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A Framework for Construction and Analysis of Juvenile Abundance Indices for American Shad (Alosa sapidissima) in the York River, Virginia

Mary Lynn Aiken

College of William and Mary - Virginia Institute of Marine Science

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A FRAMEWORK FOR CONSTRUCTION AND ANALYSIS OF JUVENILE

ABUNDANCE INDICES FOR AMERICAN SHAD (ALOSA SAPIDISSIMA)

IN THE YORK RIVER, VIRGINIA

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A Thesis

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

Master of Science

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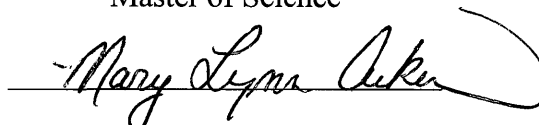
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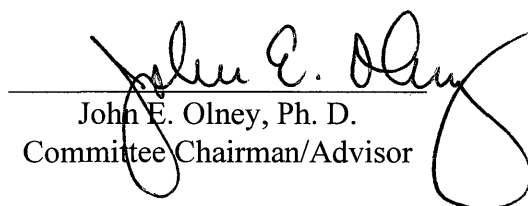
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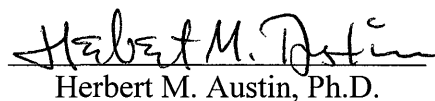
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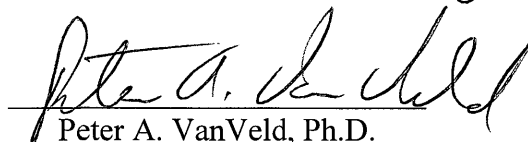
Approved, December 2000

John E. Olney, Ph. D.
Committee Chairman/Advisor

Herbert M. Austin, Ph.D.

John M. Hoenig, Ph.D.

Peter A. VanVeld, Ph.D.

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CHAPTER I

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ABSTRACT

The two major objectives of this research were to (1) critically evaluate the significance of the juvenile abundance index (JAIs) for American shad in the York River and (2) investigate the relationship between the JAI and life of the American shad in the Pamunkey River, Virginia. This first objective was accomplished by investigating the relationships between different methods of calculation of the JAI, comparing indices from independent monitoring surveys, and examining catch rates by river block (5 river-mile sections). Accomplishing the second objective required identification of common and distinguishing developmental characteristics of surviving juvenile American shad in two years of similar abundance (1998,1999) in the Pamunkey River nursery habitat.

The JAI was calculated based on catches of young shad on weekly nighttime sampling with a bow-mounted pushnet in the Mattaponi River and Pamunkey River. Indices from 1979-1999 were calculated as arithmetic, geometric, maximum geometric, and areal means. Indices were compared ends in relative abundance depend critically on the form of the index. All indices were related, but the maximum geometric mean was less tightly correlated with other indices. Comparisons of Mattaponi River, Pamunkey River, and York River indices indicated the Mattaponi River had a larger juvenile population than the Pamunkey River. Thus, the Mattaponi River drives trends in the combined York River index. York River JAIs were also compared to indices from a concurrent, independent seine survey in the York River. Aside from the lesser correlated maximum geometric mean, indices were highly correlated suggesting the relative abundance of juvenile shad is measured similarly in independent surveys. Within the Mattaponi River and Pamunkey River habitats, the area in which juveniles are captured appeared to expand during years with large JAIs and contract in years with low JAIs. Additionally, catch rates were generally higher upriver than down river in most years.

Saggita of juvenile shad, collected during the summer of 1998 and 1999, were aged using to estimate age, hatch dates, and cohort growth and mortality rates. The hatchdate distribution in 1998 was dome-shaped and included the dates April 7 to June 22. The hatchdate distribution in 1999 was flat-topped, slightly broader, and included the dates from 4 April to 22 June. Stabilization of river flow was associated with time of hatch of surviving juveniles. Comparisons of the temporal distributions of hatchdates with catch rates of ripe females, eggs, and larvae collected during other studies on the Pamunkey River indicated that shad hatched later in the spawning season experienced greater survival. Because the mean M/G in 1998 (3.73) was significantly higher than that in 1999 (0.92) and the period of stable river flow (hypothesized to promote good recruitment) was greater in 1999, it seemed like the 1999 year-class should have been larger than that of 1998, but this was not the case. The most parsimonious explanation for this difference is early emigration of juveniles, as suggested by the steeper decline in cruise catch rates after the peak, and smaller mean length, weight, and age of individuals in 1998 (40.6mm, 1.1g, 46 days - 1998; 46.1mm, 1.4g, 50days - 1999).

GENERAL INTRODUCTION

The American shad, *Alosa sapidissima*, is an anadromous member of the family Clupeidae. Although most abundant from Connecticut to North Carolina, the species ranges from the St. Lawrence River, Canada, to the Tomaka River, Florida (Walburg and Nichols 1967). This planktivorous fish generally matures at ages 3 - 7 for females (Leggett 1969, Maki et al., submitted) and about four years for males (Leggett and Carscadden 1978). Adults enter rivers in the spring to spawn. At the southern latitudes, shad are generally semelparous, but iteroparity increases with increasing latitude (Leggett and Carscadden 1978). Juveniles spend the summer in oligohaline and freshwater nurseries along the east coast of North America before returning to the open ocean. Environmental and biological events during this first summer are believed to be critical to the fluctuation of adult populations years later (Crecco and Savoy 1983, Crecco and Savoy 1985, Houde 1989).

American shad were once one of the most important commercial fisheries along the east coast of the United States. In the early 1800's, landings of American shad were approximately 23,000 metric tons (ASMFC 1999). Atlantic records of landings compiled by the National Marine Fisheries Service dating back to 1950 were the highest on record in 1957 at 5,156 metric tons (http://www.nmfs.gov/). Since then, landings for the Atlantic coast have decreased dramatically, reaching record lows of 260.4 metric tons in 1996 (Fig. 1). American shad in-river fisheries are currently not permitted in Maine, New Hampshire, Massachusetts, and Rhode Island. A moratorium on the capture and sale of American shad has existed in Maryland since 1980, and in Virginia, since 1994 (ASMFC 1999) in hopes of a resurgence of populations. In the eighties, approximately

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89% of the Atlantic harvest of shad was attributed to in-river fisheries; however, this contribution decreased yearly to approximately 33% in 1996. The construction of dams, alteration of natal habitats, and increased fishing pressure have threatened the survival of shad populations. Ocean intercept fisheries are scattered along the east coast and in-river fisheries exist in many states. Rivers in Massachusetts, Rhode Island, Pennsylvania, Maryland, Virginia, and Florida are closed to fishing. All other Atlantic Coast rivers possess in-river fisheries (ASMFC 1999). Restoration efforts and scientific investigations began in the mid-eighties, but no significant recovery of the population has occurred in the Chesapeake Bay. However, in some rivers (e.g., Merimack, Delaware rivers) stocks are stable and fishable (ASMFC 1998).

Acknowledging the need for protection and restorative action, the Atlantic States Marine Fisheries Commission (ASMFC) adopted a cooperative Interstate Fishery Management Plan (IFMP) for American Shad and River Herrings in 1985. This plan was later supplemented (1998) and amended (ASMFC 1999) to set specific regulations for the states. The goal of the amendment is to protect, restore, or maintain healthy levels of spawning stocks. Accordingly, states have instituted management plans including extensive hatchery efforts, in-river moratoria, and reductions in offshore fisheries. The IFMP mandates that certain producing states report an annual juvenile abundance index (JAI) which is intended to provide a measure of annual recruitment success, prediction of potential fishery yields, and triggers for either relaxing or restricting fisheries (Rago et al. 1995). Other management plans (e.g. those for striped bass and blue crab) also use juvenile abundance indices (Kahn et al. 1998, Rago et al. 1995) for these purposes.

The Virginia Institute of Marine Science (VIMS) began an annual American shad stock assessment program for the York River, Virginia in 1998. The in-river shad fishery on the York River has been closed since 1994, providing a unique opportunity for study (Olney and Hoenig, in pres). The program has three primary objectives. The first objective is to monitor the size of the spawning run by comparing contemporary catch rates of the staked gill net to those recorded in logbooks completed voluntarily by fishers prior to the closure of the fishery in 1980-1992. The second objective is to develop restoration targets for spawning runs based on the logbook data from the 1980's and older records collected in the 1950's. The third objective of the program is to develop methods for assessing the status of the population if the fishery is reopened, including a JAI-based method. In 1979, VIMS initiated a juvenile shad abundance monitoring program which produces an annual JAI intended for assessing adult populations 3-7 years in advance. However, after 19 years of monitoring (no sampling occurred in 1988-1990), the question still remains as to whether the index measures juvenile abundance on the spawning grounds, future recruitment, spawning stock biomass, hatching success and larval survival, or cannot be interpreted.

In the York River, the spawning season for American shad is protracted (late February through June) and individuals spawn in batches every 3-4 days (Olney et al., submitted). Timing of the in-river migration to the spawning grounds varies annually and by sex. The spawning grounds encompass a large section of the river including two biologically and physically different tributaries (the Mattaponi and Pamunkey Rivers). These reproductive, migratory, and spatial patterns suggest that multiple cohorts of

juvenile shad are produced during the spawning season at different times and in different places. Detection of these cohorts and knowledge of their vital characteristics require detailed studies of the age composition, size distribution, and catch rates of juveniles on the spawning grounds. Revealing this cohort-specific information should provide insight into the construction and value of the JAI. No such studies exist. JAIs have been positively correlated with recruitment of adult females 4-6 years later in the Connecticut River (Crecco et al. 1983), however, no models have been developed to relate juvenile abundance to subsequent adult abundance of American shad in any other system. The purpose of this study is to develop a framework for construction and analysis of the juvenile abundance indices for American shad in the York River, Virginia.

This study is divided into two parts. In section one, the calculation of the JAI is critically evaluated using juvenile shad catch data (1979-1999) from the nursery grounds on the York River. Four different methods of calculating the JAI are compared to determine whether trends in relative abundance depend critically on the form of the index. Each method is compared to an independent measure of shad abundance (the VIMS seine survey) to determine whether similar trends in abundance exist for different survey methods. Section two explores hatchdate distributions and cohort-specific vital rates of juvenile American shad in two years of average abundance (1998,1999). The number, hatchdates, and abundance of cohorts produced within a given season are determined. Early life history and juvenile survival are examined to judge whether years of similar juvenile production exhibit common or unique patterns of cohort growth and mortality. Cohort-specific vital rates are estimated and compared to relative abundance

and environmental conditions to determine whether the appearance of strong cohorts

correlates with any particular spawning times or environmental conditions.

STUDY AREA

The Pamunkey and Mattaponi rivers are adjacent watersheds that converge in West Point, Virginia to form the York River that flows to the Chesapeake Bay (Fig. 2). The Pamunkey River has a larger watershed (3,768 km^2) and average discharge rates (47.5 m^3/s) than the Mattaponi River (2,274 km^2; 27.2 m^3/s, respectively) (Bilkovic et al., in press).

American shad spawning grounds span from river kilometer 98 to km 150 on the Pamunkey River with highest egg densities located from km 104 to km 131. Spawning grounds on the Mattaponi River extend from km 81 to km 124 with highest densities of eggs located from km 96 to km 124 (Bilkovic et al. in press). Sampling cruises for juveniles in the Virginia JAI surveys began on the Pamunkey River at km 130 and on the Mattaponi River at km 111. Further upstream sampling was precluded by a 1.5m depth requirement of the sampling gear. Because the nursery zone is considered the freshwater area of each river, the absolute down river end of sampling fluctuates based on low summer river flows and salt wedge movement (Loesch and Kreite, 1983).
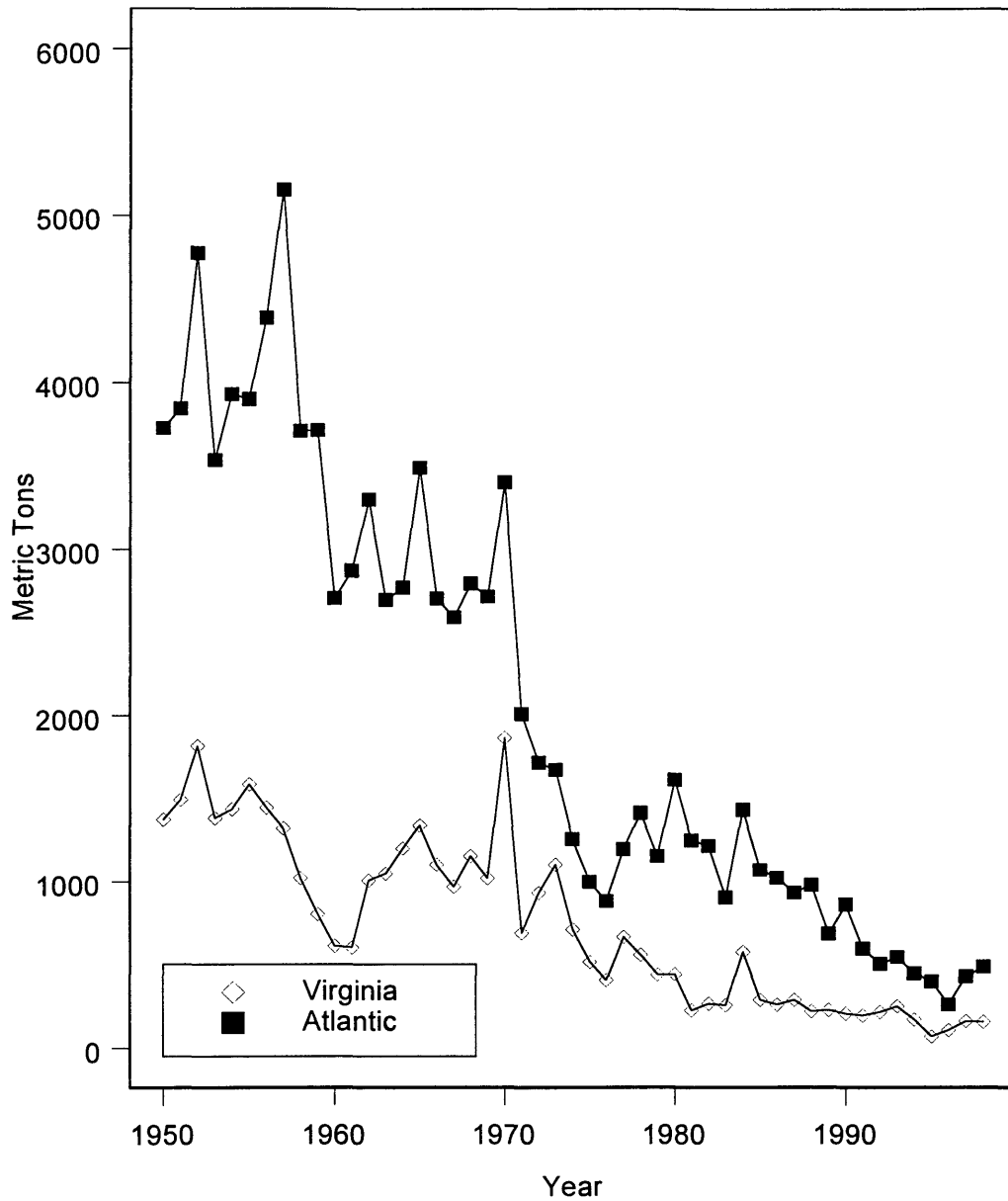
Figure 1: Landings of American shad, Atlantic Coast and Virginia (1950 - 1998).
Data from National Marine Fisheries Economics and Statistics division website
http://www.st.nmfs.gov/st1/commercial/index.html.

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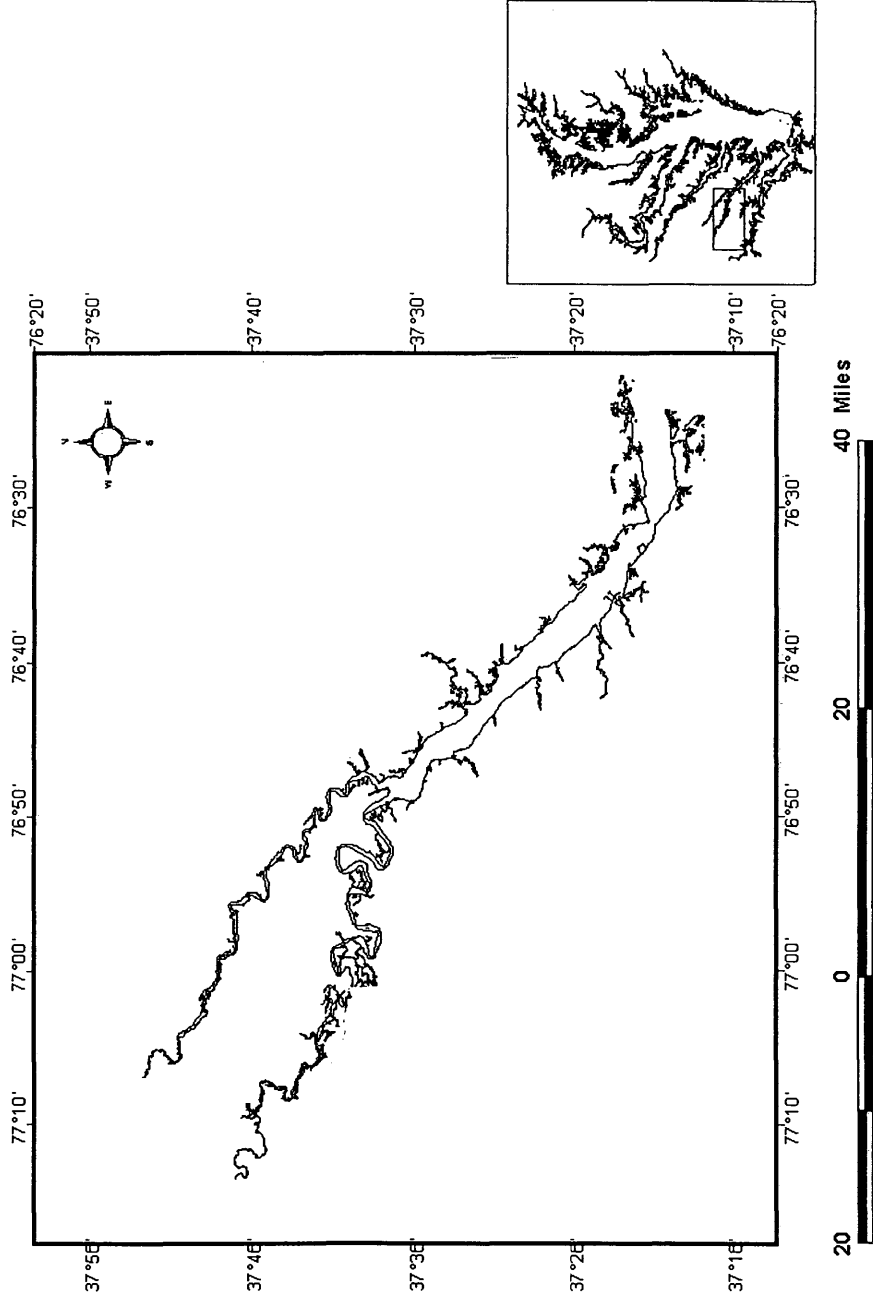
York River

Figure 2: Map of the York River with reference to the Chesapeake bay.

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CHAPTER 1: CONSTRUCTION OF JUVENILE ABUNDANCE INDICES FOR AMERICAN SHAD (*ALOSA SAPIDISSIMA*) IN THE YORK RIVER, VIRGINIA

ABSTRACT

The significance of the juvenile abundance index for American shad in the York River was critically evaluated. The JAI was calculated based on catches of young shad on weekly nighttime sampling with a bow-mounted pushnet in the Mattaponi River and Pamunkey River. Indices from 1979 - 2000 were calculated as arithmetic, geometric, maximum geometric, and areal means and were compared to determine whether trends in relative abundance depend critically on the form of the index. All indices were related. Comparisons of Mattaponi River, Pamunkey River, and York River indices indicated the Mattaponi River had a larger juvenile population than the Pamunkey River. Thus, the Mattaponi River drives trends in the combined York River index. York River JAIs were also compared to indices from a concurrent, independent seine survey in the York River. Aside from the lesser correlated maximum geometric mean, indices were highly correlated, suggesting the relative abundance of juvenile shad is measured similarly in independent surveys. When JAIs of rivers from the East Coast were compared, no regional trends in abundance were evident. Within the Mattaponi River and Pamunkey River habitats, the area in which juveniles were captured appeared to expand during years with large JAIs and contract in years with low JAIs. Additionally, catch rates were generally higher upriver than downriver in most years which implies that juveniles prefer upriver habitat or that emigration is reflected in catch rates as juveniles migrate downstream. The implications of each calculation method, the differences encountered when sampling with greater or lesser effort, and the limitations involved in measuring juvenile abundance based on a static survey area are discussed.

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INTRODUCTION

A monitoring program for juvenile fishes contributes a single annual value to a time series of abundance (the JAI) and produces a hierarchy of data (Fig. 3). Information content and data complexity increase with each descending level of the hierarchy, and each level possesses a unique spatio-temporal setting. On the lowest level, individual juvenile fishes may be captured in a single tow (average length, 500 m), at a particular time of night and at an individual station in a single stratum on some river. The otolith of each specimen yields information on age, hatch date, individual growth rate, and origin (wild or hatchery). Individuals with similar ages constitute cohorts that possess unique characteristics and exist through the time series (weeks of sampling) in a dynamic environmental milieu. Cohort fate is monitored and the number of abundant cohorts is variable. Cohort characteristics and the catch rate at each station can be associated with measured environmental and biological variables. Catch rates at each station are used to estimate stratum- or cruise-specific catch rates, and these are monitored to determine when sampling should end (after a peak in the catch followed by several cruises with little or no catch). Ultimately, at the highest level of organization, the station or cruise catch rates are used to calculate an annual index of abundance.

A number of methods have been used to estimate an annual index of relative abundance of juvenile American shad on nursery grounds. In the past, JAIs for American shad in the Hudson and Kennebec rivers were calculated as arithmetic mean catch rates (Rago et al. 1995). The Connecticut River JAI was calculated as a geometric mean catch rate and the York River JAI was calculated as a maximum geometric mean

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catch rate (Rago et al. 1995). However, recently the Atlantic States Marine Fishery

Commission (ASMFC) has required all JAIs to be calculated as seasonal geometric mean

catch rates for states monitoring the abundance of American shad juveniles (ASMFC

1999). This calculation is a geometric average of all station-specific catch rates. The

geometric mean is considered superior to the arithmetic mean because the effects of rare

large or small catches are dampened. Many methods of calculation of indices exist, and it

is not well understood which index best represents year-class strength.

The most accurate measure of juvenile abundance cannot be resolved on purely

theoretical grounds. As a management tool, the index should represent a relative measure

of recruitment to later stages of life. If a peak catch rate is calculated as the index, an

untestable assumption is made that all or a fixed proportion of the cohort is present in the

sampling area (Hoenig 1995). The validity of this assumption becomes suspect when

calculating a JAI for juveniles in a system which commonly exhibits multi-modal peaks

in catch rates over time. However, two potentially positive aspects of using a peak catch

rate as an index are (1) the dampening of the effects of emigration from the nursery zone

and (2) an abbreviated sampling season. In the first case, if late catch dates are included

in the calculation of relative abundance, fish hatched early in the season may have begun

migration from the nursery habitat. If timing of emigration is not annually consistent,

then comparison of indices may not show true trends in abundance. In the second case,

bracketing the peak catch will require frequent sampling. However, sampling will occur

over a shorter time period than that observed when bracketing the entire season within

which juveniles are present in the nursery habitat (which is required for arithmetic,

geometric, and the area under the curve methods of measuring relative abundance).

An alternative to the maximum catch rate is the area under the curve JAI, relating catch rates to time of season. One assumption of this methodology is that the average time a fish spends in the nursery habitat is constant from year to year. This forces sampling efforts to be extensive in order to bracket the timing of entrance and exit from the nursery zone. The arithmetic and geometric mean catch rates also have this assumption.

As aforementioned, the geometric average provides a better measure of central tendency and is less influenced by sporadic large catches (Colvocoresses 1984). In addition, the geometric mean normalizes data to the greatest extent possible with a conventional logarithmic transformation and reduces relative sample variation. Utilization of the geometric average is thought to decrease variance among catch rates, but may not represent year-class strength more accurately than other methods. Therefore, in the absence of empirical validation of the juvenile index, indices should be computed in several ways to determine whether conclusions depend critically on a particular form of the index (Hoenig 1995). Similar temporal trends in various forms of the JAI would support the notion that the methods of calculation generate indices that are representative of relative year-class strength.

Superimposed on the choice of calculation are the complications encountered with sampling design. Juvenile shad trickle into and out of the Hudson River nursery habitat throughout the spring and summer as a function of size and age (Limburg 1996). Thus, initial design planning becomes a gamble to determine the timing and area within which

the juveniles are located. Different nursery areas may be more productive and have
higher catch rates, producing strong, weighted station effects on the JAI when simple
averages are used (Hoenig 1995). Thus, in addition to multiple calculations of the index,
the spatial distribution of juveniles and the productivity of sampling areas should be
realized by examining station catch rates.

Comparing JAIs to measures of relative abundance in a time-series from an
independent survey is a reasonable way to validate an index. Similar trends exhibited by
both surveys would suggest that both measures were meaningful independently
producing correlated measures of the same natural phenomenon. In the Chesapeake Bay,
anadromous species tend to simultaneously experience successful or unsuccessful years
of juvenile production (Wood 2000). Regional comparisons of juvenile abundance
indices for anadromous species might be synchronous, providing another way to assay
the value of the indices.

In this section of the study, JAIs based on VIMS pushnet monitoring surveys for
American shad in the York River from 1979-2000 were critically evaluated. Indices were
calculated using four methods (arithmetic means, geometric means, maximum geometric
means, and areal means) for the Mattaponi River and Pamunkey River, and indices were
summed to generate a York River index. Indices were compared to determine whether
trends in abundance depend critically on a particular form of the index. JAIs from
pushnet surveys were also compared to JAIs generated from the VIMS beach seine
survey using linear regression to determine whether these independent surveys yield
similar trends in the relative abundance of juvenile shad. Agreement in trends of each

survey would provide supportive evidence that juvenile abundance is monitored similarly in independent programs. Catch rates of juveniles in the pushnet survey were also examined by station to test whether certain areas of the Pamunkey and Mattaponi river nursery habitats are consistently more productive seasonally. The spatial distribution of juveniles was also examined to determine whether the nursery zone varies annually. If the nursery zone is not static, the magnitude of the index may be artificially deflated in years when the zone is shifted upstream or downstream. The purpose of this section of the study is to move toward validation of the juvenile abundance index.

MATERIALS AND METHODS

Juvenile American shad were collected during pushnet cruises (Kriete and Loesch 1980) on the Pamunkey and Mattaponi rivers from June through August of 1979-2000. Sampling was modified in 1991 to the current methods after a 3-year hiatus in monitoring from 1988-1990. Current sampling procedures, described herein, include increased effort and an increased number of cruises. In addition, a shorter time was observed between recent cruises than was characteristic of the period from 1979-1987. Thus, the JAIs from each time period are considered separately in the following analysis. Shad were captured weekly using a bow-mounted pushnet on a 23-ft deep-v, center-console fiberglass boat powered by a 150-hp outboard engine (Fig. 4). The pushnet is a 5.2-m long (body 3.0-m, cod end 2.2-m), four-panel, 1.5 x 1.5-m Cobb trawl net modified to fit the pushnet frame.

The sampling area was divided into 9.3-km (5 nautical miles) river blocks beginning at river mile 69 on the Pamunkey River and 59 on the Mattaponi River (Fig. 5). Each river block was further divided into five 1.9-km (1 nautical mile) stations. Three sampling stations were randomly chosen for every river block. A minimum of twelve stations were sampled that cover four sampling blocks or approximately 20 nautical miles. On certain occasions, the sampling area was expanded by the addition of more stations when catches of alosines were high in the last block of sampling. Cruises occurred weekly and sampling began 45 minutes after sunset when alosines are most catchable using the pushnet apparatus (Loesch et al. 1982). Water surface temperature and air temperature were recorded on cruises. Time, tide, tow duration, and flowmeter

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readings were recorded for each tow. Specimens were returned to the laboratory for identification and processing (fork length, wet weight).

Annual juvenile indices of abundance were calculated as an arithmetic mean catch per unit effort (cpue), geometric mean cpue, maximum geometric mean cpue, and an areal cpue. Indices were calculated for the Mattaponi and Pamunkey rivers, tributaries of the York River.

The number of juvenile shad collected at each station is standardized for volume of flow through the net according to the following equation:

$$C_i = \frac{n_i w}{r_i a f}$$

where C_i = the number of fish caught per ith tow standardized for flow, n_i = number of fish caught on ith tow, w = standard volume of water filtered by the net when traveling a specific constant speed for a given amount of time (655 m^3 at 1200 rpm for 5 min for this study), r_i = revolutions of the flowmeter on the ith tow, a = area of the net (2.25 m^2 for this study), and f = standard unit of conversion on the flowmeter (0.0267 m/revolution).

The arithmetic mean catch is an average of all catches in a given season and is calculated as follows:

$$JAI_{arith} = \frac{1}{n}\sum_{i=1}^{n} C_i$$

where n = number of stations sampled in a given season and C_i = cpue corresponding to the ith sampling tow in a given season.

The geometric mean averages the logarithmic transformation of the catch rates over a season and is calculated as follows:

$$JAI_{geo} = anti\log\left(\frac{1}{n}\sum_{i=1}^{n}\log(C_i+1)\right) - 1$$

The maximum geometric mean is the largest geometric mean cpue for a given cruise in a season. The cruise geometric mean is calculated as follows:

$$R = anti\log\left(\frac{1}{j}\sum_{k=1}^{j}\left(\log Cj+1\right)\right) - 1$$

where R = geometric mean cruise cpue, j = number of tows for a given cruise, and C_j = cpue corresponding to the jth tow.

The areal catch commonly called the "area under the curve method" is an integrated seasonal catch per unit effort calculated as follows:

$$JAI_{areal} = \left[\sum_{i=1}^{n}D_iR_L\right] + \left[\frac{1}{2}\sum_{i=1}^{n}D_i|R-R_{i+1}|\right] + \frac{1}{2}D_1R_1 + \frac{1}{2}D_nR_{n-1}$$

where D_i = the number of days between cruise i and cruise i+1, and R_L = the lower geometric mean cruise cpue between R_i and R_{i+1}.

Arithmetic, maximum geometric, and areal indices for the York River were calculated by summing the JAIs of each tributary from 1979-2000. The geometric mean was calculated by averaging the logarithmic transformations of all catch rates from the Mattaponi and Pamunkey rivers in a given season.

The relative standard error for each time series of JAIs was calculated based on the following equation:

$$rse = \frac{s^2}{x}$$

Where s^2 = the sample variance and $\overline{x}$ = the sample mean. Relative standard errors describe the variance in relation to the mean. Thus, comparisons between the relative standard error of indices calculated by different methods were made.

Because an increase in one form of the index is expected with an increase in any other form of the index, annual arithmetic (AM), geometric (GM), maximum geometric (MGM), and areal (RM) JAIs were compared using regression analyses to determine whether the calculations produce similar year-to-year trends in relative abundance. The JAI time series were separated into two data sets, early sampling (under the old methodology, 1979-1989) and current sampling (under the new more standardized methodology, 1991-2000). Comparisons were made between the four forms of the index for the Pamunkey River, Mattaponi River, and York River to determine whether any river index depended upon the calculation method. Comparisons among like indices were made between rivers (eg. Mattaponi GM vs. Pamunkey GM, Mattaponi RM vs York River RM, etc) to determine whether tributaries experienced the same trends in juvenile abundance. Additionally, between river comparison were performed to determine whether a single river JAI dominated the York River JAI.

The area under the curve method was used to integrate the average cpue for 5-mile river-blocks in a season. Integrated average cpues were calculated for all river-blocks on the Mattaponi and Pamunkey rivers from 1991-2000. Data from 1979-1989 were not used because the sampling program differed from the current protocol. Integrated average cpues for a given river block are calculated as follows:

$$R_B = \left[\sum_{i=1}^{n} D_i J_L \right] + \left[\frac{1}{2} \sum_{i=1}^{n} D_i \left| J_i - J_{i+1} \right| \right] + \frac{1}{2} D_1 J_1 + \frac{1}{2} D_{n-1} J_n$$

where B = 5-mile river block (1 = uppermost river block, 2 = 2nd uppermost river block, etc), D_i = the number of days between cruise i and cruise i+1, J = average cpue for a given river block on cruise i, and J_L = the lower cpue between C_i and C_{i+1}. The catch is assumed to be zero, ½ D_1 days before the first cruise and ½ D_{n-1} days after the last cruise. R_B values for each river were compared within and between years to note any spatial trends in juvenile abundance.

The main goal of the VIMS beach seine survey is to develop an index for juvenile striped bass in the Chesapeake Bay, but the program also monitors the abundance of other species including juvenile American shad. Seines are hauled by hand during the summer (July - September) at stations in the Pamunkey, Mattaponi, and York rivers. The gear is a 1.2m x 30.5m seine with a 6.4mm mesh. Based on an analysis of length frequency distributions, shad within a given size range are considered young of the year (01-15 July - 65mm; 16 July- 15 September - 70mm). For additional information on the survey see Austin et al. (1995) and the VIMS Fisheries Department web site (http://www.fisheries.vims.edu/seinedata/). Seine survey JAIs for American shad in the York River were calculated as seasonal geometric mean cpues, the recommended calculation method for the VIMS beach seine. Calculations are similar to formulas utilized for the pushnet surveys, but C equaled the total number of juvenile shad captured for a given beach seine. York River indices are actually geometric means of all hauls on the Mattaponi and Pamunkey rivers. Regressions were performed on pushnet versus

seine survey JAIs to determine whether an independent survey reveals the same measures of relative abundance of juvenile shad in the York River annually. Indices from 1991-2000 were compared.

The relative abundance of juvenile American shad has also been monitored in other rivers along the east coast (Maryland - Upper Chesapeake Bay (Mowrer pers. comm.), New Jersey - Delaware River, New York - Hudson River, Connecticut - Connecticut River, Maine - Kennebec (ASMFC 1998)). Linear regression was used to compare JAIs from these rivers to determine whether East Coast rivers experienced similar trends in shad abundance annually.

RESULTS

Mattaponi and Pamunkey River Comparisons

Mean catch rates per cruise on the Mattaponi and Pamunkey rivers are shown in figures 6 and 7. The peak catch rate was observed on the first of six cruises (1979-1982, 1985, and 1991) in the Pamunkey River and the first of three cruises (1979, 1980, 1991) on the Mattaponi River. Multi-modal peaks occurred in eight years (1983, 1991, 1992, 1995, 1996, 1998-2000) on the Pamunkey River and nine years (1983-1987, 1991-1996, 1998-2000) on the Mattaponi River. Thus, single peaks in catch rates occurred in eleven and seven years on the Pamunkey and Mattaponi rivers, respectively. Juvenile abundance indices, summarizing the cruises on the Mattaponi and Pamunkey rivers, are shown in Table 1. The relative standard error for each form to the index varies little among calculation methods.

Ratios of Mattaponi to Pamunkey river JAIs indicate that the relative abundance of shad is almost always greater on the Mattaponi River (Table 2). By all calculations, the greatest difference in relative abundance was observed in 1993 when the abundance of juveniles on the Mattaponi River was 40-80 times larger than the Pamunkey River. Similarly, differences are also large in 1984 (12-17 times), 1987 (18-40 times), 1997 (9 - 12 times), and 1998 (14 - 28 times). Juvenile abundance may have been greater in the Pamunkey River in 1979 and 1991, but agreement among ratios is not unanimous.

Table 3 shows comparisons of forms of the JAI for the Mattaponi (A) and Pamunkey (B) rivers. Column 1 shows the x and y values, which are different methods of calculation of an index for a given tributary. Other columns present regression

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equations, R^2 values, and p values for designated time series being compared. When considering forms of the index for the Mattaponi and Pamunkey rivers separately, all comparisons were significant for indices from 1979-1988 for the Pamunkey River, whereas three comparisons (MGM vs RM, p = 0.08; RM vs. GM, p = 0.10; AM vs RM, p = 0.12) are insignificant for the same indices for the Mattaponi River (Table 3). All comparisons are highly significant and correlated for 1991-2000 indices. However, R^2 values are larger for Mattaponi comparisons (min - 0.90, max - 0.99) than Pamunkey comparisons (min = 0.84, max = 0.97).

The maximum geometric mean appears to be the calculation least related to other indices based on comparisons of indices from the Mattaponi River. Comparisons involving the areal mean appear to have lower agreement among trends in relative abundance for the Pamunkey River. When indices are compared for the Mattaponi and Pamunkey rivers, all JAIs are correlated from 1991-2000. Indices from 1979-1987 are correlated for the areal mean (Table 4).

York River Comparisons

Juvenile abundance indices for the York River, calculated as arithmetic, geometric, maximum geometric, and areal means, are shown in Table 1. The relative standard error for each form of the JAI varies little among calculation methods. All methods of calculation indicate 1996 was the largest year and 2000 was the second largest year on record for juvenile abundance in the York River when indices are ranked from highest to lowest (Table 5). However, no other year has the same rank for all forms of the JAI. In three cases (1986, 1991, 1997), the rank is the same for three forms of the

indices. Other rankings of years possess less agreement among indices.

Forms of the JAI are more correlated under the current sampling protocol (1991-2000) than during the previous survey protocol (1979-1989) (Table 6). R^2 values are higher for regressions comparing JAIs from 1991-2000 than 1979-1989 with values ranging from 0.83 - 0.97 and 0.52 - 0.90, respectively. Two regressions (MGM vs GM, RM vs GM) were non-significant ($p > 0.05$) under early protocol. The arithmetic mean has the strongest correlation with other indices (RM, GM, MGM) for regressions based on JAIs from early sampling years. Under the current survey methodology, all comparisons were highly significant. Regressions of the maximum geometric mean against other measures of relative abundance have lower R^2 values, suggesting that the maximum geometric mean has a weaker relationship with the other measures.

Tributary indices were also compared to indices for the York River (Table 7). The strongest relationships occur between the Mattaponi and York rivers in latter sampling years.

Independent Survey Comparisons

Mattaponi, Pamunkey, and York river indices for the seine survey are shown in Table 8. Both the maximum geometric mean and geometric mean forms of the JAI based on pushnet data were compared to the geometric mean JAI based on seine survey catches (Table 9). Both forms of the pushnet index are strongly correlated with the seine survey JAI for the York River (Table 9). Indices are more strongly related for geometric mean comparisons than maximum geometric mean - geometric mean comparisons.

Station Effects

Average catch rate by station is depicted in Figure 8. The largest number of river

blocks inhabited by shad occurred in 1996 on both tributaries. This was also the largest

index according to all indices from 1991-2000. The smallest number of river blocks

inhabited by shad occurred in 1992 and 1993 on the Pamunkey River. The smallest

numbers on the Mattaponi River were observed in 1991, 1992, and 1997. According to

all indices from 1991 - 2000, 1992 had the lowest juvenile abundance. Thus, the number

of sampling river blocks at which shad are captured is largest in years of the highest JAIs

and smallest in years of the lowest JAIs. The average sizes of each nursery habitat for the

largest year of juvenile abundance shown in the figure are 50% and 20% larger than the

other years on the Pamunkey and Mattaponi rivers, respectively. In addition, catches in

the up-river stations appear to contribute most heavily to the overall annual catch on each

river, especially on the Pamunkey River. It is not clear which river blocks are more

productive in several years of greater abundance on the Mattaponi (1996-1998). The

average catch rate per river block is variable. In 1991, 1992, and 1996, downriver

stations are more productive than upriver stations. In other years on the Mattaponi River,

upriver stations are more productive.

Regional JAIs

Juvenile abundance indices for various river systems are shown in Table 10.

Aside from Virginia surveys, no significant trends in abundance exist on a regional basis.

Relative standard errors indicate that the Delaware River and secondly the Connecticut

River have the greatest variance among annual indices. The Upper Bay indices posses

the smallest relative standard error. Although trends are not synchronous, 1996 was the

largest index for the Kennebec, Hudson, and York rivers. In addition, 1996, was the

second largest year on record for the upper Chesapeake Bay.

DISCUSSION

Increased sampling effort is the most probable cause of tighter correlations among indices from 1991-2000 than in earlier years. Average number of cruises per season increased to 8.8 in 1991-2000 (compared to 5.9 in 1979-1987) with approximately 30 or more additional stations visited annually after 1987. Increased effort should produce a better estimate of relative abundance by bracketing the rise, peak, and decline in catches and simply by providing a larger sample size. Before 1991, sampling was often initiated later in the season, and the peak catch commonly occurred during the first cruise. JAIs in these years would underestimate the relative abundance of juveniles if the true peak in abundance occurred prior to the first cruise.

The arithmetic, geometric, and areal means are generally correlated forms of the JAI under the current sampling design. The difference between the arithmetic mean and geometric mean is the logarithmic transform of the cpue which decreases variability in the values averaged for the geometric mean. Because these are both basic averages, a tight correlation is expected. When the areal JAI is divided by the number of days within a season (number of days from the first to last cruise), it is similar to an arithmetic mean. Thus, the areal mean should be tightly correlated with the other two means, as well.

Although still relatively high, many of the lowest R^2 values observed under the current sampling design are in comparisons involving the maximum geometric mean. The maximum geometric mean is designed to be utilized when catches rise to a peak and then fall during a season. However, the majority of seasonal catch rates on the Mattaponi and Pamunkey rivers posses multi-modal peaks. When years with both multi-modal peaks

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and large catches are excluded (ie. 1996), R^2 values increase in comparisons involving the maximum geometric mean. The magnitude of the largest cpue with respect to other cpues in a season affects the correlation between the maximum geometric mean and other JAI calculations.

The results suggest that the geometric mean is not a superior measure of abundance. The geometric mean is the official index reported to the ASMFC and is assumed to be the best approximation to the true abundance. However, overall, the four forms of the index (GM, MGM, AM, RM) show similar trends in the relative abundance of juvenile shad in the York River. The geometric mean may reduce variability among station catches, but relative standard error for indices is similar among calculation methods. Areal means may be superior for sampling programs that have difficulty bracketing the time shad are present in the nursery zone, because catches of zero fish will not deflate the areal JAI. Catches of zero deflate arithmetic means, and the also deflate geometric means, although to a lesser extent.

The York River JAI is more heavily influenced by the abundance of shad in the Mattaponi River than the Pamunkey River, despite the physical similarities of the two tributaries and their proximity. American shad juvenile recruitment is generally much greater on the Mattaponi River than the Pamunkey River. Similarly, shad egg and larval abundance in 1997 and 1998 were higher on the Mattaponi River than the Pamunkey River by a factor of 5.5 and 4.4, respectively (Bilkovic et al., in press). The JAIs for the Mattaponi and Pamunkey rivers and JAIs for the Pamunkey and York rivers are related. However, JAIs for the Mattaponi and York river indices are more highly correlated.

Therefore, the abundance of juveniles in the Mattaponi River appears to be responsible for the trends in abundance from 1979-2000 in the York River. As a result, future sampling designs could omit the Pamunkey River and still potentially retain a meaningful time series.

In general, the nursery habitat expands during years of larger indices, particularly for the Pamunkey River. Density-dependent competition appears to only significantly affect juvenile shad at relatively large population sizes (Savoy and Crecco 1988). Interspecific and intraspecific competition among juvenile clupeids may influence the spatial distribution of shad during years of high abundance. Competition for food and suitable habitat may force young shad to inhabit additional areas of the river. However, the American shad population is currently depleted and juvenile abundance may not be large enough to be greatly affected by density-dependent processes. Expanded nursery habitat could also be explained by early outmigration of juveniles from the nursery habitat. Larger juvenile shad have been observed leaving the nursery habitat earlier than smaller shad (Limburg 1996). If hatchdate distributions are broad, older larger fish may migrate from the nursery early while shad hatched later are still developing. The early outmigration would cause the nursery zone to appear expanded.

Within the nursery zone, upriver stations appear to be more highly productive than downriver stations and may heavily influence the magnitude of the JAI. One assumption underlies this theory. The time of night must not affect catch rates. American shad school during light hours (Ross and Backman 1992). Thus, sampling begins 45 minutes after sunset to ensure schools have dissipated. Blueback herring and

alewives have constant nocturnal availability to the pushnet sampling gear (Jessop and Anderson 1989). American shad, their congeners, may also exhibit similar behavior, but this has not been tested. If the above assumption is valid, juveniles may prefer upriver habitat from June to August in the York River. This is supported by Dixon's findings (pers comm.) that hatchery-reared shad were colleted upriver far from their downriver release site (Dixon, pers. comm). Juveniles do not require fresh water for survival (Limburg and Ross 1995). Additionally, DO and pH levels are well within suitable ranges for survival (Bilkovic et al. in press). Therefore, upriver areas must have additional characteristics which make them more suitable for juvenile life. Shallow water, greater amount of woody debris, and overhang at upriver stations (Bilkovic et al. in press) provide greater protection from predators. Increased water flow also stirs detritus which can support a larger planktonic population upon which to feed. The abundance of insects is also greater at upriver station and may provide additional food for juveniles (Massman 1963). The high catches at upriver stations may also reflect the outmigration and mortality of juveniles. The upper stations of the sampling area cover approximately 62% of the lower spawning habitat defined by Bilkovic et al. (in press). As cohorts move downstream from the spawning grounds and nursery habitat, the size of the cohort is decreasing due to mortality, which could result in a decreasing trend in catch rates as one moves downstream.

The large catches at the most upriver stations suggests that sampling farther upriver would result in larger catches. The area monitored in the survey is assumed to be a constant proportion of the entire nursery habitat. This assumption should be further

examined. During years of little rainfall and decreased flow, the nursery habitat could be shifted upstream and during wet years the nursery habitat could be shifted downstream. Shifts in the positioning of the habitat may cause the proportion sampled to fluctuate. Measuring the abundance of juveniles based on static stations in a fluctuating habitat will artificially inflate or deflate the index.

Regardless of annual shifts in the nursery zone or the potential inadequacy of the station grid to bracket the zone, both pushnet and seine survey indices show the same trends in relative abundance of American shad from 1991 to 2000. Indices for the Mattaponi River are more tightly correlated than indices for the Pamunkey River. Tighter correlation may result from an additional seine station on the Mattaponi River. Agreement among these two independent surveys provides supportive evidence that both surveys are producing similar measures of the relative abundance of juvenile shad in the York River. Although not an explicit validation of either survey as a predictor of year-class strength, the result does suggest that JAIs of American shad in the York River reflect true abundance. The seine survey is less expensive, easier to perform, and is used in most states to monitor the relative abundance of shad. Thus, the seine survey may be a more practical and compatible method of measuring juvenile abundance.

Interjurisdictional comparisons of JAIs revealed no general trend in juvenile abundance along the east coast. Localized weather patterns, environmental quality, predator, and prey densities are among many factors that may cause of lack of synchronicity among regional indices. However, 1996 was the largest index on record for the Kennebec, Hudson, and York rivers. Perhaps unusually large years are caused by

regional weather patterns. Currently, sampling protocols and gears are not standardized. If procedures were similar, the magnitude of indices also may be compared.

Further understanding of the JAI for the York River can be founded on additional studies. The assumption that catchability of juveniles does not change on a given cruise as a function of time remains untested. A study should be performed to further evaluate the sampling protocol. Sampling should also be performed upstream of the first sampling blocks to determine the uppermost reaches of juvenile inhabitation. Several years of monitoring upriver and a continuance of the pushnet survey may determine whether the entire nursery zone shifts during drought and wet years. Lastly, the framework designed for examining juvenile indices should be performed on JAIs for American shad and other species in different river systems.

Table 1: Forms of an index of abundance of juvenile American shad in the York River (1979-2000). AM = arithmetic mean, GM = geometric mean, MGM = maximum geometric mean, RM = areal mean, M = Mattaponi River, P = Pamunkey River, Y = York River (M + P), rse = relative standard error.

Year	AM$_M$	GM$_M$	MGM$_M$	RM$_M$	AM$_P$	GM$_P$	MGM$_P$	RM$_P$	AM$_Y$	GM$_Y$	MGM$_Y$	RM$_Y$
1979	14.2	7.4	24.3	1134.0	16.5	5.1	32.0	1258.9	30.7	5.9	56.3	2392.9
1980	16.2	6.6	18.5	636.2	4.1	1.1	6.5	228.1	20.3	3.3	25.0	864.3
1981	5.0	1.2	13.5	43.6	2.3	1.1	3.3	106.4	7.2	1.2	16.8	150.0
1982	9.9	4.4	9.3	342.2	1.0	0.6	1.9	32.0	10.9	2.9	11.2	374.2
1983	7.5	3.6	7.3	300.5	3.4	1.7	3.6	105.4	10.9	2.6	10.9	405.9
1984	20.1	9.5	22.6	446.2	1.3	0.7	1.5	25.7	21.4	4.1	24.1	471.9
1985	17.6	9.6	26.0	410.8	8.7	3.3	10.1	156.5	26.3	6.7	36.1	567.3
1986	19.8	10.7	26.1	598.2	5.6	3.2	4.4	112.8	25.4	6.8	30.5	711.0
1987	5.0	2.6	7.3	228.9	0.1	0.1	0.4	6.0	5.1	1.7	7.7	234.9
1988-1990							No sampling					
1991	2.7	1.4	7.0	93.5	3.8	1.8	6.3	129.0	6.5	1.6	13.3	222.5
1992	0.4	0.4	1.5	37.3	0.0	0.0	0.1	1.9	0.5	0.1	1.6	39.2
1993	27.0	15.2	30.3	973.4	0.3	0.2	0.7	12.0	27.3	6.3	31.0	985.4
1994	29.4	14.7	51.5	1055.0	5.1	2.2	9.5	571.0	34.6	5.6	61.0	1626.0
1995	8.7	4.2	6.4	273.2	1.7	0.9	2.2	88.6	10.4	2.8	8.6	361.8
1996	125.3	88.9	144.2	6325.1	26.1	14.8	31.5	1082.5	151.4	34.8	175.7	7407.6
1997	47.6	29.8	95.4	2103.4	5.0	2.4	8.2	169.2	52.5	7.4	103.6	2272.5
1998	40.8	26.8	77.3	2544.2	2.8	1.0	3.5	89.2	43.6	5.3	80.8	2633.4
1999	9.2	3.0	11.8	298.0	1.7	0.8	2.2	79.8	10.9	1.6	14.0	377.8
2000	80.9	57.9	115.7	3627.7	19.9	8.6	26.3	567.0	100.8	23.0	142.0	4194.7
rse	1.3	1.5	1.2	1.5	1.3	1.5	1.3	1.5	1.2	1.5	1.1	1.4

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Table 2: Ratios of JAI values for American shad (Mattaponi JAI / Pamunkey JAI). Ratios <1 are underlined. Abbreviations are: MGM = maximum geometric mean; RM = areal mean; GM = geometric mean; AM = arithmetic mean

Year	AM	GM	MGM	RM
1979	0.9	1.5	0.8	0.9
1980	4.0	6.0	2.8	2.8
1981	2.2	1.1	4.1	0.4
1982	9.5	7.3	4.9	10.7
1983	2.2	2.1	2.0	2.9
1984	15.5	13.6	15.1	17.4
1985	2.0	2.9	2.6	2.6
1986	3.6	3.3	5.9	5.3
1987	39.6	26.0	18.3	38.5
1991	0.7	0.8	1.1	0.7
1992	12.7	20.0	11.2	19.6
1993	79.4	76.0	43.3	81.5
1994	5.7	6.7	5.4	1.8
1995	5.0	4.7	2.9	3.1
1996	4.8	6.0	4.6	5.8
1997	9.6	12.4	11.6	12.4
1998	14.6	26.8	22.1	28.5
1999	5.4	3.7	5.3	3.7
2000	4.1	6.7	4.4	6.4

Table 3: Regression equations ($y = mx + b$), R^2 values, and p -values for comparisons of forms of an index of abundance of juvenile American shad on the Mattaponi River (A) and the Pamunkey River (B). MGM = maximum geometric mean; RM = areal mean; GM = geometric mean; AM = arithmetic mean.

A)

x	y	1979-1987			1991-2000		
		mx+ b	R^2	p	mx+ b	R^2	p
MGM	RM	23.7x + 52.6	0.37	0.08	37.1x - 271.7	0.90	< 0.001
MGM	GM	0.4x - 0.3	0.77	0.001	0.5x - 4.5	0.90	< 0.001
RM	GM	0.006x + 3.3	0.32	0.1	0.01x - 0.4	0.98	< 0.001
AM	GM	0.5x - 0.7	0.94	< 0.001	0.7x - 2.7	0.99	< 0.001
AM	RM	28.1x + 1.0	0.30	0.12	50.2x - 135.2	0.98	< 0.001
AM	MGM	1.1x + 2.6	0.76	0.002	1.2x + 8.0	0.91	< 0.001

B)

x	y	1979-1987			1991-1999		
		mx+ b	R^2	p	mx+ b	R^2	p
MGM	RM	39.5x - 54.0	0.96	< 0.001	29.9x + 1.1	0.86	< 0.001
MGM	GM	0.1x + 0.9	0.73	0.003	0.4x - 0.7	0.94	< 0.001
RM	GM	0.003x + 1.2	0.62	0.01	0.01x - 0.2	0.86	< 0.001
AM	GM	0.3x + 0.3	0.91	< 0.001	0.5x - 0.2	0.97	< 0.001
AM	RM	70.0x - 108.2	0.83	< 0.001	36.1x + 30.8	0.84	< 0.001
AM	MGM	1.8x - 1.7	0.92	< 0.001	1.2x + 1.3	0.98	< 0.001

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Table 4: Regression equations (y = mx + b), R^2 values, and p-values for comparisons of forms of an index of abundance of juvenile American shad on the JAIs for Mattaponi versus Pamunkey rivers (1979 - 1988, 1991-2000). M = Mattaponi River; P = Pamunkey River; AM = arithmetic mean; GM = geometric mean; MGM = maximum geometric mean; RM = areal mean

x	y	Index	1979-1987			1991-2000		
			mx+ b	R^2	p	mx+ b	R^2	p
M	P	AM	0.3x + 1.0	0.12	0.30	0.2x - 1.2	0.87	< 0.001
M	P	GM	0.3x + 0.03	0.27	0.15	0.1x - 0.3	0.90	< 0.001
M	P	MGM	0.6x - 3.2	0.24	0.18	0.2x - 0.01	0.71	0.002
M	P	RM	1.1x - 268.1	0.71	0.003	0.1x + 24.5	0.71	0.002

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Table 5: Years of monitoring juvenile abundance on the York River (1979- 2000) ranked in ascending order for each form of the JAI. Like years are underlined and the number of agreements noted. Abbreviations are: AM = arithmetic mean; GM = geometric mean; MGM = maximum geometric mean; RM = areal mean; # agree = number of agreements among indices.

AM	GM	MGM	RM	# agree
1992	1992	1992	1992	4
1987	1981	1987	1981	2
1991	1991	1995	1991	3
1981	1999	1983	1987	0
1995	1987	1982	1995	2
1982	1983	1991	1982	2
1983	1995	1999	1999	2
1999	1982	1981	1983	0
1980	1980	1984	1984	2
1984	1984	1980	1985	2
1986	1998	1986	1986	3
1985	1994	1993	1980	0
1993	1979	1985	1993	2
1979	1993	1979	1994	2
1994	1985	1994	1997	2
1998	1986	1998	1979	2
1997	1997	1997	1998	3
2000	2000	2000	2000	4
1996	1996	1996	1996	4

Table 6: Regression equations (y = mx + b), R^2 values, and p -values for comparisons of forms of an index of abundance of juvenile American shad in the York River. Juvenile abundance monitoring changed after 1989 by increasing effort (number of cruises) and standardizing the time between cruises (6 days). Current monitoring occurs from June - August, which is less protracted in time than past monitoring (spring - early fall). Abbreviations are: MGM = maximum geometric mean; RM = areal mean; GM = geometric mean; AM = arithmetic mean

x	y	1979-2000			1979-1987			1991-2000		
		mx+ b	R^2	p	mx+ b	R^2	p	mx+ b	R^2	p
MGM	RM	36.1x - 234.4	0.92	< 0.001	38.7x - 253.3	0.77	0.002	8.4x - 294.	0.92	< 0.001
MGM	GM	0.2x - 0.6	0.82	< 0.001	0.1x + 1.3	0.60	0.06	0.2x - 1.7	0.83	< 0.001
RM	GM	0.004x - 0.5	0.89	< 0.001	0.002x + 2.7	0.90	0.35	0.01x - 5.4	0.93	< 0.001
AM	GM	0.2x - 0.5	0.96	< 0.001	0.21x + 0.23	0.85	< 0.001	0.2x - 1.2	0.97	< 0.001
AM	RM	48.2x - 130.5	0.96	< 0.001	54.8x - 301.5	0.52	0.03	7.7x - 79.	0.98	< 0.001
AM	MGM	1.3x + 5.1	0.93	< 0.001	1.5x - 2.3	0.83	0.001	1.2x - 9.7	0.93	< 0.001

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Table 7: Regression equations (y = mx + b), R^2 values, and p-values for comparisons of forms of an index of abundance of juvenile American shad on the York River (1979 - 1998, 1991 - 2000). P = Pamunkey River, Y = York River, M = Mattaponi River; AM = arithmetic mean; GM = geometric mean; MGM = maximum geometric mean; RM = areal mean

x	y	Index	1979-1987			1991-2000		
			mx+ b	R^2	p	mx+ b	R^2	p
P	Y	AM	1.4x + 11.4	0.63	0.01	5.1x + 9.7	0.91	< 0.001
P	Y	GM	1.0x + 2.0	0.63	0.01	2.3x + 1.3	0.96	< 0.001
P	Y	MGM	1.4x + 14.4	0.79	0.002	5.0x + 16.9	0.80	< 0.001
P	Y	RM	1.6x + 308.9	0.94	< 0.001	5.8x + 392.6	0.77	< 0.001
M	Y	AM	1.2x + 2.4	0.69	0.005	1.2x - 1.2	0.99	< 0.001
M	Y	GM	0.6x + 0.4	0.82	< 0.001	0.4x - 0.4	0.96	< 0.001
M	Y	MGM	1.6x - 3.2	0.67	0.005	1.2x - 0.03	0.99	< 0.001
M	Y	RM	2.1x - 268.0	0.91	< 0.001	1.1x - 24.5	0.99	< 0.001

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Table 8: Indices of abundance of juvenile American shad collected in beach seine surveys (1980 - 1999). Indices are calculated for the Mattaponi, Pamunkey, and York rivers. st. dev. = standard deviation

	Mattaponi		Pamunkey		York	
	Index	st. dev.	Index	st. dev.	Index	st. dev.
1980	1.75	1.06	0.51	0.82	1.30	1.02
1981	0.35	0.56	0.33	0.59	0.34	0.57
1982	13.03	1.26	0.51	0.54	4.40	1.50
1983	2.80	0.95	0.63	0.77	1.65	0.97
1984	16.97	1.12	0.06	0.20	4.34	1.66
1985	7.21	1.37	0.56	0.63	3.03	1.38
1986	0.87	0.90	0.00	0.00	0.43	0.74
1987	0.17	0.46	0.00	0.00	0.09	0.35
1988	0.00	0.00	0.00	0.00	0.00	0.00
1989	0.41	0.63	0.00	0.00	0.21	0.50
1990	0.18	0.47	0.00	0.00	0.10	0.36
1991	0.04	0.25	0.02	0.11	0.03	0.20
1992	0.00	0.00	0.00	0.00	0.00	0.00
1993	0.18	0.49	0.00	0.00	0.10	0.37
1994	1.69	1.14	0.15	0.43	0.86	0.99
1995	0.03	0.14	0.00	0.00	0.02	0.10
1996	14.61	1.35	1.97	1.29	6.48	1.56
1997	2.23	1.11	0.36	0.67	1.20	1.03
1998	2.11	1.21	0.06	0.36	0.93	1.07
1999	0.14	0.41	0.00	0.00	0.08	0.31

Table 9: Regression equations (y = mx + b), R^2 values, and p -values for comparisons of forms of an index of abundance of juvenile American shad between two independent surveys monitoring juvenile abundance on the York, Mattaponi, and Pamunkey rivers (1991-1999). GM = geometric mean; MGM = maximum geometric mean; Y = York River; M = Mattaponi River; P = Pamunkey River.

Pushnet	Seine	1991-1999		
		mx+ b	R^2	p
GM - Y	GM - Y	0.1x - 0.4	0.97	< 0.001
GM - M	GM - M	0.07x - 0.4	0.95	< 0.001
GM - P	GM - P	0.1x - 0.09	0.98	< 0.001
MGM - Y	GM - Y	0.03s - 0.7	0.81	< 0.001
MGM - M	GM - M	0.03x - 0.6	0.74	0.003
MGM - P	GM - P	0.05x - 0.04	0.78	< 0.001

Table 10: Time series of indices of abundance for juvenile American shad in rivers along the Atlantic Coast. All indices are calculated as geometric means except for the Connecticut River (arithmetic mean). rse = relative standard error.

Year	ME Upper Kennebec	CN Connecticut	NY Hudson	NJ Upper Delaware	MD Upper Bay and Potmac	VA York seine
gear	seine	seine	seine	seine	haul seine	seine
1979	0.2	47.9	23.9	17.3	NA	NA
1980	0.0	21.3	23.9	25.0	NA	NA
1981	1.0	12.5	19.1	31.2	NA	0.3
1982	0.0	4.8	12.2	52.0	NA	4.4
1983	0.2	16.6	18.2	136.8	NA	1.6
1984	0.9	11.2	7.8	83.2	NA	4.3
1985	0.7	15.9	26.5	60.3	NA	3.0
1986	0.1	17.0	46.3	98.9	NA	0.4
1987	0.2	44.3	20.2	77.3	NA	0.1
1988	0.1	24.0	27.6	65.4	0.1	0.0
1989	1.3	61.6	47.3	60.1	0.2	0.2
1990	3.5	43.0	41.2	124.1	0.0	0.1
1991	1.2	50.6	24.1	44.0	0.1	0.0
1992	0.1	97.4	35.2	32.0	0.0	0.0
1993	0.0	79.6	11.6	137.5	0.1	0.1
1994	0.0	107.9	26.1	39.4	0.2	0.9
1995	0.2	28.8	5.7	60.8	0.4	0.0
1996	4.2	38.7	30.6	213.5	1.3	6.5
1997	0.0	60.9	13.1	91.6	1.2	1.2
1998	0.0	41.1	3.2	20.3	1.6	0.9
rse	1.97	20.11	6.88	33.12	0.74	2.76
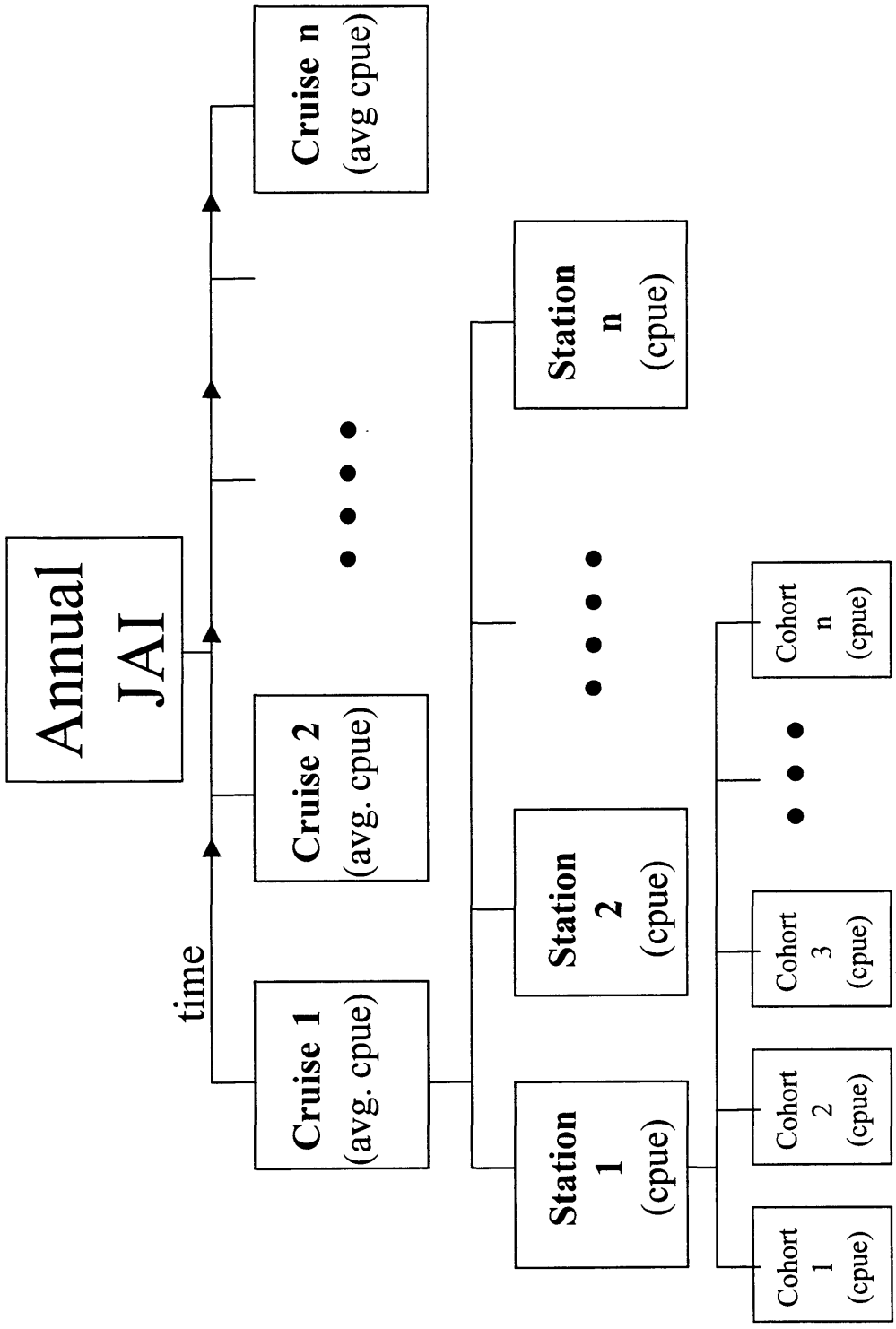
Figure 3: Levels of complexity for a juvenile abundance monitoring survey.
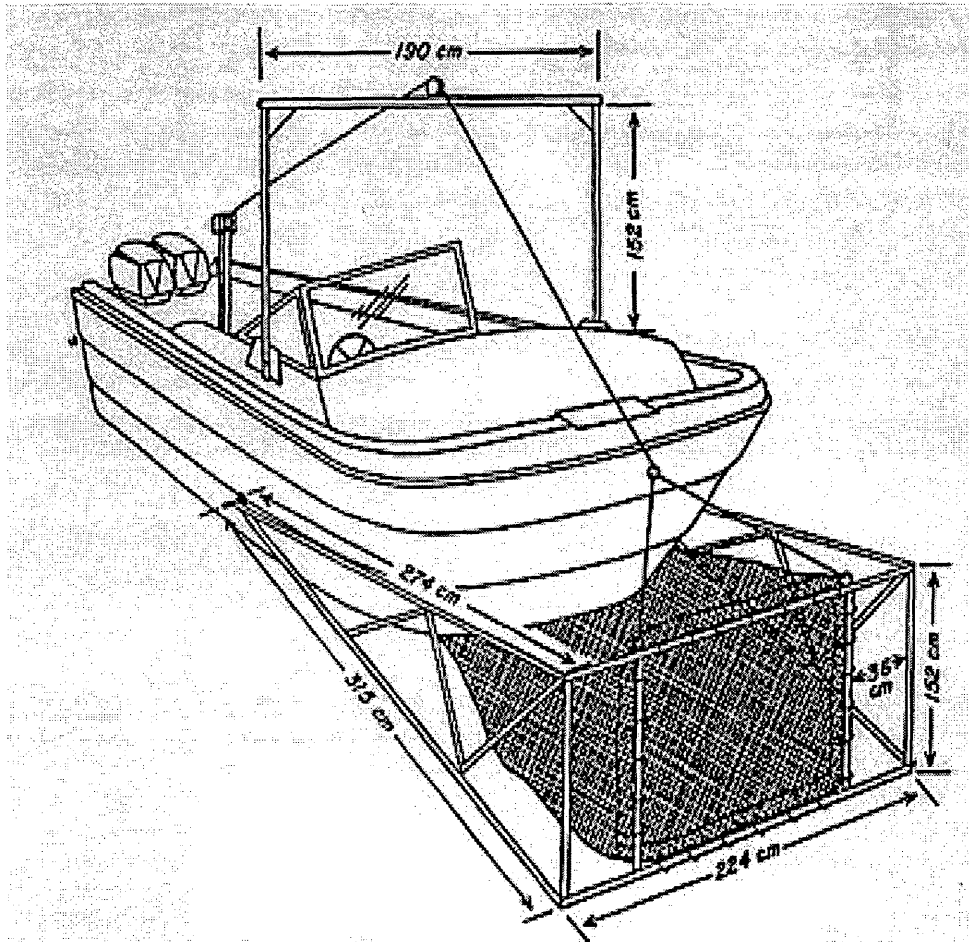
Figure 4: VIMS pushnet sampling gear designed specifically to collect pelagic juvenile fishes (Kriete and Loesch 1980).
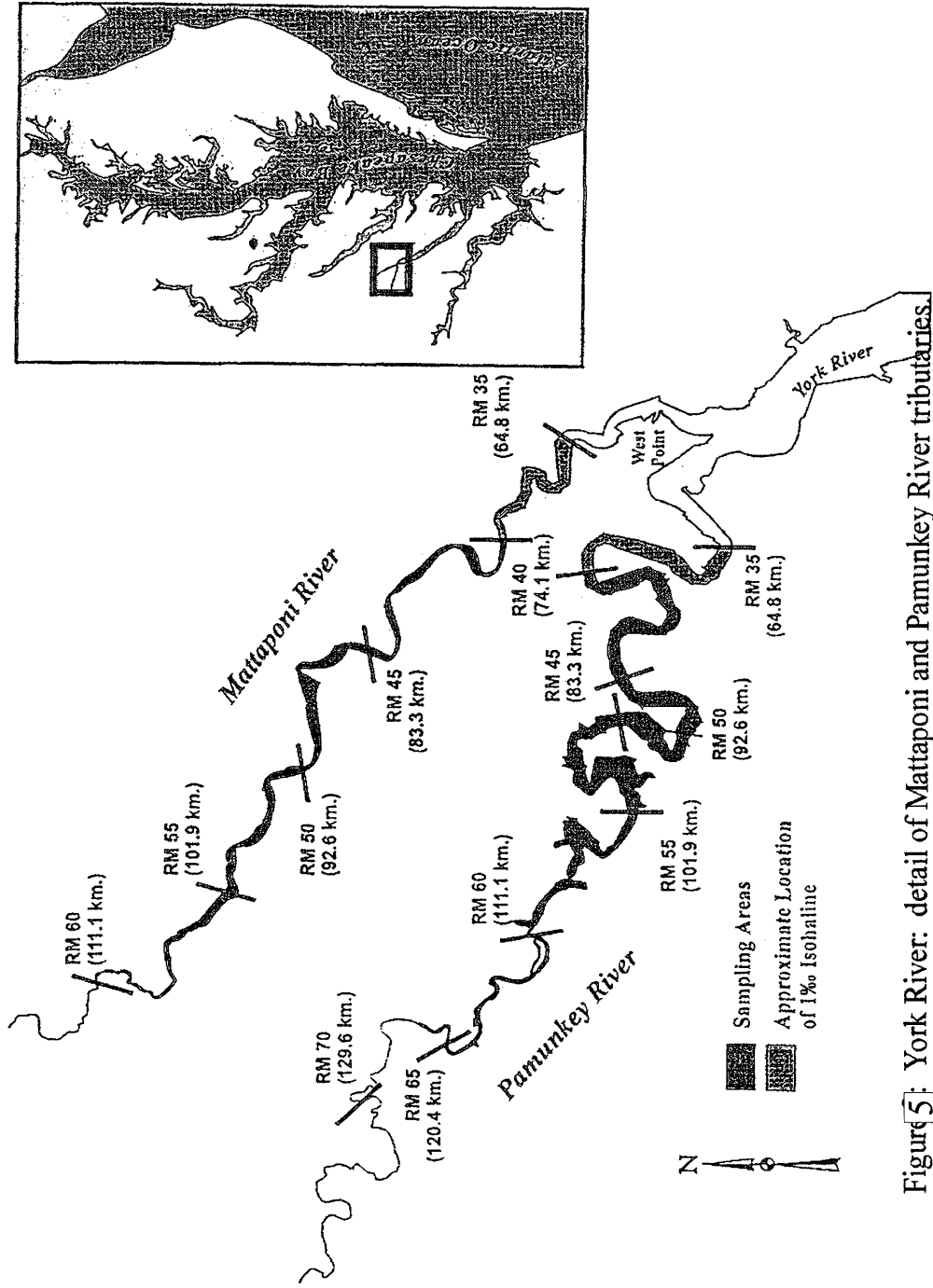
Figure 5: York River: detail of Mattaponi and Pamunkey River tributaries. Juvenile abundance sampling area is designated by bars. Image from Dixon(1996).
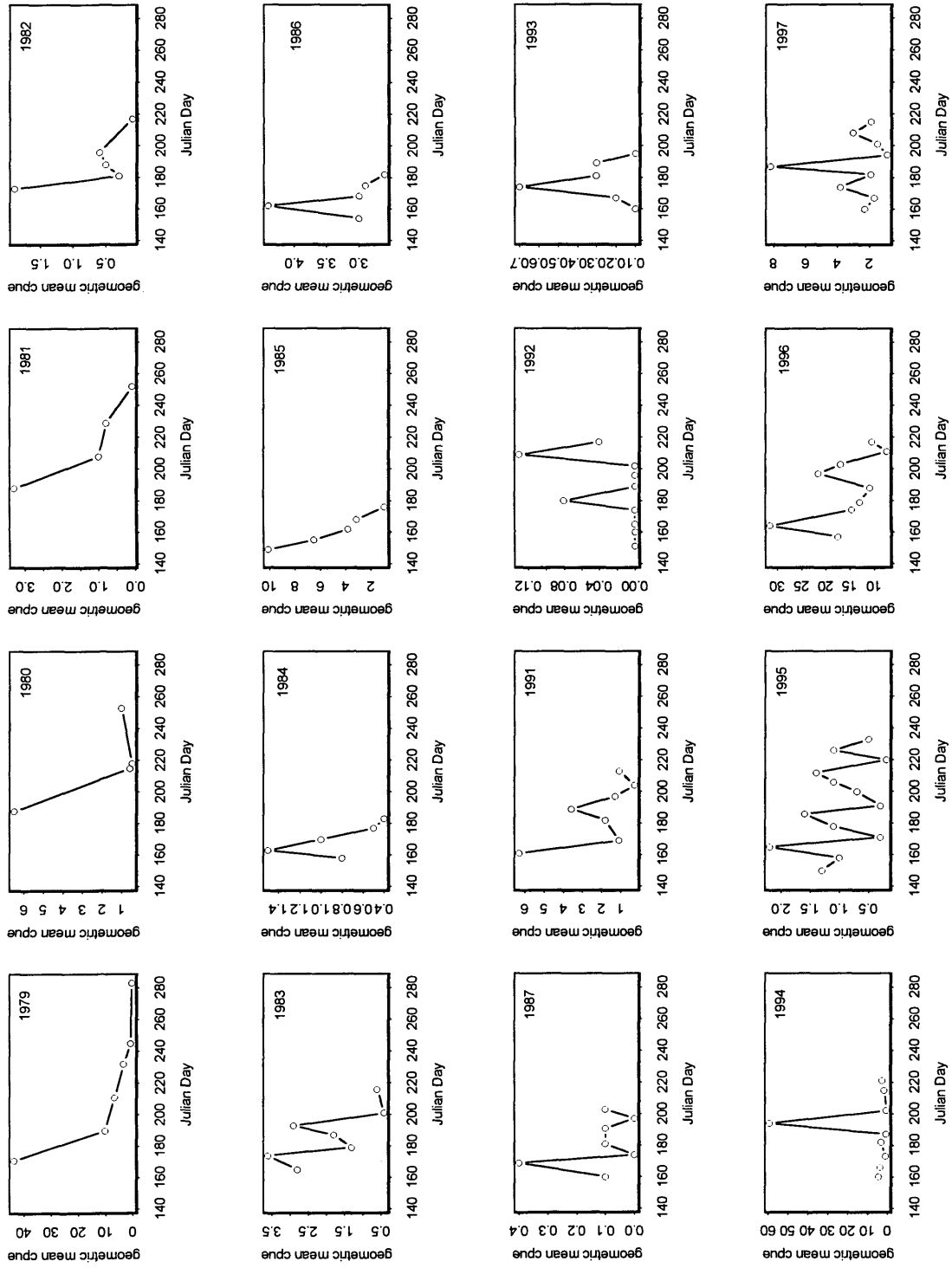
Figure 6: Average catch rate of juvenile American shad per pushnet cruise, Pamunkey River (1979-2000).

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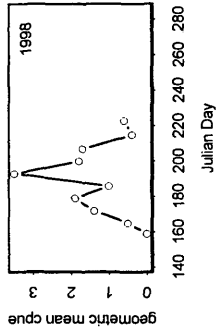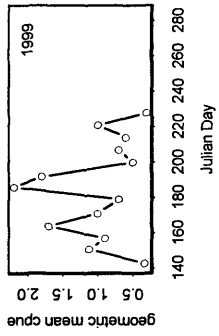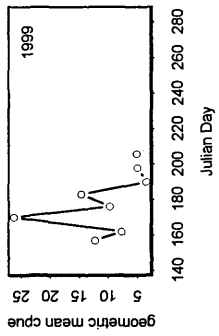
Figure 6 continued.

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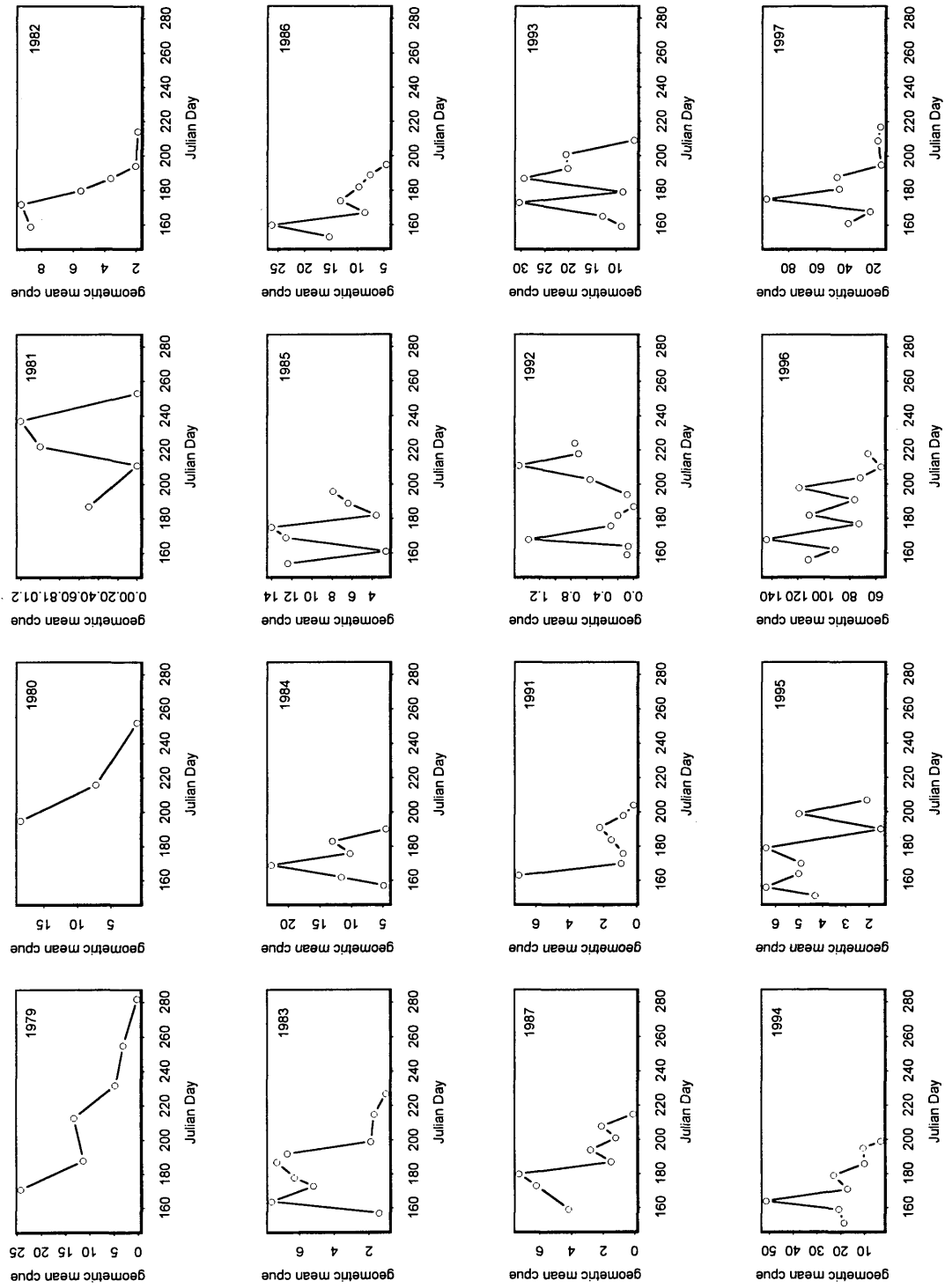
Figure 7: Average catch rate of juvenile American shad per pushnet cruise, Mattaponi River (1979-2000)
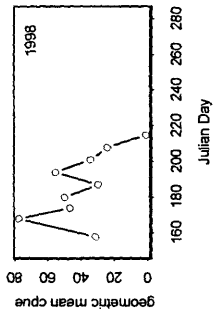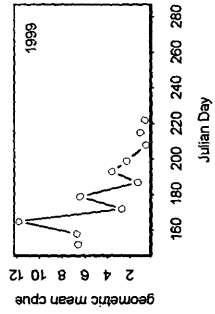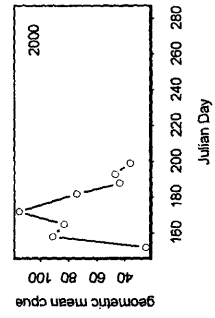
Figure 7 continued.

52
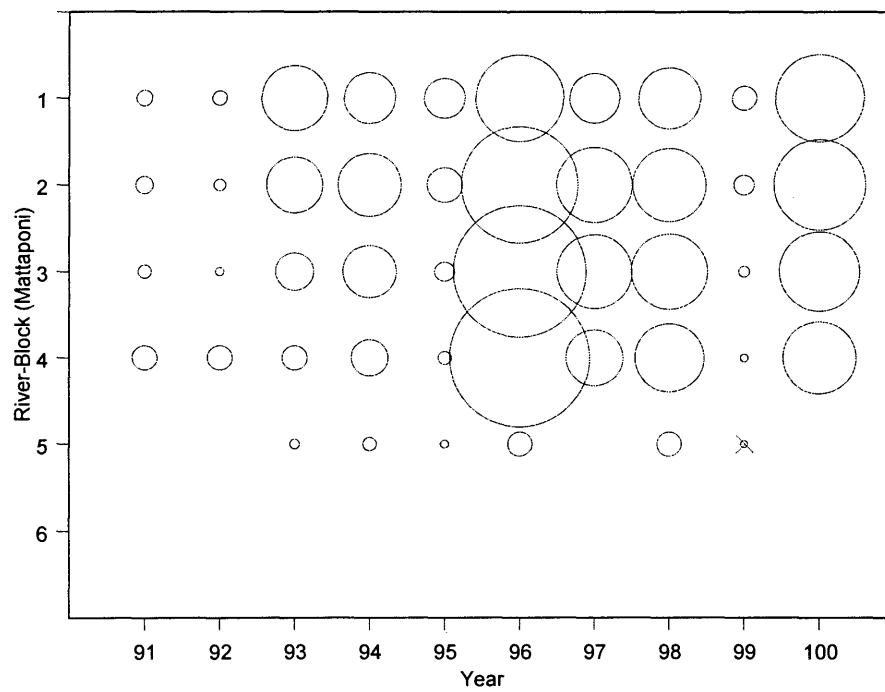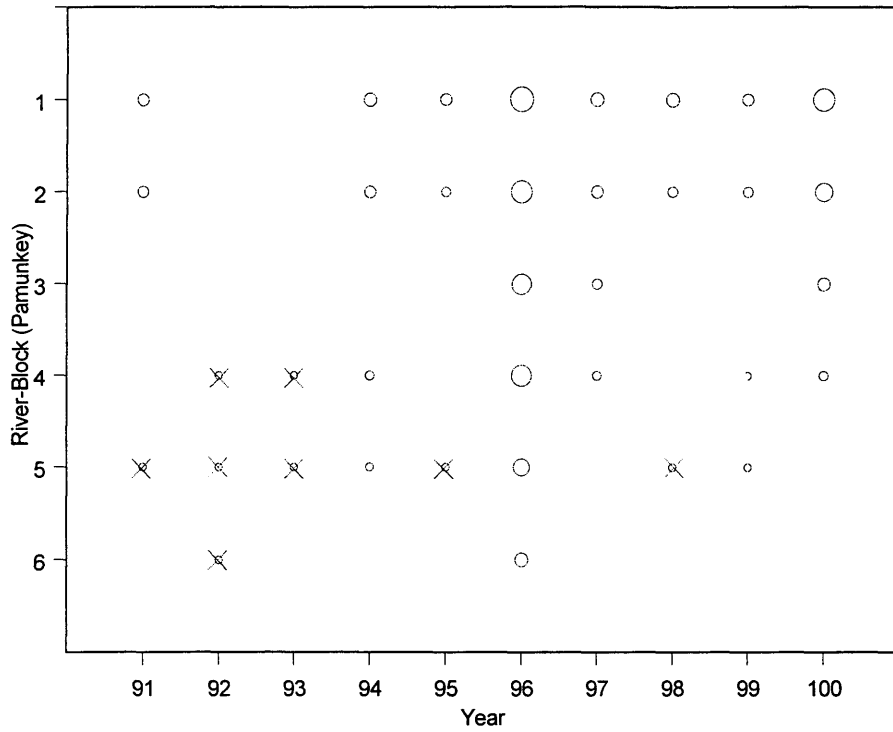
Figure 8: Spatial distribution of juvenile American shad in the Pamunkey River
(a) and Mattaponi River (b) (1991-2000). Bubble size is proportional to mean
catch per unit effort. X represents sampled river blocks where no juveniles
were caught. River block 1 is river miles 69-65 on the Pamunkey River and
river miles 59-55 on the Mattaponi River. The largest bubble 12,719
(Mattaponi River - 1996)the smallest bubble is 1.86 (Pamunkey River - 1993).

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CHAPTER II. COHORT DYNAMICS OF JUVENILE AMERICAN SHAD
(*ALOSA SAPIDISSIMA*) IN THE PAMUNKEY RIVER, VIRGINIA: TWO YEARS
OF SIMILAR ABUNDANCE, 1998 AND 1999

ABSTRACT

In this study, common and distinguishing developmental characteristics of surviving juvenile American shad were identified in two years of similar abundance (1998,1999) in the Pamunkey River nursery habitat. Juvenile shad, collected during the summer of 1998 and 1999, were aged using daily increments in their otoliths. The hatchdate distribution in 1998 was dome-shaped and included the dates April 7 to June 22. The hatchdate distribution in 1999 was flat-topped, slightly broader, and included the dates from 4 April to 22 June. The first surviving cohorts were hatched after fluctuations in water flow subsided in each year suggesting that the time of hatch is heavily influenced by hydrological conditions. Comparisons of the temporal distributions of hatchdates with catch rates of ripe females, eggs, and larvae collected during other studies on the Pamunkey River indicated that shad hatched later in the spawning season experienced greater survival. Cohorts were designated as juveniles hatched within 5-day intervals. Mean cohort-specific instantaneous growth was 0.02/d based on wet weight and fork length in 1998, and 0.02/d (wet weight) and 0.05/d (fork length) in 1999. Cohort-specific mortality ranged from 5% to 9% (mean - 7%) in 1998 and 2% to 8% (mean - 5%) in 1999, but most regressions of log(catch rate) versus time were not significant. M/G ranged from 1.67 to 5.00 in 1998 and 0.40 to 1.60 in 1999. Because the mean M/G in 1998 (3.73) was higher than that in 1999 (0.92) and the period of stable river flow (hypothesized to promote good recruitment) was greater in 1999, it seemed like the 1999 year-class should have been larger than that of 1998, but this was not the case. There were no obvious causes for unexpectedly high mortality of juvenile American shad at the end of the nursery period in 1998. Thus, a likely explanation for the observed discrepancy is the early emigration of juveniles in 1998, as suggested by the steeper decline in cruise catch rates after the peak, and smaller mean length, weight, and age of individuals (40.6mm, 1.1g, 46 days in 1998 versus 46.1mm, 1.4g, 50 days in 1999). The impacts of varying residence times of cohorts in the sampling area on the calculation of juvenile abundance indices are discussed.

INTRODUCTION

Subtle variability associated with growth and mortality experienced during the early life of fishes has significant affects on recruitment (Houde 1989). Mortality appears to be growth dependant and declines steadily with increasing body size. The physiological mortality rate (M/G) is often used as a measure of the success of a given cohort of fish. This is because larval biomass increases only after larvae surpass the transition size (M/G = 1.0). In general, cohorts that reach transition size early have the advantage of an earlier gain in biomass. Thus, annual variability in the age at which transition is reached can act to control recruitment. Measures of larval growth alone can not predict recruitment, but the combination of back-calculated birth dates and cohort specific M/G ratios can provide an indicator of the time periods in which the most successful cohorts of fish were hatched.

A common goal among fisheries scientists is the unveiling of the mechanisms responsible for variability in recruitment patterns. Highly variable mortality and growth experienced during the early life of fishes are responsible for fluctuating recruitment levels and year-class strength. The dynamics of larval growth, mortality, and fluctuations in recruitment are well known (Houde 1989, Houde 1994, Letcher et al. 1996, Houde 1997, Rutheford et al. 1997). The relationship between larval growth and mortality, mediated by hydrographic and meteorological conditions, is generally considered the major cause of fluctuating recruitment.

Factors controlling the abundance of juveniles are not well studied. If year-class strength is set during the larval stage of life, relative juvenile abundance should

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theoretically be a tool used to predict future adult recruitment, but this remains a difficult task for managers of many species. Juvenile growth and mortality are rarely considered, but also may be factors affecting recruitment variability. Post-juvenile life may affect the relationship between young-of-the year and adult recruitment. Comparison of many years of data related to the characteristics of juvenile life may reveal processes responsible for successful juvenile production.

The early life history of American shad is not well known, particularly the juvenile stage. At a minimum of 10-12C , American shad spawn in the mainstreams of rivers in shallow water with moderate current (Massmann 1952, Chittenden 1969). Hatching time is temperature dependent (Barton 1972). Egg development is prolonged and mortality increased when water temperatures are below 16C (Marcy 1972), but eggs can survive at suboptimal conditions (Schmidt et al. 1988). Young shad reach transition size at first feeding, which is earlier than many species (Houde 1997). Larvae are planktonic and passively drift downstream (Schmidt et al. 1988). Shad metamorphose to the juvenile stage at approximately 28mm (Savoy and Crecco 1988). They feed on planktonic crustacea, chironomid larvae (Liem 1924), copepods, and insects (Hildebrand and Schroeder 1928, Massman 1963). Feeding peaks in the early evening (Massman 1963). Down stream oceanic migration of juveniles is size (Chittenden 1969, Marcy 1976, Schmidt et al. 1988, Limburg 1996)and temperature dependent (O'Leary and Kynard 1986). Decreasing temperatures also cause a decline in hyperosomoregulatory ability, which also may serve as a proximate cue for autumnal migration (Zydlewski and McCormick 1997).

Although poorly understood, density-independent environmental variables

mediated by density-dependant processes are generally considered primary factors

affecting growth and mortality of young shad stages (Crecco and Savoy 1987a). Shad

spawn in the mainstreams of rivers during the spring when environmental conditions,

such as water flow, temperature, dissolved oxygen, and turbidity are highly variable.

These episodic fluctuations in meteorological and hydrological conditions have been

shown to greatly affect early life recruitment (Crecco and Savoy 1985, Crecco and Savoy

1987a, Crecco and Savoy 1987b, Dixon 1996, Limburg 1996, McGovern and Olney

1996, Rutheford and Houde 1995). On the Connecticut River, mortality rates of

American shad larvae were highest in late May when river temperatures were below 18C

and river flow exceeded 800 m^3/s. Mortality rates were lowest when the river

temperatures rose above 21C and river flows fell below 300 m^3/s (Crecco and Savoy

1987a). Similarly, on the Hudson River, the 1990 year-class of American shad was

established mainly by cohorts hatched when waters were warm and river flow was

minimal, allowing food sources to build up and promoting larval survival (Limburg

1996).

Year-class strength is generally considered to be set during the larval stage for

American shad. However, little is known about juvenile growth and mortalities. Juvenile

abundance is monitored on eight rivers on the Atlantic coast (ASMFC 1999), but juvenile

abundance indices (JAIs) have only been related to adult abundance on the Connecticut

River (Savoy and Crecco 1988). Investigation of juvenile vital rates may reveal that

dynamics of this stage of life are variable, suggesting that year-class strength may be

strongly influenced by cohort dynamics in the juvenile stage.

In this study, common or distinguishing developmental characteristics of surviving juvenile American shad were identified in two years of low abundance (1998,1999) in the Pamunkey River nursery habitat. Patterns in hatchdate distributions, mortality, growth, M/G ratio, and related parameters were examined to judge how they differ among year classes or cohorts. Water flow, temperature, spawning stock biomass, and larval abundance, which were hypothesized to be linked to survival and hatchdate distributions of juvenile shad, were included in the analysis. The objective was to interpret how linked M and G processes during the juvenile stage act to shape a cohort's contribution to recruitment, and to examine between-year or between-cohort variability in the process. The overall goal of this section is to contribute towards an understanding of the dynamics of recruitment of American shad in the York River.

MATERIALS AND METHODS

Environmental Data

Continuous temperature recordings were not available on the spawning grounds for an extended time period. Water temperatures on the Pamunkey River were collected at Rockahock (RM 45) by the Virginia Department of Game and Inland Fisheries (VDGIF) during shad broodstock monitoring (16 March to 17 May in 1998 and 17 March to 8 May in 1999), but not on a daily basis. Complete time series of temperatures were generated by regressing temperatures collected by VDGIF with VIMS ferry pier (RM 5) mean daily temperatures collected in 1998 and 1999 (Pamunkey temp. = 1.046 (ferry temp) + 1.006, r^2 = 0.79, p < 0.001; Pamunkey temp. = 0.70(ferry temperature) + 3.42, r^2 = 0.87, p < 0.001, respectively) to generate daily temperatures in the nursery habitat. Daily Pamunkey River mean water flow from March 1 to August 31 was collected at the USGS gauging station in Hanover County, Virginia (RM 97).

Otolith Preparation and Analysis

Saggital otoliths from juvenile American shad were collected during 1998 and 1999 weekly pushnet surveys. Otoliths were mounted and ground, and daily increments were counted under 100X magnification using methods described in Secor et al. (1991). Ages were determined by averaging two independent counts of otolith increments. The validity of otolith increments as estimators of age in days for American shad has been established, with first increment deposition occurring on day 1 for larvae raised at 15C and 18 C (Savoy and Crecco 1987). Age extimates were discarded if the difference in replicate counts of increments was greater than 10% of the average (Dixon 1996, Kline

1990). A test of symmetry was used to determine whether the method of increment enumeration applied to the first aging trial was compatible with increment enumeration in the second aging trial (Evans and Hoenig 1998). Cohorts were defined as all fish hatched within a 5-day span, similar to cohorts definitions of Crecco and Savoy (1987a) and Dixon (1996).

Hatchdate Distributions and Residence Time

Hatchdates were back calculated as the day of capture minus the age at capture for each shad. Hatchdates were related to mean daily water flow at hatch, and temperature occurring at hatch. Hatchdate frequency distributions were plotted for each cruise, and the first appearance of the earliest and latest hatched cohorts were plotted to elucidate recruitment patterns. Residence time was defined as the number of days between the first and last cruises in which individuals of any cohort were captured. Residence time was calculated for each cohort and compared to determine whether the time spent in the nursery is the same for all cohorts. A Kolmogorov-Smirnov test was used to determine whether distributions of cohort-specific residence times were different in 1998 and 1999.

Growth and Mortality

Cohort-specific instantaneous growth rates (G), instantaneous mortality rates (M), and their ratios (M/G) were calculated. Slopes of regressions of log(fork length) and log(wet weight) on date of capture were used as estimates of instantaneous growth rates (d^{-1}). Slopes of regressions of size (fork length or wet weight) on date of capture were used as estimates of finite growth rates (mm/d or g/d). Growth was only estimated for cohorts present on six or more cruises. A Kolmogorov-Smirnov test was used to

determine whether length and weight distributions in 1998 and 1999 were different.

Slopes of regressions of log (catch rates) over time were used as estimates of natural

mortality. Mortality was estimated for cohorts with 10 or more individuals, present on 6

or more cruises. Each regression was performed beginning on the date of the cruise with

the highest catch rate assuming juveniles were fully recruited to the gear at this time

(Hilborn and Walters 1992). It was also assumed that vulnerability to the push net was

constant for all ages of juveniles collected. Catchability is assumed to be constant over

time.

Broodstock, Eggs, and Larvae

Catch rates of ripe (hydrated) female American shad in drift gill nets are recorded

during egg taking activities on the Pamunkey River spawning grounds annually by the

Virginia Department of Game and Inland Fisheries (VDGIF). During the spawning run,

300 ft drift gill nets (4.5" - 5.75" varying stretch mesh sizes) are fished nightly at

Rockahock (RM 45). Sex, fork length, and reproductive stage were recorded for each

fish captured in 1998 and 1999. Water temperature was also recorded (see VDGIF 1998

and VDGIF 1999) for additional details).

Patterns in catches of broodstock were plotted with juvenile hatchdate

distributions and patterns of catches of eggs and larvae on the Pamunkey River spawning

grounds to determine whether temporal overlaps occurred. Eggs and larvae were

collected in a separate study in 1998 and 1999 (Bilkovic et al., in press).

RESULTS

Variability in Temperature and Flow

The average temperatures for March through August in 1998 and 1999 were 22.4

C (min - 9.3 C March 17; max -30.9 July 23) and 17.5 C (min - 8.2 C March 13, max -

31.0C July 31), respectively. As expected, temperatures increased throughout the spring

and summer in both years (Fig. 9).

Patterns of water flow differed in 1998 and 1999 (Fig. 10). Four fluctuations in

flow above 100 m^3/s occurred between March 1 and August 30 in 1998, whereas only one

such peak occurred in 1999. Mean flows in 1998 and 1999 were 46.8 m^3/s (min - 2.0

m^3/s August 29, max - 438.9 m^3/s March 23) and 11.9 m^3/s (min - 1.3 m^3/s August 8, max

- 175.6 m^3/s March 18), respectively.

Juvenile Catch Rates and Size Distribution

Temporal patterns in catch rates of juvenile American shad on the Pamunkey

River 1998 and 1999 are depicted in Figure 11. Juveniles were captured on weekly

cruises from 8 June (Julian day 159) to 11 August (Julian day 223) in 1998 and 23 May

(Julian day 143) to 16 August (Julian day 228) in 1999. Two peaks in catches occurred in

both years. In 1998, the smaller peak occurred on 28 June (Julian day 170) and a second

larger peak occurred 12 July (Julian day 193). In comparison, the catch in 1999 rose to a

first peak (13 June) and a second somewhat larger peak 5 July (Julian day 186).

After the second peak, a steep decline in catch rate occurred in 1998 and a gradual decline

occurred in 1999.

Despite differences in peak catch rates (3.5 vs 2.2) , the juvenile indices were

similar in both years (geometric mean - 1.15 in 1998 and 1.04 in 1999).

The fork length and wet weight distributions of juvenile American shad captured in 1998 and 1999 were statistically different (p > 0.05) (Fig. 12 and 13). Mean fork lengths in 1998 and 1999 were 40.6mm and 46.1mm, respectively. The size range in 1999 was larger than in 1998 (26.8mm - 99.1mmfor 1998; 25.4mm - 75.1mm for 1999). Mean weights in 1998 and 1999 were 1.1g and 1.4g, respectively. The range of weights was greater in 1998 than in 1999 (0.2g- 12.4g for 1998; 0.1 - 5.4g - 0.1g for 1999).

Age Estimation, Cohort Catch Rates, Hatchdate Distributions, and Residence Times

A total of 416 shad were captured in 1998 and 328 shad in 1999. Otoliths of 365 (89%) juvenile shad collected in 1998 and 280 (86%) shad collected 1999 were used in this study. Thus, 11% of the specimens in 1998 and 14% of the specimens in 1999 were not used because the percent difference in aging exceed 10% or the otoliths were damaged during preparation . A contingency test showed no systematic bias in aging. Age frequency distributions for shad in 1998 and 1999 are shown in Figure 14. The means of the distributions were 46 days and 50 days, respectively. The youngest juveniles captured in 1998 and 1999 were 23 days and 28 days old, and the oldest juveniles were 89 days and 85 days old, respectively.

Definition of cohorts and cruises upon which they were captured are shown in Tables 11 and 12. Sixteen cohorts were identified in 1998. Cohort 11, hatched between May 26-30 (Julian days 146-150) had the largest number of individuals in 1998. The cohorts with the fewest individuals were those that hatched early (cohorts 1-6, Julian days 96-125) or late in the season (cohort 16, Julian days 171-175). Seventeen cohorts were

identified in 1999. The cohort with the largest number of individuals (cohort 6) hatched

between 26 April and April 30 (Julian days 116-120). The cohorts with the fewest

individuals were those that hatched early (cohorts 1 -3, Julian days 91-105) or late

(cohorts 16 and 17, Julian days 166-175) in the season.

Several similarities exist in the appearance of cohorts in cruises (Fig. 15 and 16,

Table 13). The oldest cohorts (those hatched first) were not collected on initial cruises.

In 1999, cohorts 1-2 were observed sporadically in the second, third, and fourth cruises.

In 1998, cohorts 1 and 2 were only observed once (in cruise 4). The youngest cohorts

(those hatched last) disappeared quickly from cruise catches. In 1998, cohorts 15 and 16

were only observed on two cruises (8 and 9). In 1999, cohorts 16 and 17 were present

only in the last three cruises. Persistent cohorts were observed in both years. In both

years, six to seven cohorts (1998: 8-13; 1999: 4, 7-11, 14) were observed on six or more

cruises (42 or more days).

Hatchdate distributions were also plotted compared by cruise date. The

appearance of cohorts in 1998 cruises was gradual and peaked on cruise 4 (Julian day

179: 12 cohorts). In 1999, cohorts appear earlier and more abruptly. Six cohorts were

present on the second cruise (Julian day 151) in 1999 and only two cohorts were present

on the second cruise (Julian day 165) in 1998. The cruise with the greatest number of

cohorts was cruise 7 (Julian day 186 : 10 cohorts) in 1999. On average, juveniles were

present in more cruises in 1999 (4.6) than in 1998 (3.6). Additionally, the average

number of cohorts per cruise was greater in 1999 (6.4 cohorts/cruise) than 1998 (5.2

cohorts/cruise).

Hatchdate distributions were unique (Figure 17). The hatchdate distribution for the 1998 year-class was dome-shaped with a long left-hand tail and included the dates April 7 to June 22 (Julian days 96-175). In 1999, the hatchdate distribution was broader and plateau-like, and included the dates from 4 April to 24 June (Julian days 91-175).

When hatchdate distributions were plotted against environmental variables (Fig. 18 and 19), several patterns were apparent. Water temperature generally increased throughout the season and during the hatch of successful cohorts (Fig. 18). Surviving juveniles were hatched at warmer temperatures in 1998. All juveniles were hatched at temperatures above 16C in 1998, whereas in 1999, many juveniles were hatched at temperatures below 15C. Juveniles were also generally hatched after fluctuations in water flow stabilized (Fig. 19). However, in 1998, one fluctuation in flow did occur at the beginning of the time period within which surviving juveniles were hatched. In 1999, no fluctuations in flow occurred during hatch of surviving shad.

The distribution of residence times plotted by successive cohorts in 1998 and 1999 was generally dome-shaped (Fig. 20). The earliest and latest hatched cohorts had the shortest residence times and cohorts hatched in mid-season had the longest residence times in both years. However, the distributions of cohort-specific residence times in the two years were significantly different (ks test - alpha = 0.05, p = 0.059). The mean residence time of cohorts hatched in 1998 was 37 days while in 1999 mean residence time was 45 days.

Growth and Mortality

Cohort-specific instantaneous growth (G) was estimated by regressing both

log(wet weight) and log(fork length) to date of capture for cohorts 7 - 14 in 1998 and

cohorts 3-13 in 1999 (Fig. 21-24). Cohorts present on less than 6 cruises were excluded

due to insufficient sample size. All regressions were significant ($p < 0.02$). Mean finite

growth rates were similar in 1998 (wet weight - 0.06 gd^{-1}, fork length - 0.71 mmd^{-1}) and

1999 (wet weight - 0.08gd^{-1}, fork length - 0.77mm d^{-1}). Mean instantaneous growth

rates were also similar in 1998 (wet weight - 0.02 d^{-1}, fork length - 0.02 d^{-1}) and 1999

(wet weight - 0.05 d^{-1}, fork length - 0.02 d^{-1}). Cohort 10 had the highest instantaneous

growth rate (wet weight - 0.03 d^{-1}, fork length - 0.03 d^{-1}) in 1998 (Table 11). Cohorts 7

and 11 had the highest growth rates in 1999 (wet weight - 0.06 d^{-1},0.07 d^{-1}, fork length -

0.02 d^{-1}, 0.02 d^{-1}, respectively) (Table 12).

Regressions of the declines in log(catch rates) of juveniles were used to estimate

cohort-specific mortality rates in 1998 and 1999 (Fig. 25 and Fig. 26). Only one

regression was significant ($p < 0.05$) in each year. Analysis was restricted to cohorts 9 -

13 in 1998 and 4,7-12 in 1999. Mortality rates per day ranged from 0.05 (cohorts 10 and

13) to 0.09 (cohorts 11and 12) in 1998 and 0.02 (cohort 7) to 0.08 (Cohort 10) in 1999

(Table 11 and 12). The average mortality was 0.07 in 1998 and 0.05 in 1999.

Ratios of M/G ranged from 1.67 (cohort 10) to 5.00 (cohort 13) in 1998 and 0.40

(cohort 7) to 1.60 (cohorts 10) in 1999. The mean M/G ratio was 3.73 in 1998 and 0.92

in 1999. M/G decreased with increasing relative cohort size in both years, but the

regressions were not significant ($p>0.05$). A summary of characteristics of cohorts is

shown in tables 11 and 12.

Broodstock, Eggs, and Larvae

Catch rates of hydrated female American shad used for egg taking from 16 March

to 17 May in 1998 (Julian days 75 - 137) and 17 March to 8 May in 1999 (Julian days 76

- 128) are depicted in Figure 27. Spawning females were captured from 16 March to 15

May with the peak catch rate occurring on 2 April in 1998 (14.0 females per net).

Spawning females were captured throughout monitoring in 1999 with the peak catch of

females on 5 April (40.8 females per net).

Eggs and larvae were collected in a separate study in 1998 and 1999 (Bilkovic et

al. , in press). Catches of eggs and larvae were low and sporadic on the Pamunkey River

in both years. The number of days when eggs were present is depicted as a bar in Figure

29. American shad eggs and/or larvae were collected in seven cruises (2 April - 14 May)

in 1998 using bongo nets or a pushnet. In 1999, cruises only occurred on three dates (9

April, 13 April, 6 May). Shad eggs and larvae were collected on 12-April and 19 April.

Hatchdate distributions overlapped the dates of capture of eggs and larvae, but hatchdates

of juveniles continued past the last date of capture of eggs and larvae. Hatchdates

overlapped the later dates of catches of adult females and eggs/larvae in the Pamunkey

River (Fig. 28). Catch rates and the distribution of hatch dates had a greater proportion of

overlap in 1999.

DISCUSSION

Spawning by American shad on the Pamunkey River, Virginia produces multiple cohorts of juveniles that exhibit wide variability in spatio-temporal occurrence, abundance, and catchability. During two years of average JAIs, 16 to 17 surviving cohorts were produced and most were hatched late in the spawning season. Table 14 summarizes comparisons made between these two years. Cohorts that were hatched early in the spawning season did not survive and their abundances were small. The surviving cohorts inhabited a large stretch of freshwater nursery habitat (at least 20 river miles in length) during the summer on the Pamunkey River. As each cohort grew older and became available to the sampling gear, cohort-specific catch rates over the summer peaked once. The strongest cohorts were persistent, remaining withing the nursery habitat for 6 - 8 weeks. Multiple peaks in the catch of all juveniles (Fig. 11) were caused by the successive appearance of strong cohorts during the season. Eventually, catch rates descended as juveniles died, grew large enough to avoid the gear, or emigrated from the nursery area.

Hydrological conditions shaped the distributions of hatch dates of juvenile shad on the Pamunkey River in 1998 and 1999. A successive series of cold fronts brought rain to central and eastern Virginia in the spring of both years. Depending on their magnitude, these rainfalls produced fluctuations in water flow and temperature in the Pamunkey River that typically lagged behind the precipitation events (Bilkovic 2000). Hatchdates of juvenile American shad were closely linked to these fluctuations. Of those surviving cohorts in 1998, 76% of the juveniles collected were hatched after May 20 when river

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flow stabilized and water temperature remained above 10 C. Similarly, all surviving

cohorts were produced well after a shorter period of fluctuation in river flow in 1999.

Those individuals that were hatched during periods of unstable flow in 1998 (Fig. 19)

formed weak cohorts that were not persistent. Less sporadic water flow in 1999 may

have lead to a broader, flat topped hatchdate distribution, because environmental

conditions were more consistent throughout the season. In the latter portion of the 1998

and 1999 seasons, low flow and warm water may have lead to greater densities of

zooplankton. The combination of stable environmental conditions and high zooplankton

density is commonly associated with greater survival of shad (Crecco and Savoy 1985,

Limburg 1996).

Stream flow appears to affect the time of hatch, but the significance, if any, of

variable flow on the proliferation of surviving juvenile cohorts remains obscure.

Bilkovic (2000) explored the relationship between water flow and the juvenile abundance

index for American shad in the Mattaponi and Pamunkey rivers for the period 1990 to

1999. Although mean, minimum, and maximum low flow in May was positively

correlated with the JAI in the Mattaponi River, no strong relationship was detected in the

Pamunkey River. Mean water flow in May and the JAI for the Pamunkey River were

inversely related, but it was suspected that this relationship was spurious.

The contribution of juvenile cohorts of American shad spawned late in the

spawning season to juvenile abundance is higher than that of earlier-spawned cohorts.

Although ripe adult females were captured between 16 March - 6 April in 1998 and 16

March - 3 April in 1999, shad hatched during these times apparently did not survive.

Greater survival of later hatched shad has also been observed in the Hudson and

Connecticut rivers (Limburg 1996, Hoenig et. al 1990). A laboratory study revealed

optimum pH, temperature, and prey levels for larval survival and explained that these

conditions are most likely to occur in tributaries of Chesapeake Bay between mid-May

and early June (Leach and Houde 1999). Thus, it appears that the small proportion of the

adult shad population that spawn late in the season, during conditions favorable for

survival of young, contribute more to juvenile production than do all other shad.

Temporal patterns of spawning inferred from collections of American shad

broodstock during egg taking on the spawning grounds are generally unrelated to

production of cohorts of juveniles. In both 1998 and 1999, the earliest hatchdates of

American shad juveniles overlapped the trailing end of catches of hydrated females

suggesting other factors, such as the relationships between growth and mortality, more

heavily influenced the relative abundance of cohorts. Similar disjunct has been observed

for American shad in other rivers, as well as for other species. For example, hatchdate

distributions that are shifted later in the season have been observed for American shad in

the Hudson River (Limburg 1996), striped bass in the Pamunkey River (McGovern and

Olney 1991), and northern anchovy in the California Current (Methot 1983).

The broad range of juvenile hatch dates suggests that successful spawning

occurred well past the last date of broodstock collection. While the collection of

broodstock diminished, cohorts of juveniles continued to be produced as late as June in

both years (Table 14). Broodstock collections cease when the volume of eggs stripped

from females is large enough to support the hatchery for a season, regardless of continued

spawning. Furthermore, eggs and larvae are rare in ichthyoplankton collections (Bilkovic et al. 2000). As a result, very little is known about the spawning patterns of adults on the Pamunkey River. Juvenile hatchdates in this study reveal that adults stay on the spawning grounds until late May or early June. These findings are consistent with the temporal patterns of emigration of post-spawning females (Olney and Hoenig, 1999 and Hoenig and Olney, 2000). Pound nets catches at the mouth of the York River indicated that adult American shad were exiting the system as late as early and mid-June in 1998 and 1999, respectively.

Although the geometric mean JAIs were similar in each year, size- and age-frequency distributions of juvenile American shad in the Pamunkey River differed between 1998 and 1999. On average, the juveniles captured in 1999 were larger (40.6mm, 1.1g in 1998; 46.1mm, 1.4g in 1999) and older (46 days in 1998; 50 days in 1999) (Table 14). These differences are not attributable to sampling error since sampling in 1999 began 16 days prior to the date of the first cruise in 1998. Thus, the smallest and youngest juveniles produced in 1999 should have been available to the gear.

The earliest surviving cohorts of American shad produced did not appear first in pushnet collections. In both years, early cohorts (1 and 2) were not captured by the pushnet until cruises 2 - 4. Numbers of individuals in these cohorts were small and they may have been incidentally collected. Alternatively, retarded growth caused by cooler temperatures at hatch could have prevented individuals in these early cohorts from reaching a catchable size until an older age than individuals hatched later (Leach and Houde 1999). However, the mean ages (80 days - 1998; 69 days - 1999) and sizes

(48.4mm, 1.56g - 1998; 59.0mm, 2.32g - 1999) of juveniles in cohorts 1 and 2 on the date

of first capture were older and larger than those sizes and ages at first capture of all other

juveniles in either year. Thus, slow growth does not explain their late capture. Instead, it

is more likely that early cohorts in both years were hatched farther upstream and

transported a larger distance before capture each year. Drift down river would have

provided additional time to grow and age before entering the pushnet sampling area.

Shad eggs have been captured as far as 11 river miles above the most upriver sampling

station occupied in the juvenile survey (Bilkovic 2000). The most upriver stations are

commonly the areas within which the largest catchrates of juveniles are observed (Fig. 8

in chapter 1). As a result, farther upstream monitoring would increase total catches of

juveniles, but is constrained by gear deployment limitations.

Hatchdate frequency distributions can be misleading because they are the

combined reflection of abundance, natural mortality, and residence time of individual

cohorts in the sampling area. Cohorts that hatch late in the season and outmigrate early

could be under represented in the sample if recruitment occurs throughout the sampling

season. If recruitment of new cohorts continues throughout a sampling season, hatchdate

frequency distributions could be biased by mortality and residence times. For example,

suppose three cohorts are hatched in a season. Cohort A is hatched before cohort B, and

cohort B is hatched before cohort C. Assume the abundance of all cohorts is equal and

that sampling brackets the residence time of all cohorts. Cohort A is recruited to the gear

first and is collected on all cruises (Fig. 29). Cohort B is collected on the last 4 cruises

and cohort C is collected on the last 3 cruises. Thus, cohort A is recruited before cohort

B, and cohort B is recruited before cohort C and the residence times are A>B>C. The number of individuals collected from cohort A is larger than the number collected from cohort B, which is larger than the number collected from cohort C. Thus, the relative abundance represented by the catches suggests cohort A is the largest and cohort C is the smallest, when all cohorts are equal in abundance. This bias is difficult to remove since extimates of natural mortality are confounded by outmigration.

Instantaneous and finite growth rates of juveniles were high relative to those in other systems (Tables 11 and 12). Crecco and Savoy (1985) estimated that growth of American shad between the ages of 35 to 63 days ranged from 0.01mm/d to 0.04mm/d in the Connecticut River in 1983. Estimates of instantaneous growth were higher for juveniles in this study than were those for larval shad (0.21/d) in the Connecticut River (Houde 1997). The instantaneous growth rates of larval shad in the Connecticut River were also more variable (CV = 0.075) than those estimated for juvenile shad in this study (CV = 0.35 - weight and length in 1998; CV = 0.26 - weight, CV = 0.37 length 1999).

Instantaneous mortality rates were low and small variation among cohort-specific estimates was observed. Mortalities ranged from 5%/day to 9%/day in 1998 and 2%/day to 8%/day in 1999 (Table 11 and 12). As expected, juvenile mortality rates were generally lower than those estimated for larvae in the Connecticut River (7.7%/day to 33.3%/day, Houde 1997). The highest mortality rate observed for juvenile cohorts in the Pamunkey River was larger than that estimated for juvenile American shad in the Connecticut River. Crecco et al. (1983) calculated rates between 1.8 and 2.0%/day during a four-year period (1979 - 1982). For the Pamunkey River data, regressions of

catch rate versus time were not significant and R^2 were often low. Gear avoidance, patchy

distribution of juveniles, and insufficient sampling probably influenced the estimation of

mortality rates. Determining survival rates for larval and juvenile fishes is extremely

difficult, even when cohorts can be identified using daily increments (Hoenig et al. 1990).

Larger shad may only be sporadically captured because they are large enough to avoid the

pushnet. Coefficients of variation of estimates of late larval-stage mortality of American

shad in the Connecticut River (CV = 0.25 in1979 to 1984, Houde 1997) were just below

those of juveniles in the Pamunkey River (CV = 0.28 in 1998, CV = 0.40 in 1999). This

may suggests that gear avoidance (or some related attribute that would reduce

vulnerability to the gear) may be somewhat higher in juveniles than in larvae.

Relatively high growth and low mortality were characteristic of most cohorts in

1999. Of these, cohorts 4, 7, and 8 (excluding cohorts 5 and 6 for which M/G could not

be estimated) had large numbers of individuals. Low M/G ratios (0.40 - 0.83) of cohorts

in 1999 suggest that these cohorts reached the transition stage (M=G) as larvae sooner

than others and benefitted from an earlier gain in biomass. These patterns are consistent

with the inverse relationship observed between M/G ratios and cohort abundances of

larval American shad in the Connecticut River (Houde 1997). Rutherford and Houde

(1995) found larval M/G ratios were inversely correlated with the abundance of juvenile

striped bass in the Potomac River.

In contrast, relatively higher mortality and slower growth were characteristic of

cohorts with the largest number of individuals in 1998 (Table 11). As a result, M/G

ratios were unexpectedly (and unrealistically) high (1.67 - 5.00, mean = 3.73) suggesting

that these cohorts were continuing to lose biomass late into the juvenile stage.

Furthermore, the period of stable river flow, a hydrological regime that apparently

influenced appearance of survivors and is thus hypothesized to promote good recruitment,

was shorter in 1998 than in 1999. Given these contrasts in cohort dynamics and

developmental conditions, one might predict that recruitment in 1998 should have been

far less than observed in 1999. However, this was not the case. A satisfactory treatment

of this question could serve to either elucidate some underlying causes of variable year

class strength or the nature of the JAI survey methodology.

In late August or early September, juvenile American shad are no longer available

to capture by the pushnet or seine on the freshwater nursery grounds in the York River

system, and are believed to have started the annual out-migration to the lower estuary.

Occasionally, large juveniles (80-130 mm TL) are captured in trawl samples during

routine monitoring in the middle and lower York River in late fall and winter months but

their occurrence is sporadic. In general, the habits and distributions of young-of-the-year

shad after they leave Chesapeake Bay nursery areas are not known. Furthermore, the

biological and environmental factors that affect the timing and rates of departure from the

Pamunkey River nursery habitat are not described. In the Hudson River, downstream

movement of juvenile shad is a function of size and age, and the movement of the oldest

cohorts in the nursery zone has been observed as early mid-June in the Hudson River

(Limburg 1995). Other factors influencing the downstream migration of juvenile

American shad have been identified as either increasing river flow, decreasing water

temperature (O'Leary and Kynard 1986), moon phase (Stokesbury and Dadsweel 1989),

and a physiological changes causing a decline in hyperosomoregulatory ability

(Zydlewski and McCormick 1997).

Varying rates and timing of emigration of juvenile American shad could explain

the puzzling similarities in juvenile abundance indices in 1998 and 1999. Several lines of

evidence suggest that juveniles departed the nursery grounds earlier in 1998 that in 1999.

First, the mean number of cruises in which juveniles were captured was 3.6 in 1998 and

4.6 in 1999 (Table 14), suggesting that juveniles remained on the nursery grounds a week

longer in 1999. Second, juveniles captured in 1998 were slightly smaller (in mean weight

and length) than those observed in 1999 (Table 14), a likely result of shorter residence

time since water temperature and zooplankton densities were similar in both years

(Bilkovic 2000). Catch rates descended rapidly in 1998 and gradually in 1999 in the

cruises that followed the highest peak catch in each year (Fig. 30) . As a result, the

number of days from the last observed peak catch in 1998 and 1999 were 4 and 6 days,

respectively. Cohorts that peaked on or after the peak cruise catch were present on an

average of 2.8 and 3.4 cruises after this event in 1998 and 1999, respectively.

Recognizing that emigration and natural mortality are indistinguishable in such catch

data, the rapid decline in catch in 1998 could have been the result of either higher rates of

emigration, higher mortality or both. Importantly, there were no obvious causes for

unexpectedly high mortality of juvenile American shad at the end of the nursery period in

1998. Thus, a more likely explanation for the rapid decline in catch at the end of the 1998

sampling season and the resulting high M/G ratios is early emigration of juveniles.

If the timing and rate of emigration of juvenile shad from the nursery habitat

varies among cohorts, inter-annual comparisons of JAIs may not be meaningful. The predictive value of the index depends on its ability to scale estimates of juvenile catch to the true abundance of survivors. If immature survival remains constant after juveniles exit the nursery habitat and if maturity rates are known, the juvenile index can be used to estimate the run strength of mature adults entering the rivers to spawn in subsequent years. Certain forms of the JAI (specifically, the geometric, arithmetic, or areal forms) are especially sensitive to emigration since longer residence times can result in larger indexes. The maximum geometric mean may be less sensitive to emigration but does not account for multiple peaks in catch that may occur within a given year. Thus, if leakiness in the nursery habitat (i.e., emigration) alters catch rates of juveniles, the JAI will not be a reliable measure of juvenile production and has no relationship to subsequent run size.

Migration distance of spawning adults and the size of the nursery habitat varies for each stock of American shad along the US east coast. In rivers where spawning grounds are distant from the ocean and freshwater habitats (and the juvenile survey area) are extensive, the effects of emigration on catches of juveniles may be dampened. Surveys that encompass a greater stretch of river may be able to better estimate year class strength because the juvenile monitoring area is long enough to encompass the downstream migration of cohorts. Therefore, all shad may remain in the sampling area until the completion of the survey. As a result, juvenile indexes may have more predictive capacity for certain stocks than for others. For example, the survey to monitor juvenile shad in the Connecticut River is about 120km long and the juvenile index of abundance have been positively correlated with recruitment levels of adult females 4-6

years later on the Connecticut River (Crecco et al. 1988). Perhaps sampling such a large area dampened any effects of emigration thus, providing a good estimate of year-class strength. In the case of the York River system, migration distances are relatively short (about 80 km) and the sampled nursery habitat is relatively small (about 40 km). Thus, the amount of time necessary for cohorts to migrate out of the nursery zone is shorter than that of the Connecticut (assuming juveniles from the Connecticut and Pamunkey rivers have similar swimming speeds), and perhaps more variable, making estimates of relative juvenile abundance more difficult.

Biological information gained from aging juveniles can be used to test assumptions of various forms of the JAI. Arithmetic, geometric, and areal means assume that the residence time of individuals is constant year to year. By determining the first and last dates of capture, residence times were estimated in 1998 and 1999. On average, cohort-specific residence times in 1998 and 1999 differed by one week suggesting that the assumption of constant residence time may have been violated. Indices calculated as means also assume that the time of arrival and departure from the sampling area is constant annually. This assumption also appeared to be met because examination of the dates of first and last appearance of cohorts in cruise catches revealed these times were similar in each year. In order to make meaningful comparisons of the magnitude of indices, the maximum geometric mean, arithmetic mean, and geometric mean assume that a constant fraction of the population is present in the nursery area annually. Similar numbers of cohorts were captured in each year and approximately 50% of the cohorts (8/16 cohorts - 1998, 10/17 cohort - 1999) were present during the peak catch in both

years. These similarities imply that the assumption is met. However, all assumptions were tested using only two years of data. Thus, it is recommended that further detailed examination of indices be continued.

The utility of the index of juvenile abundance on the York River system may be linked to patterns of emigration and not to patterns of survival. Without a full understanding of the effects of emigration, efforts to monitor abundance of juvenile shad in Virginia rivers may be fruitless. Thus, it is critical that future studies explore the nature and timing of emigration. Three questions that remain unanswered are (1) how variable is the residence time of individual cohorts? (2) when do juveniles leave the nursery habitat? and (3) when do juveniles emigrate from the York River system? Juvenile abundance should be monitored on the nursery grounds, downstream of the nursery grounds, and close to the mouth of the river in attempts to answer these questions. Marking of otoliths with unique OTC marks for dates of release would facilitate estimating date of hatch. An in-depth examination of the catch rates of juvenile American shad in seine survey catches on the York River may also provide insight into the emigration of juvenile shad. In addition, inspection of declines in catch rates after peak catches in historical monitoring data may suggest that emigration rates are highly variable. These suggested studies as well as more detailed studies such as this one would provide information for greater understanding of the dynamics of American shad juvenile life in the Pamunkey River, and thus move closer toward determining the meaning and utility of the juvenile abundance index.

Table 11: Cohort-specific hatchdates, first and last dates of capture, number captured, number of cruises during which individuals were captured, estimates of growth, estimates of mortality, and M/G ratios during juvenile life of American shad in the Pamunkey River (1998). Abbreviations are: F = first Julian date of capture, L = last Julian date of capture, num. = number, g = finite growth rate estimated from wet weight (ww) or fork length (fl), G = instantaneous growth rate estimated from wet weights(ww) or fork length (fl), M = instantaneous mortality, M/G$_{ww}$ = physiological mortality rate (growth is estimated by wet weight), CV = coefficient of variation (standard deviation/ mean).

Cohort	hatchdate range	F	L	num. captured	num. cruises	g$_{ww}$ (g d^{-1})	g$_{FL}$ (mm d^{-1})	G$_{ww}$ (d^{-1})	G$_{FL}$ (d^{-1})	M	M/G$_{ww}$
1	96-100	179	179	1	1	*	*	*	*	*	*
2	101-105	179	179	1	1	*	*	*	*	*	*
3	106-110	159	179	4	2	*	*	*	*	*	*
4	111-115	172	200	4	3	*	*	*	*	*	*
5	116-120	179	179	4	1	*	*	*	*	*	*
6	121-125	179	179	2	1	*	*	*	*	*	*
7	126-130	179	200	11	3	*	*	*	*	*	*
8	131-135	165	207	23	6	*	*	*	*	*	*
9	136-140	165	207	46	7	0.03	0.65	0.02	0.02	0.06	3.00
10	141-145	172	223	70	7	0.10	0.85	0.03	0.03	0.05	1.67
11	146-150	179	207	78	6	0.08	0.78	0.02	0.02	0.09	4.50
12	151-155	179	223	55	7	0.06	0.70	0.02	0.02	0.09	4.50
13	156-160	186	207	30	6	0.04	0.59	0.01	0.01	0.05	5.00
14	161-165	193	214	24	4	*	*	*	*	*	*
15	166-170	207	214	9	2	*	*	*	*	*	*
16	171-175	214	214	3	1	*	*	*	*	*	*
CV						0.42	0.14	0.35	0.35	0.30	0.37
Mean						0.06	0.71	0.02	0.02	0.07	3.73

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Table 12: Cohort-specific hatchdates, first and last dates of capture, number captured, number of cruises during which individuals were captured, estimates of growth, estimates of mortality, and M/G ratios during juvenile life of American shad in the Pamunkey River (1999). Abbreviations are: F = first Julian date of capture, L = last Julian date of capture, num. = number, g = finite growth rate estimated from wet weight (ww) or fork length (fl), G = instantaneous growth rate estimated from wet weights(ww) or fork length (fl), M = instantaneous mortality, M/G_ww = physiological mortality rate (growth is estimated by wet weight), CV = coefficient of variation (standard deviation/ mean).

Cohort	hatchdate range	F	L	num. captured	num. cruises	g_{ww} (g d⁻¹)	g_{FL} (mm d⁻¹)	G_{ww} (d⁻¹)	G_{FL} (d⁻¹)	M	M/G_ww
1	91-95	151	164	2	2	*	*	*	*	*	*
2	96-100	151	164	2	2	*	*	*	*	*	*
3	101-105	151	164	11	3	*	*	*	*	*	*
4	106-110	143	192	26	8	0.09	0.85	0.06	0.02	0.05	0.83
5	111-115	151	186	29	5	*	*	*	*	*	*
6	116-120	151	186	37	5	*	*	*	*	*	*
7	121-125	151	192	32	6	0.06	0.70	0.05	0.01	0.02	0.40
8	126-130	157	192	32	6	0.06	0.80	0.06	0.02	0.04	0.67
9	131-135	164	214	21	8	0.03	0.41	0.03	0.01	0.04	1.33
10	136-140	171	207	20	6	0.06	0.63	0.05	0.01	0.08	1.60
11	141-145	179	228	19	7	0.20	1.22	0.07	0.02	0.05	0.71
12	146-150	186	221	14	5	*	*	*	*	*	*
13	151-155	186	221	13	5	*	*	*	*	*	*
14	156-160	192	228	8	6	*	*	*	*	*	*
15	161-165	207	221	8	2	*	*	*	*	*	*
16	166-170	214	228	2	2	*	*	*	*	*	*
17	171-175	221	221	4	1	*	*	*	*	*	*
CV						0.72	0.35	0.26	0.37	0.42	0.49
Mean						0.08	0.77	0.05	0.02	0.05	0.92

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Table 13 : Dates of pushnet monitoring survey cruises on the Pamunkey River and number of cohorts of juvenile American shad present in the catches (1998, 1999).

Cruise	1998		1999	
	Julian Day	# cohorts	Julian Day	# cohorts
1	159	1	143	1
2	165	2	151	6
3	172	4	157	6
4	179	12	164	9
5	186	6	171	6
6	193	8	179	5
7	200	9	186	10
8	207	7	192	9
9	214	5	200	4
10	223	4	207	7
11	*	*	214	5
12	*	*	221	6
13	*	*	228	3

Table 14: Comparison of environmental data, juvenile American shad dynamics, collections of eggs/larvae, and dates of capture of hydrated females in the Pamunkey River (1998, 1999). Ichthyoplankton data reported from Bilkovic et al. (2000). Broodstock data reported from VDGIF (1998 and 1999).

Comparison	1998	1999
average water temperature (March 1 - Aug 30)	22.4C	17.5C
average water flow (March 1 - Aug 30)	46.8m^3/s	11.9m^3/s
water flutuations above 100m^3/s	4	1
# peaks in mean cruise catches	2	2
decline in mean cruise catches after final peak	steep (faster)	gradual (slower)
JAI (geometric mean)	1.15	1.04
mean fork length	40.6mm	46.1mm
mean wet weight	1.1g	1.4g
mean age	46 days	50 days
youngest juveniles captured	23	28
oldest juveniles captured	89	85
# of surviving cohorts	16	17
# cohorts/cruise	5.2	6.4
# cruises/cohort	3.6	4.6
range of hatchdates	April 7 - June 22 (Julian days 96-175)	April 4 - June 24 (Julian days 91-175)
mean G of cohorts (length)	0.02/d	0.02/d
mean G of cohorts (weight)	0.02/d	0.05/d
mean M cohorts	0.07/d	0.05/d
mean M/G of cohorts	3.73	0.72
dates of capture of broodstock	March 16 - May 17 (Julian days 75 - 137) peaked on April 2	March 17 to May 8 (Julian days 76 -128) peaked on April 5
dates of capture of eggs and larvae	April 2 - May 14 (Julian days 92 - 134)	April 9 - May 6 (Julian days 99 - 126)

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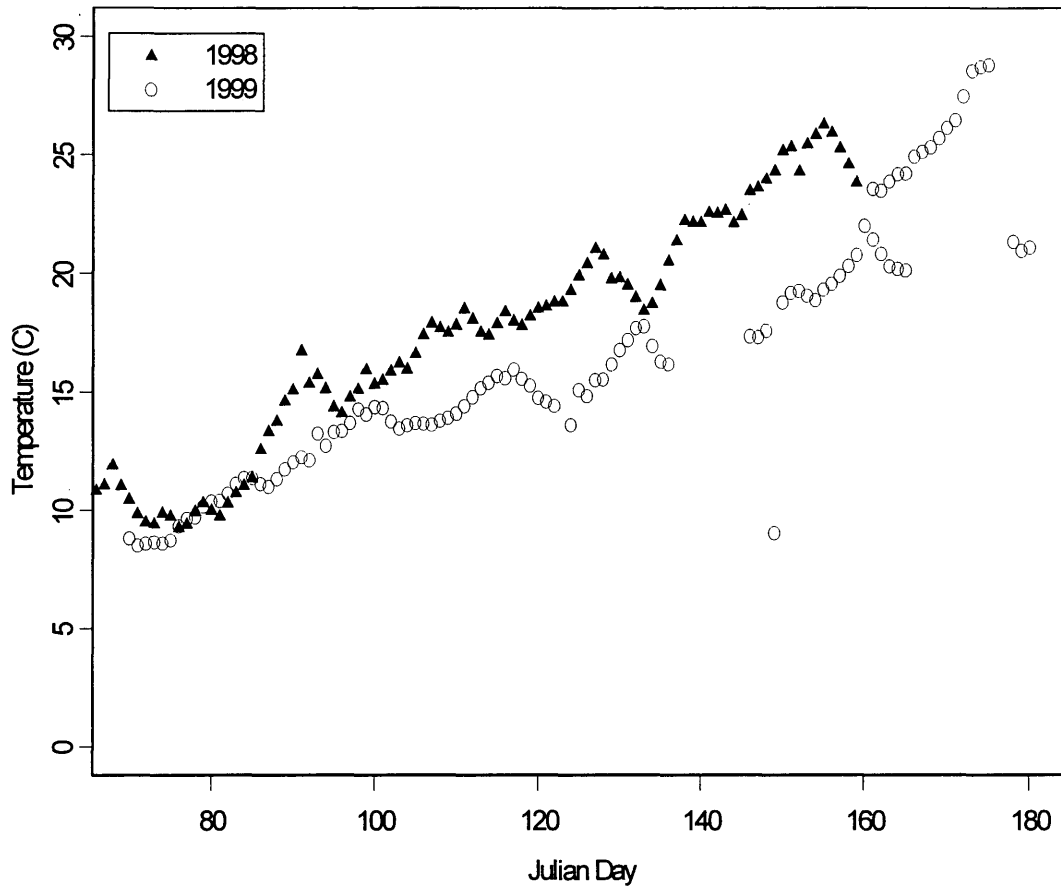
Figure 9: Average daily temperature on the Pamunkey River spawning grounds (1998, 1999). Temperatures were converted from average daily temperatures at the VIMS ferry pier.
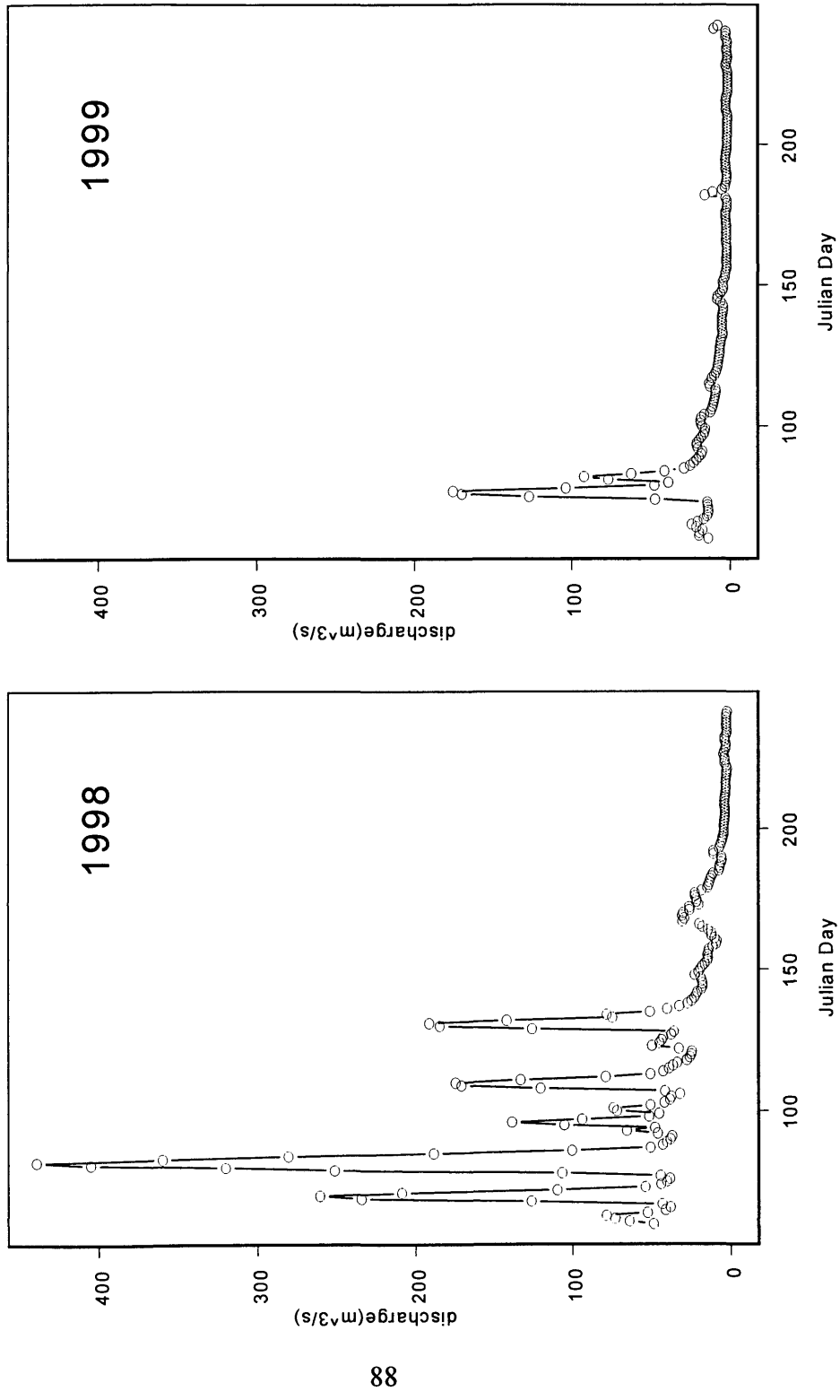
Figure 10: Discharge rates (m³/s) for the Pamunkey River (1998, 1999) measured by USGS gauge (01673000), Hanover, VA.
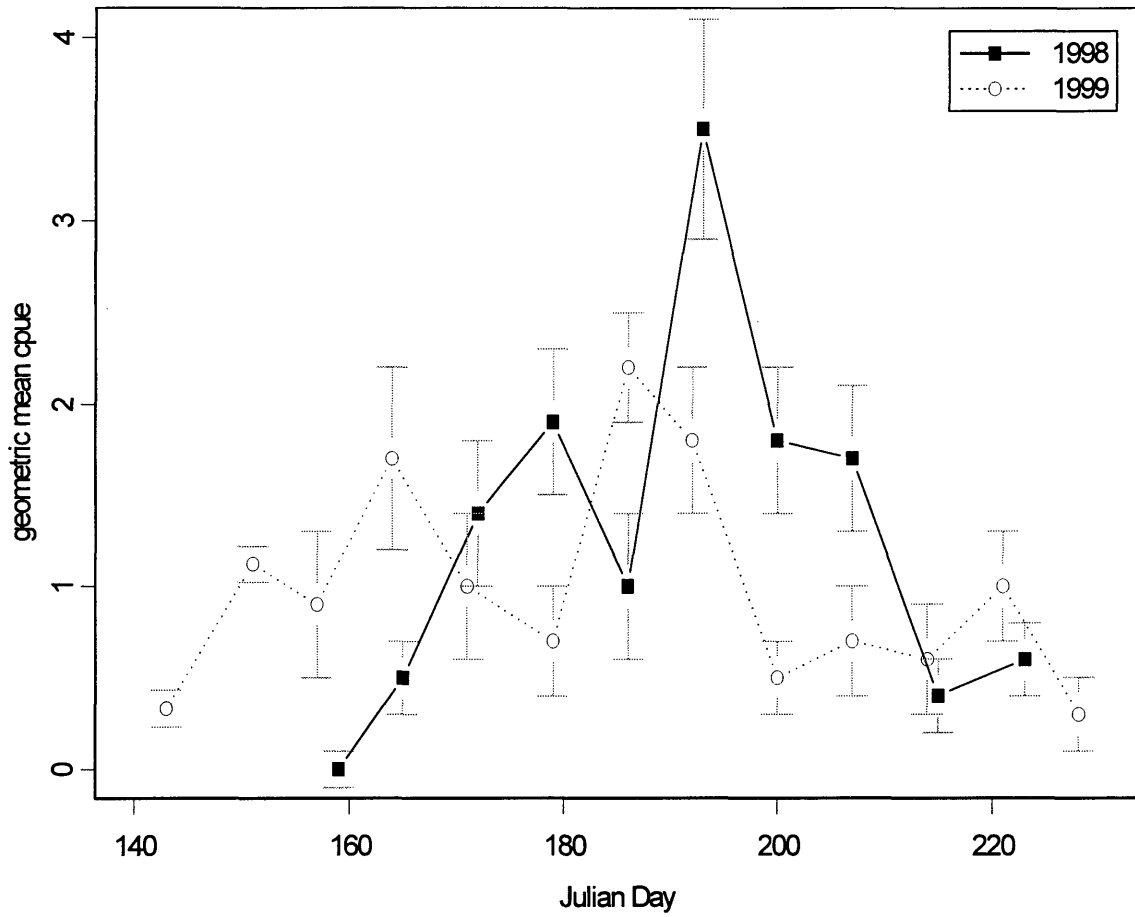
Figure 11: Mean cruise catchrates of juvenile American shad, Pamunkey River (1998, 1999). Standard deviations are indicated by bars.
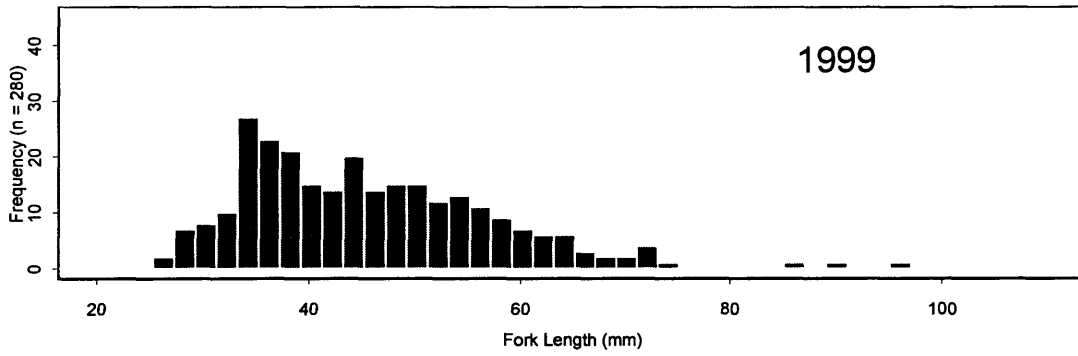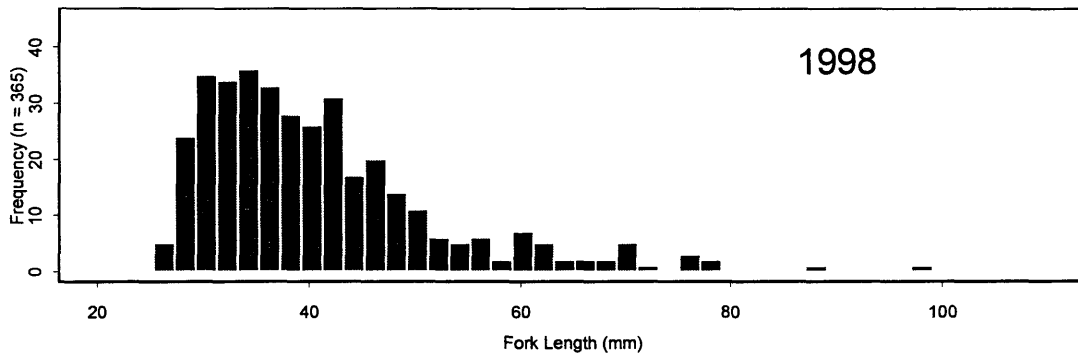
Figure 12: Fork length distributions for juvenile American shad, Pamunkey River (1998, 1999).
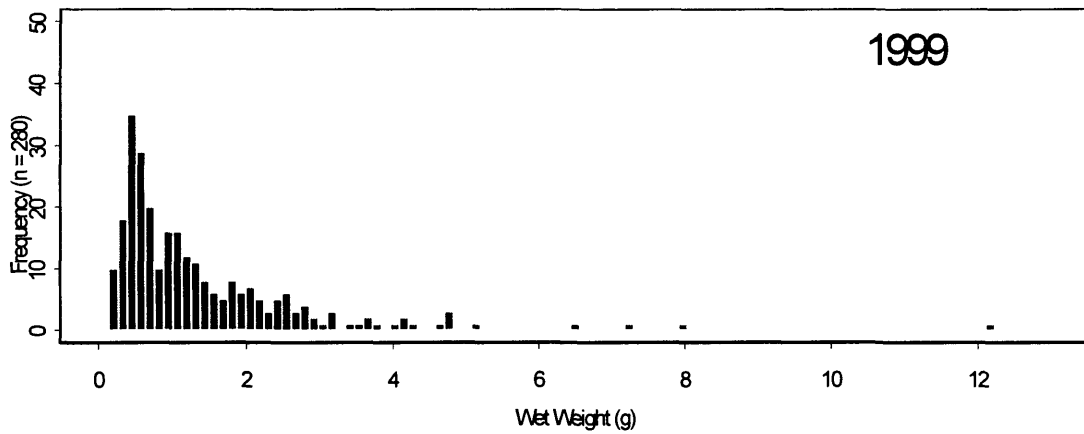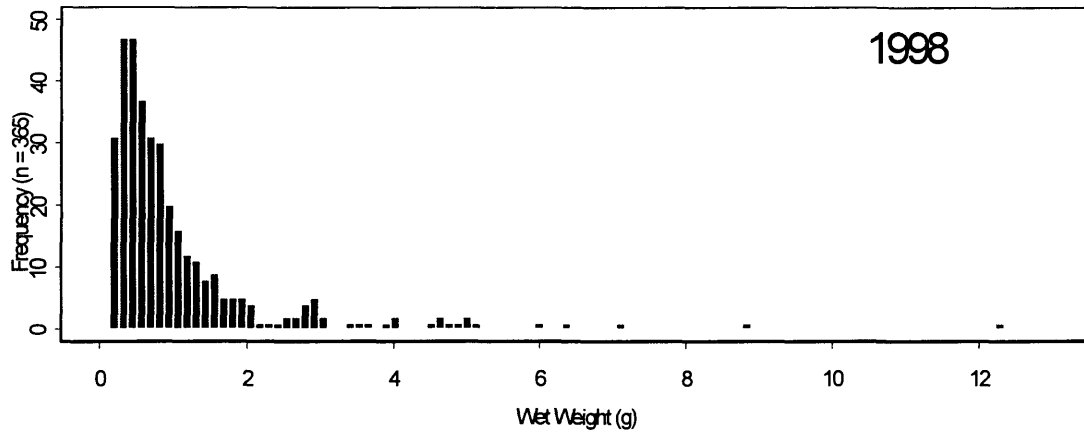
Figure 13: Wet weight distributions of juvenile American shad, Pamunkey River (1998, 1999).
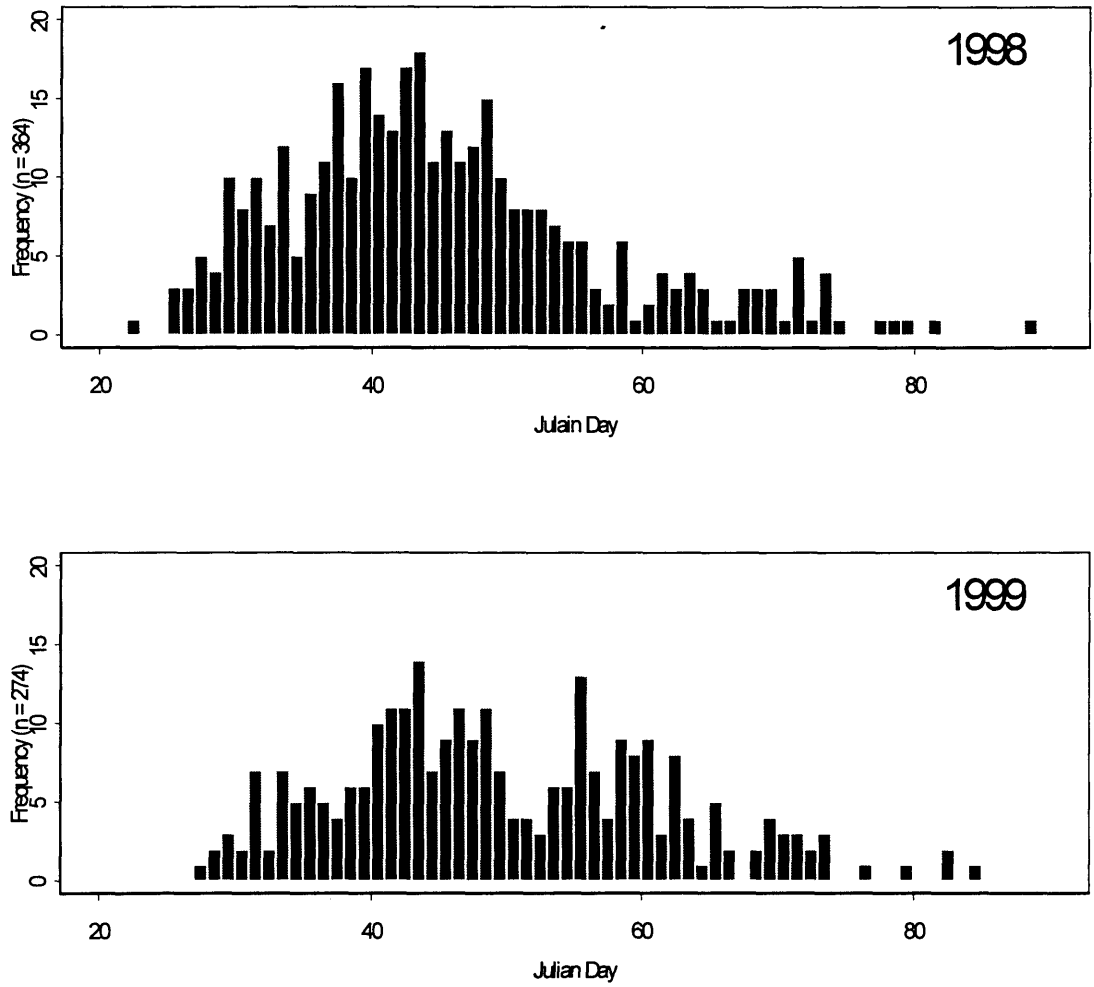
Figure 14: Age at capture of juvenile American shad collected during the pushnet monitoring survey, Pamunkey River (1998, 1999).
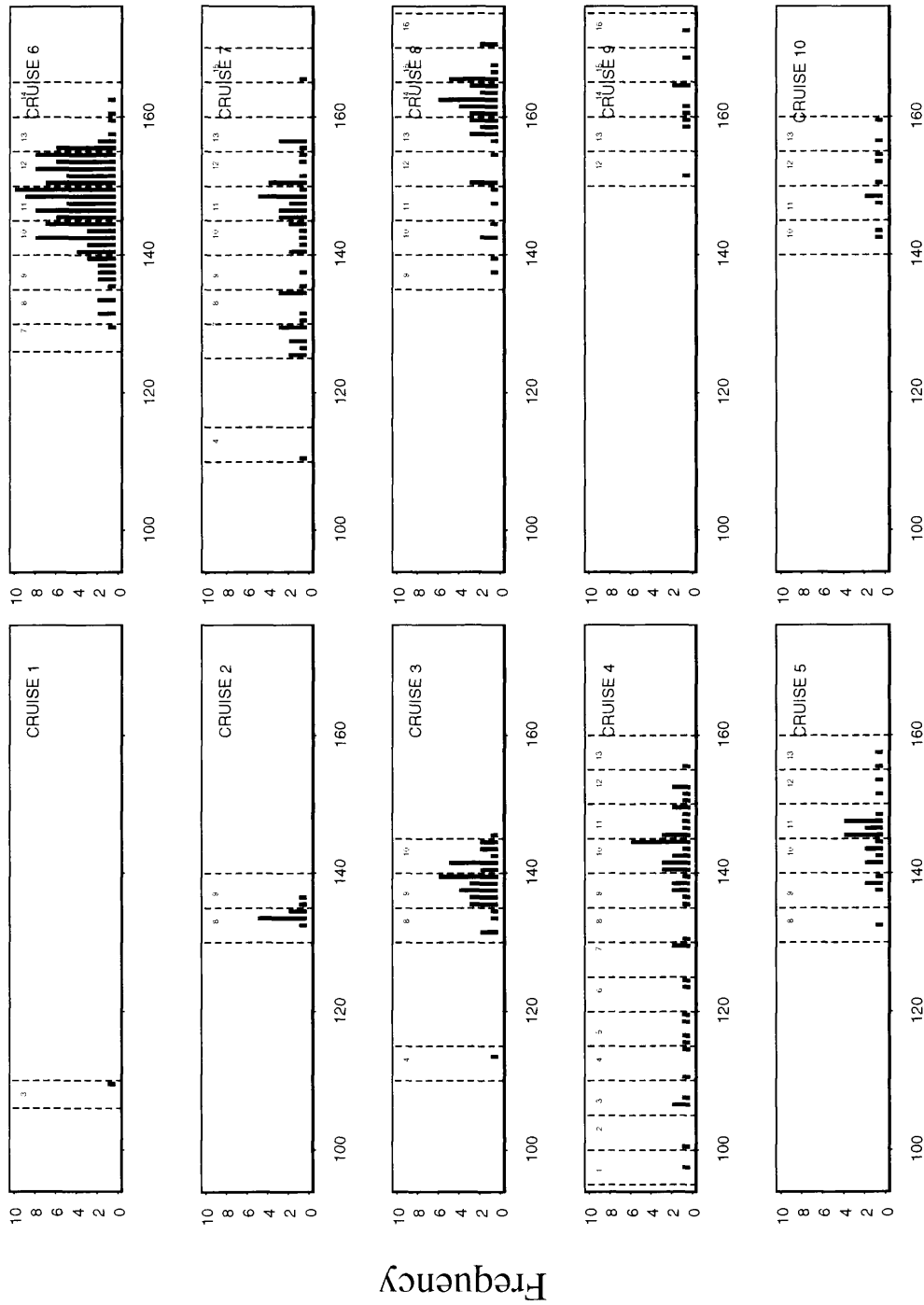
Figure 15: Juvenile American shad hatchdate distributions by cruise date, Pamunkey River (1998). Cohorts are labeled by number. Vertical dotted lines represent the beginning and end of hatchdates designated for given cohorts.
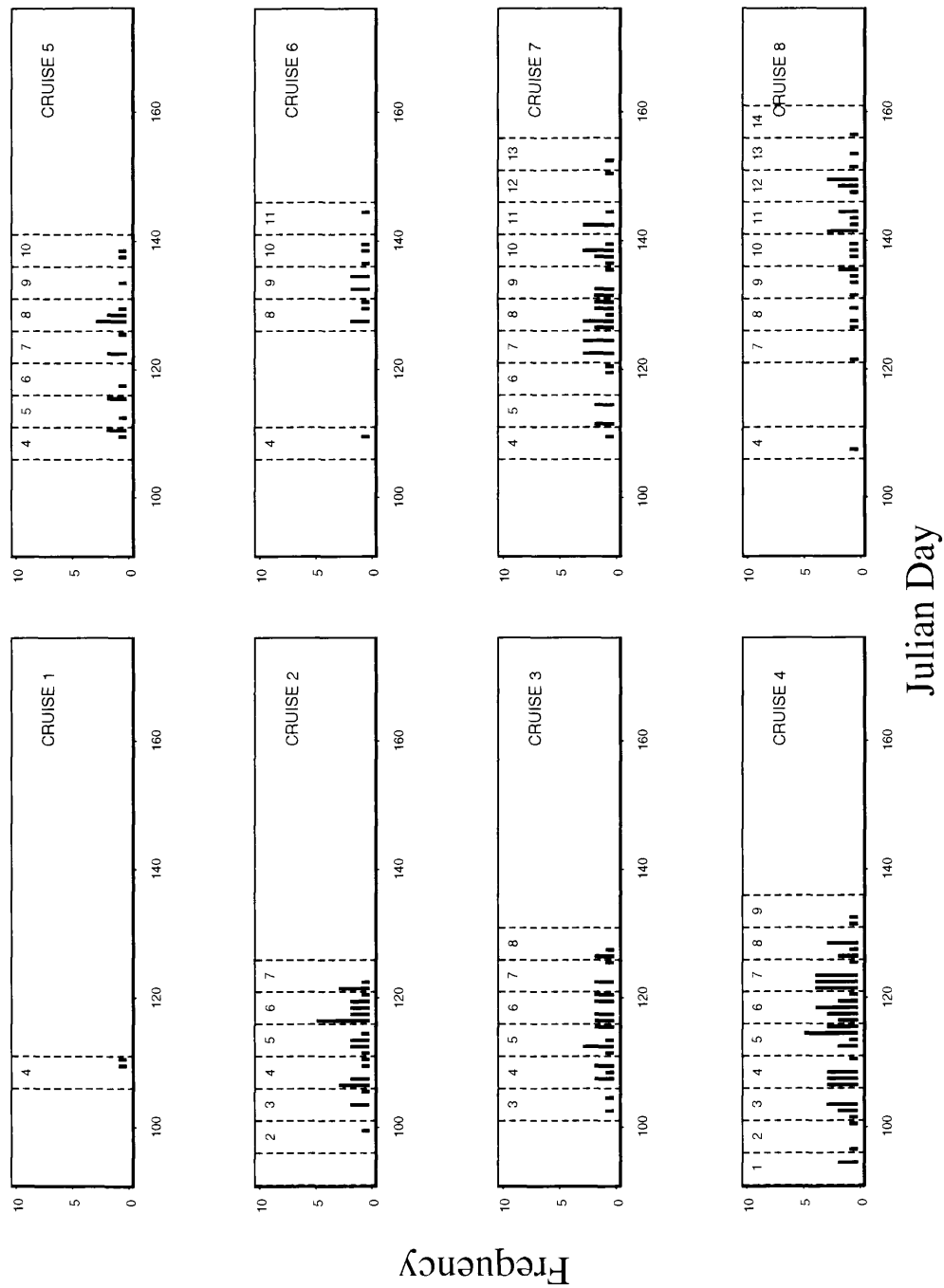
Figure 16: Juvenile American shad hatchdate distributions by cruise date, Pamunkey River (1999). Cohorts are labeled by number. Vertical dotted lines represent the beginning and end of hatchdates designated for given cohorts.
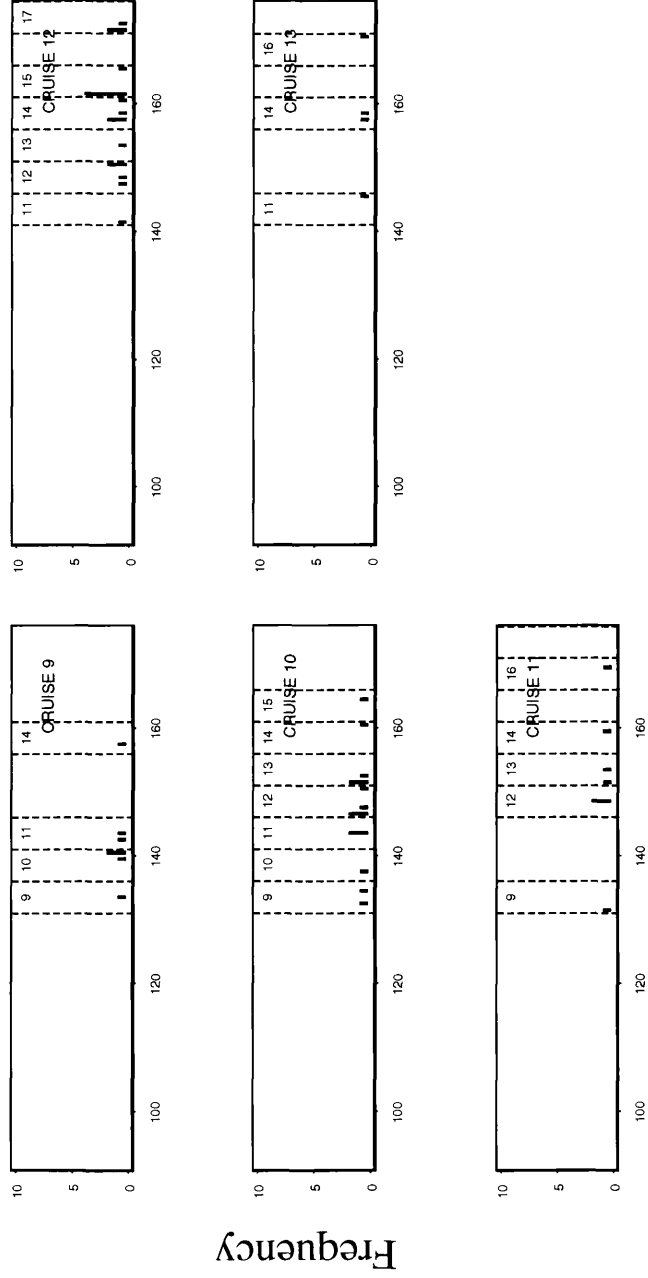
Julian Day

Frequency

Figure 16 continued.
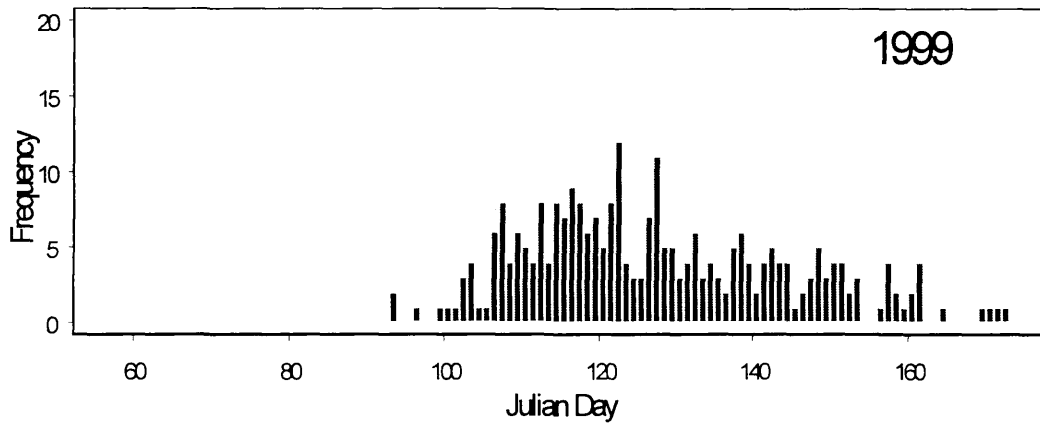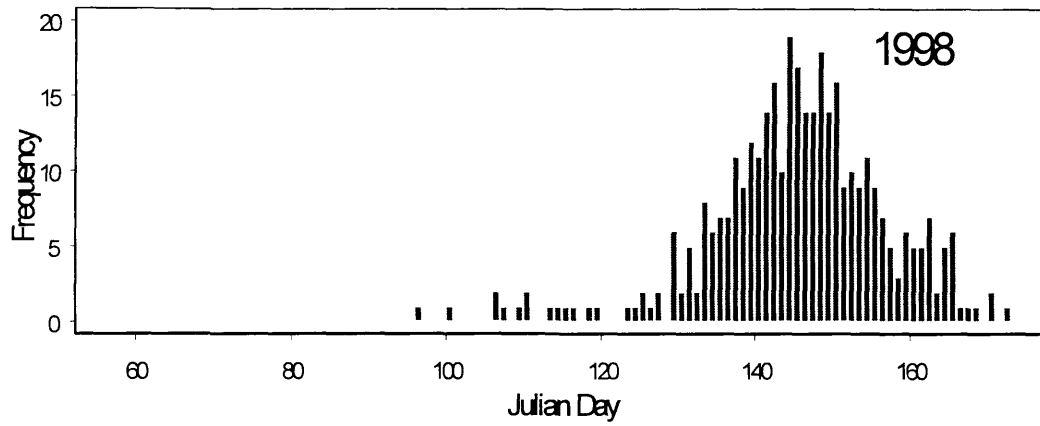
Figure 17: Hatchdate distributions for juvenile American shad captured during summer pushnet cruises on the Pamunkey River (1998, 1999).
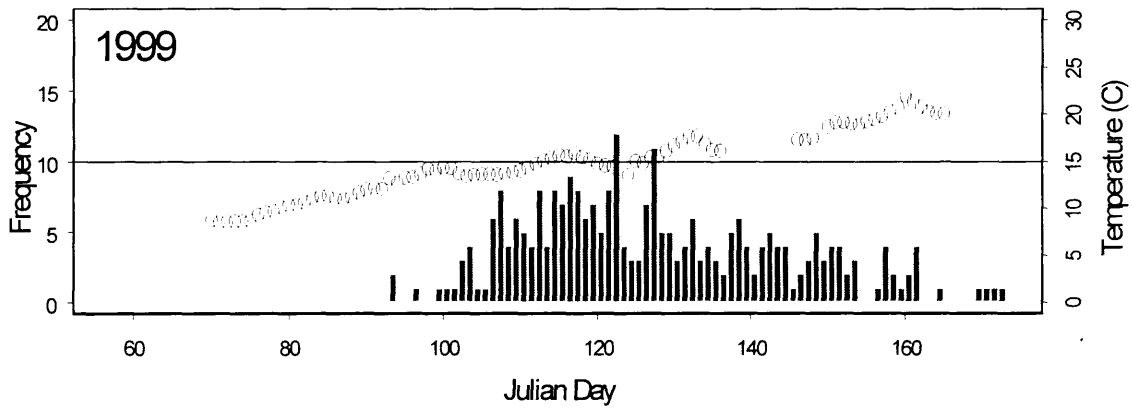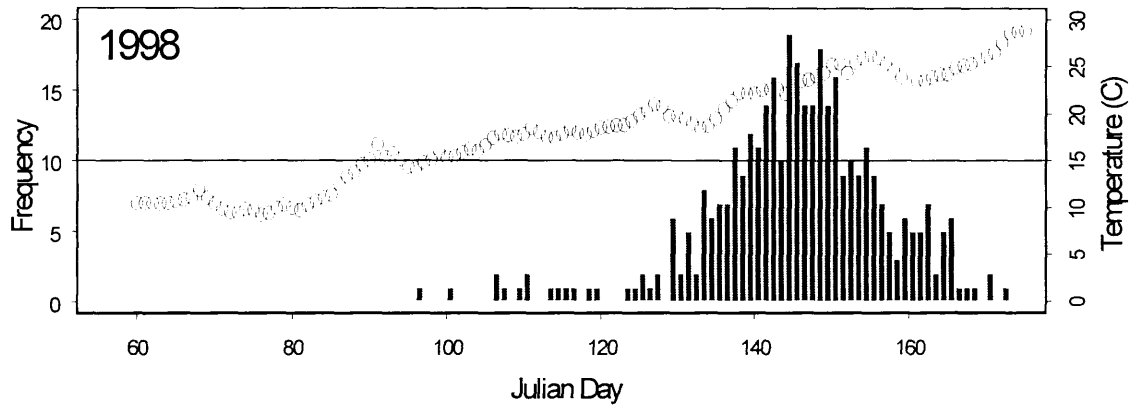
Figure 18: Hatchdate distributions for juvenile American shad and mean daily water temperature, Pamunkey River (1998, 1999).

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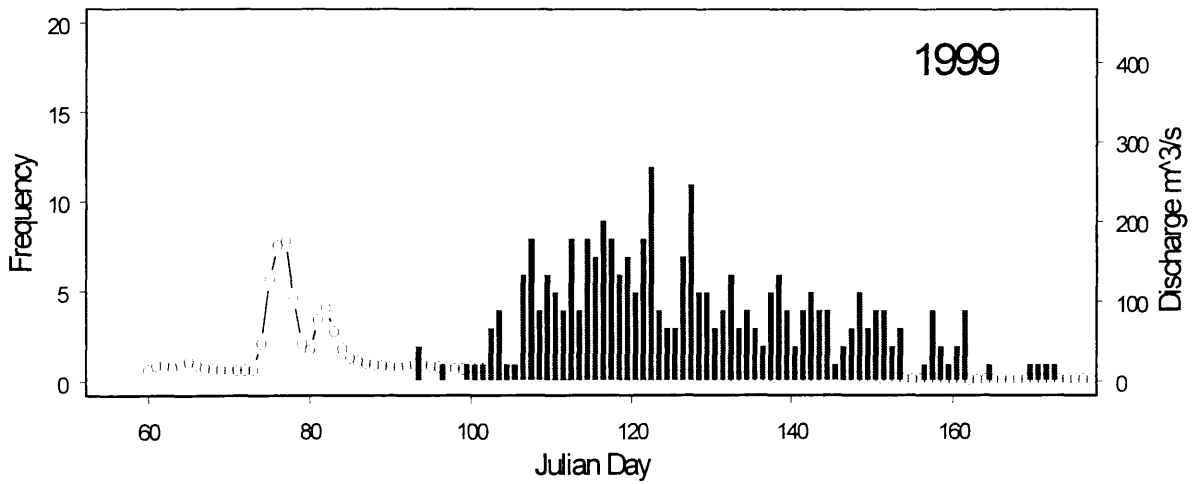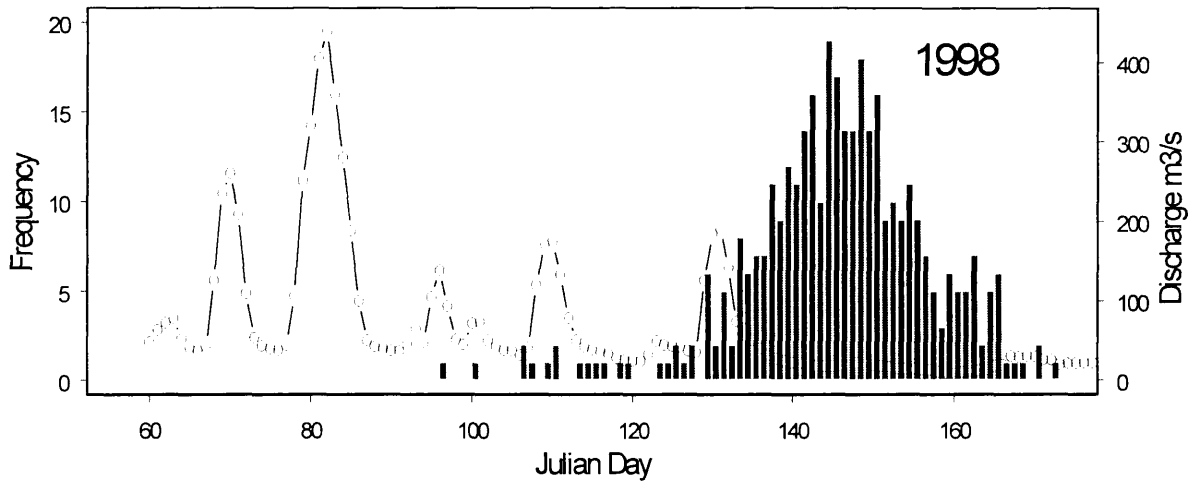
Figure 19 : Hatchdate distributions for juvenile American shad and discharge, Pamunkey River (1998, 1999).

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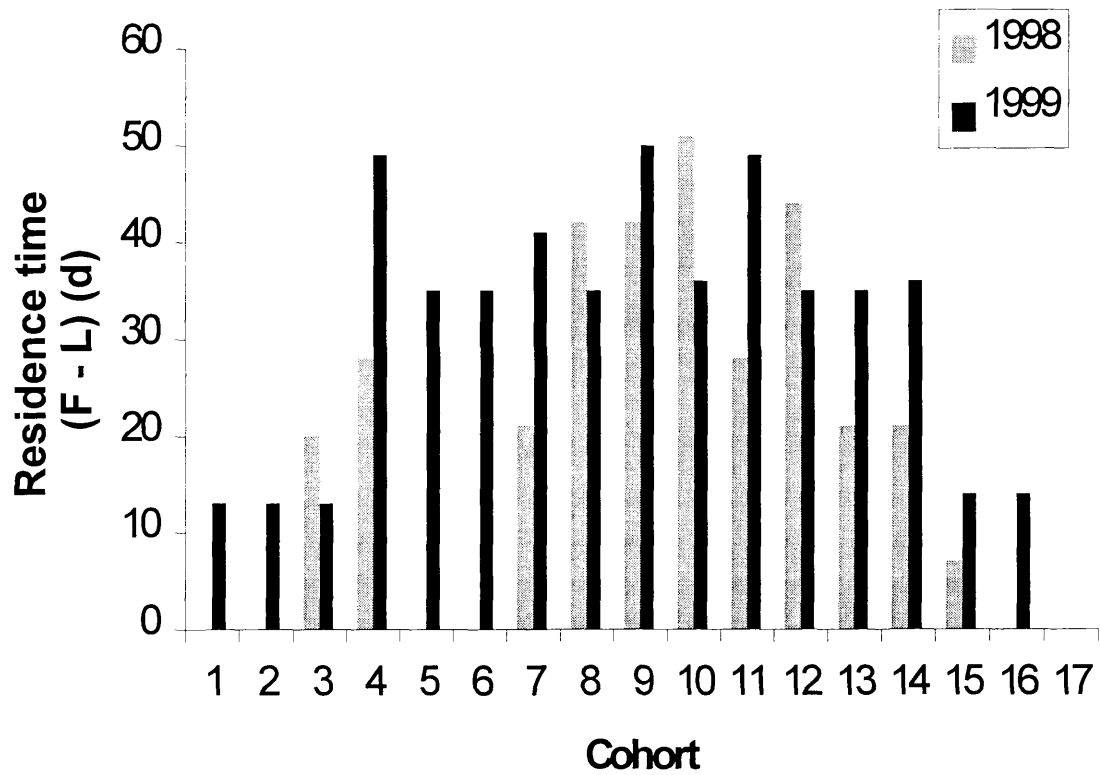
Figure 20: Cohort-specific residence times of juvenile American shad, Pamunkey River (1998, 1999). Residence time was estimated as the time between the dates of first and last appearance of cohorts in cruise catches.
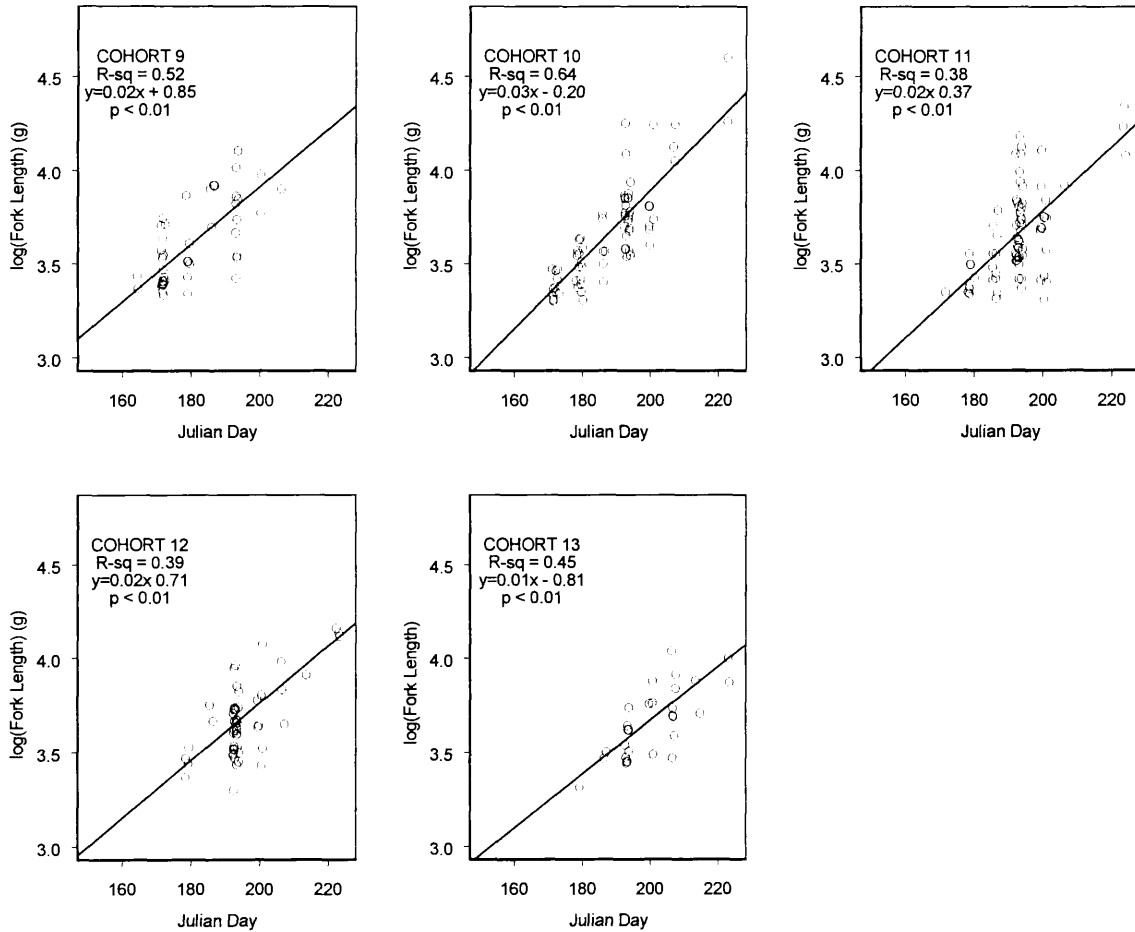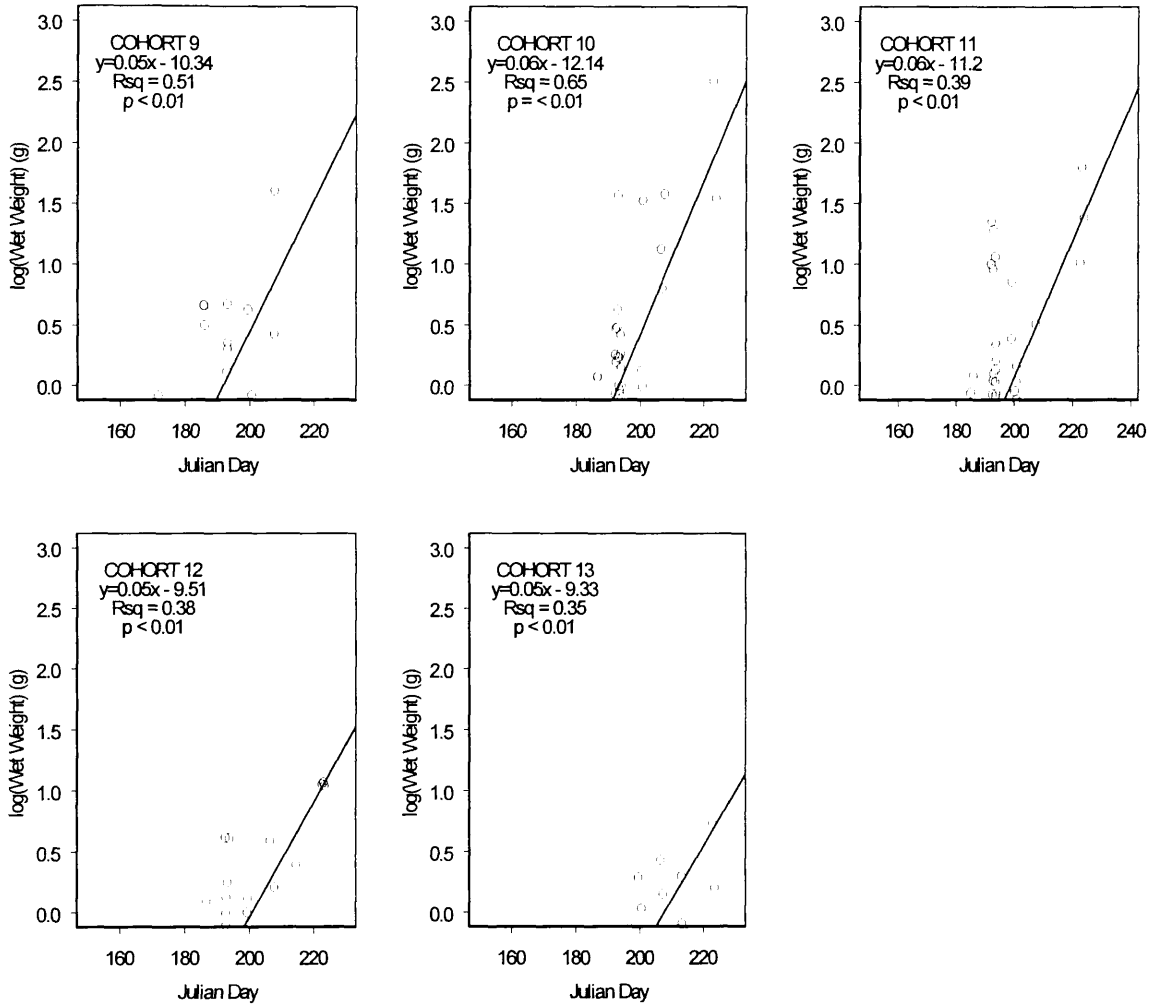
Figure 21: Regressions of log(fork length) (mm) versus day of capture of juvenile American shad in the Pamunkey River, summer 1998. Estimates of cohort-specific instantaneous growth are the slope (m) of the regression equation (y = mx + b). Date of capture is jittered. Only those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported.
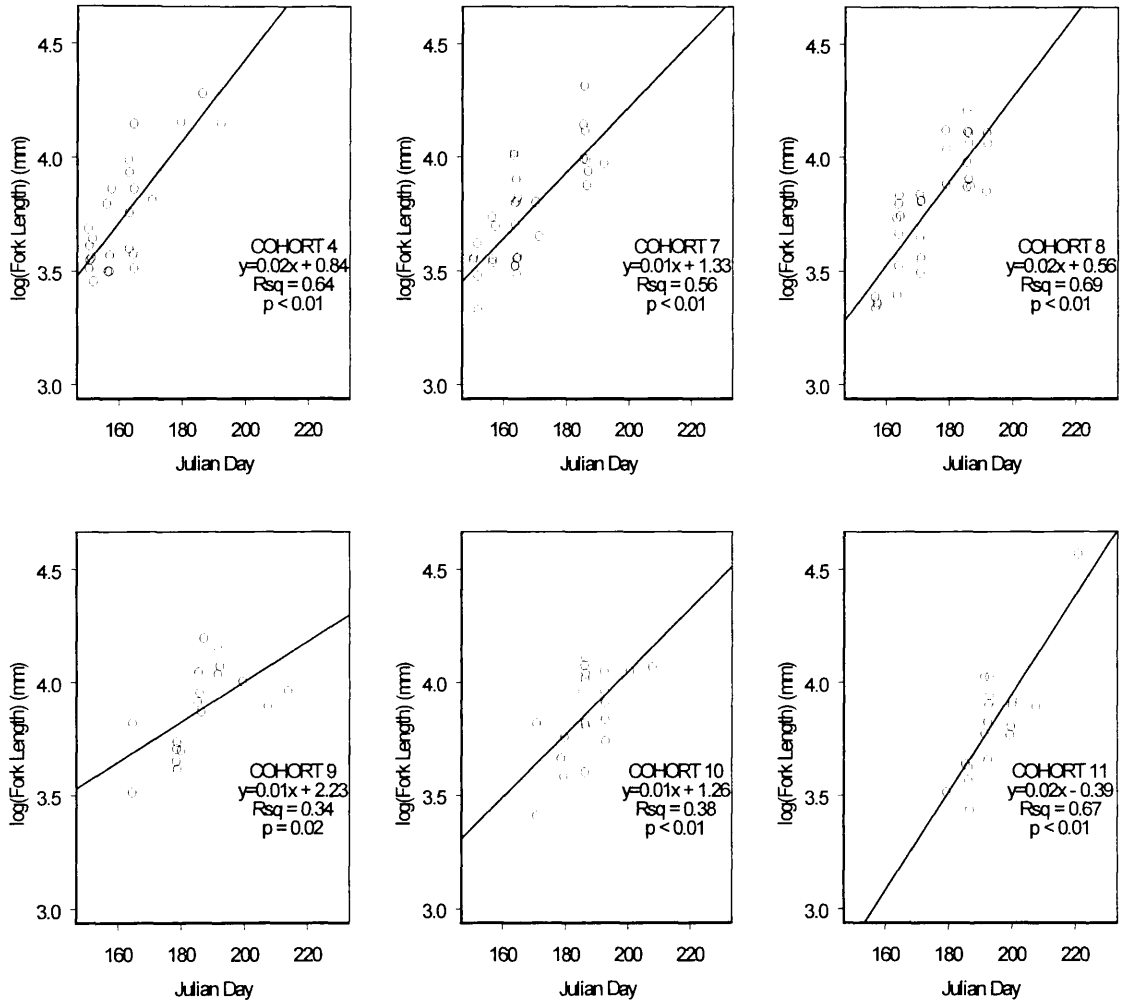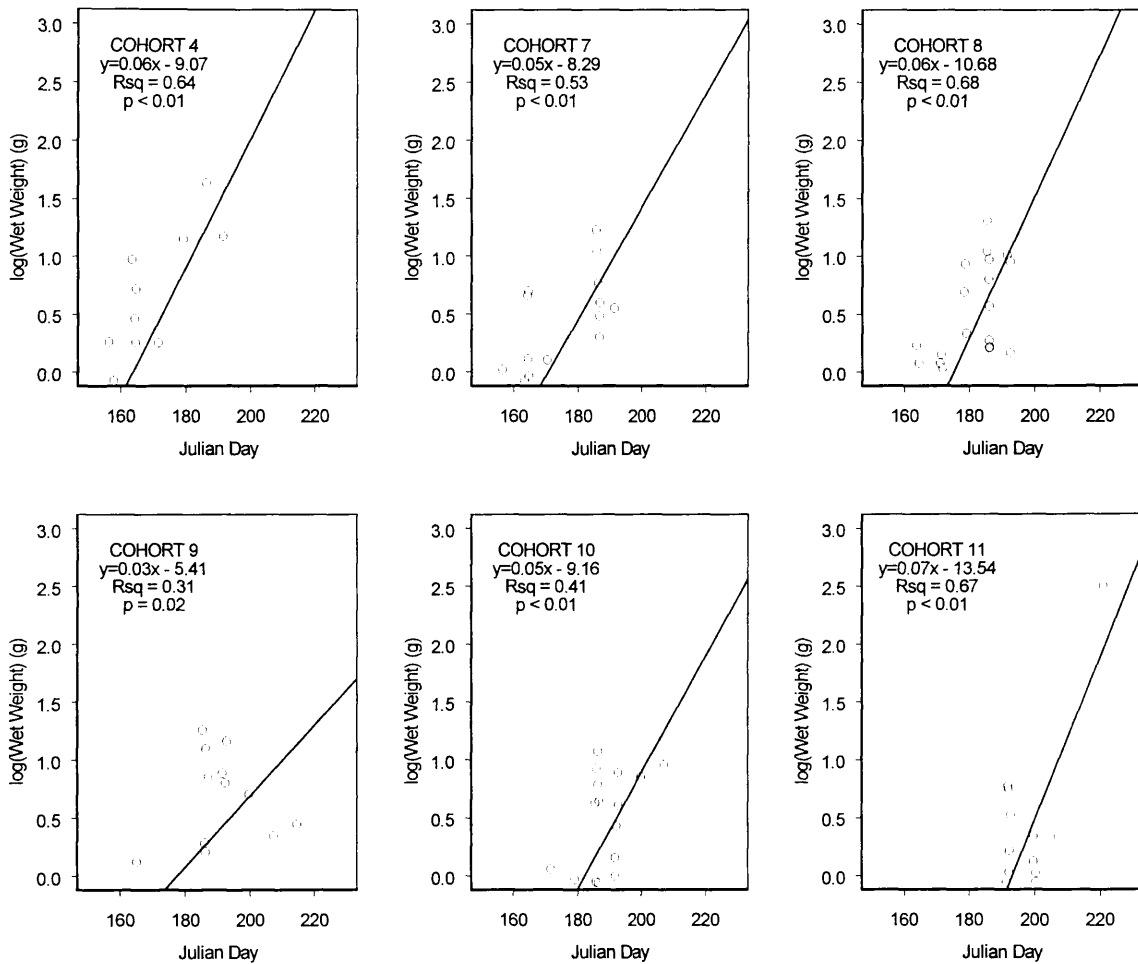
Figure 22: Regressions of log(wet weight) (g) versus day of capture of juvenile American shad in the Pamunkey River, summer 1998. Estimates of cohort-specific instantaneous growth are the slope (m) of the regression equation (y = mx + b). Date of capture is jittered. Only those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported

Figure 23 : Regressions of fork length (mm) versus day of capture of juvenile American shad in the Pamunkey River, summer 1999. Estimates of cohort-specific growth are the slope (m) of the regression equation (y = mx + b). Date of capture jittered. Only those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported

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Figure 24: Regressions of log(wet weight) (g) versus day of capture of juvenile American shad in the Pamunkey River, summer 1999. Estimates of cohort-specific instantaneous growth are the slope (m) of the regression equation (y = mx + b). Date of capture is jittered. Only those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported.
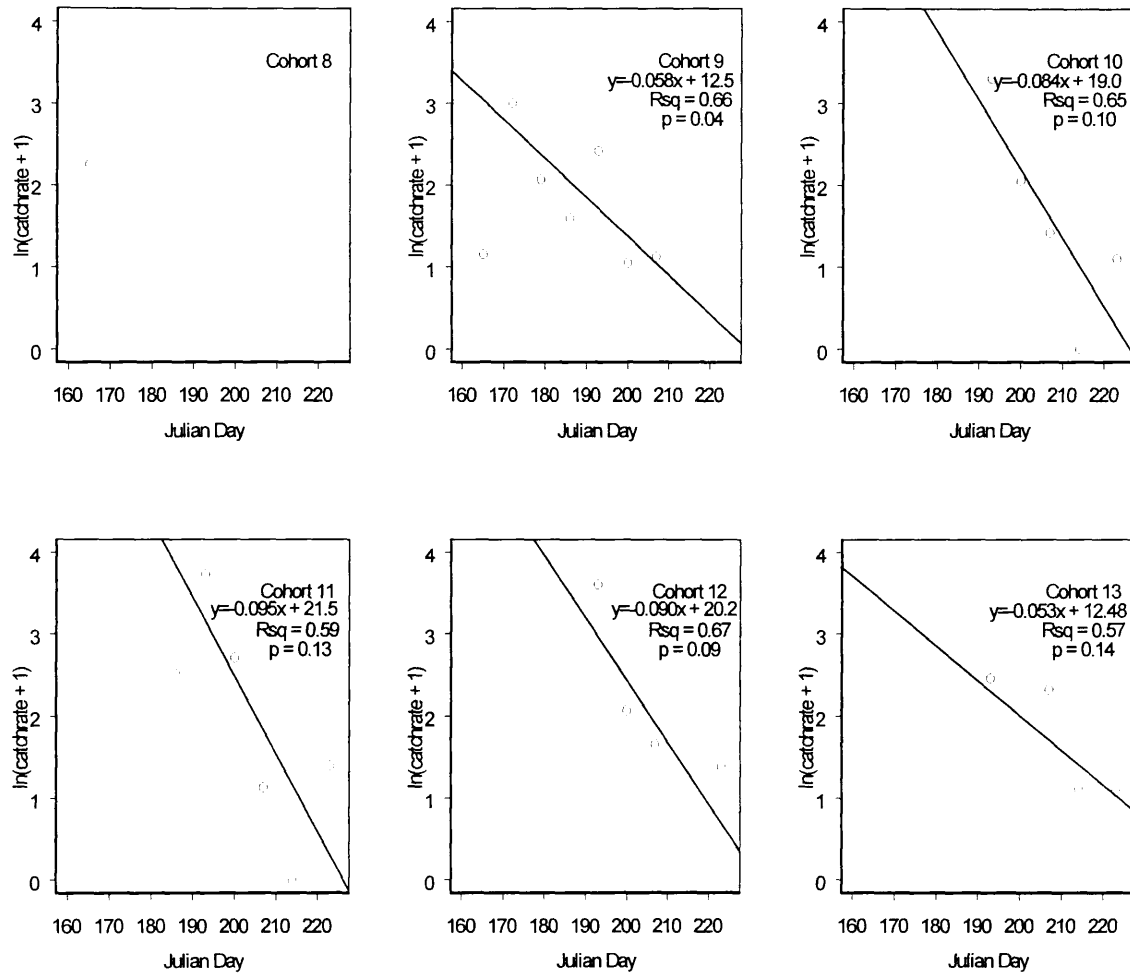
103

Figure 25: Regressions of abundance versus day of capture of juvenile American shad in the Pamunkey River, summer 1998. Estimates of mortality are the slope (m) of the regression equation (y = mx + b). Those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported.
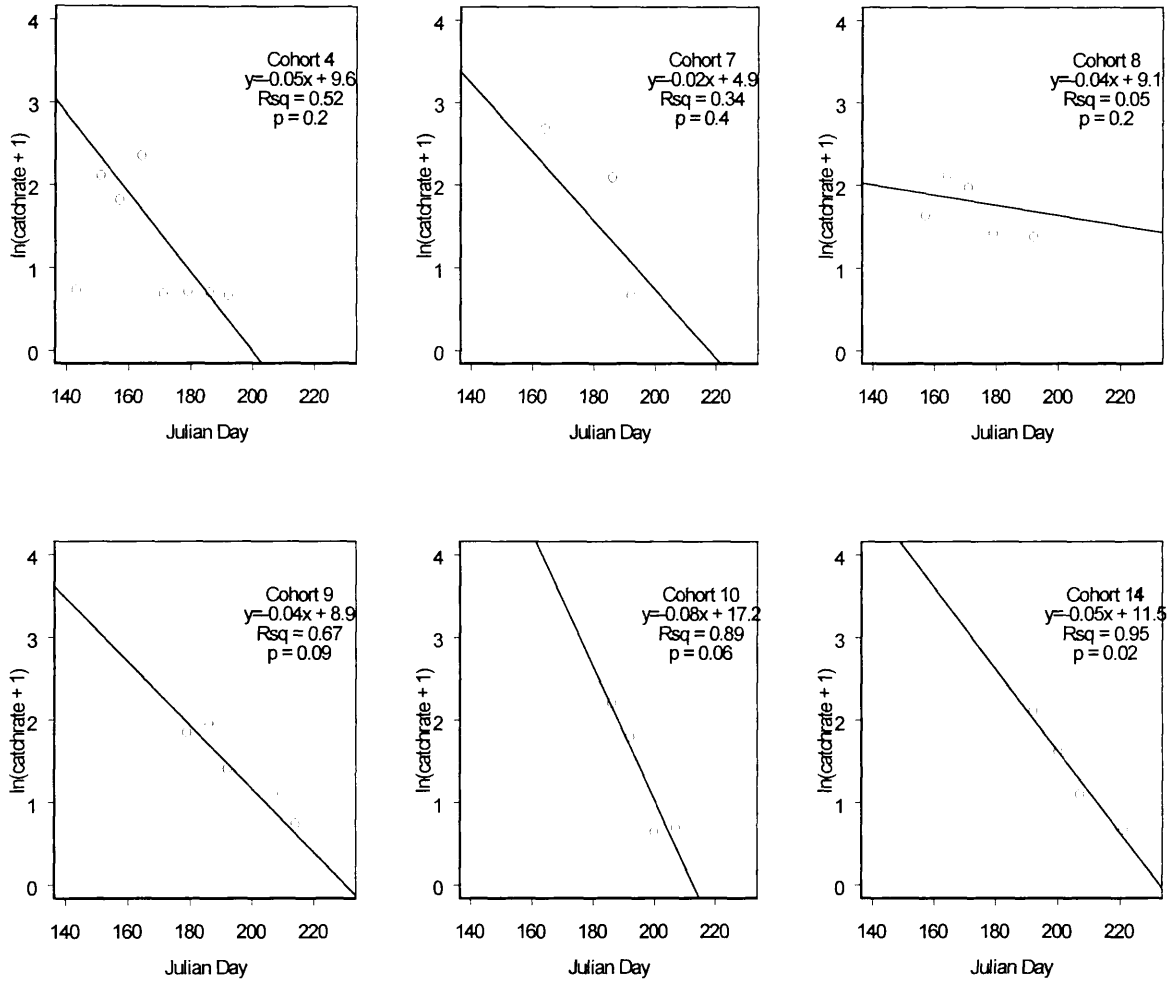
104

Figure 26: Regressions of abundance versus day of capture of juvenile American shad in the Pamunkey River, summer 1999. Estimates of mortality are the slope (m) of the regression equation (y = mx + b). Those cohorts present on 6 or more cruises were considered. R^2 and probability values are reported.
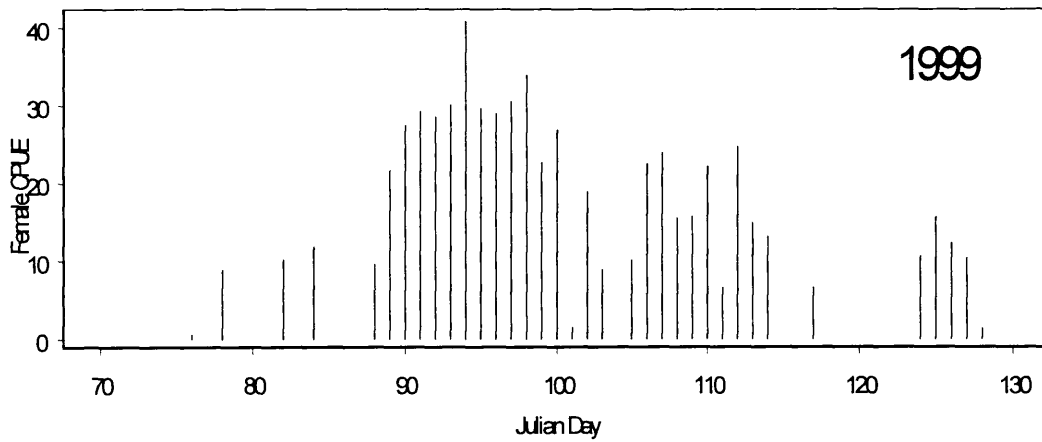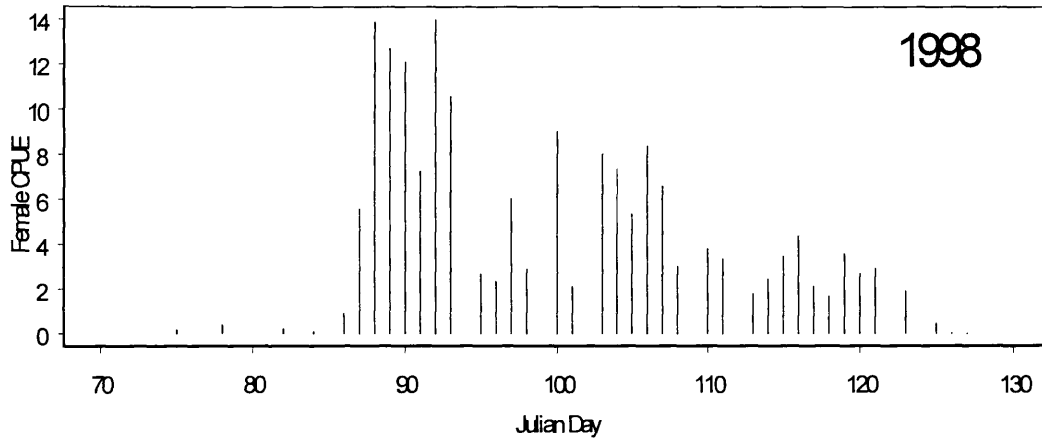
Figure 27: Catch rates of hydrated female American shad broodstock in drift gill nets, Pamunkey River (1998, 1999).
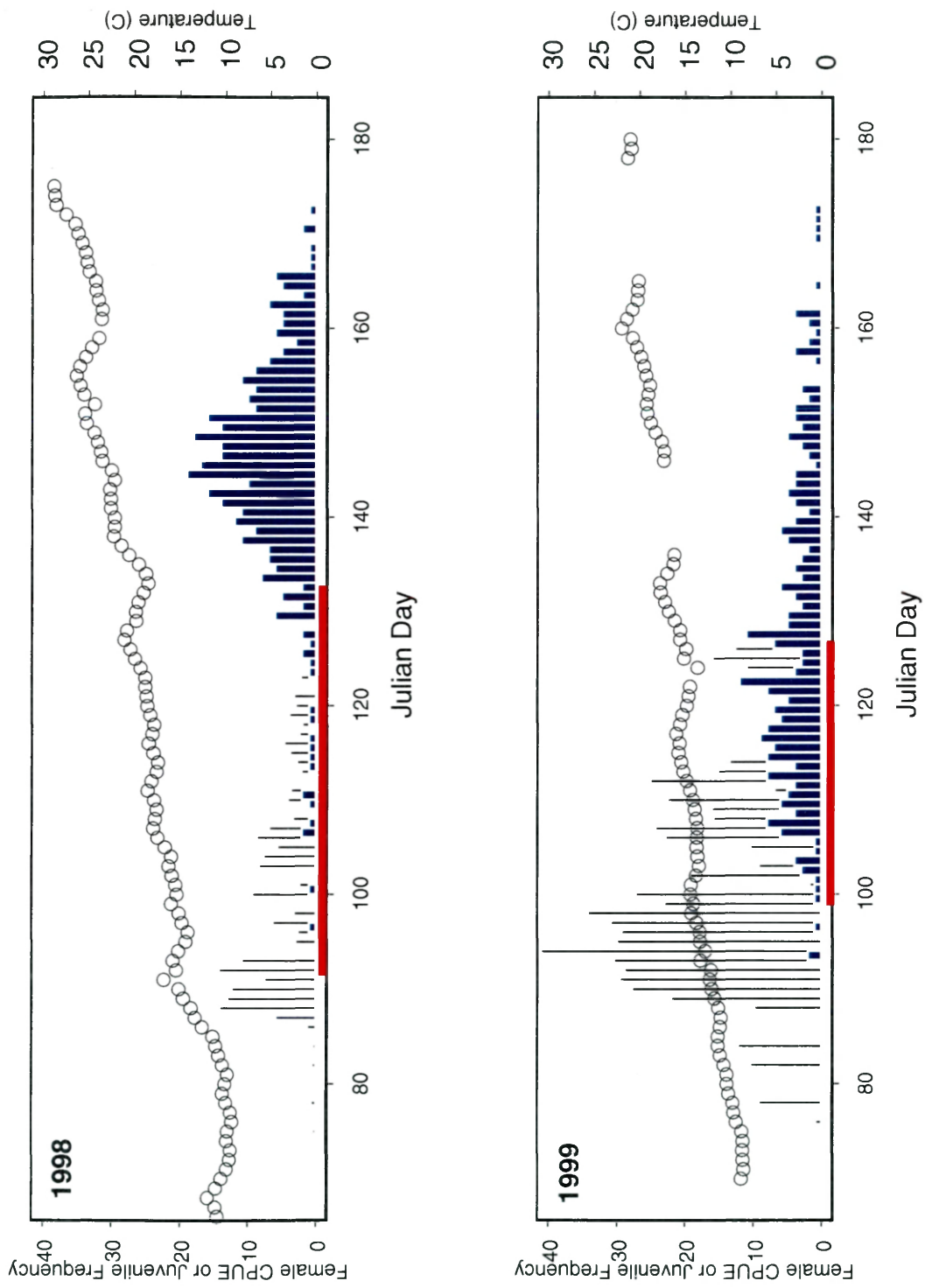
Figure 28: Catch rates of female brood stock (|), eggs and larvae (|),juvenile hatchdate distributions (■) of American shad, and water temperature (O) on the Pamunkey River (1998, 1999).

Figure 29: Example of the effects of recruitment and residence time on the relative abundance of cohorts of fish. If cohorts A, B, and C have equal total numbers of individuals, and if catch rates are proportional to abundance, then the sum of individuals captured from individual cohorts misrepresents the relative abundance of each cohort. n = number of fish caught during season. When cohorts were present in cruises, a total of 20 fish from each was collected.
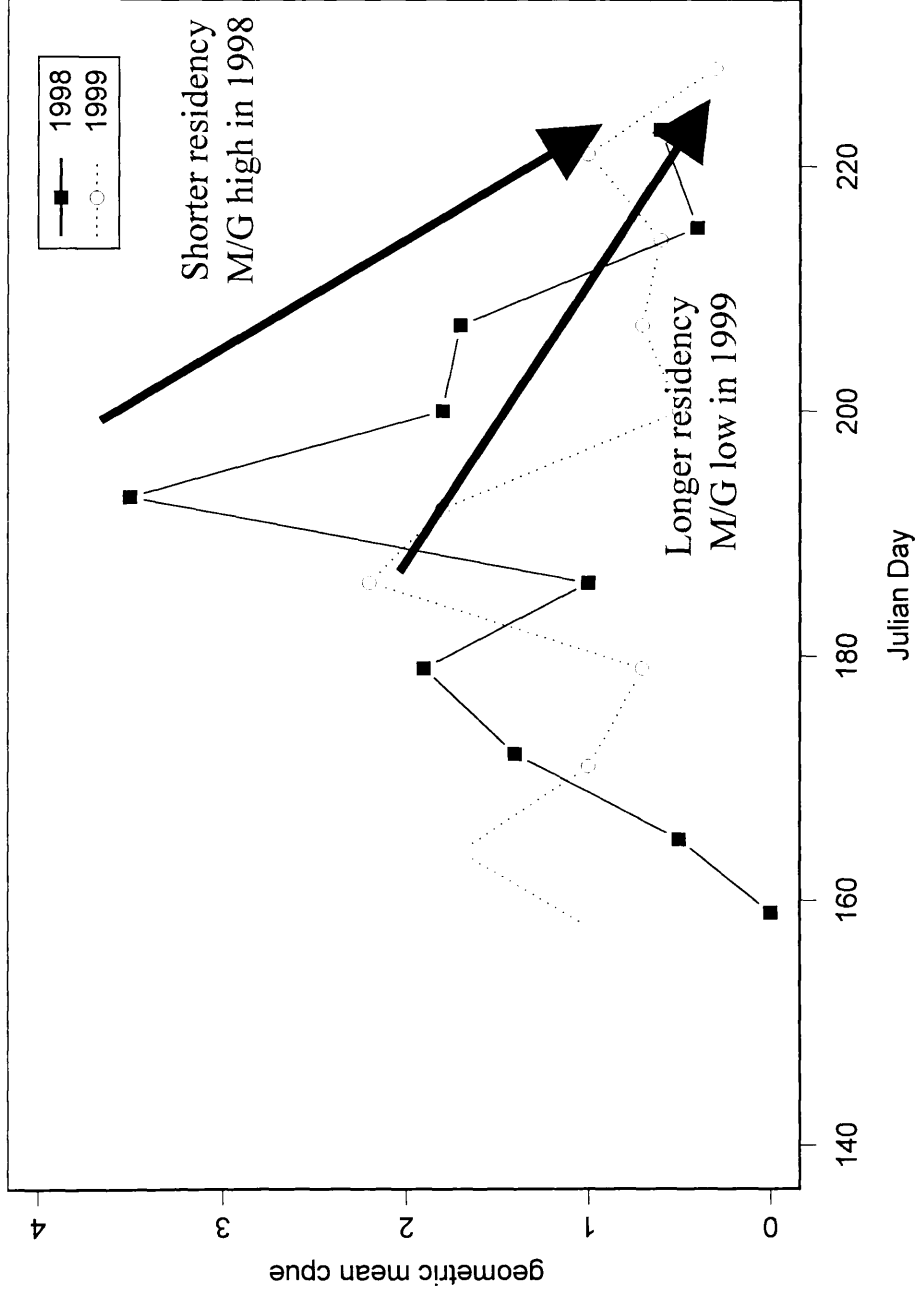
Figure 30: Stylistic drawing of differences in declines in mean catch rates in 1998 and 1999.

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VITA

Born in Newport News, Virginia , October 23, 1975. Graduated from Denbigh

High School, Newport News, Virginia in 1994. Earned a B.A. Echols Scholar

Interdisciplinary degree from University of Virginia, Charlottesville, Virginia in 1998.

Entered the masters program of the School of Marine Science, College of William and

Mary in 1998.