysids					
Neomysis americana	0-6.5	+			
Water mites	0.4-2.7	+-0.2	0.4-1.1	0.2-0.4	0.2-1.6
Insect larvae	0.5-2.6	0-0.3	+-1.2	0.3-0.6	+-0.2
			Water characteristics		
Average temperature (C)	16.2	16.5	16.6	17.4	18.3
Average salinity (0/00)	0.5	0.1	0.1	0.1	0.1

TABLE 2. Percent composition of fishes captured by all gears on a 23-mile transect of the Pamunkey River, Virginia, April - May 1985. Station designations are mid-points of three mile strata. Asterisks indicate percentage values less than 1.0.

TAXA	STATION NUMBER							
	P-34	P-37	P-40	P-43	P-46	P-49	P-52	P-55
Bay anchovy	96.0	91.0	53.5	60.5	26.6	66.1	17.2	13.8
White catfish	*	*	1.5	1.8	2.6	2.1	4.0	*
Atlantic menhaden	2.6	*	23.5	15.9	52.1	24.4	64.4	79.8
Hogchoker	*	5.7	14.3	4.8	14.9	4.2	8.0	4.6
Channel catfish			*	*	1.9	*	*	
Atlantic croaker	*	*	3.8	4.3	1.1	1.0	*	
Spot	*	*	2.5	11.6	*			
White perch	*	2.0	*	*	*	*	2.3	
Striped bass				*	*	*	*	
Spottail shiner						*	1.1	
Others	*		*	*	*	*	*	*
Number of specimens collected	1196	659	840	775	734	829	1021	109

Table 3.-Consumption of larval striped bass during initial presentations of prey to potential fish predators. Species are ranked in decreasing order of number of prey eaten. Asterisk indicates fish collected for gut analysis.

Potential predators			
Species	Length (mm)	Number of individuals tested	Prey consumed per individual
Spottail shiner*	82-93	4	19;18;19;19
Bluegill	37-90	4	15;8;20;20
White perch*	60-125	4	16;20;15;12
Pumpkinseed	39-120	4	20;20;20;0
Channel catfish*	63-98	5	0;18;12;14;0
Satinfin shiner*	44-73	5	0;10;10;4;2
White catfish*	50-95	5	10;0;8;0;7
Striped bass	15-18	4	4;2;7;3
Tessellated darter*	58-60	4	4;1;8;2
Inland silverside	70	2	1;0
Yellow perch	110-150	3	1;0;0
Atlantic needlefish	47-52	3	0;0;0
Hogchoker	48-50	5	0;0;0;0;0
American eel	40-70	5	0;0;0;0;0

Table 4.-Mean rates at which satinfin shiner and spottail shiner preyed on striped bass yolk-sac larvae at various prey densities.

Prey density (number/m^3)	Mean number of larvae consumed per hour (range)	Mean percentage of prey items consumed
	Satinfin shiner	
20	1.0 (0-1)	60
100	4.4 (4-5)	88
333	15.0 (8-17)	88
1,650	37.5 (2-65)	45
3,300	40.6 (8-81)	24
	Spottail shiner	
20	2.0 (2-2)	100
100	2.8 (2-5)	56
333	14.8 (14-16)	92
1,650	82.2 (81-83)	99
3,300	108.7 (80-150)	65

Table 5.-Stomach contents of fishes collected in the Pamunkey River, Virginia, April and May 1985-1986. Values are percentages of total contents (by number) observed for each prey category.

Prey taxon	Satinfin shiner (N=18)	Spottail shiner (N=12)	White catfish (N=60)	Channel catfish (N=13)	Atlantic menhaden (N=11)	Bay anchovy (N=24)	Tessel-lated darter (N=12)	White perch (N=4)	Atlantic croaker (N=32)	Hogchoker (N=9)
Fish eggs	4		28	38	<1			3		
Amphipods	4		47	30		<1	18	96	98	53
Ostracods	46	68		2	<1	<1	2			
Insects	4	22	1	25		<1	3		1	16
Water mites	1			<1						
Bivalves	8	10	1	<1			1			
Gastropods	<1					<1	2			
Cladocerans	30				99	16	35			
Copepods	1		23		<1	84	18			
Polychaetes							22			29
Isopods			<1	5				1		2
Mysids				<1					2	

Figure 1.-Scatter diagram of striped bass egg density versus depth for samples taken 23-24 April 1987 on the Pamunkey River, Virginia.

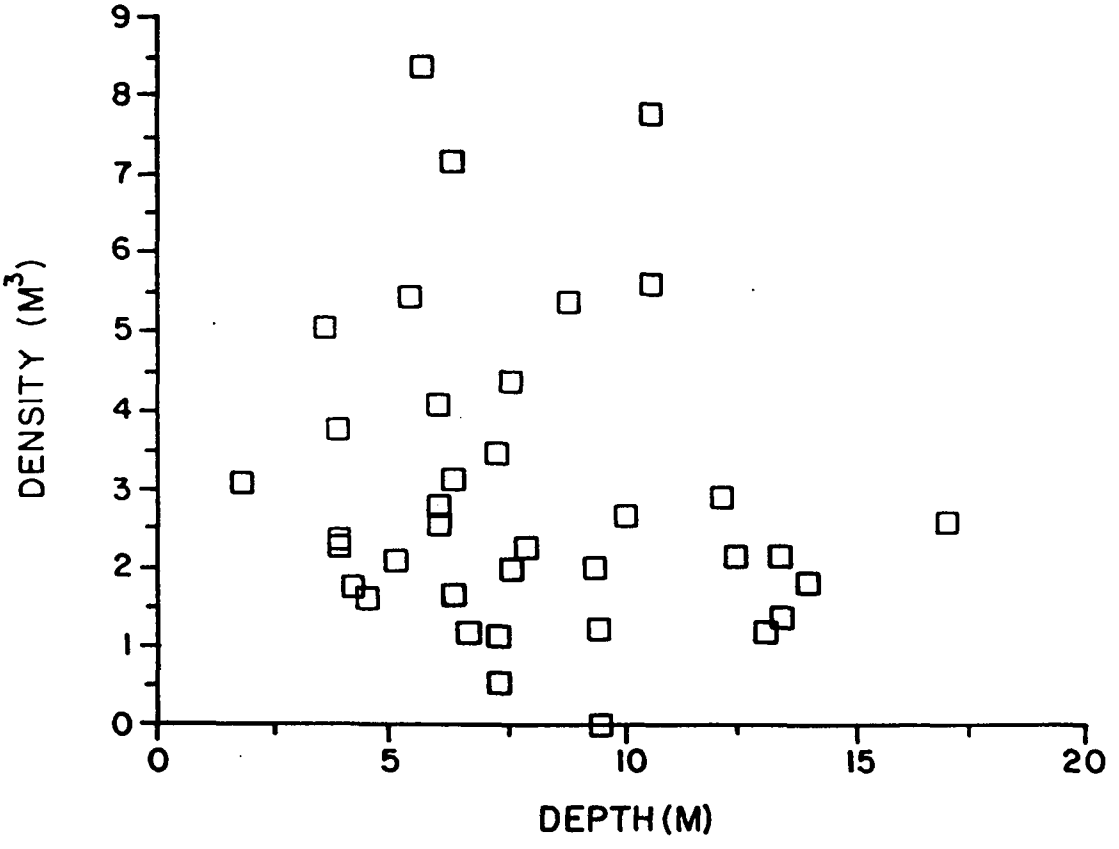
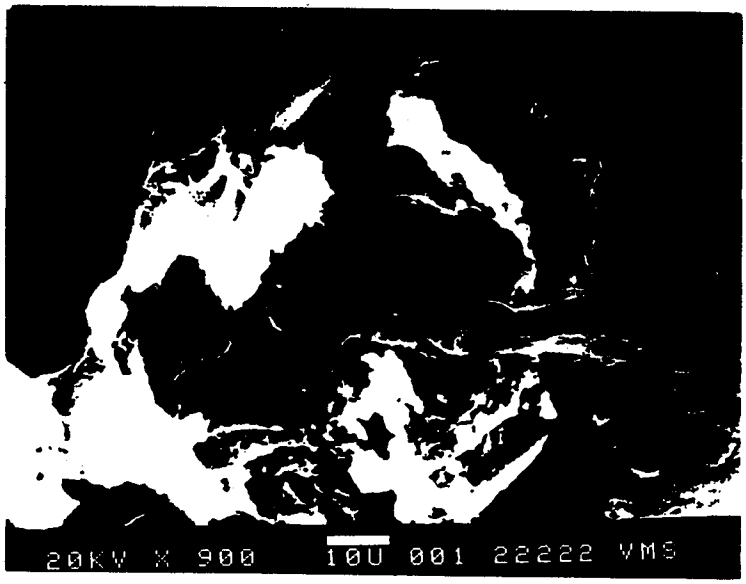

DENSITY (M^3)
9
8
7
6
5
4
3
2
1
0
0
5
10
15
20
DEPTH (M)

Figure 2.-**A**: Photomicrograpgh of head region of a striped bass yolk-sac larva damaged by the cyclopoid copepod Acanthocyclops vernalis. Wounds (W) are visible on head and nape of neck. **B**: Cloe-up of neck wound (panel A), showing irregular edge. White material is abraded tissue. **C**: Mouth parts of A. vernalis. White bars represent 100 µm in A and C and 10 µm in B.


A
20KV X180 100U 003 22222 VMS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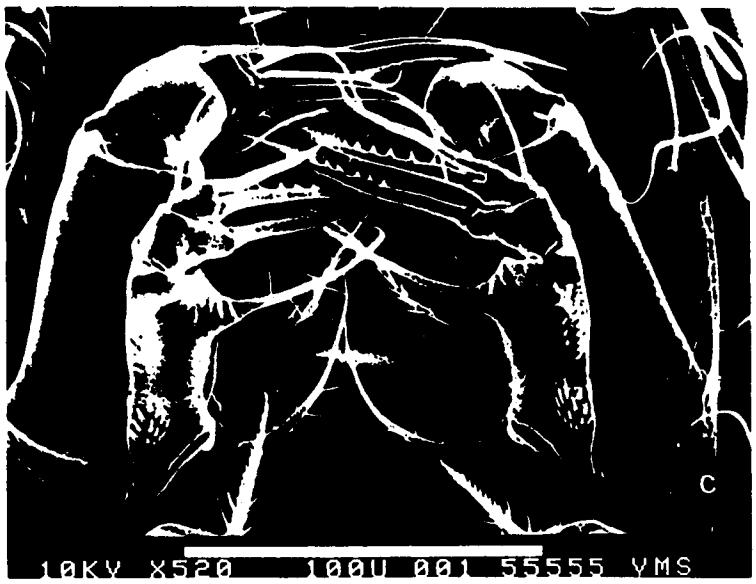
C
10KV X520 100U 001 55555 VMS

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PHYSICAL AND BIOLOGICAL FACTORS AFFECTING SURVIVAL AND RECRUITMENT SUCCESS OF STRIPED BASS, *Morone saxatilis*

INTRODUCTION

Many studies have included estimates of mortality rates of striped bass eggs or larvae (Dahlberg 1979, Stauffer and Picquelle 1981, Alheit 1986, Leak and Houde 1987, Olney et al. 1991) and demonstrated the potential effect of variability in mortality rates on recruitment (Houde 1987, 1989). However, some investigators (Rice et al. 1987; Miller et al 1988) have suggested that average mortality rates may contain less information than an analysis based on individual survivors. Since most fish eggs and larvae die during the first week of life, it may be more informative to determine how survivors differ from other fish spawned, or if birthdates of survivors co-occur with any biological or physical conditions that help explain their success (Fritz et al. 1990). Several studies (Methot 1983; Crecco and Savoy 1985; Rice et al. 1987) have used otolith analysis to compare patterns of growth and the distribution of hatchdates of individuals that survived the rigors of early development with abiotic and biotic variability during the spawning season. These investigations have provided some evidence of recruitment mechanisms that appear to explain why certain individuals from a cohort may survive.

Back-calculation of hatchdates by examination of daily growth rings on otoliths was used by Methot (1983) to determine seasonal patterns of recruitment variability in the northern anchovy, Engraulis mordax. The method was intended to test a corollary of Cushing's (1975) match-mismatch hypothesis that larvae hatched during favorable environmental conditions constituted most of the year-class. Methot (1983) reported that while abundance of larvae of northern anchovy was greater in 1979 than in 1978, survival of juveniles was greater during April and May of 1978 than during the same period in 1979. This interannual difference was reflected in the fishery since catch data indicated that the 1978 year-class was twice as large as the 1979 year-class. Methot (1983) did not measure ambient conditions during the spawning seasons and was able only to speculate on factors affecting observed temporal patterns of recruitment.

Crecco and Savoy (1985) compared birthdates and growth rates of larval and juvenile American shad, Alosa sapidissima, with biological (zooplankton abundance) and physical factors (river flow and water temperature) in the Connecticut River. They found that survival was low for cohorts hatched early in the spawning season (May 21-June 12), but rose among cohorts hatched later (June 21- July 6) when river flows were low and water temperatures and zooplankton densities were high.

Mechanisms regulating survival of larval bloaters, Coregonus hoyi, in Lake Michigan were examined by comparing characteristics of survivors during the first two months of life with various attributes of larvae (Rice et al 1987). Otoliths were examined to determine ages, periods of stress, dates of first-feeding (a close approximation of hatchdate) and average growth rates of larvae from hatching to two months. Differences between first-feeding dates of newly hatched and one-month old larvae indicated that those hatched early in the spawning season experienced higher initial mortality than late-hatching larvae. Early-hatched larvae grew half as quickly during their first three weeks of life and had a higher frequency of stress marks on otoliths than those hatched later. These data suggested that growth-dependent mortality factors such as predation may have been an important mechanism affecting recruitment.

The otolith analysis method employed by Methot (1983), Crecco and Savoy (1985), and Rice et al. (1987) may offer some insight into the mechanisms responsible for variable recruitment of striped bass. Although the size of the spawning stock has increased during the past few years in Virginia waters (Olney et al. 1991), an study of recruitment mechanisms may help to elucidate causes of fluctuating population abundance. Striped bass have historically undergone distinct patterns of alternating high and low abundances at fairly regular intervals (Koo 1970). Periods

of abundance have usually been attributable to a single, very large year class (Merriman 1941) that dominated landings for a considerable period of time. In addition, Olney et al. (1991) found that recruitment was poorly related to egg production and spawning biomass. This evidence suggests that despite the present abundance of striped bass, high recruitment will still probably be a rare event. The present study is intended to help identify some of the factors and their interactions responsible for patterns of striped bass population dynamics.

The primary objective of this study was to compare the frequency distribution of hatchdates of juvenile striped bass with various physical and biological data collected during the early developmental period of the survivors. In order to examine the utility of the hatchdate method (Methot 1983, Crecco and Savoy 1985 and Rice et al. 1987) to determine factors affecting survival, two spawning seasons (1988 and 1989) were selected, each representing contrasting patterns of recruitment. To better understand the predation component of striped bass survival, additional goals of this study involved field and laboratory experiments with bay anchovy, Atlantic menhaden and the cyclopoid copepod, Acanthocyclops vernalis.

METHODS

Study site

The study site was located on the Pamunkey River, VA, above the York River, along the western shore of the Chesapeake Bay (Fig.1). Data were collected within a 35-km section from river kilometer (Rkm) 53 to Rkm 88, a section encompassing historical spawning grounds (Grant and Olney 1991, Olney et al. 1991).

Laboratory experiments on predation

Bay anchovy and Atlantic menhaden were presented with striped bass yolk-sac larvae under laboratory conditions. Fishes were collected at night in the York River at the Virginia Institute of Marine Science with a 202 µm Hansen net and transferred to aquaria containing filtered York River water. Salinities were gradually reduced to 1-2 $^{\circ}/_{oo}$ over a series of days. Individual predators were acclimated in 18.96-l aquaria for 1-h after a 48-h starvation period. Forty striped bass larvae (hatchery reared) were then placed in the aquaria for a 1-h test period. At the completion of each test predators were removed, contents of aquaria were filtered through a 110-µm mesh plankton sieve and remaining prey were counted. Consumption rates of bay anchovy were determined following methods described in Chapter 1. Mortality rates of striped bass larvae in experiments were estimated using the equation: $N_t=N_0\ e^{-zt}$

Where: N_t= the number of larvae at time t; N_0= the initial number of larvae; -Z= the instantaneous mortality rate; and t= 1 day.

To measure predation rates of A. vernalis, trials were carried out using groups of 1, 5, 10, 20 and 30 adult A. vernalis, each presented with 20 striped bass yolksac larvae as prey in 1-l jars for a period of 24 h. Three replicates and one control were used for each density treatment. Dead larvae were removed from experimental chambers every 2 h. At the end of the experiment, the contents of the 1-l jar were filtered and surviving prey counted.

Field assessment of predation

Gut content analysis of bay anchovy was conducted to provide direct evidence of predation on striped bass eggs and larvae. Bay anchovy collected by push-net (see following section) from three cruises during peak spawning in 1988 (26 April, 1 May, 8 May) and 1989 (24 April, 2 May, 8 May) were dissected. Each stomach was removed, placed in a petri dish and teased open. Food items were identified to the lowest possible taxon, enumerated and expressed as a percent of total number of organisms consumed per anchovy. In addition, taxa of microzooplankton collected by pumps from three cruises in 1988 (25 April, 27 April, 8 May) and 1989 (26 April, 3 May, 8 May) were compared with the diet of

bay anchovy (see following section for details of microzooplankton sampling and sorting).

Assessment of survival

Field collection: A 60-cm bongo sampler with 335-µm mesh nets was used to estimate densities of striped bass eggs and larvae as well as the cyclopoid copepods A. vernalis and Mesocyclops edax during spring 1988 and 1989. Collections were obtained twice a week from the beginning of April until the end of May. Both nets were equipped with flow meters for volumetric measurements and catches were combined and preserved in 5-8% buffered formalin.

Food for first-feeding larvae was collected weekly by pumping 20-l of water through a 63-µm mesh sieve. The pump was deployed in a continuous oblique fashion until the required amount of water had been filtered. Collections were placed in 50-ml jars and preserved in 5-8% buffered formalin.

Potential fish predators were collected weekly, at night with a bow-mounted push-net (Kriete and Loesch 1980). The push-net was a 5.2-m long, 1.5 X 1.5-m modified Cobb trawl with 1.9-cm stretch mesh in the body, 1.27-cm stretch mesh in the cod end and a 10-mm cod end liner. The push net frame was metered for volumetric measurements. Immediately after capture, specimens were preserved in 5-8% buffered formalin, and taken to the laboratory.

Juvenile striped bass were collected at three stations on the Pamunkey River (km 68, 73, 85) by the Virginia Striped Bass Seine Survey biweekly during July through September of both years with a 30.5m long, 1.2m deep, 0.6cm bar mesh minnow seine (Colvocoresses 1989). In addition, collections were made with a 4.9m semi-balloon otter trawl during June 1988 and 1989. Striped bass were preserved in 10% buffered formalin for one day, rinsed with water, and transferred to 45% isopropanol or 70% ethanol until otoliths were removed.

An environmental station located within the spawning grounds of the Pamunkey River (Rkm 63 in 1988 and Rkm 78 in 1989) was used to measure physical variables including pH, dissolved oxygen, water temperature, salinity and rainfall. All data were recorded on a data logger which was programmed to collect information every 30 min from the end of March to the beginning of June of both years. Data were transferred to a computer diskette weekly and sensors were recalibrated. In addition, salinity and temperature were measured along the length of the Pamunkey River spawning grounds during 1988 and 1989 ichthyoplankton cruises.

Laboratory procedures: Plankton collections from the 60-cm bongo nets were sorted for striped bass early life stages and cyclopoid copepods. Striped bass eggs and larvae were sorted from whole samples, whereas A. vernalis and M. edax

were removed from successive splits ($^1/_2$ - $^1/_{1024}$). Densities of striped bass eggs and larvae were reported as number $100m^{-3}$, cyclopoid copepods as number m^{-3}. Egg production estimates for the Pamunkey River in 1988 and 1989 were obtained from Olney et al. (1991).

Microzooplankton from pump collections were identified and counted in a 2-ml subsample taken with a Stempel pipette. Densities were reported as individuals per liter of water filtered.

Fishes taken in push-net samples were identified, counted and measured (standard length in mm). Water volume filtered was determined for each sample and densities were expressed as the number $100m^{-3}$.

Otoliths from juvenile striped bass were removed, embedded in Spurr's medium (Spurr 1969), cut with an Isomet saw, ground to the primordium using 400 and 600 grit sandpaper and polished (Haake et al. 1982). Otoliths were read at least twice (non-consecutively), with the aid of a video system consisting of a camera and a compound microscope interfaced to a computer. Reading pairs were discarded if differences were large (>10%). A value of three was added to the mean increment count to compensate for the delay in deposition of the first otolith ring (Jones and Brothers 1987). Light microscope readings accurately reflected age up to 80 days after which a correction factor was necessary (Kline 1990). One day was added to the age of

fishes 81-88 days old, two days to fishes 89-100 days old and three days to fishes aged 101-110 days. Fishes older than 110 days were not included in analysis as Kline (1990) found that they could not be reliably aged. Growth rates of individual fishes were determined from the equation:

$$GR = (SL - 3.1 \text{ mm}) / AGE$$

where: GR is the average growth rate (mm d^{-1}) for a fish during its life and SL is the standard length of the fish in mm. A value of 3.1mm was subtracted from the standard length to account for the size of the larva at hatching (Kline 1990).

Data analysis: A modification of the egg production model of Olney et al. (1991) was used to calculate an estimate of larval production during both years. For the present purpose, it was assumed that daily mortality rates of larvae (-Z) ranged from 0.08 to 0.39 averaging 0.20 (Houde et al. 1989). This average value was used in Olney et al.'s (1991) equation 3 for the calculation of egg production:

$$P_j = \left(\frac{n_j}{e^{-zt}}\right) x\, V_j \qquad (3)$$

Where: P_j= estimated total number of larvae in stratum j; n_j= number of larvae per m^3 of river water at station j; V_j= volume of stratum j in m^3; Z= instantaneous rate of mortality; t= 0.5d.

It was also assumed that the median size of larvae was 5mm total length since Uphoff (1989) found that striped bass larvae collected by plankton gear ranged from 3.0 to 8.0 mm TL. Grant and Olney (1991) reported that the modal length of larvae collected by bongo nets in the Pamunkey and Mattaponi was 5mm notochord length. Using an average growth rate of 0.29mm d^{-1} (Houde et al. 1989) larvae would be susceptible to plankton collection gear for 17.2 days ($^{5mm}/_{0.29mm/d}$=17.2 d). This value (17.2 days=d_i) was incorporated into Olney et al.'s 1991 equation 5:

$$S_{P_i}^2 = D_i^2 \sum_{j=1}^{k_i} \frac{V_{ij}^2 S_i^2}{d_i^2} \qquad (5)$$

Where: S_p^2= the variance estimate on the abundance of larvae collected during the period represented by the cruise; D_i= number of days represented by cruise i, defined as the day of the cruise plus one-half the days since the last cruise plus one-half the days until the next cruise; V_{ij}= volume of the j^{th} stratum on the i^{th} cruise; S_i^2= the variance estimate for the

number of eggs/m^3 of river water for cruise i; K_i = number of stations included in the variance estimate for cruise i; d_i= duriation in days larvae are susceptible to the plankton gear. No other modifications were made to the model (Olney et al. 1991) to estimate production of larvae.

Between week and within week variability were examined for the physical (water temperature, dissolved oxygen, pH, salinity) and biological factors (densities of eggs, potential fish predators, cyclopoid copepods, microzooplankton) collected during 1988 and 1989. Prior to analysis, data were partitioned into weekly time periods, $\log_{10}$-transformed, and then tested for between week variability using Analysis of Variance (SAS). The Kruskal-Wallis test was used in place of ANOVA for nonnormal data after transformation. The mean and coefficient of variation (CV) were also calculated on data pooled by week to examine within week variability. Salinity was not included in analysis since the STD employed in 1989 did not accurately measure values $<0.8°/_{oo}$ along the length of the river.

RESULTS

Laboratory studies on predation

Bay anchovy and Atlantic menhaden fed on striped bass yolk-sac larvae in laboratory experiments (Table 1). Three of five Atlantic menhaden consumed 10 to 65% of available prey

during the trial period, and the remaining two fishes ingested no larvae. As prey density increased, the consumption of yolk-sac larvae by bay anchovy increased to a maximum of 42 larvae h^{-1} at densities of 1650 m^{-3}. Instantaneous mortality coefficients ranged from 0.14 at densities of 3300 larvae m^{-3} to 0.36 at densities of 20 larvae m^{-3} (Table 2). At the highest prey densities tested (1650 m^{-3}, 3300 m^{-3}) anchovies consumed an average of 22.4 larvae h^{-1}.

Predation rate experiments with A. vernalis and striped bass larvae, showed that as predator density increased, more yolk-sac larvae were killed. The maximum number of deaths (13 yolk-sac larvae) occurred at a density of predators at 30 copepods/l and corresponded to an instantaneous mortality coefficient (Z) of -1.04 (65% d^{-1}) (Table 3, Fig. 2). Mortality in control experiments varied from 5 to 25% d^{-1} and occasionally exceeded experimental mortality. Mean control mortality was 16% d^{-1}.

Gut content analysis: Direct evidence of predation on striped bass eggs and larvae was derived from examination of 229 stomachs of bay anchovy collected by the push-net in 1988 and 1989. Striped bass eggs made up 0.01% of the diet (by number) of bay anchovies collected during peak spawning in 1988 and occurred in 4% of the stomachs examined. These eggs were well digested and late stage embryos were the only remaining components. Fish larvae constituted 0.4% of the gut contents

of bay anchovy collected during 1989 peak spawning and occurred in 7% of bay anchovy stomachs. However, most larvae were too digested for positive identification. Based on descriptions by Olney et al. (1983), two specimens were determined to be Morone spp.

The diet of bay anchovy was very similar to the composition of plankton (Table 4). Twelve invertebrate taxa were identified in bay anchovy guts and plankton samples during 1988 and 1989. Ostracods, gastropods and insects occurred in higher proportions in anchovy guts than in the plankton; harpacticoids and adult copepods were observed less frequently. Plankton samples and bay anchovy gut contents consisted primarily of cladocera and copepodites. Relative proportions of cladocera and copepodites were similar between anchovy gut contents and plankton samples for a given year. Cladocera and copepodites comprised 87.3% of the total number of individuals in 17 samples of the plankton during peak spawning of striped bass in 1988. These taxa made up 82% of the gut contents of bay anchovies (n=134) during the same period of time. In 1989, 88.1% of the zooplankton (20 samples) contained cladocera and copepodites and represented 68.4% of bay anchovy gut contents. Fish larvae constituted 0.4% of the organisms in anchovy guts from 1989 and striped bass eggs made up 0.01% of the gut contents of bay anchovy collected during peak spawning in 1988.

Assessment of survival

Egg and larval abundance: Thirty-one ichthyoplankton cruises were conducted during spring 1988 and 1989 to determine the time, location and magnitude of striped bass spawning. Spawning in 1988 occurred along a 29-km segment of the river from Rkm 59 to Rkm 88 (Fig. 3). Estimates of egg density estimates from the analysis of 81 samples taken during 13 ichthyoplankton cruises indicated that peak spawning activity (>100 eggs/100m^3) was in a 19-km segment of the river from Rkm 65 to Rkm 84. Highest densities of larvae were also found in this section of the river (Fig. 3). In 1989, striped bass eggs were collected in a larger portion of the river (35-km) from Rkm 53 to Rkm 88 (Fig. 4). Data from bongo collections (18 cruises; 115 collections) made in 1989 showed that peak spawning activity was displaced down river from that of 1988, to an 11-km section from Rkm 59 to Rkm 70. Greatest densities of larvae in 1989 were in a larger section of the river than larvae (19-km) from Rkm 58 to Rkm 77. Although, total egg production was very similar in 1988 (2.66 X 10^9) and 1989 (2.29 X 10^9), more larvae were produced in 1989 (1.56 X 10^9) than in 1988 (1.73 X 10^8) (Fig.5). Egg mortality, based on total egg and larval production was estimated to be 93.5% d^{-1} in 1988 and only 31.9% d^{-1} in 1989. In 1988, only 1.66 X 10^6 larvae were produced one week after peak spawning (8 May) when egg production was estimated at 7.02 X 10^8. In contrast, the

production of larvae (3.92×10^8) was greatest the week following peak spawning in 1989.

Variability in physical parameters: Spawning activity was closely related to water temperature during both years. In 1988, striped bass eggs were collected on the first cruise (4 April) when water temperature was 19°C (Fig. 6). Spawning declined dramatically between 10 and 20 April as water temperatures fell to 12°C (Figs. 6, and 7). A very large peak in spawning activity occurred on 1 May when 822 eggs/100m^3 were collected at water temperatures of approximately 16.5°C. In 1989, eggs were also collected the first week of April when water temperatures rose rapidly to about 16°C (Fig. 6). Above Rkm 78, spawning ceased on 14 April 1989 when water temperatures fell below 12°C (range = 11.1 to 11.5°C; Figures 4 and 7), however, it continued in the lower part of the spawning grounds where water temperatures ranged from 12.4 to 12.8°C. The temporal distribution of egg densities was more normally distributed in 1989 than in 1988 (Fig. 6); with the highest densities of eggs coinciding with water temperatures > 18°C.

Temporal fluctuations in water temperature during the spawning season were great in 1988 and 1989 (Figs. 6 and 7). Water temperature unseasonally rose to 19°C on 4 April 1988 and declined steadily to 12°C on 15 April. This was followed by a gradual warming trend to 16°C on 1-8 May when peak

spawning occurred and remained there until 8 May. Water temperatures then rose to 25°C by 26 May. A similar trend was observed in the beginning of April 1989 when water temperature rose quickly, reached 16°C on 6 April and fell to 12°C by 12 April. However, unlike the trend of 1988, water temperatures then rose steadily to 19°C coinciding with peak spawning. After peak spawning, the water cooled to 15°C on 15 May and then warmed steadily for the rest of the month. Mean monthly water temperatures were lower in April 1988 (14.9°C) than in April 1989 (15.4°C). Average water temperatures higher in May 1988 (19.5°C) than in May 1989 (18.0°C).

Salinity decreased with increasing distance from the mouth of the Pamunkey River (Fig. 8). Salinity was less than 1 $°/_{oo}$ above Rkm 63 in 1988 and Rkm 64 in 1989. The lower limit of spawning during both years followed the 1 $°/_{oo}$ contour and was displaced downriver in 1989 from the 1988 area of spawning (Figs. 3 and 4). No striped bass eggs and 9 striped bass larvae (7 at one station) were taken in 12 collections during 1988 and 1989 with salinities >1$°/_{oo}$. Data from the 1988 environmental station (located at RKM 63) showed tidal variability with salinity > 2$°/_{oo}$ to as high as 5 or 6 $°/_{oo}$ during late flood and approaching 1$°/_{oo}$ or less during late ebb (Fig 9). Between 13 and 15 April 1988, salinity exceeded the usual extremes observed during the spawning season and reached 11$°/_{oo}$. In contrast, salinity at the environmental station

(RKM 78) in 1989 was much lower (0.02-0.05 °/$_{oo}$, i.e. fresh water) and less variable than the 1988 values.

Dissolved oxygen concentrations was usually inversely related to water temperature during 1988 and 1989 with highest values occurring when water temperatures were low (Fig. 10). Lowest dissolved oxygen levels (6 mg/l) were at the end of the 1988 spawning season at a water temperature of 26°C. Again in 1989 lowest dissolved oxygen values (6.5 mg/l) occurred after spawning had ceased and water temperatures reached 24°C (Fig. 10).

During 1988, pH values were approximately 7.0 but at least two episodes of pH depression occurred simultaneously with rain events (Fig. 11A). Between 6 and 8 May after >1.3cm of rain fell, the largest drop in pH occurred and lasted 51 hours. Beginning on 6 May, at 0550hrs, pH values declined steadily from 6.9 to 6.3 at 0800hrs on 8 May. Values of pH quickly rebounded to 7.08 by 1000hrs. Most rain events during spring 1988 had little or no effect on pH. For example, on 12 May 1988 2.9cm of rain failed to depress the pH depression, and on 25 May after 0.5cm of precipitation, pH rose. In 1989, pH usually ranged from 7.0 to 8.5; however, most rain events were associated with detectable depressions in pH (Fig. 11). Drops in pH were usually minor, but at least two prolonged depressions were recorded. On 1 May 1989, when 3.9cm of rain was measured, after three previous days of rain (1.1cm), pH began to decline from 7.0. The low of 6.38 on 2 May at

0630hrs was followed by a rise to 6.9 on 3 May at 1630hrs. A 10-day depression in pH below 6.9 occurred between 9 and 19 May. A long, gradual decline in pH began on 9 May when 1.7cm of rain fell. Values reached 6.6 at 0430hrs on 14 May and rose to 6.7 by 1430hrs. Three consecutive days of rain (1.8cm) from 15 to 17 May caused another drop in pH to 6.23 on 17 May. Values remained between 6.2 and 6.3 until 0900hrs on 18 May when pH started to rise to 7.00 at 1000hrs on 19 May. Periods of extreme daily fluctuation were noted during the 1989 spawning season, such as on 11 April when pH went as low as 6.8 during the day and as high as 8.5 at night.

Potential fish and invertebrate predators: The bow-mounted push-net captured 15 species of fishes during the two-year study comprising 5,038 (916/100m^3) specimens in five cruises in 1988 (31 collections) and 4,912 (668/100m^3) specimens in nine cruises (87 collections) during 1989 (Tables 5, 6). The bay anchovy was the most abundant species representing 75.5% (1988) and 73.3% (1989) of the fishes collected. Atlantic menhaden was the second most numerous species in 1988 (19.7%) and third most abundant in 1989 (9.5%). Although both species occurred in all strata, the abundance of bay anchovy decreased upriver whereas the abundance of Atlantic menhaden increased upriver.

During 1988, the density of potential predators (fishes that ate striped bass larvae in laboratory trials), was

greatest during the week of peak spawning (62/100m^3; Fig.12). No samples were taken after 8 May due to a breakdown of the push-net boat. The 1988 distribution of potential predatory fishes (Fig. 13) overlapped in time an space with peak densities that of striped bass eggs and larvae (Fig. 14). Fishes (>30/100m^3) encompassed 10km of the 20km portion of the river which included peak spawning during the end of April and beginning of May. During this time, fishes were collected in densities <10/100m^3 above Rkm 75. Considerable numbers of larvae were collected below Rkm 75 when potential predators first became abundant; however, very low densities of larvae were collected in this region in the following weeks. The abundance of potential predatory fishes was lower for all of the 1989 spawning season (Figs. 12 and 13), and densities rarely reached above 5/100m^3 on the spawning grounds.

Cyclopoid copepods, A. vernalis and M. edax, were most abundant at the end of the 1988 spawning season when densities were greater than 100/m^3 (Fig. 15). Highest densities of striped bass larvae (>10/100m^3) during 1988 were not coincidental, in time or space, with high densities of cyclopoid copepods. In 1989, densities of cyclopoid copepods were also high at the end of the spawning season (Fig. 15). However, unlike 1988, high cyclopoid abundance (>100/m^3) occurred shortly after peak spawning in 1989 and overlapped, to some degree, with peak densities of larvae.

Food for first-feeding larvae: Potential prey items for first-feeding striped bass larvae collected by pump sampling during 1988 and 1989 consisted of 13 invertebrate taxa (Table 7). Cladocera and copepod nauplii were dominant, and combined made up 85.9% and 86.8% of the total number of plankton collected in 1988 and 1989, respectively. Densities of microzooplankton peaked at 194/l during peak spawning of striped bass and then declined to 74/l the following week when few larvae were collected (Fig 16). There was little overlap in time and space between high densities of microzooplankton (>100/l) and striped bass larvae (>10/100m^3) during spring 1988 (Figure 17). Most larvae (>10/100m^3) were exposed to food in densities <75/l. In 1989, microzooplankton densities were 92/l during peak spawning but increased to 173/l the following week when the greatest number of larvae were collected (Figure 16). Although the very high densities of larvae (>100/100m^3) were exposed to food concentrations >100/l (Figure 17) from about 26 April to 6 May, the abundant larvae between Rkm 65 and Rkm 59 produced prior to 26 April, were subjected to food concentrations <50/l.

Juvenile survival: Sixteen of 190 otoliths from juvenile striped bass collected in the Pamunkey River during 1988 and 1989 had a difference >10% between readings and were not included in analysis. Distribution of hatchdates of juveniles

collected in 1988 and 1989 were based on data from 77 and 97 otoliths, respectively.

The hatchdates of juveniles collected during June and July 1988 were most frequent in the weeks of 5 May and 12 May with the mode occurring one week earlier for juveniles collected in July than in June (Fig. 18). The mode of the distribution of hatchdates of fishes collected in August was in the week of 19 May and no juveniles having April hatchdates were found. However, only eight individuals were aged from August collections as only nine individuals were taken in the seine survey (Colvocoresses 1989). Distributions of hatchdates for combined data from June, July and August in 1988 had modes during the weeks of 5 May and 12 May. At least 44% of the juveniles aged in 1988 were hatched in the weeks following peak spawning despite the decline in abundance of striped bass eggs (Fig.20). Juveniles hatched during the week of 5 May 1988 may have been part of the cohort associated with peak spawning.

In 1989, the mode of the distribution of hatchdates was within the week of 28 April for fishes collected in June, 28 April and 5 May for fishes collected in July and 5 May for fishes collected in August (Fig. 19). The greatest frequency of hatchdates for all collections of juveniles combined occurred during the weeks of 28 April and 5 May. The temporal distribution of these hatchdates closely followed egg production and at least 59% of the hatchdates of juveniles

occurred when egg production was at a maximum (Fig.20). During both 1988 and 1989 the temporal distribution of juvenile hatchdates closely matched the peaks in production of larvae.

The average growth rate of 1988 juvenile striped bass was 0.51mm d^{-1}. The mean growth rate for those hatched in April 1988 was 0.48mm d^{-1} while fishes which hatched in May averaged 0.51mm d^{-1}. Variability in average growth rates was observed for birthdates of cohorts pooled by week in 1988 with no apparent seasonal trends (Fig. 21). Confidence intervals (±1SE) around the mean growth rates of all cohorts overlapped and no significant differences were observed.

The mean growth rate of 1989 juveniles (0.53mm d^{-1}) was slightly higher than the growth rate calculated for 1988 fishes. Average growth rate for fishes with hatchdates in April and May 1989 was also 0.53mm d^{-1}. Little variability in growth rates was observed for cohorts during weeks in April or May 1989 (Fig. 21). Except for the four individuals hatched during the week of 7 April, average growth rates ranged from 0.51-0.55mm d^{-1}.

Variability in factors: Statistical analysis indicated that there were similar trends in variability for factors collected during the 1988 and 1989 spawning seasons. All biotic factors showed high within-week variability during both years (Tables 8a and 9a). Analysis of Variance also indicated that between-

week variability was high for striped bass egg abundance and densities of cyclopoid copepods during the spawning seasons of 1988 and 1989 (Tables 8b and 9b). Microzooplankton densities showed significant variability between weeks in 1989. The Kruskal-Wallis test indicated that microzooplankton collected during weeks in 1988 were not as variable ($p \leq 0.05$) in abundance as during the 1989 spawning season. However, significant variability between weeks in microzooplankton abundance in 1988 was observed at $p \leq 0.1$. Although abundance of potential predatory fishes was much higher in 1989 than in 1988, there was little variability in abundance between weeks during either spawning season. Abiotic factors including water temperature, pH, and dissolved oxygen showed little within-week variability during 1988 and 1989, but between-week variability was highly significant. In contrast to other abiotic factors, significant differences in rainfall were not observed between weeks during either spawning season but tremendous within-week variability occurred during both years.

DISCUSSION

Laboratory studies on predation

Laboratory results of predation on striped bass yolk-sac larvae by bay anchovy and Atlantic menhaden, increased a list of potential predators in the Pamunkey River, VA to 11 fishes and one cyclopoid copepod (Table 10). These data indicated

that a wide variety of fishes which have temporal and spatial coincidence with striped bass spawning may prey on striped bass early life stages. In addition, experiments on consumption rate demonstrated that bay anchovy could eat up to 42 yolk-sac larvae in an hour. As bay anchovy dominated push-net samples, this species may have a significant impact on survival of striped bass early life stages. These results were similar to Dowd (1986) who found that bay anchovy could consume up to 44.5 larval sea bream (Archosargus rhomboidalis) per hour. The presence of striped bass eggs and larvae in the guts of field collected bay anchovy further stresses the importance of this species on the spawning grounds. Comparison of the diet bay anchovy with abundance of specific taxa in the plankton revealed generalized feeding habits. Predation by bay anchovy on early life stages of striped bass would probably increase during peak spawning simply due to an increase in striped bass eggs and larvae relative to the total plankton available for food. Although over 61% of striped bass eggs were spawned during a single week in 1988, eggs made up only 0.01% of the gut contents of bay anchovy collected during peak spawning. Due to the extremely fragile nature of striped bass eggs, only well developed and recently ingested eggs were likely to be detected. Thus, predation on striped bass eggs was probably not accurately represented by the analysis of gut contents. While densities of striped bass larvae were an order of magnitude greater in 1989 than in

1988, larvae were relatively rare in the plankton constituting <0.01% of the taxa taken in 20 samples during peak spawning in 1989. Fish larvae represented 0.4% of bay anchovy diet suggesting that larvae may be selectively consumed. Further, these larvae were well digested and may have also been underestimated as a food item of bay anchovy.

Predation rates as high as 4 larvae killed/d implicated A. vernalis as an important predator should densities of newly hatched yolk-sac larvae coincide with patches of A. vernalis. Similar ingestion rates of <2 larval Atlantic menhaden and spot (Leiostomus xanthurus) per copepod/d were measured for the calanoid copepod Centropages typicus at densities as great as 12 larvae per copepod (Turner et al. 1985). Mortality rates of four northern anchovy larvae per copepod/d were recorded for Labidocera trispinosa at densities of 15 larvae per copepod. In other experiments predation rates were as great as 12-14 fish larvae killed per copepod per day for L. jollae (Lillelund and Lasker 1971) and Anomalocera ornata (Turner et al. 1985).

Factors affecting survival of juveniles

Egg production of striped bass in the Pamunkey River (Olney et al. 1991) was nearly equal in 1988 (2.6×10^9) and 1989 (2.2×10^9), yet egg and larval survival, as estimated by the recruitment index (the average number of juveniles per seine haul), was four times larger in 1989 (14.50;

Colvocoresses 1990) than in 1988 (3.14; Colvocoresses 1989). Ninety-five percent confidence intervals for egg production were low for 1988 (0.11×10^9) and 1989 (0.18×10^9) indicating that these values were good estimates of spawning activity. The 1988 juvenile index for the Pamunkey River was slightly lower than the historical average of 3.49 juveniles and the 95% confidence interval ranged from 1.80 to 4.92 juveniles. The 1989 juvenile index was three and a half times higher than the historical average with a 95% confidence interval ranging from 8.66 to 23.5 juveniles (Colvocoresses 1990). The 95% CI for the 1988 and 1989 juvenile indices did not overlap indicating that juvenile production was significantly higher in 1989 on the Pamunkey River than in 1988.

Since the frequency modes of hatchdates of juveniles collected during June and July of 1988 and during the summer of 1989 were very similar, otolith analysis of juveniles probably provided good estimates of hatchdates for the seven day cohorts. In addition, the temporal coincidence between trends in larval production and hatchdates of juveniles also suggested that juvenile hatchdates were accurately estimated. The shift in hatchdate distribution to mid-May for juveniles collected in August 1988 may have been due to age underestimation. Kline (1990) found that the ages of juveniles collected in September were consistently underestimated; however, any age underestimation from August samples were adjusted with a correction factor. Since, the

same criteria used by Kline (1990) were employed followed for otolith analysis in this study, and no shift in hatchdates were observed for fishes collected in August 1989, age underestimation appears to be unlikely. It is more probable that the shift in hatchdates of August 1988 juveniles was an artifact of the small number of individuals (n=8) aged.

The average growth rates of juvenile striped bass from 1988 (0.51mm d^{-1}) and 1989 (0.53mm d^{-1}) were very similar to the growth rate of juveniles collected in the Pamunkey River during summer 1987 (0.53mm d^{-1}; Kline 1990). Similar to the results of this study, Kline (1990) also found no seasonal increase in average growth rates of 1987 juvenile striped bass from the Pamunkey River.

Poor survival was noted for individuals hatched during peak spawning in 1988. Most survivors had hatchdates late in the spawning season when egg production was declining. In contrast, the greatest number of surviving juveniles were hatched in 1989 when egg production was at a maximum. A number of physical and biological factors and their interactions may be responsible for the observed patterns of recruitment.

Physical factors: Although average water temperatures were lower during peak spawning in 1988 (16.5°C) than in 1989 (19.0°C), values were within the suitable range (12 - 24°C) for the survival of striped bass early life stages (Setzler et al.

1980). However, water temperatures encountered by striped bass eggs and larvae during peak spawning in 1989 may have been more conducive to development of these early life stages than 1988 water temperatures. More survivors were hatched during peak spawning in 1989 when water temperatures were between 18°C and 19°C. Morgan et al. (1981) reported that the optimal temperature for survival of striped bass eggs and larvae was 18.2°C. The lower water temperatures in 1988 may have prolonged development of eggs and slowed growth of larvae, thereby increasing susceptibility of these early life stages to predation. A striped bass egg requires 58 h to hatch at 16°C, but only 42 h at 19°C (Polgar et al. 1976). Rogers and Westin (1981) also concluded that growth rates of larvae were lower at 16°C than at 19°C. Few juveniles (<4%) survived from early spring spawning in 1988 and 1989 when 8-14% of the eggs were produced. A drop in water temperature to 12°C during spring of both years may have stressed these early life stages. Crance (1984) reported that water temperatures at or below 12°C were considered to be lethal to striped bass eggs and larvae. Morgan et al. (1981) found that percent survival of striped bass eggs and larvae was reduced at water temperatures around 12°C. They reported that eggs incubated at water temperature <11°C did not hatch and larvae incubated at 12°C had physical abnormalities, larger yolk sacs and smaller lengths at hatching.

The temporal and spatial distribution of spawning

activity was related to water temperatures during 1988 and 1989. Olney et al. (1991) found that the passage of cold fronts early in the spawning season during several years on Virginia rivers decreased egg production and prolonged the spawning season. Setzler et al. (1980) stated that lowest temperatures for striped bass spawning in the Chesapeake Bay were between 11°C and 12°C. In this study, data indicated that spawning ceased at or below 12°C. In 1988, very few eggs were collected between 10 and 15 April when water temperatures fell to 12°C. On 15 April 1989 spawning occurred only in the lower half of the spawning grounds where water temperatures were >12°C.

The spatial distribution of spawning activity was also related to salinity; the lower limit of spawning in both years followed the $1°/_{oo}$ contour. No eggs and few larvae were collected in water with salinities $>1°/_{oo}$ during 1988 and 1989 confirming the observation of Hardy (1978) that spawning outside of freshwater is minimal and eggs collected in higher salinities are probably expatriated.

Dissolved oxygen was usually within the range suitable for the survival of early life stages of striped bass and probably had little effect on survival during the two-year study. Dissolved oxygen reached minimum values of 6 mg/l after spawning was completed in both years. Setzler et al. (1980) reported that dissolved oxygen values <5 mg/l were stressful to striped bass eggs and larvae.

Although pH was usually within a range (7.0 to 8.5) considered suitable for survival of striped bass (Hall et al. 1984; 1984; 1985; 1987a; 1987b), several pH depressions associated with rainfall were noted during 1988 and 1989. Several of these depressions occurred during periods of peak survival. For example, between 6 and 8 May 1988, a drop in pH to 6.3 was associated with 0.5-in of rain; however, this week accounted for 22% of the juveniles hatched that spring. A depression in pH to 6.4 occurred when 1.5-in of rain fell during the week of peak spawning in 1989 when 39% of the juveniles were hatched. The longest depression in pH (< 6.9) occurred between 9 and 19 May 1989 when 20.6% of the juveniles were hatched. However, during this period of time extreme low values (<6.3) were only encountered for two days (17-18 May). Although it appears that the duration and extent of depressions in pH may not have been severe enough to have deleterious effects on survival of striped bass early life stages, it is possible survival may have been improved in the absence of these pH depressions. Regan et al. (1968) reported that a pH range of 6.0 to 10.0 was favorable for survival of striped bass larvae. Hall et al. (1985) concluded that pH values of 6.3 on the Nanticoke River, MD were not acutely toxic but potentially stressful for striped bass larvae.

The majority of rain events in 1988 had little or no effect on pH values; however, rainfall in 1989 was usually associated with detectable depressions in pH. This difference

may have been due to the location of the environmental station during the two years. In 1988, the environmental station was located in the lower part of the spawning grounds (Rkm 64) where salinities consistently exceeded $1°/_{oo}$ during the last of the flood tide. In 1989, the station was moved to Rkm 78 where salinities were usually $< 0.05°/_{oo}$. The higher salinities at the 1988 environmental station may have served to buffer the water against great changes in pH that might have developed from the addition of acids during rain events (Reid and Wood 1976).

Extreme daily fluctuations of pH were probably due to the increased photosynthetic activity of phytoplankton during daylight hours. Removal of inorganic carbon from the water column during daylight hours results in an increase in pH. Values subsequently fall when photosynthesis ceases after dark. Sanders and Riedel (1987) noted that a persistent bloom of Microcystis sp. in the freshwater section of the Potomac River, MD caused variability in pH with maximums greater than 10.0. They reported that long-term elevations of pH increased the mobility of phosphorus and maintained the high level of algal growth and high pH.

Biological factors: Differences in predator abundance and the spatiotemporal coincidence of predators and prey in 1988 and 1989 may have influenced recruitment. Potential predatory fishes, mainly bay anchovy, were collected in greater numbers

during the 1988 spawning season than during the same period in 1989. Also in 1988, a coincidence in time and space was observed with high densities of eggs and fishes below Rkm 75. It is interesting to note that in the area of peak spawning, few larvae were taken within the >30/100m^3 contour for predators. Reduced densities of larvae may have been a result of predation on the high densities of eggs. This period of peak spawning and high densities of fishes also produced comparatively few survivors. Most juveniles were hatched during the week after peak spawning when densities of predatory fishes started to fall.

In 1989, there was little coincidence between high densities of potential predatory fishes and spawning activity. For most of the spawning season, densities of fishes exceeding 10/100m^3 were taken below the 1°/$_{oo}$ contour, where little spawning activity occurred. Only eggs and larvae produced during the last week of May were subjected to high densities of fishes, and 1% of the survivors were produced by this cohort. In addition to high densities of fish predators, early life stages produced that week were subjected to high water temperatures (>24°C) that may have had severely stressed them. Hardy (1978) reported that mortality was high for striped bass eggs at water temperatures above 21°C and for larvae at temperatures above 23°C.

The push-net was designed to eliminate some of the problems encountered in sampling pelagic juvenile fishes in

near-surface waters (Kriete and Loesch 1980). Loesch et al. (1982) found that catches of juvenile Alosa spp. were significantly greater in the surface at night than during the day. Based Loesch et al.'s (1982) results, the push-net probably efficiently sampled anchovies and menhaden, while densities of other predators may have been underestimated. Many of the species that tested positively as potential predatory fishes (see Chapter 1) are bottom dwellers and were probably unavailable to the push-net. However, some fishes usually associated with the bottom (i.e. hogchoker, white catfish, white perch, spottail shiner) did appear in pushnet collections and some of these species are known to feed in the water column (Stevens 1959, Goodson 1965). In addition, collection of fishes by other gear types during 1985 and 1986 (Chapter 1) indicated that anchovy and menhaden were, by far, the most abundant fishes on the spawning grounds of the Pamunkey River. These abundance data as well as laboratory results and gut analysis suggests that bay anchovy as well as Atlantic menhaden may be very important predators of striped bass early life stages.

Despite laboratory data that showed Acanthocyclops vernalis killed striped bass larvae, cyclopoid copepods may not have had a great effect on larval survival in 1988. During 1988 spawning season there was little temporal coincidence between high densities of larvae and cyclopoid copepods. Densities of cyclopoid copepods were greatest at

the end of the 1988 spawning season when few larvae were taken. In 1989, high densities of cyclopoids were not only taken at the end of the spawning season but also during the week of peak spawning. As otolith analysis of juveniles indicated that the greatest number of survivors were from the cohorts associated with peak spawning, it is difficult to determine what effect predation by cyclopoids may have had on survival of larvae. Data from predation rate experiments with varying densities of A. vernalis and extremely high densities of striped bass larvae indicated that predation by cyclopoid usually is probably not an important factor affecting survival of striped bass larvae at concentrations usually observed on the spawning grounds.

Food availability for first-feeding larvae may also have had an effect on recruitment. Following the week of peak spawning in 1988, food densities fell to an average of <75/l and there was very little coincidence throughout the 1988 spawning season between high densities of striped bass larvae (>10/100m^3) and densities of microzooplankton >100/l. Chesney (1989) reported that striped bass larvae could feed and grow well at food concentrations as low as 50/l (at 19°C), but better survival and growth occurred at higher food densities. At Eurytemora affinis densities of 250/l, growth of striped bass larvae was 0.40 mm d^{-1} with an expected survival of 86.5%. However, at food densities of 50/l, growth rates were only 0.30mm d^{-1} with 61% survival Chesney (1989).

For a two week period in 1989, that included peak spawning, high densities of larvae >100/100m^3 were temporally and spatially coincident with food densities >100/l. More food combined with warmer water and fewer predators may have contributed to increased survival of juveniles hatched during peak spawning in 1989.

Interactive effect of physical and biological factors: It is unlikely that poor survival of striped bass early life stages during 1988 could be attributed to either sparse food, or low water temperatures alone. These factors may have caused a reduction in the growth and development of eggs and larvae that may have made them more susceptible to elevated predator levels (Post and Prankevicius 1987; Miller et al. 1988). The escape capability and swimming speeds of larvae may have also been affected by these factors thereby increasing the risk of predation (Frank and Leggett 1982; Rice et al. 1987). In addition, recruitment may have been poorer in 1988 because the majority of eggs were spawned during a one-week period when the interactive effects of abiotic and biotic factors may not have been conducive to the survival of this very large cohort. Evidence for its poor survival was indicated by the low number of larvae collected the week after peak spawning, the extremely high mortality experienced by eggs produced during the 1988 spawning season and the low number of juveniles which survived from peak spawning. A more uniform distribution of

egg production in 1989 and good survival of the larger cohorts may have been responsible for the higher juvenile index observed the following summer.

The high within-week variability exhibited by biological factors during 1988 and 1989 may have been a result of samples being collected along the length of the Pamunkey River. During both years daily cruises were designed to bracket the 35 km area of the Pamunkey River which encompasses striped bass spawning activity (Grant and Olney 1991). Therefore, it is expected that within a week, there would be tremendous variability in egg abundance. The spatial heterogeneity of the sampling scheme also explains the within-week variability in other biological factors. Salinities changed from 5 to 6 $^{\circ}/_{oo}$ in the lower part of the sampling area to completely fresh water (<0 $^{\circ}/_{oo}$) at the upper limits of striped bass spawning. Species compostion and abundance of fishes, microzooplankton and cyclopoid copepods would also change as habitat and salinities varied along the length of the Pamunkey River. Between-week variability was high for striped bass eggs. As the sampling scheme was also designed to temporally bracket the spawning season, this result was not surprising. Between-week variability was noted for cyclopoid copepods, and microzooplankton during 1988 and 1989 whose abundance was probably a response to seasonal changes in water temperature and food availability. However, despite annual differences in abundance, Analysis of Variance indicated that potential

predatory fish densities were fairly constant during 1988 and 1989 spawning seasons. Water temperature, pH, and dissolved oxygen did not exhibit within-week variability. Unlike the biological factors, these data were collected at only one location on the spawning grounds of the Pamunkey River (the environmental station) and did not possess the spatial component to within-week variability. However, between week variability was high for aforementioned abiotic factors. Variability in water temperature and salinity were the result of seasonal changes with neither parameter ever approaching levels that, when considered alone, endangered survival of eggs and larvae. Values of pH also were significantly variable during both spawning seasons as mean weekly values fluctuated between 6.8 and 7.2 and occasionaly approached levels considered to be stressful for eggs and larvae. Rainfall showed extreme within-week and very little between-week variability as total rainfall was similar between weeks but extremely unpredictable during the week.

Variability in these biotic and abiotic factors probably had an affect the patterns of survival of eggs and larvae inferred by otolith analysis of juveniles. However, the affect of these factors on changes in mortality and developmental rates of eggs and larvae need not be great. Even small changes in rates of growth and mortality can have a very large effect on recruitment (Houde 1987, 1989). Although fish predators did not exhibit significant between-

week variability during the 1988 spawning season, the high abundance of fishes in 1988 relative to 1989 still may have had an affect on the distribution of hatchdates determined by otolith analysis. Due to the complex nature of a fishes environment no factor, alone, is likely to be the cause of recruitment variability (Rothschild 1986). The pattern of survival is a function of many different factors and their interactions. A factor such as predation does not need to exhibit tremendous seasonal changes to cause variable recruitment if the factors it interacts with vary. For example, variability in factors such as water temperature and food abundance mediated by temporally fluctuating egg abundance can change a larva's susceptibility to relatively constant predator levels and result in variability in the distribution of hatchdates of juveniles.

The role of other factors: While it appears that the interactive effects of factors such as predation, food availability and water temperature were important in determining recruitment in 1988 and 1989, there are other factors that may also play a role in recruitment variability. Uphoff (1989) used correlation and regression analysis to examine the relationships between population characteristics (growth, abundance and mortality) of larval striped bass and minimum water temperature, river flow, rainfall and feeding incidence. Uphoff (1989) found that year-class success during

1980-1985 on the Choptank River, MD was significantly related to water temperature during peak spawning and to rainfall during the early postlarval stage.

Coutant (1987) suggested that a decrease in the amount of summer habitat with suitable temperature and dissolved oxygen concentration stressed adult striped bass in Cherokee Reservoir, TN. He stated that poor body condition caused by unfavorable temperature and dissolved oxygen concentrations early in oogenesis may have reduced the reproductive potential of striped bass as more energy reserves would be required for increased metabolic demand (Rothschild 1986). Coutant (1987) hypothesized that the decline of striped bass in the Chesapeake Bay may be related to poorly oxygenated, deeper waters in the main-stem of the Bay during the summer. Coutant and Benson (1990) evaluated late-July water temperatures and dissolved oxygen concentrations as well as striped bass distribution and juvenile indices in the Chesapeake Bay. Criteria for habitat suitability were determined from fresh water reservoirs in Tennessee and were "confirmed" for the York-Pamunkey estuary in Virginia based on 1956-1959 water temperature data (Massman 1962) and 1967-1971 striped bass distributions (Grant 1974). Based on correlations between suitable summer habitat (water column thickness where temperature is below 25°C and D.O. > 2mg/l) and the striped bass juvenile index, Coutant and Benson (1990) concluded that there has been a progressive degradation of suitable habitat

for striped bass in the Chesapeake Bay over a 25-year period (1962-1987). A sill of warm water off the mouth of the Rappahannock River is believed to have formed a "thermal barrier" preventing a seaward migration of Maryland striped bass thereby reducing the reproductive capabilities of females. However, they ignored the fact that migration might take place several months before the barrier formed. Since Virginia striped bass had no barrier and therefore free access to coastal waters in summer, their reproductive success (= juvenile index) was not similarly affected.

Conclusions of habitat suitability for striped bass based on sketchy annual data are questionable in an estuarine system that is as highly dynamic as the Chesapeake Bay. Spawning females which are subjected to nutritional deficiencies or stressful environmental conditions may have reduced egg quality. However, there are so many different physical and biological factors that may affect survival of eggs and larvae to the juvenile stage that speculation on the condition of spawners can never be attributed to the magnitude of the juvenile index. A more accurate representation of the effects of low dissolved oxygen and high water temperature on the reproductive capability of striped bass would include an assessment of egg production, egg viability and survivorship of larvae after spawning.

While it is possible that low dissolved oxygen concentrations and high water temperatures in the deeper

waters of the Chesapeake Bay may have had some effect on recruitment during the early 1980's, results from this study indicate that these factors most likely, represent only a piece to the puzzle explaining recruitment. A fishes environment is very complex, composed of a vast array of physical and biological variables whose interactions are very poorly understood (Rothschild 1986). Recruitment will vary from year to year as biotic and abiotic factors and the connection between these factors change. Since so many different factors may be involved it will often be difficult to determine, in a given year, which factors or combinations of factors will be most important.

In this study otolith analysis was used to compare birthdate frequency distribution of juvenile striped bass with the various biotic and abiotic conditions encountered by their early developmental stages during the spawning season. The technique was successful in identifying at least some of the factors which may have affected survival of eggs and larvae. However, this investigation could have been strengthened by and examining some of the characteristics of eggs (i.e. mortality rates) and larvae (i.e. mortality rates, growth rates, gut contents, condition). For example, growth rates of juveniles were very similar for both the 1988 and 1989 spawning seasons and showed little seasonal variability. However, juveniles represented only those individuals that were able to survive the hardships of recruitment and most

likely had growth rates very different from larvae that died. Post and Prankevicius (1987) demostrated through the use of otolith analysis of larvae and juveniles that juveniles of yellow perch (Perca flavescens) which survived the early developmental stages were the larger and faster growing members of their cohort. Growth rates and data on nutritional status of larvae for individual weeks during the 1988 and 1989 spawning seasons, together with the biological and physical data, would have been extremely valuable in explaining the observed distributions of hatchdates of juveniles.

Fritz et al. (1990) stated that to better understand recruitment mechanisms investigators should focus on "the unique features of survivors" rather than explaining "why over 99% of the eggs and larvae die". However, Houde (1989) showed that extremely small changes in growth or mortality of eggs and larvae may have a very large effect on recruitment. Houde's (1989) results suggested that explaining why such a large percentage of early developmental stages die may also be an essential component in understanding recruitment. Therefore, mechanisms of recruitment in fishes can be better understood through an approach that not only concentrates on the unique features of survivors but also on the attributes of larvae that will most likely die. Much information can be gleaned from both approaches and adopt one method while ignoring another probably results in a poorer interpretation of the actual factors determining recruitment.

Table 1.-Consumption of larval striped bass by bay anchovy and Atlantic menhaden in laboratory presentations. Forty larvae were presented to each potential predator.

Potential predators species	length (SL)	#tested	Prey consumed per individual
Bay anchovy	39-43 mm	5	25; 12; 14; 22; 4
Atlantic menhaden	30-40 mm	5	22; 14; 0; 26; 0

Table 2.-Mean rates at which bay anchovy preyed on striped bass yolk-sac larvae at various prey densities.

Prey density (number/m^3)	Mean number of larvae consumed per hour (range)	Mean percentage of prey items consumed	Z
20	0.6 (0-2)	30	-0.36 (30% d^{-1})
100	1.4 (0-5)	28	-0.32 (28% d^{-1})
333	6.0 (1-14)	38	-0.48 (38% d^{-1})
1650	22.4 (3-42)	27	-0.31 (27% d^{-1})
3300	22.4 (11-29)	14	-0.14 (14% d^{-1})

Table 3.-Mortality rates (-Z) and total number of striped bass yolk-sac larvae killed (in parenthesis) by different numbers of Acanthocyclops vernalis. In each experiment 20 larvae were presented to 1 or more copepods in 1-l vessels for 24-h. Control test vessel contained only yolk-sac larvae.

	Number of copepods/l									
Replicate	1		5		10		20		30	
1	-0.16	(3)	-0.29	(5)	-0.43	(7)	-0.91	(12)	-1.04	(13)
2	-0.22	(4)	-0.29	(5)	-0.16	(3)	-1.04	(13)	-0.91	(12)
3	-0.16	(3)	-0.29	(5)	-0.36	(6)	-0.43	(7)	-0.91	(12)
control	-0.05	(1)	-0.16	(3)	-0.29	(5)	-0.11	(2)	-0.22	(4)

Table 4.-Percent composition of zooplankton from 37 plankton samples (excluding copepod nauplii) and stomach contents of 229 bay anchovy collected in the Pamunkey River, Virginia during three cruises associated with peak spawning in 1988-1989.

Taxa	Plankton 1988 (n=17)	Plankton 1989 (n=20)	Anchovy guts 1988 (n=134)	Anchovy guts 1989 (n=95)
cladocera	76.8	67.9	72.1	56.1
copepodites	10.5	20.2	9.9	12.3
harpacticoids	11.7	6.6	5.9	2.9
ostracods	<0.1	0.5	0.6	13.4
gastropods	0.2	<0.1	6.5	4.1
insects	0.1	<0.1	0.1	3.1
adult copepods	0.6	4.4	0.6	<0.1
amphipods	<0.1	<0.1	4.3	7.7
other inverts	0.1	0.3	<0.1	<0.1
eggs	<0.1	<0.1	<0.1	0.0
larvae	<0.1	<0.1	0.0	0.4

Table 5.-Percent composition of fishes collected by push-net along a 28-km transect of the Pamunkey River, VA, April-May, 1988 (31 collections). Station designations are midpoints of 5-km strata. Asterisk indicates percentage value less than 1.0.

Station	Rkm 61	Rkm 66	Rkm 71	Rkm 76	Rkm 81	Rkm 86	total
Total #/100m^3	247	357	195	57	27	32	916
Taxa							
Bay anchovy	92.3	68.0	84.2	63.9	41.0	33.9	75.5
Atlantic menhaden	1.8	29.1	13.3	28.4	35.3	56.8	19.7
Inland silverside	*	*	1.2	2.7	9.8	4.2	*
Spot	3.4	1.6	*	*	*	*	1.7
Blueback herring	*	*	*	*	7.8	*	*
White catfish	*	*	*	3.9	*	*	*
Spottail shiner	*	*	*	*	4.0	4.0	*
Others	*	*	*	*	2.1	*	*

Table 6.-Percent composition of fishes collected by push-net along a 28-km transect of the Pamunkey River, VA, April-May, 1989 (56 collections). Station designations are midpoints of 5-km strata. Asterisk indicates percentage value less than 1.0.

Station	Rkm 61	Rkm 66	Rkm 71	Rkm 76	Rkm 81	Rkm 86	Total
Total #/100m^3	272	106	59	52	87	93	668
Taxa							
Bay anchovy	84.7	69.6	58.4	61.7	56.4	80.0	73.3
Atlantic menhaden	4.8	19.6	20.5	10.4	11.5	3.4	9.5
Inland silverside	6.8	8.3	*	19.7	26.0	9.4	11.7
Hogchoker	2.4	1.8	*	*	*	2.5	1.7
Blueback herring	*	*	2.2	3.4	*	4.0	1.1
Gizzard shad	*	*	*	2.8	4.7	*	*
Spottail shiner	*	*	*	1.1	*	*	*
Others	1.1	*	*	*	*	*	*

Table 7. Percent composition of taxa collected in microzooplankton samples om the Pamunkey River, Virginia during spring 1988 and 1989.

Taxa	1988	1989
Cladocerans	73.3	45.1
Copepod nauplii	12.6	41.7
Copepodites	6.6	7.0
Calanoid copepods	1.6	2.5
Harpacticoid copepods	4.7	2.5
Cyclopoid copepods	0.3	0.9
Insects	0.1	<0.1
Bivalves	0.1	<0.1
Amphipods	<0.1	<0.1
Nematodes	<0.1	<0.1
Ostracods	<0.1	0.2
Watermites	<0.1	<0.1

Table 8a.–Within week values of n (number of observations), X (mean) and CV (coefficient of variation) for factors including striped bass eggs (#/100m^3), potential fish predators (#/100m^3), cyclopoid copepods (#/m^3), water temperature (°C), pH, dissolved oxygen (mg/L) and rain (inches). Data were collected during April and May 1988 in the Pamunkey River, Virginia. Biological observations reflect data collected at positive stations. * indicates mean value <0.1.

	WEEKS																							
	1			2			3			4			5			6			7			8		
% Juv Hatched	1.2%			7.8%			6.5%			11.7%			28.6%			29.9%			13.0%			1.0%		
	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV
Eggs	15	38	131	2	2	141	10	131	98	16	285	189	5	27	57	5	48	80	3	14	66			
Fish	7	11	95	6	29	82	6	31	45	6	60	132	6	20	74									
Cyclopoids	16	0.5	152	5	1	145	6	0.2	66	13	3	128	5	2	96	5	0.8	123	6	52	237	6	11	91
Microzoo				5	86	53	12	127	40	11	123	111	6	62	50	5	156	67	5	65	27	5	61	43
Temperature	8	17	4	14	14	8	14	14	2	7	15	3	9	16	2	16	18	6	14	21	5	11	23	2
pH	8	7.0	2	13	7.2	2	14	7.1	1	9	7.2	2	9	6.8	5	14	7.2	3	16	6.9	2	11	7.3	7
DO	7	7.6	2	14	7.9	1	14	8.2	2	8	8.7	2	9	8.5	1	13	8.3	6	14	6.9	6	12	6.7	3
Rain	3	0.2	89	7	*	261	7	0.1	221	7	*	263	7	0.2	147	8	0.1	268	7	0.2	140	5	*	170

Table 8b.–Between week variability for factors collected during April and May 1988. ♦ denotes factors which were log transformed and ANOVA was used. ♣ denotes factors which could not be normalized by log transformation and the Kruskal–Wallis test was used.

Factors	DF	Probability
♦Eggs	6	0.0001
♦Fish	4	0.2728
♦Cyclopoids	7	0.0006
♣Microzoo	6	0.0707
♣Temperature	7	0.0001
♣pH	7	0.0001
♣DO	7	0.0001
♣Rain	7	0.5121

Table 9a.–Within week values of n (number of observations), X (mean) and CV (coefficient of variation) for factors including striped bass eggs (#/100m^3), potential fish predators (#/100m^3), cyclopoid copepods (#/m^3), water temperature (°C), pH, dissolved oxygen (mg/L) and rain (inches). Data were collected during April and May 1989 in the Pamunkey River, Virginia. Biological observations reflect data collected at positive stations. * indicates mean value <0.1.

	WEEKS																							
	1			2			3			4			5			6			7			8		
% Juv Hatched	4.1%			6.2%			7.2%			30.9%			29.9%			13.4%			7.2%			1.0%		
	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV	n	X	CV
Eggs	17	48	111	12	71	107	12	119	162	13	215	121	6	127	122	11	3	98	11	31	138	5	6	93
Fish	5	7	119	7	11	42	6	6	49	7	5	112	6	12	132	6	3	63	6	14	114	6	5	65
Cyclopoids	10	0.1	192	5	0.3	62	6	0.6	72	7	0.7	56	13	34	163	6	1	55				6	30	123
Microzoo	9	37	50	8	34	63	6	42	29	7	92	51	5	197	39	7	18	60	6	21	29	6	106	26
Temperature	13	15	11	13	12	6	9	16	6	11	19	1	15	18	6	14	15	4	10	16	5	13	21	4
pH	13	7.1	5	15	7.3	8	9	7.0	1	11	6.9	2	14	6.7	4	14	6.7	2	9	6.7	5	13	7.3	6
DO	13	9.8	2	13	9.9	3	10	8.6	7	11	7.7	5	12	7.1	1	14	6.8	4	10	7.2	3	13	8.1	7
Rain	7	0.3	125	7	0.2	211	7	0	0	7	0.3	192	7	0.2	189	7	0.2	172	7	*	115	7	*	114

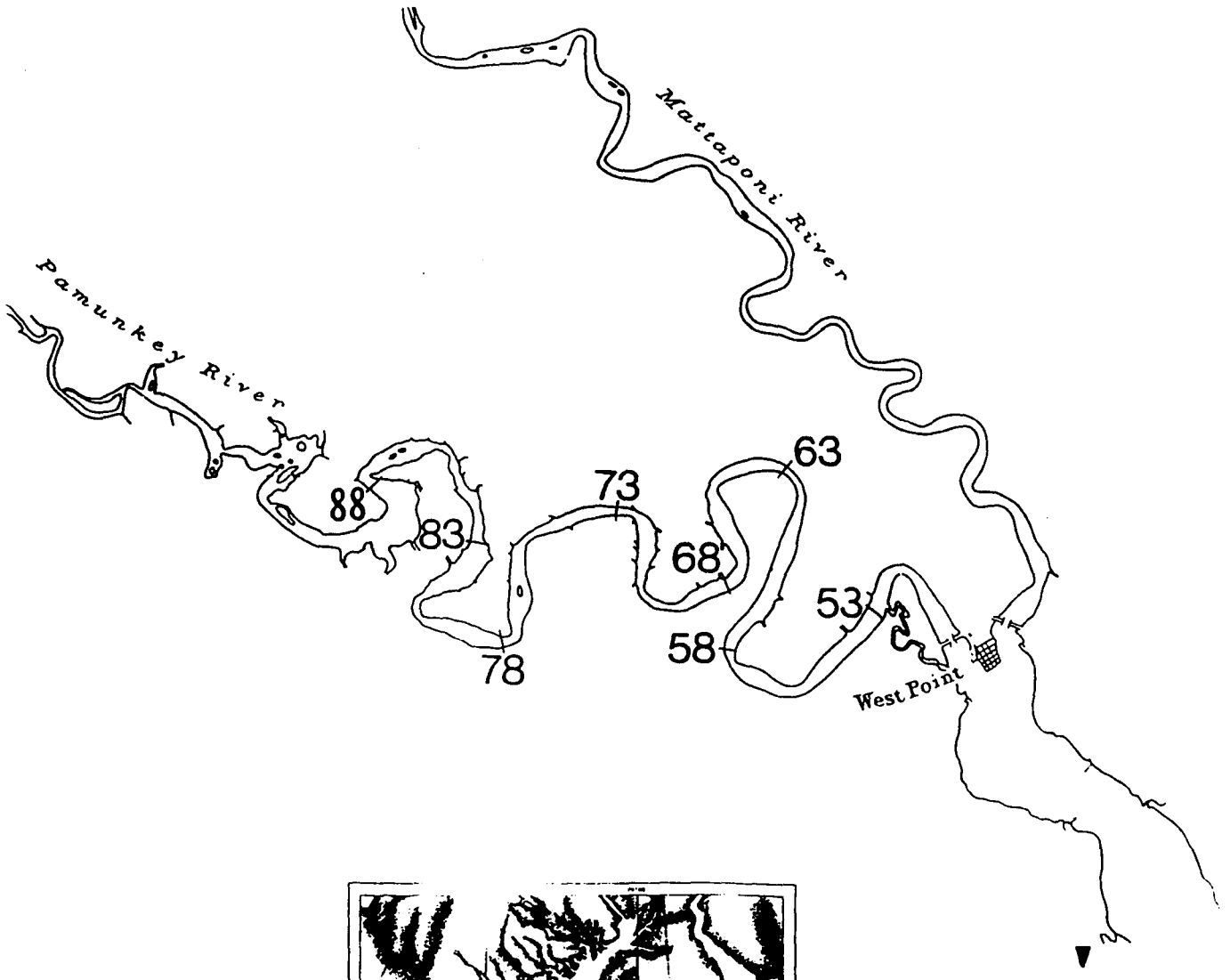
Table 9b.–Between week variability for factors collected during April and May 1989. ♦ denotes factors which were log transformed and ANOVA was used. ♣ denotes factors which could not be normalized by log transformation and the Kruskal–Wallis test was used.

Factors	DF	Probability
♦Eggs	7	0.0001
♦Fish	7	0.2805
♦Cyclopoids	6	0.0001
♦Microzoo	7	0.0001
♦Temperature	7	0.0001
♣pH	7	0.0001
♣DO	7	0.0001
♣Rain	7	0.1549

Table 10.-List of potential predators of striped bass yolk-sac larvae from the Pamunkey River, Virginia.

Atlantic menhaden	Spottail shiner
Bay anchovy	Bluegill
Channel catfish	Pumpkinseed
White catfish	White perch
Satinfin shiner	Striped bass
Tessellated darter	*Acanthocyclops vernalis*

Figure 1.- Pamunkey River location along the lower western shore of the Chesapeake Bay and station designations listed as river kilometers.


Mattaponi River
Pamunkey River
88
83
73
68
63
53
58
78
West Point

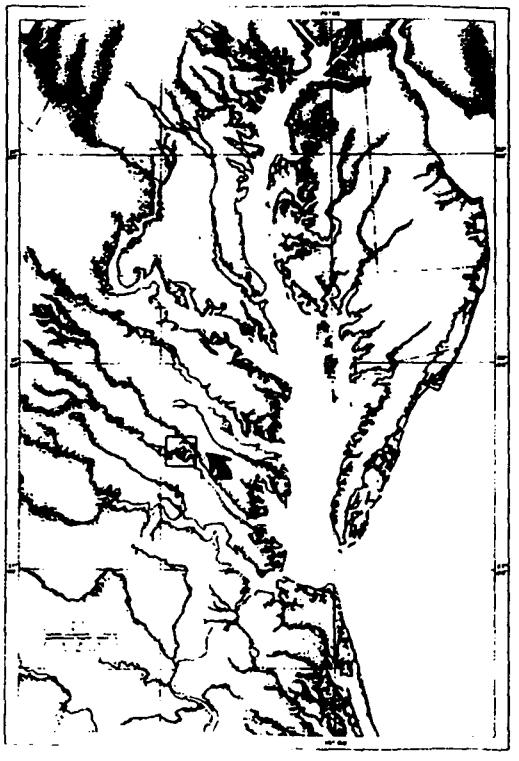


Figure 2- Predation by various densities of Acanthocyclops vernalis on fixed densities of striped bass yolk-sac larvae.

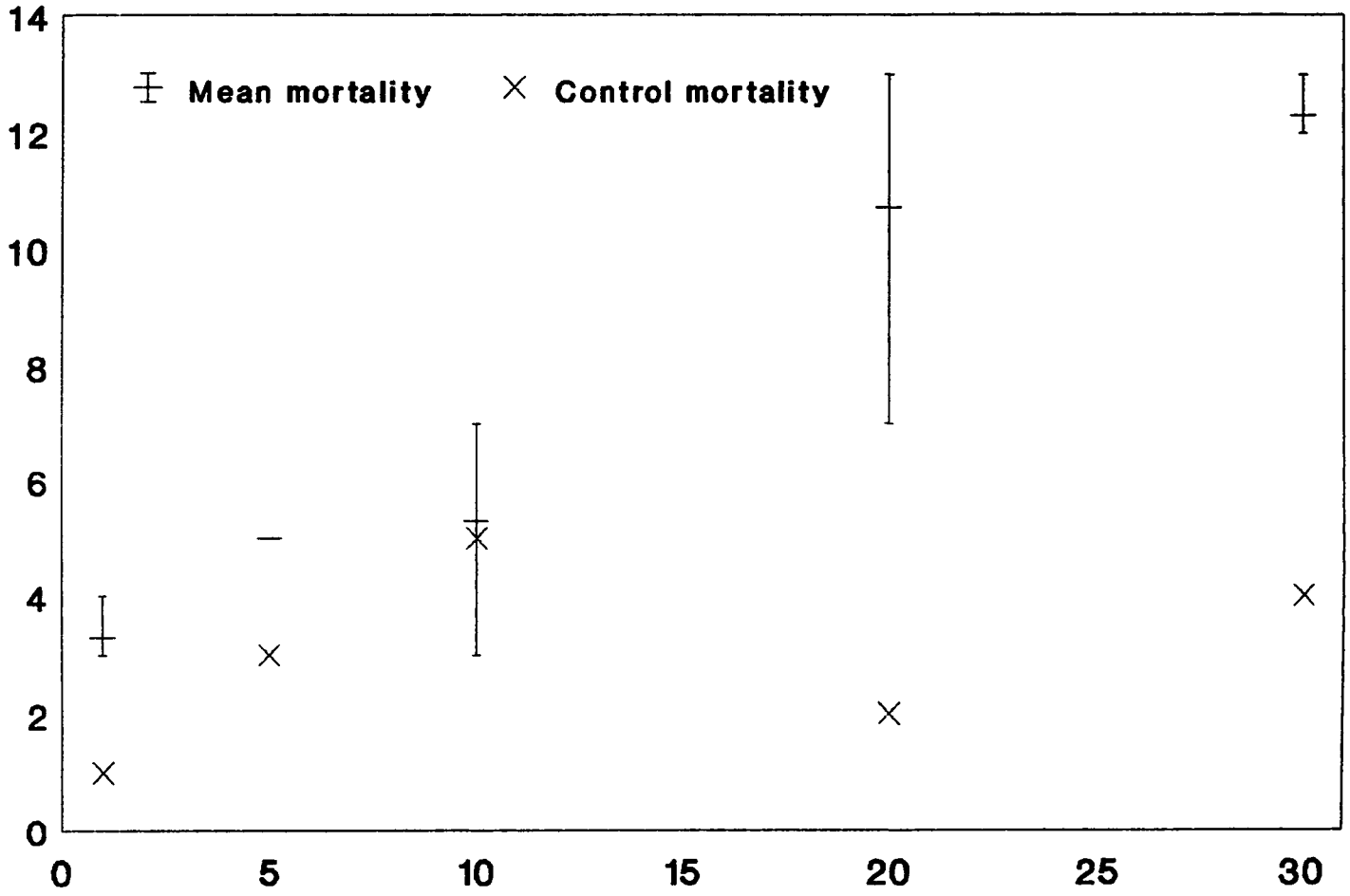

Mean mortality
Control mortality
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30

Figure 3.- Spatio-temporal distribution of striped bass eggs and larvae (#/100m^3) during 1988 for the Pamunkey River, VA. Shaded area indicated egg densities >100/100m^3.

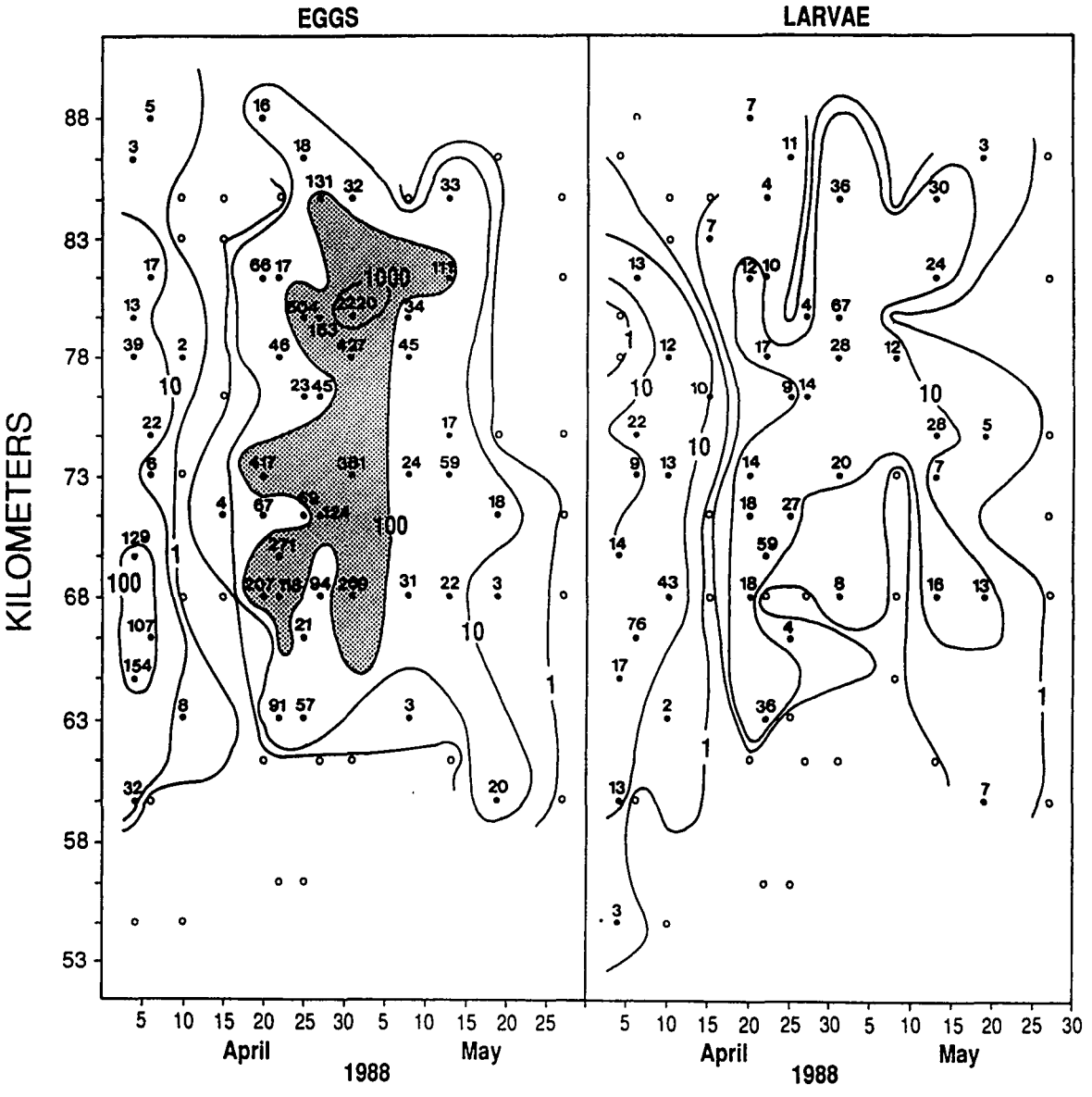

EGGS
LARVAE
KILOMETERS
88
83
78
73
68
63
58
53
5 10 15 20 25 30 5 10 15 20 25
April
May
1988
5 10 15 20 25 30 5 10 15 20 25 30
April
May
1988

Figure 4.- Spatio-temporal distribution of striped bass eggs and larvae (#/100m^3) during 1989 for the Pamunkey River, 1989. Shaded area indicates densities >100/100m^3.

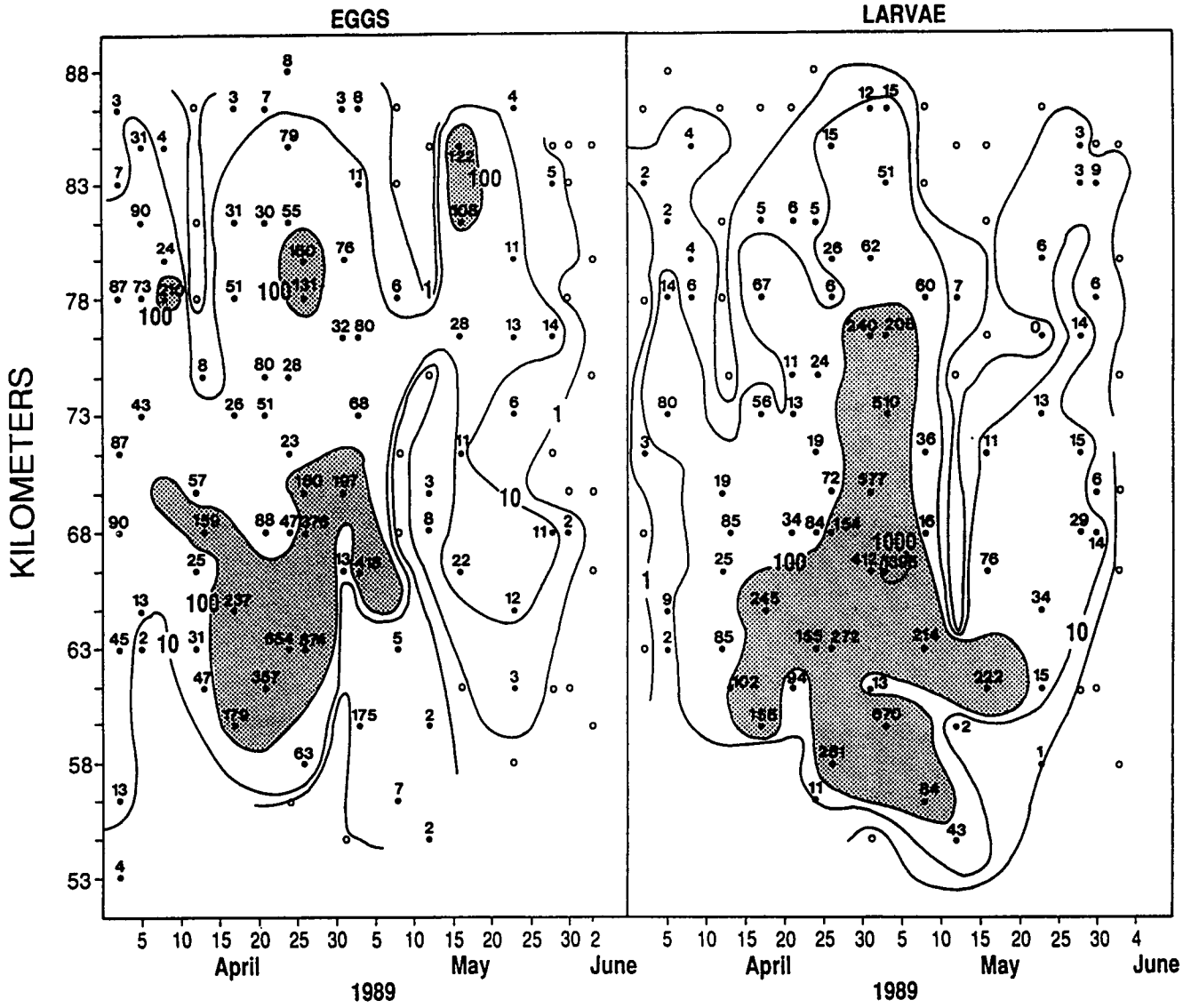
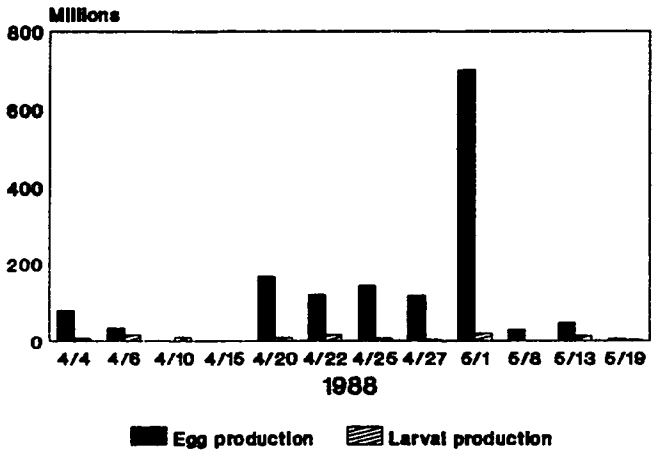

EGGS
LARVAE
KILOMETERS
88
83
78
73
68
63
58
53
5 10 15 20 25 30 5 10 15 20 25 30 2
April
May
June
1989
5 10 15 20 25 30 5 10 15 20 25 30 4
April
May
June
1989

Figure 5.- Estimates of striped bass eggs and larvae produced during **A**: 1988 and **B**: 1989. Data derived from cruises made on dates indicated.


Millions
800
600
400
200
0
4/4
4/6
4/10
4/15
4/20
4/22
4/25
4/27
5/1
5/8
5/13
5/19
1988
Egg production
Larval production

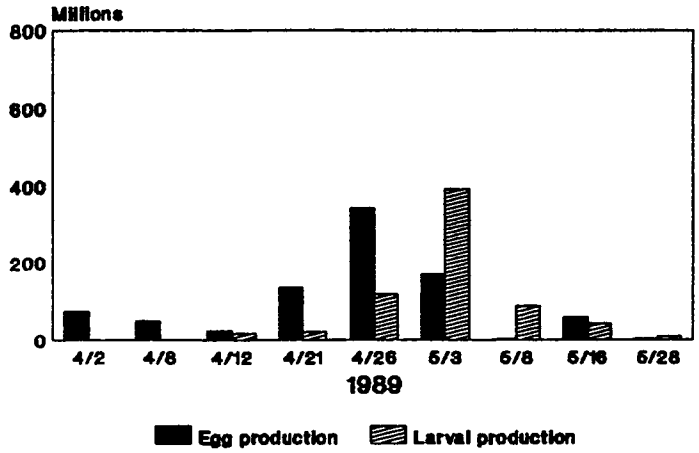
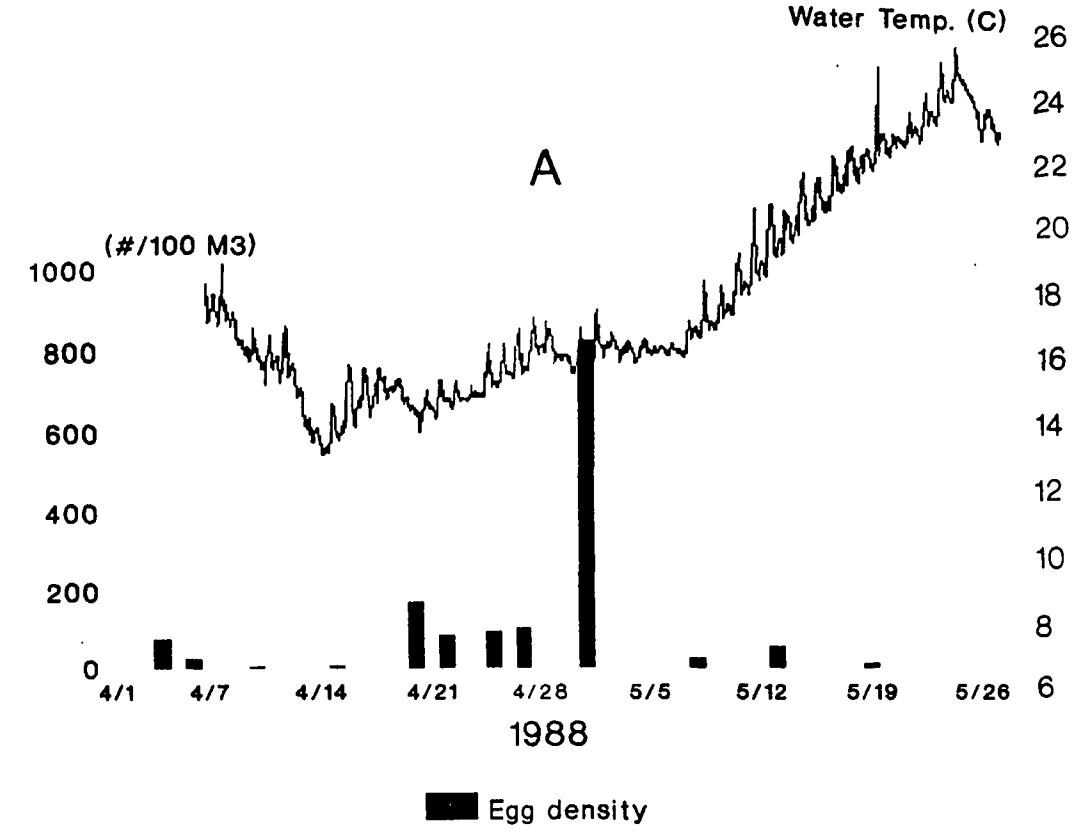

Millions
800
600
400
200
0
4/2
4/8
4/12
4/21
4/26
5/3
5/8
5/16
5/26
1989
Egg production
Larval production

Figure 6.- Egg density (total number/ total volume in #/100m^3 at positive stations) for a cruise and water temperature during **A**: 1988 and **B**: 1989.


Water Temp. (C)
A
(#/100 M3)
1000
800
600
400
200
0
26
24
22
20
18
16
14
12
10
8
6
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1988
Egg density

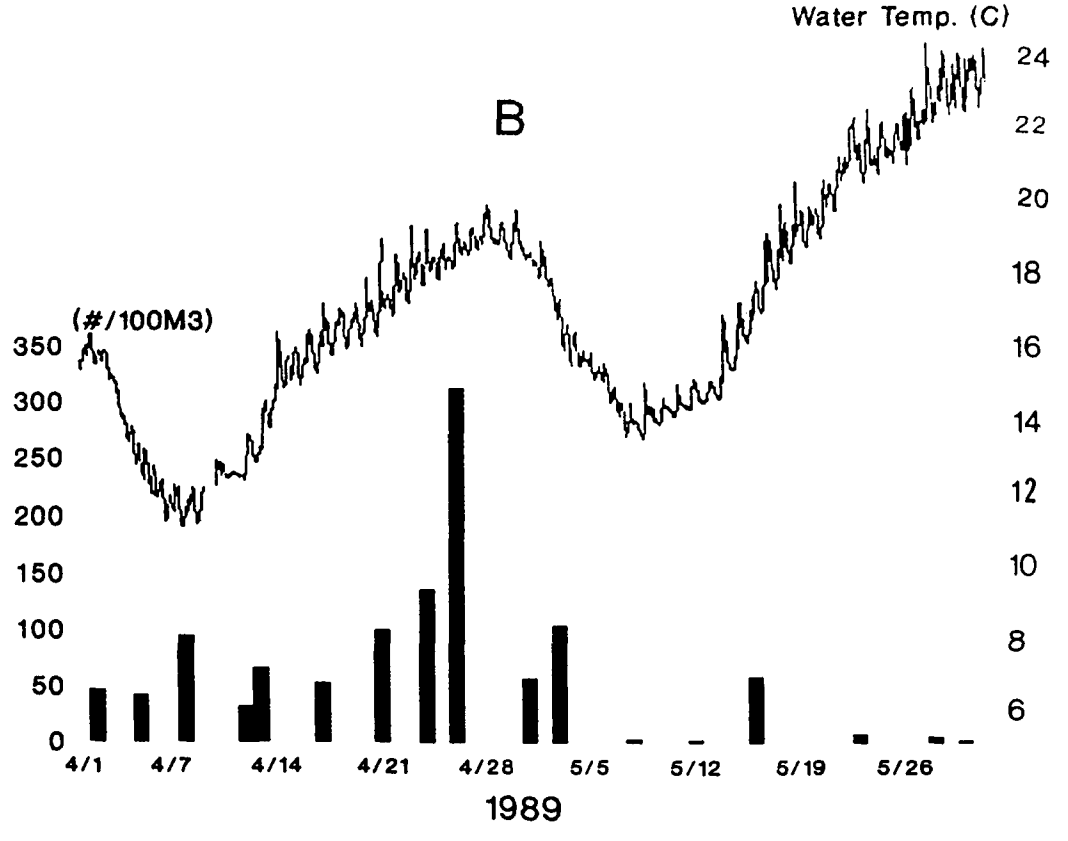

Water Temp. (C)
B
(#/100M3)
350
300
250
200
150
100
50
0
24
22
20
18
16
14
12
10
8
6
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1989

Figure 7.- Spatio-temporal distribution of water temperature (°C) during spring 1988 and 1989 for the Pamunkey River, VA.

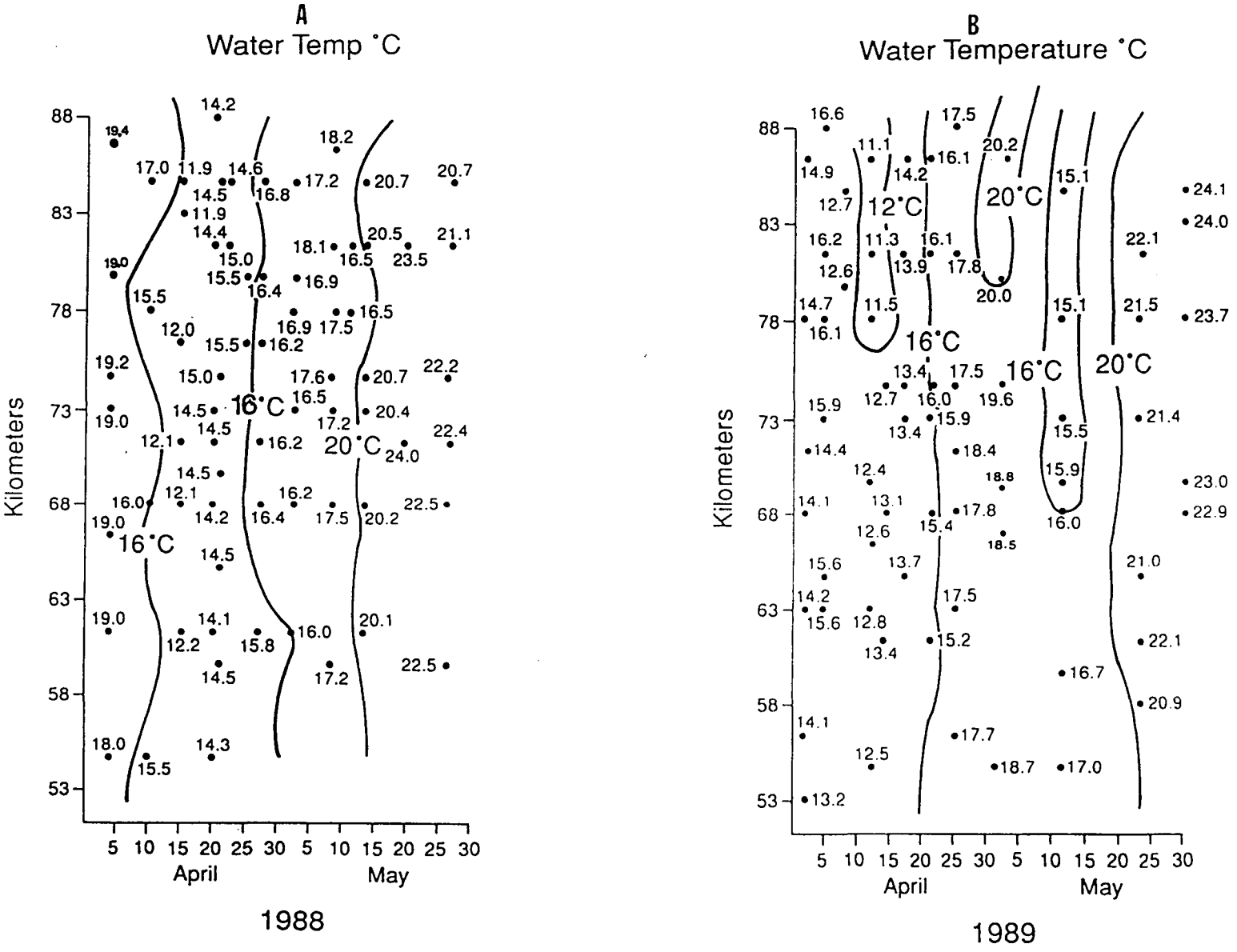
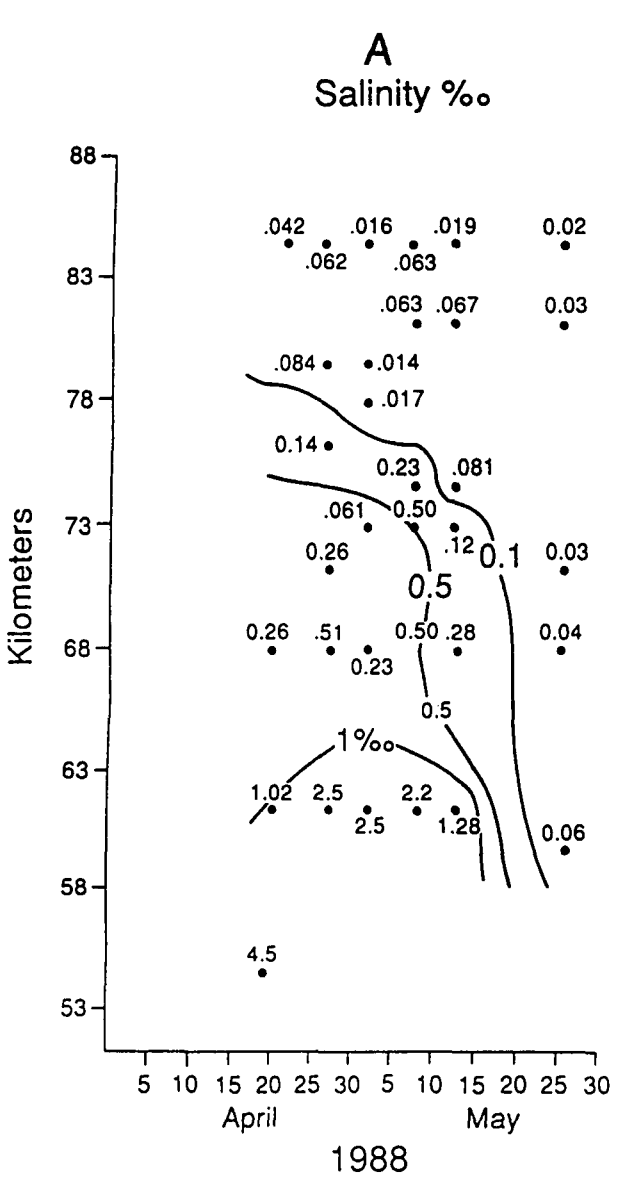

A
Water Temp °C
Kilometers
88
83
78
73
68
63
58
53
16°C
20°C
5 10 15 20 25 30 5 10 15 20 25 30
April
May
1988
B
Water Temperature °C
12°C
16°C
16°C
20°C
20°C
1989

Figure 8.- Spatio-temporal distribution of salinity ($^{\circ}/_{oo}$) for the Pamunkey River, VA during spring 1988 and 1989. No eggs were collected at densities below $1^{\circ}/_{oo}$.


A
Salinity ‰
Kilometers
88
83
78
73
68
63
58
53
.042 .016 .019 0.02
.062 .063
.063 .067 0.03
.084 .014
.017
0.14
0.23 .081
.061 0.50
.12 0.1 0.03
0.26
0.5
0.26 .51 0.50 .28 0.04
0.23
0.5
1‰
1.02 2.5 2.2
2.5 1.28 0.06
4.5
5 10 15 20 25 30 5 10 15 20 25 30
April May
1988

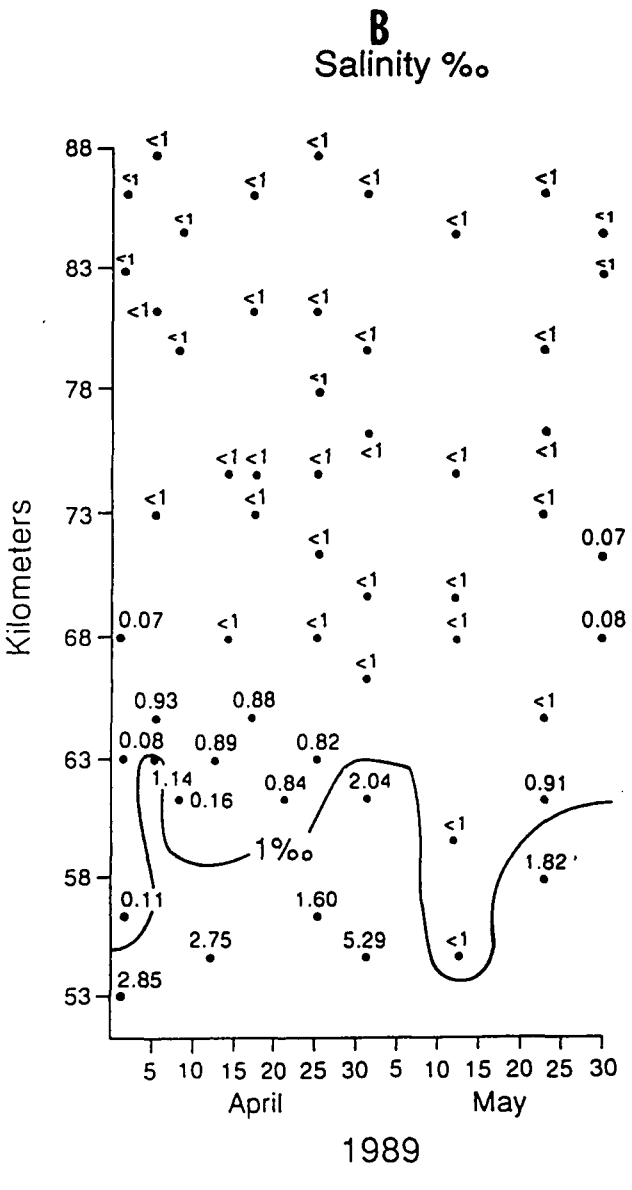
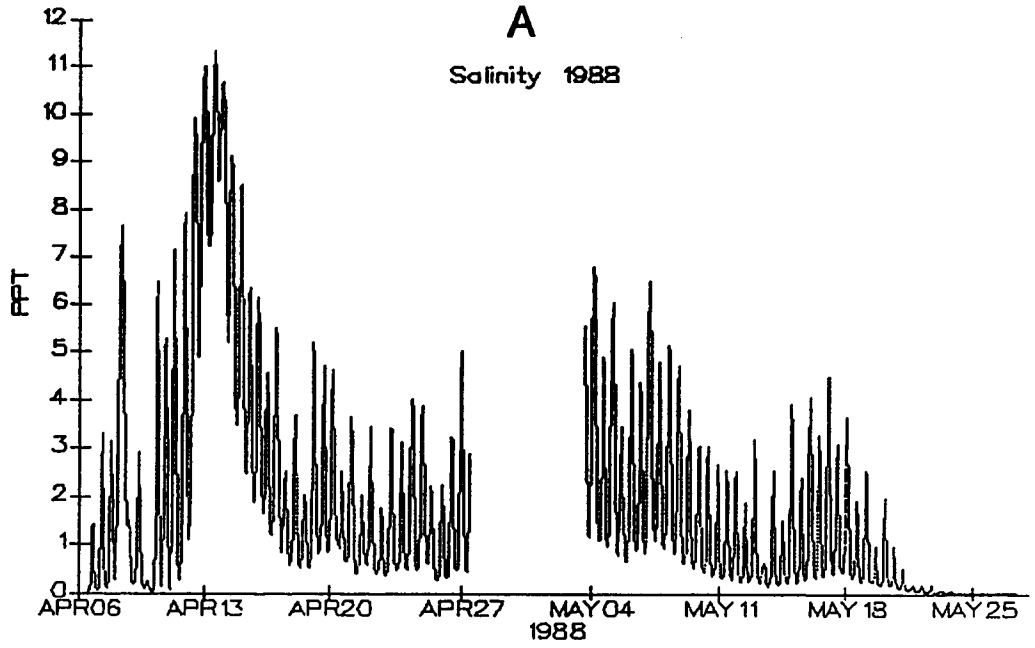

B
Salinity ‰
Kilometers
88
83
78
73
68
63
58
53
<1
0.07
0.08
0.93 0.88
0.08 0.89 0.82
1.14 0.84 2.04 0.91
0.16
1‰
1.82
0.11 1.60
2.75 5.29
2.85
5 10 15 20 25 30 5 10 15 20 25 30
April May
1989

Figure 9. Salinity values (°/$_{oo}$) at the environmental station in 1988 (Rkm 63) and 1989 (Rkm 78)


A
Salinity 1988
PPT
12
11
10
9
8
7
6
5
4
3
2
1
0
APR06
APR13
APR20
APR27
MAY04
MAY11
MAY18
MAY25
1988

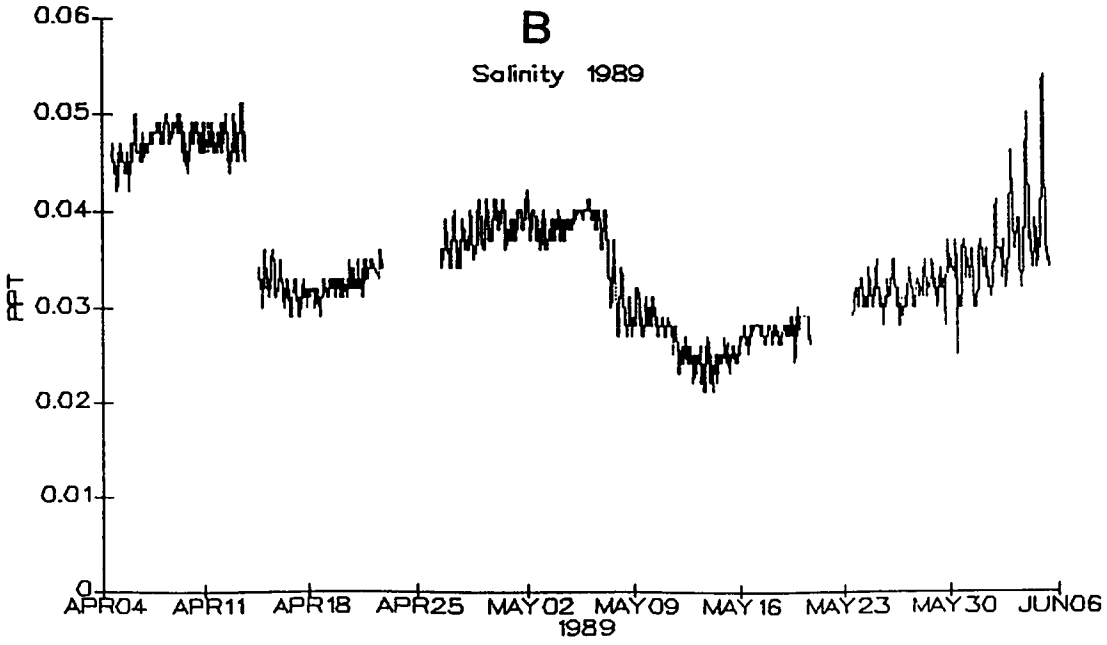
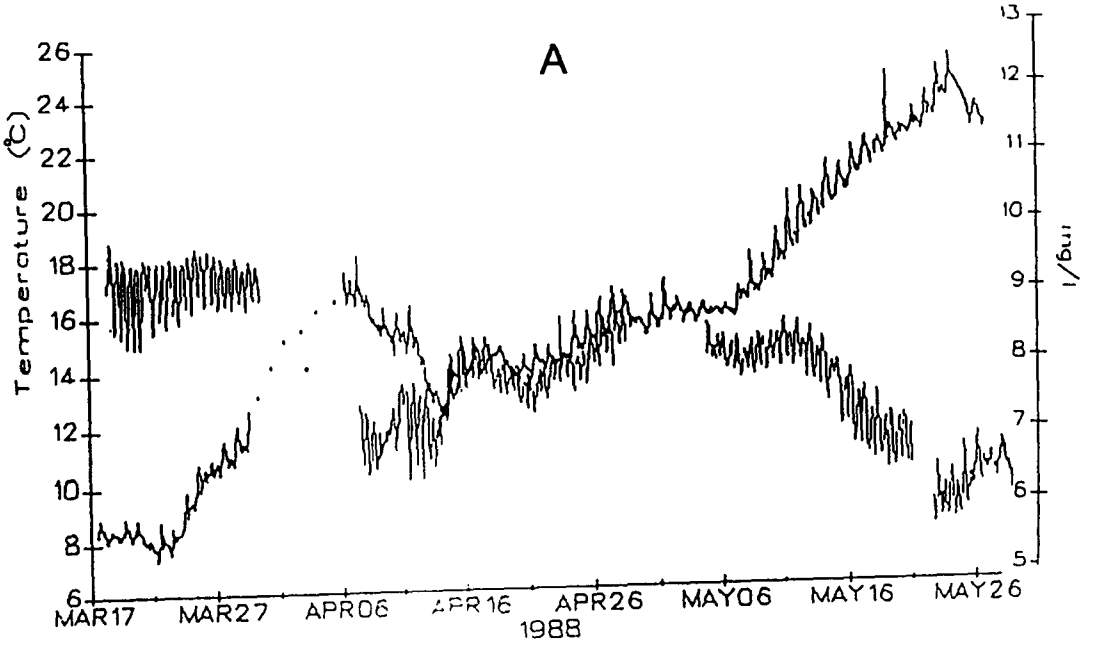

B
Salinity 1989
PPT
0.06
0.05
0.04
0.03
0.02
0.01
0
APR04
APR11
APR18
APR25
MAY02
MAY09
MAY16
MAY23
MAY30
JUN06
1989

Figure 10. Plots of dissolved oxygen (mg/l) and water temperature (°C) in the Pamunkey River, VA during spring 1988 and 1989.


A
Temperature (°C)
mg/l
MAR17
MAR27
APR06
APR16
APR26
MAY06
MAY16
MAY26
1988

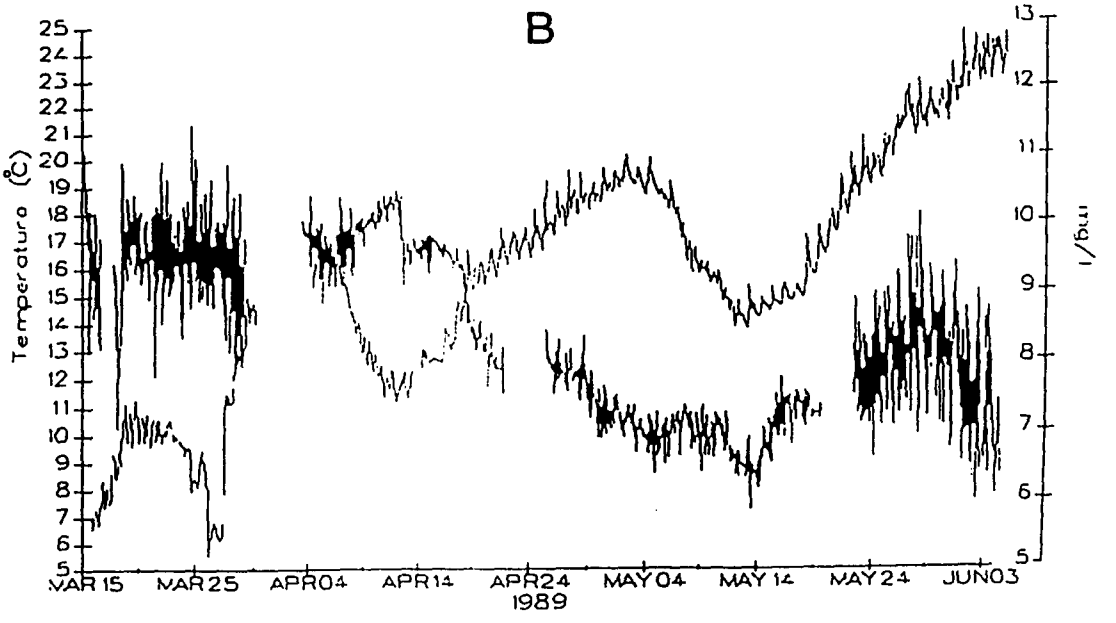
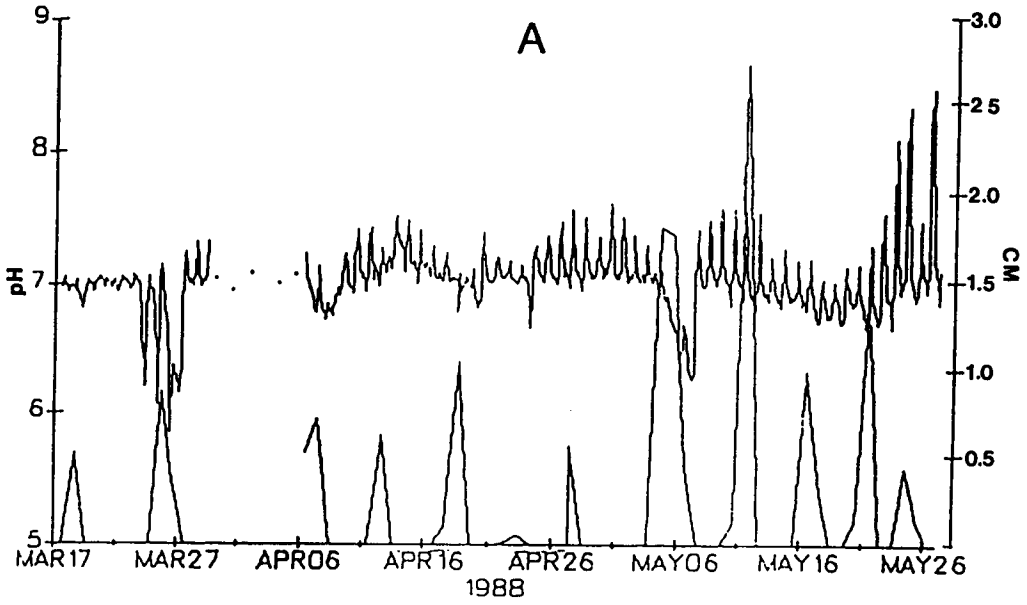

B
Temperatura (°C)
mg/l
MAR15
MAR25
APR04
APR14
APR24
MAY04
MAY14
MAY24
JUN03
1989

Figure 11. Plots of pH and rainfall for the Pamunkey River, VA during spring 1988 and 1989.


A
9
8
7
6
5
pH
3.0
2.5
2.0
1.5
1.0
0.5
CM
MAR17
MAR27
APR06
APR16
APR26
MAY06
MAY16
MAY26
1988

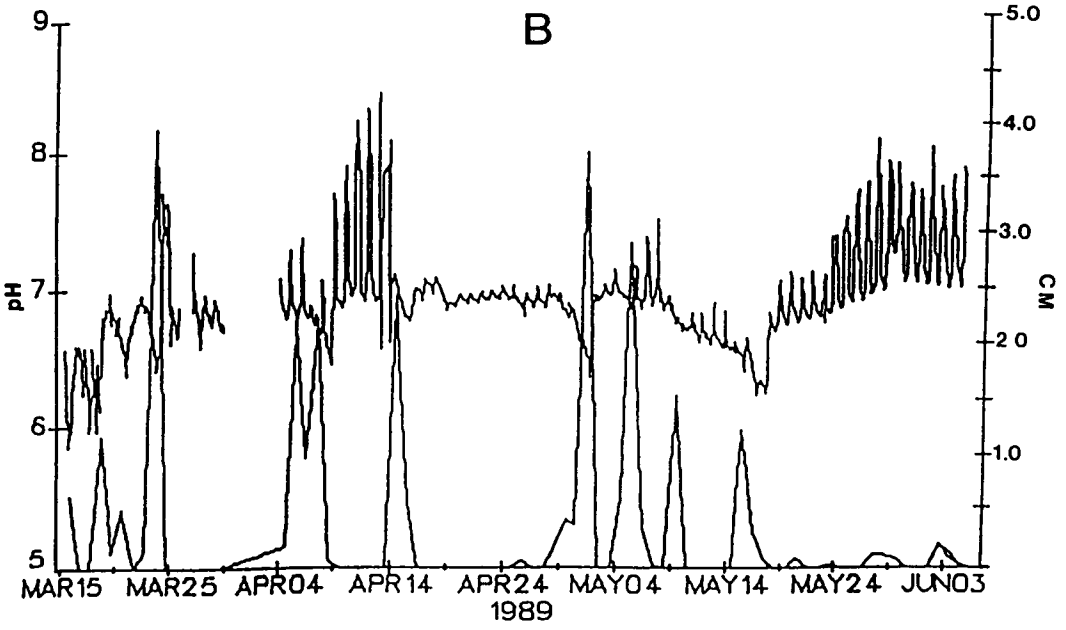
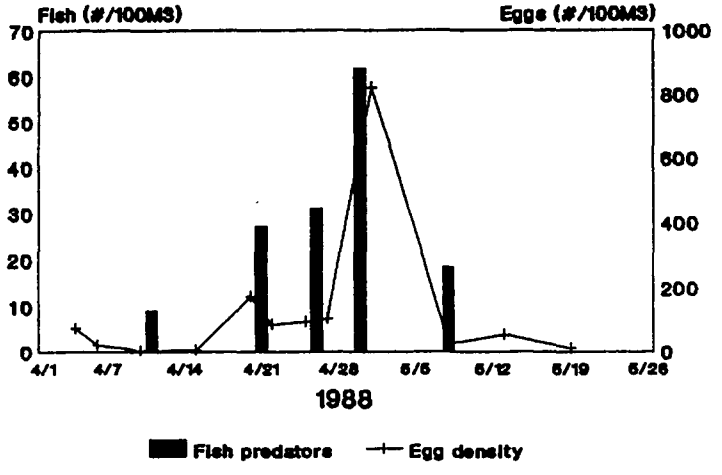

B
9
8
7
6
5
pH
5.0
4.0
3.0
2.0
1.0
CM
MAR15
MAR25
APR04
APR14
APR24
MAY04
MAY14
MAY24
JUN03
1989

Figure 12. Density (total number/total volume filtered at positive stations) of potential fish predators (those tested positive in laboratory trials), and striped bass eggs during **A**: 1988 and **B**: 1989 on the Pamunkey River, VA.


Fish (#/100M3)
Eggs (#/100M3)
70
60
50
40
30
20
10
0
1000
800
600
400
200
0
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1988
Fish predators
Egg density

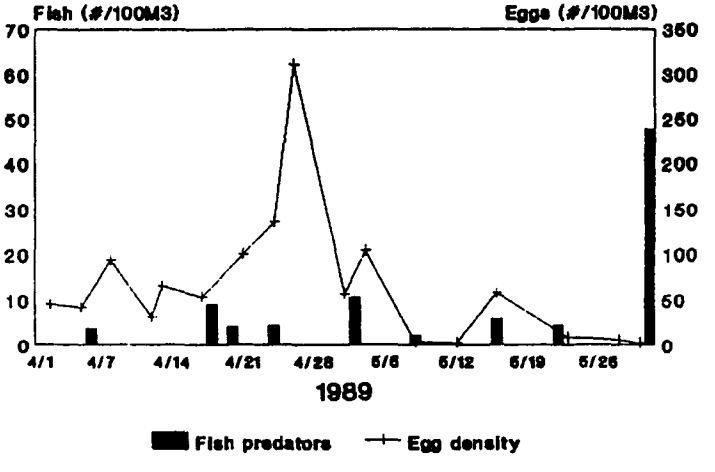
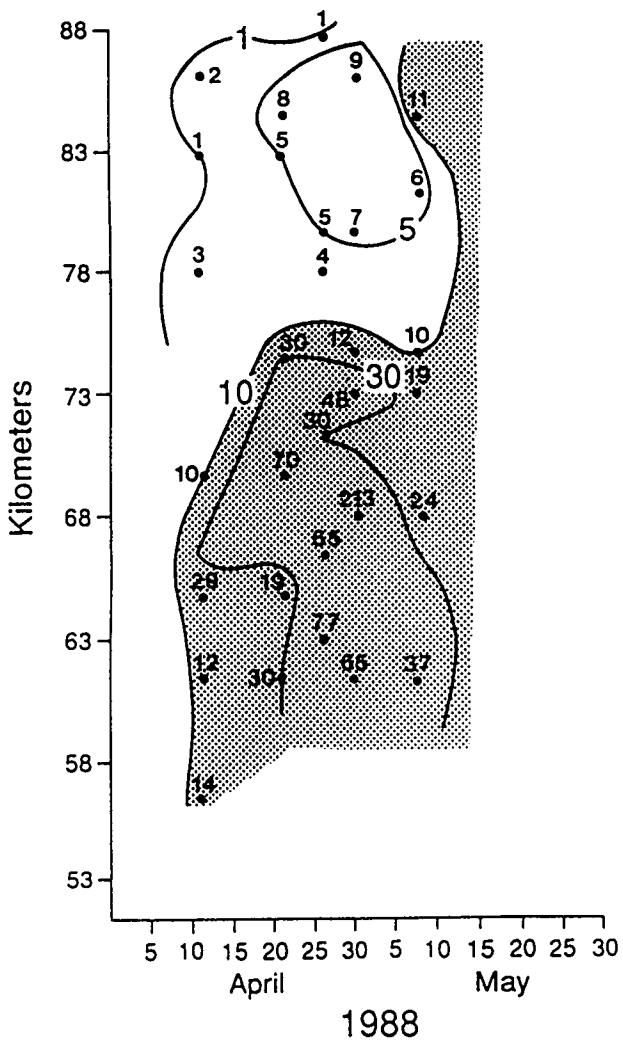

Fish (#/100M3)
Eggs (#/100M3)
70
60
50
40
30
20
10
0
350
300
250
200
150
100
50
0
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1989
Fish predators
Egg density

Figure 13.- Spatio-temporal distribution of potential fish predators (#/100m^3) in the Pamunkey River, VA during spring 1988 and 1989.

A

Potential Fish Predators #/100m³



B

Potential Fish Predators #/100m³

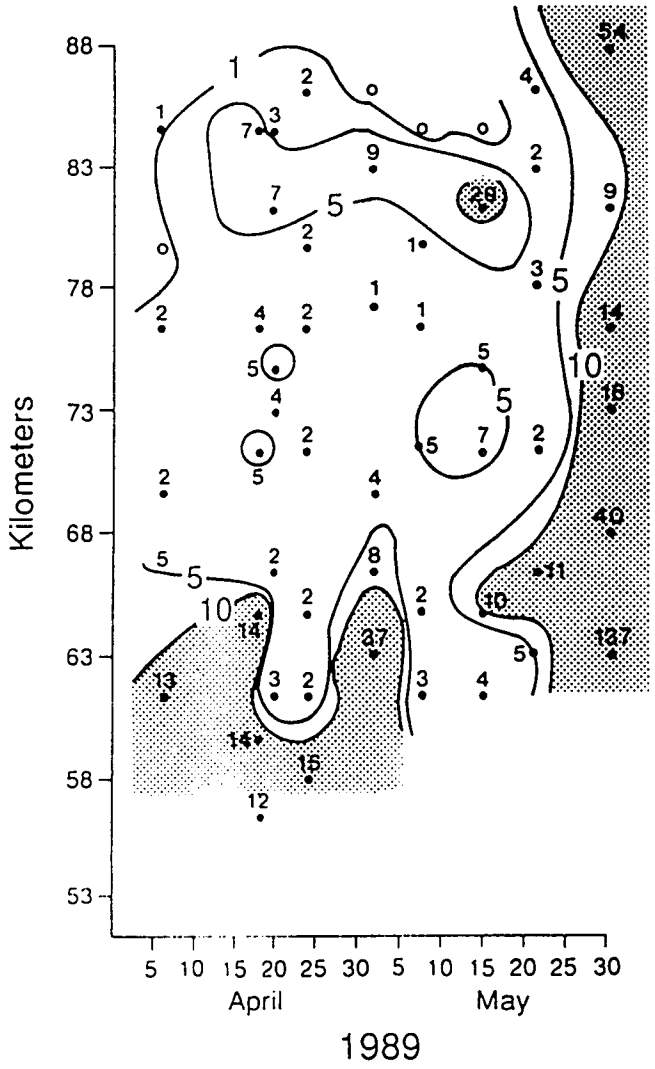
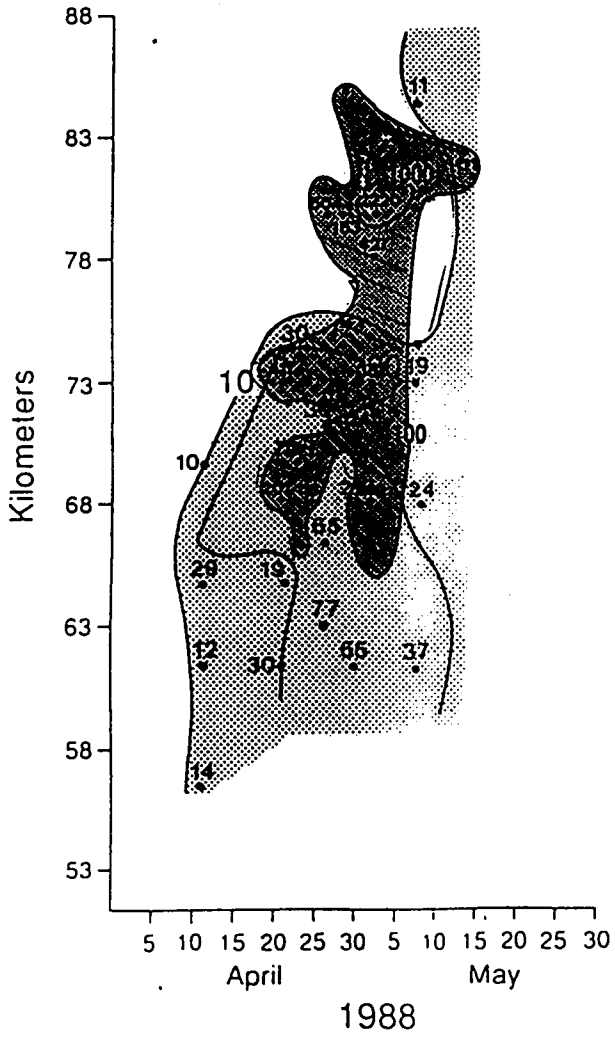


Figure 14.- A: Spatio-temporal distribution of striped bass egg densities >100/100m^3 superimposed over potential fish predators >10/100m^3. B: Spatio-temporal distribution of densities of striped bass larvae superimposed over densities of potential predators >10/100m^3.


Kilometers
88
83
78
73
68
63
58
53
5 10 15 20 25 30 5 10 15 20 25 30
April
May
1988

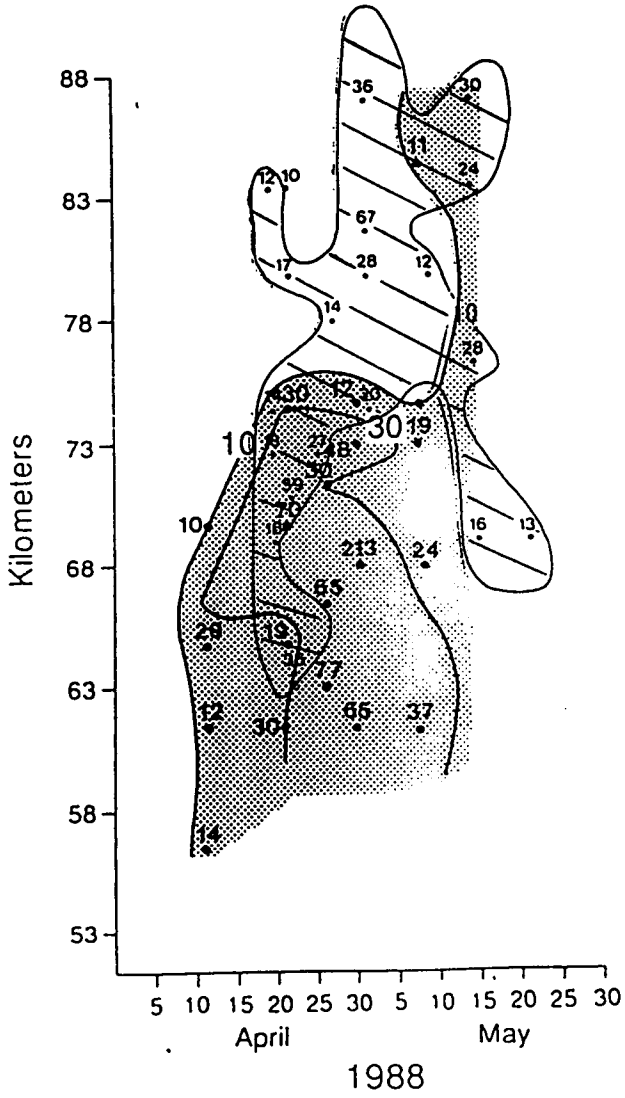
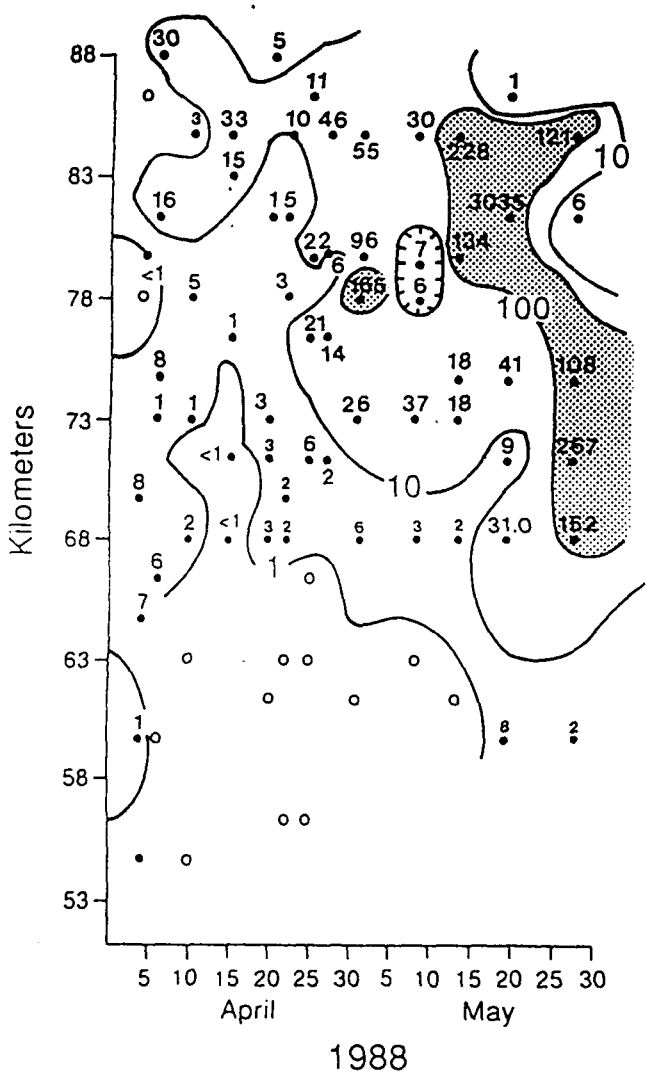

Kilometers
88
83
78
73
68
63
58
53
5 10 15 20 25 30 5 10 15 20 25 30
April
May
1988

Figure 15.- Spatio-temporal distribution of cyclopoid copepods (Acanthocyclops vernalis and Mesocyclops edax) for the Pamunkey River, VA during spring 1988 and 1989. Densities expressed as #/m^3.

A

Cyclopoid Copepods #/m³



B

Cyclopoid Copepods #/m³

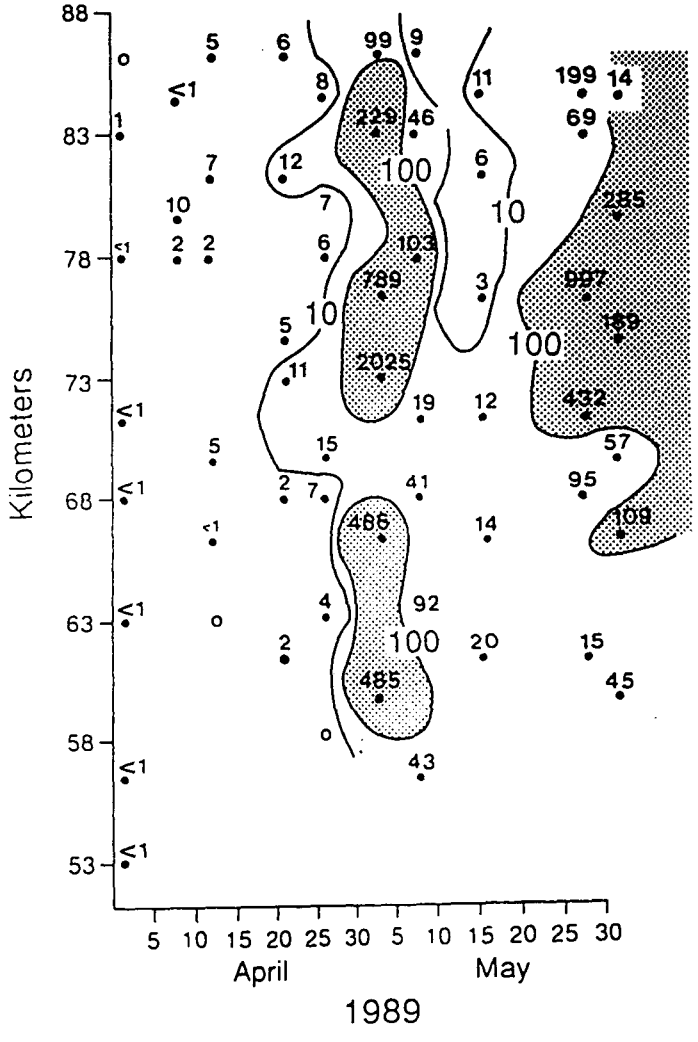
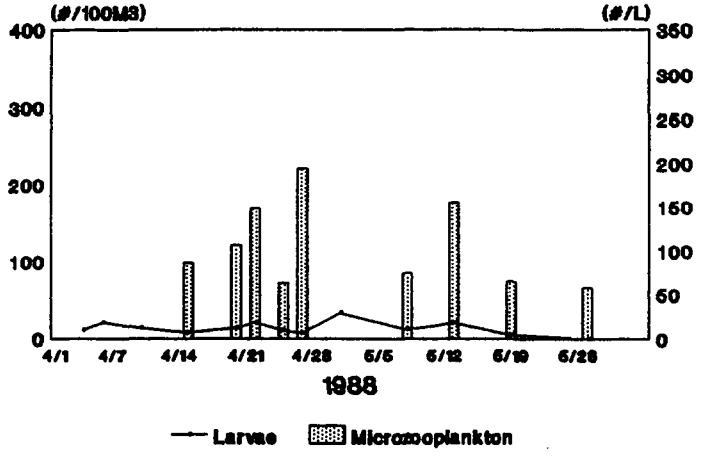


Figure 16.- Cruise densities (total number/total volume filtered at positive stations) of microzooplankton and striped bass larvae during **A**: 1988 and **B**: 1989.


(#/100M3)
(#/L)
400
300
200
100
0
350
300
250
200
150
100
50
0
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1988
Larvae
Microzooplankton

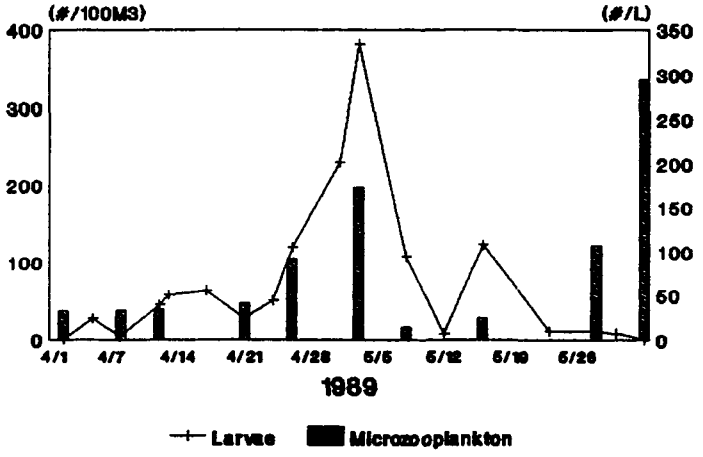

(#/100M3)
(#/L)
400
300
200
100
0
350
300
250
200
150
100
50
0
4/1
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1989
Larvae
Microzooplankton

Figure 17.- Spatio-temporal distribution of microzooplankton (#/l) for the Pamunkey River, VA during spring 1988 and 1989.

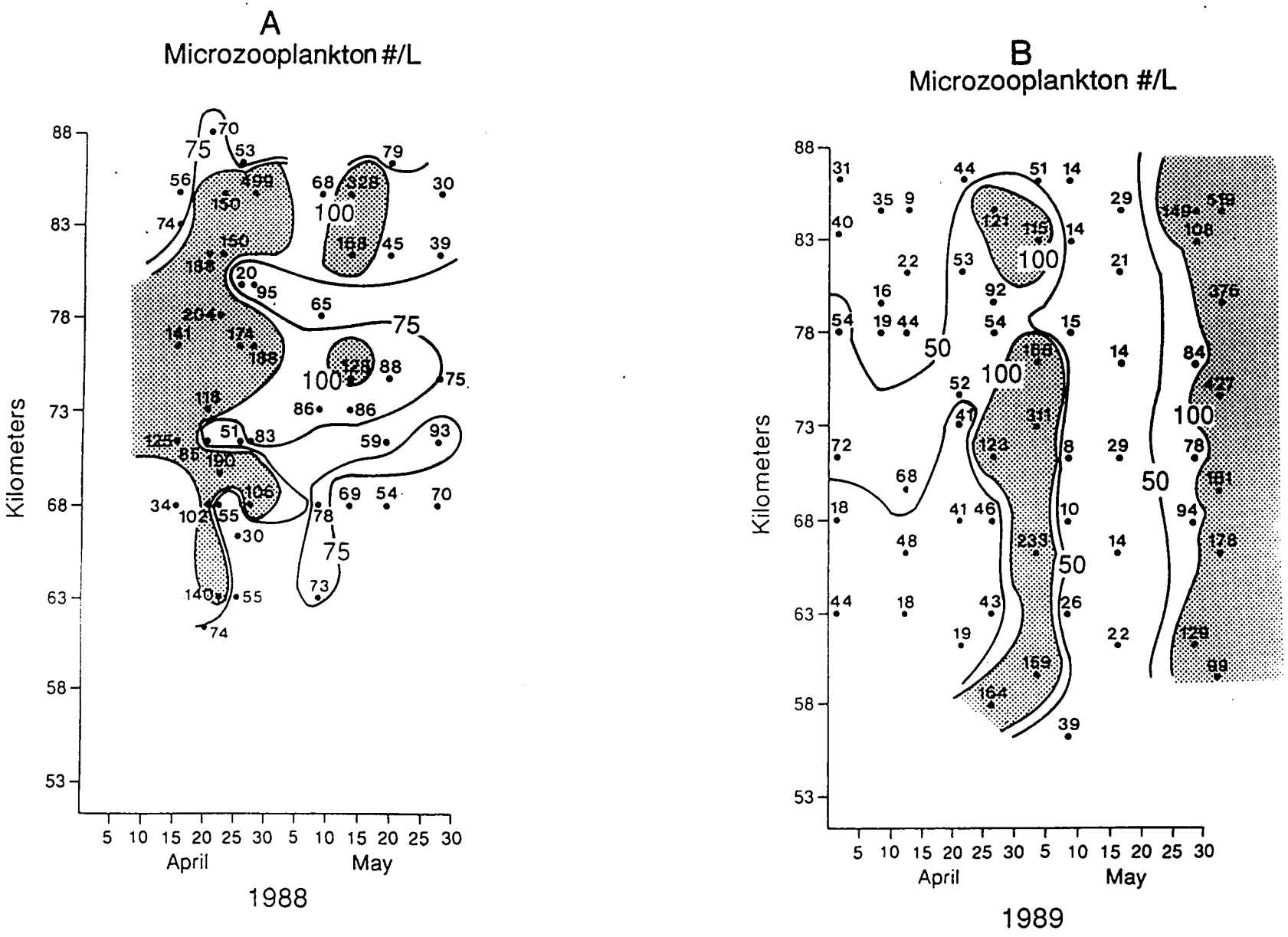
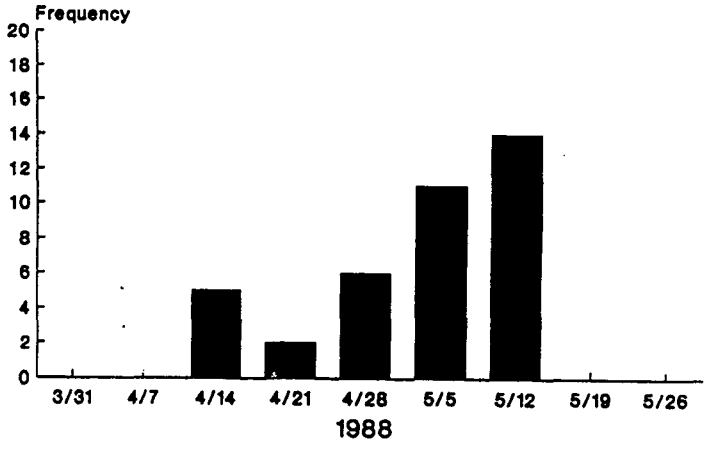

A
Microzooplankton #/L
Kilometers
88
83
78
73
68
63
58
53
5 10 15 20 25 30 5 10 15 20 25 30
April
May
1988
B
Microzooplankton #/L
Kilometers
April
May
1989

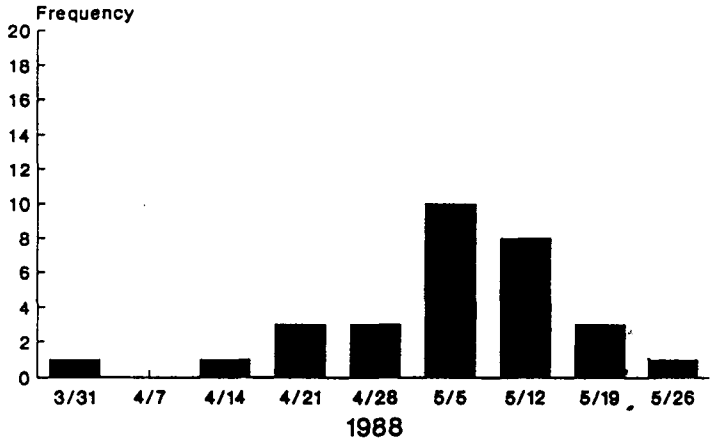
Figure 18. Juvenile birthdate distributions for the Pamunkey River in 1988. Birthdates pooled by week. **A**: June samples, **B**: July samples, **C**: August samples, **D**: Total (June, July and August).

A



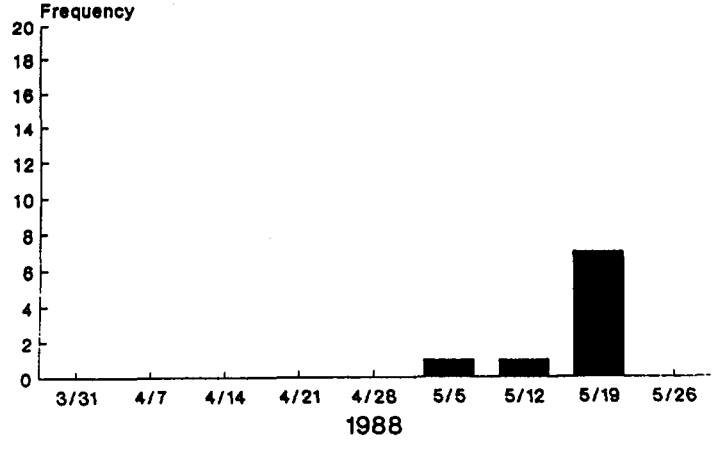
June 1988 n=38

B



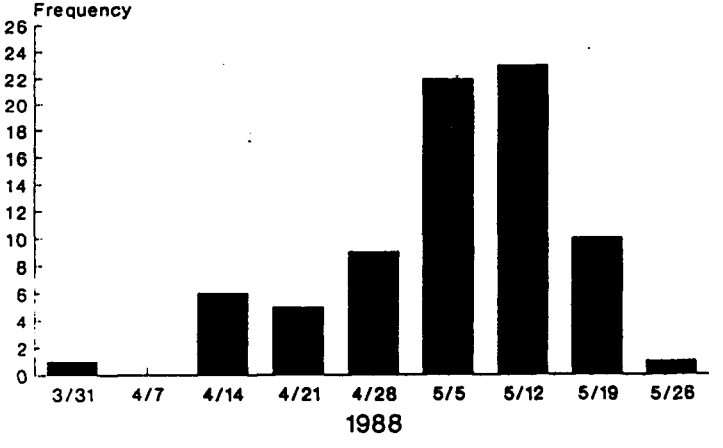
July 1988 n=31

C



August 1988 n=8

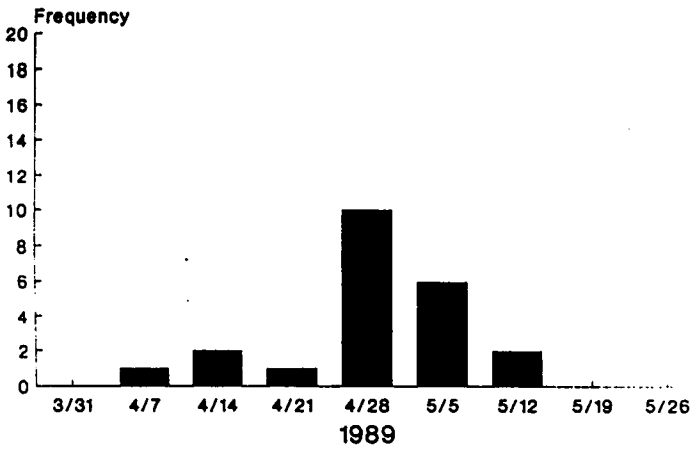
D



Total 1988 n=77

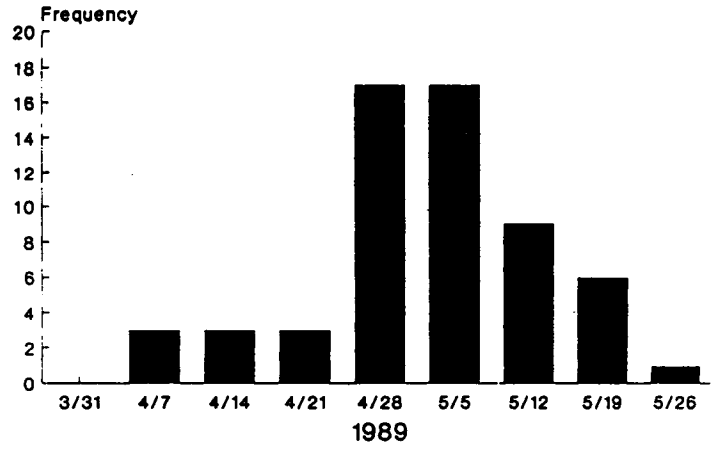
Figure 19.- Juvenile birthdate distribution for the Pamunkey River during 1989. Birthdates pooled by week. **A**: June samples, **B**: July samples, **C**: August samples, **D**: Total (June, July, August).

A



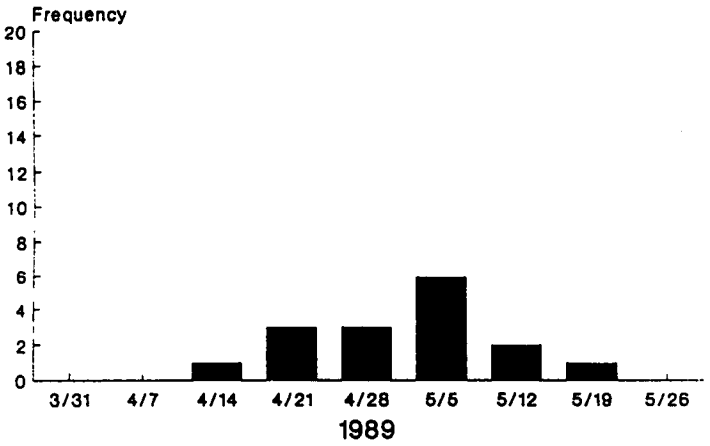
June 1989 n=22

B



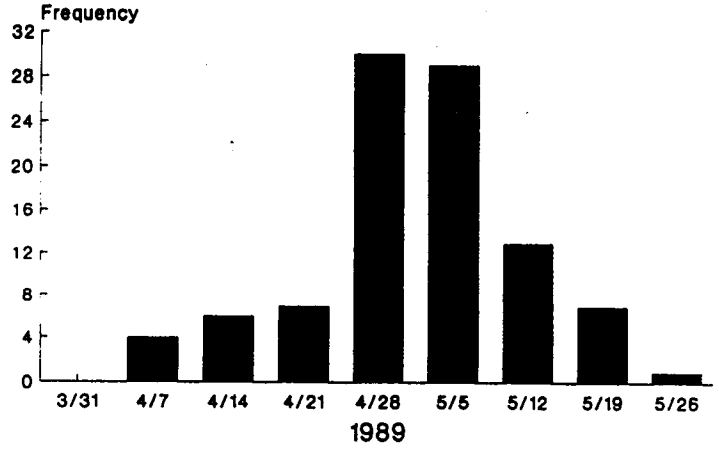
July 1989 n=59

C



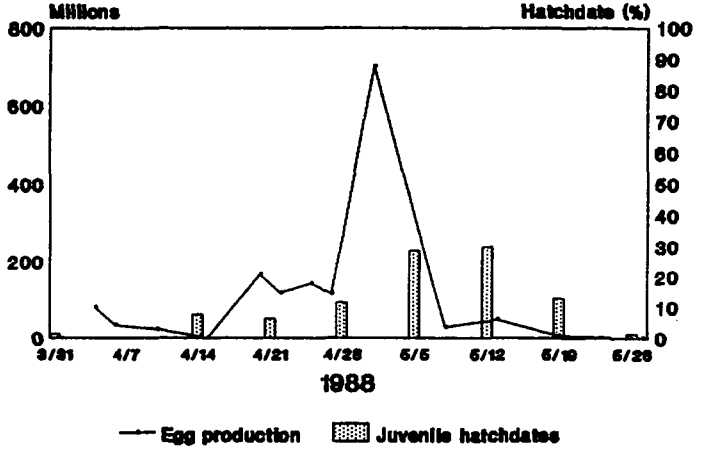
August 1989 n=16

D



Total 1989 n=97

Figure 20.- Juvenile birthdates (%), and production of striped bass eggs for the Pamunkey River, VA during **A**: 1988 and **B**: 1989.


Millions
Hatchdate (%)
800
600
400
200
0
100
90
80
70
60
50
40
30
20
10
0
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1988
Egg production
Juvenile hatchdates

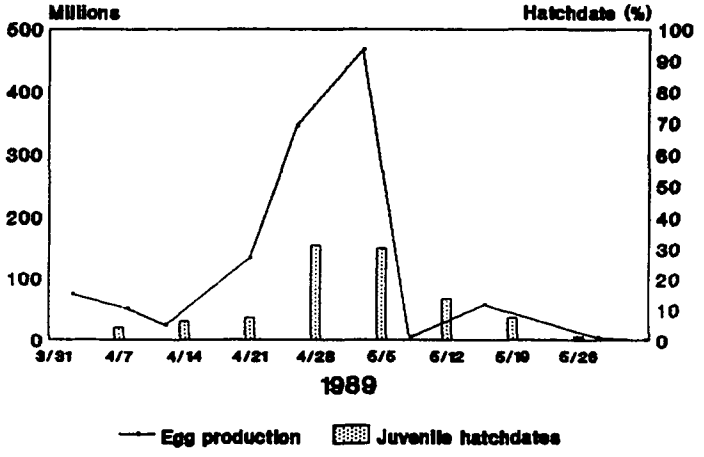
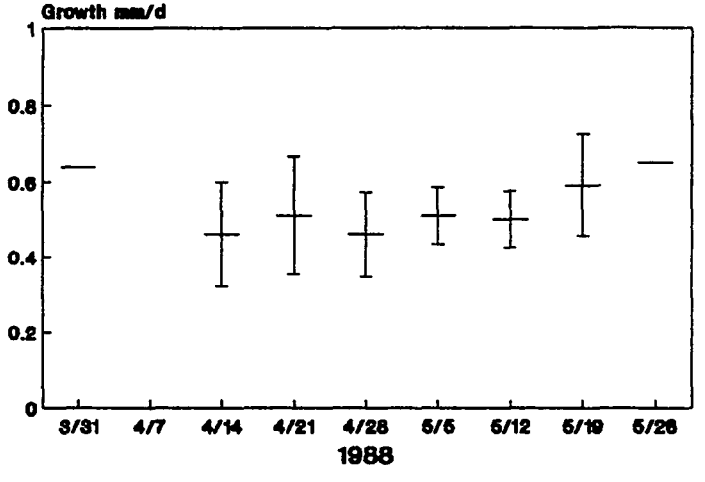
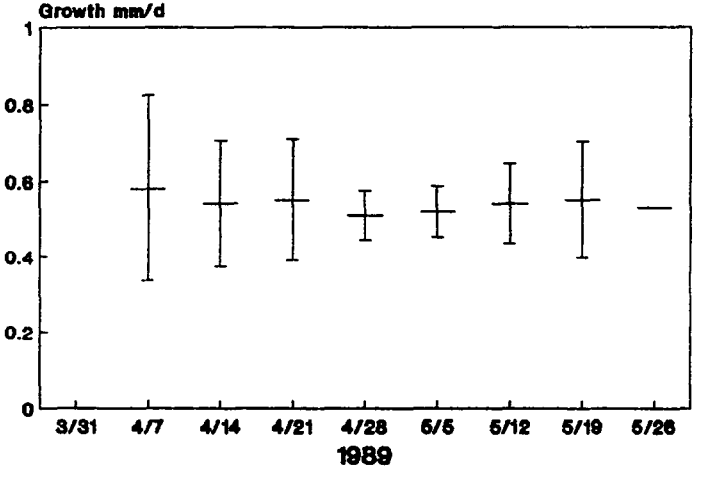

Millions
Hatchdate (%)
500
400
300
200
100
0
100
90
80
70
60
50
40
30
20
10
0
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1989
Egg production
Juvenile hatchdates

Figure 21.- Growth rates mm/d and confidence intervals (± 1 SE) for juveniles collected in the Pamunkey River during **A**: 1988 and **B**: 1989. Data pooled by week.


Growth mm/d
1
0.8
0.6
0.4
0.2
0
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1988


Growth mm/d
1
0.8
0.6
0.4
0.2
0
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
1989

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VITA

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In January 1986 he entered the The College of William and Mary, Virginia Institute of Marine Science, School of Marine Science. He married Beth in August 1988 and became a father to Molly in October 1990.