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Variability in juvenile growth, mortality, maturity, and abundance of American shad and blueback herring in Virginia

Troy D. Tuckey
Virginia Institute of Marine Science, tuckey@vims.edu

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Variability in Juvenile Growth, Mortality, Maturity, and Abundance of American Shad and Blueback Herring in Virginia

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In Partial Fulfillment
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Doctor of Philosophy

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by
Troy D. Tuckey
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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

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Troy D. Tuckey

Approved, by the Committee, December 2008

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

John M. Brubaker, Ph.D.

Mary C. Fabrizio, Ph.D.

John M. Hoenig, Ph.D.

Edward D. Houde, Ph.D.
University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory

ABSTRACT

Young-of-year (YOY) population dynamics of American shad and blueback herring in Virginia's rivers were examined with an emphasis on variability in growth and mortality rates. In addition, an analysis was conducted to relate juvenile abundance indices of American shad to adult indices to establish a stock-recruitment relationship. To accomplish the stock recruitment relationship, an additional study that examined maturation schedules and inter-annual variability in maturation schedules among stocks was perfromed. Results of population dynamics studies found that growth and mortality rates of American shad and blueback herring varied by river and year.Conspecific abundance was an important factor in predicting size at the end of summer indicating density-dependent regulation of growth. For both species, instantaneous growth was highest at 40 d and decreased by 100 d as water temperatures decreased each year. American shad mortality rates increased from 2005 to 2007 with highest rates observed in the James River, while mortality rates for blueback herring had no clear pattern. Large year-classes of *Alosa* spp. that are smaller in size prior to emigration into the coastal ocean may experience higher mortality rates resulting in recruitment stabilization. Despite the close proximity of four river systems studied, there were persistent differences in growth and mortality rates that support observed trends in year-class strength. High mortality rates observed in the James River support the observation of almost complete recruitment failure of wild American shad in this system. Furthermore, low mortality rates observed in the Rappahannock River are consistent with an increasing trend in recruitment of maturing females, while lower mortality rates and similar growth rates observed in the Mattaponi River compared with the Pamunkey River support long term observations of greater juvenile production of American shad in the Mattaponi River. Young-of-year blueback herring recruitment in Virginia rivers was an episodic process with multiple peaks observed throughout summer indicating that cohorts were not fully vulnerable to sampling and that there may be movement out of adjacent habitats. Maturation of American shad showed consistent patterns with most American shad mature by age 5. However, year-class specific estimates ranged from 50% to 85% mature in the James River, from 59% to 79% in the Rappahannock River, and from 60% to 87% in the York River. Based on current monitoring and age termination methods using scales, the age of full recruitment to the staked gillnet fishery is age 5, corresponding to the age when the largest proportion of the population reaches maturity. Harvest of age 5 females in the historical fishery was probably a contributing factor to its collapse during the 1980s. Persistent differences in maturity schedules of American shad between the James and York rivers, and to a lesser extent with those from the Rappahannock River, show that neighboring stocks that experience similar climate regimes can have stock-specific maturity patterns that persist through time. Using juvenile abundance indices (or hatchery release in the case of the James River), the estimated maturity schedule, and estimated adult mortality rates, resulted in a predicted index that matched observed trends from 1998 to 2006 for three stocks of American shad . This study demonstrates that population dynamics of juvenile *Alosa* spp. is highly variable in a temporal and spatial context involving density-dependent processes that act to regulate year class production.

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Variability in Juvenile Growth, Mortality, Maturity, and Abundance of American Shad and Blueback Herring in Virginia

INTRODUCTION

The beginning of the 20th century marks the precipitous decline of American shad (*Alosa sapidissima*) stocks on the Atlantic coast of North America (Limburg et al. 2003). Stock collapse has been attributed to a multitude of factors including overfishing, poor water quality, and the reduction of favorable spawning and rearing habitat through the construction of dams. Once comprising the greatest fishery in the United States, American shad now enjoy Federal, State, and local protection in the form of harvest restrictions and regulations to rebuild depleted stocks (ASMFC 2007a).

In Virginia, American shad have been under a nearly complete fishing moratorium since 1994 to rebuild stocks. The moratorium is not total because Native American tribal communities harvest American shad on the spawning grounds as part of a treaty agreement that dates to Colonial times. Furthermore, a bycatch allowance has been permitted in portions of Virginia rivers associated with the commercial striped bass harvest since 2006. Finally, American shad were subject to an ocean-intercept fishery until the mandated closure in 2005. Undoubtedly, American shad are taken as bycatch in coastal fisheries with unknown harvest levels that continues to reduce already depleted stocks (ASMFC 2007a). Now, more than twenty years after the moratorium took effect in VA, American shad stocks remain at very low levels, and coast-wide, a few stocks show signs of improvement, but most are still in decline (ASMFC 2007a).

A similar, but less publicized, story exists for river herring (blueback herring, *Alosa aestivalis*, and alewife, *Alosa pseudoharengus*) in North America. River herring stocks have shown declines in landings and poor recruitment throughout their range (Schmidt et al. 2003; Hightower et al. 1996). Hypotheses to explain declines include overfishing, restricted spawning and rearing habitat, poor water quality, and predation (Schmidt et al. 2003; Savoy and Crecco 2004). Unfortunately, landings of river herring species are combined hindering species-specific stock analyses. The low abundance of blueback herring and alewife stocks has resulted in harvest closures in Massachusetts, Rhode Island, Connecticut, and North Carolina, and additional management options are currently under consideration throughout their range (ASMFC 2007b).

My research was designed to examine young-of-year (YOY) population dynamics of American shad and blueback herring in Virginia's rivers with an emphasis on variability in growth and mortality rates. Furthermore, an analysis was conducted to relate juvenile abundance indices of American shad with adult indices to establish a stock-recruitment relationship for Virginia. Because landings of blueback herring are combined with alewife, there are no data available to support adult-recruitment comparisons for blueback herring.

Classic stock-recruitment analyses were considered inappropriate because of the depressed nature and low spawning stock biomass of the wild stocks of American shad in Virginia. The network of theory and knowledge gained since the early 1900s that relates spawning stock size and recruitment cannot be effectively implemented for American shad since the observed stock size is depleted and most likely near the origin on a classic stock-recruitment curve; there is insufficient contrast in observable stock size to model dynamics and limited data exists for historical spawning stock biomass and recruitment.

Therefore, a different approach was undertaken to relate the production of juveniles to returning adults. A unifying model was developed for American shad covering a wide array of research topics that include: 1) Young-of-year growth and mortality and associated variation in space and time to examine production of juveniles in Virginia Rivers with an emphasis on variability and potential sources of variability, 2) Estimation of maturity schedules for American shad for each population to evaluate population-specific characteristics and further to be used in a predictive model, and 3) a conceptual model that combines juvenile production, maturity schedules, adult mortality and an index of adult spawning potential observed through a simulation of the commercial fishery.

The first objective of my study was to understand population dynamics of juvenile American shad and blueback herring in lower Chesapeake Bay nurseries. It was hypothesized that the close proximity of rivers in Virginia (< 1° latitude) would produce similar growth and mortality rates if juvenile population dynamics are primarily determined by environmental conditions. Previous investigations have established that growth and mortality rates of YOY American shad in the Connecticut River are inversely related to water flow in May (Crecco and Savoy 1987) and that growth may be stimulated by subsequent flow events (Hoffman et al. 2007). For blueback herring, year class size is negatively correlated with water discharge during May-June in a New Brunswick river, presumably due to a reduction in food (Jessop 1990). Understanding the underlying sources of recruitment variation can aid in model development of stock-recruitment dynamics for these species.

The second objective examined the potential of stock-specific characteristics in age at maturity that may influence stock restoration or recovery. A model based on VA rivers data was developed by Maki et al. (2001) that investigated maturity schedules using a cross-sectional approach. My investigation extended the maturity schedule model to produce year-class specific estimates (longitudinal approach) of maturity and compared three separate populations: Rappahannock River, York River, and the James River stocks. The null hypothesis is that stock-specific characteristics in maturity at age do not exist, with the alternative hypothesis that maturity at age patterns do exist and are partially responsible for observed trends in VA stocks. Furthermore, assessment models have used maturity schedules to estimate yield to establish mortality thresholds for management and require an appropriate maturity schedule since each stock is managed separately (ASMFC 2007a). In addition, harvest practices must be considered since fishing pressure may alter the observed maturity pattern (ASMFC 2007a). If stock-specific maturity patterns exist, then identical fishery regulations could have different impacts on particular stocks. In depleted stocks, persistent delays in age at maturity may also affect stock recovery.

The third objective was to combine juvenile production estimates with a catch-rate index of adults taken during the spawning run in Virginia to produce a stock-recruitment model for American shad. Because limited data exists concerning adult abundance of blueback herring, no model can be developed at this time, but a similar methodology could be applied when appropriate data are available.

The three objectives, taken together, strive to characterize patterns in growth and mortality and link those patterns to environmental processes that ultimately determine year-class strength and subsequent return of adults. Although there are numerous factors that operate in the coastal ocean that can affect population dynamics of American shad and blueback herring, little information is available from that environment to address food availability, predation rates, migration patterns, or other sources of YOY recruitment variation. However, understanding aspects of *Alosa* spp. biology and ecology prior to emigration of juveniles to the coastal ocean provides insight into how those dynamics vary inter- annually and spatially during early life.

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Chapter One

Maturity schedules of American shad from the Virginia portion of Chesapeake Bay

ABSTRACT

Recent assessments of American shad used stock-specific maturity schedules in biomass-per-recruit models to establish benchmark total mortality rates for management. Because stocks of American shad are managed separately, an appropriate maturity schedule for each stock is required. Additionally, projections of adult biomass require knowledge about year class strength and the maturation process. Changes in age at maturity can occur when strong year classes enter the spawning stock and may affect stock assessment models and management decisions. Maturity schedules may also change due to fishing or other external factors. If stock-specific maturity patterns exist, then identical fishery regulations could have different impacts on neighboring stocks. Most American shad matured by age 5 in this study, with year-class specific estimates that ranged from 50% to 85% mature in the James River, from 59% to 79% in the Rappahannock River, and from 60% to 87% in the York River. Based on current monitoring, the age of full recruitment to the staked gillnet fishery is age 5, corresponding to the age when the largest proportion of the population reaches maturity. Harvest of age 5 females in the historical fishery was probably a contributing factor to its collapse during the 1980s. Persistent differences in maturity schedules of American shad between the James and York rivers, and to a lesser extent with those from the Rappahannock River, show that neighboring stocks that experience similar climate regimes can have stock-specific maturity patterns that persist through time.

INTRODUCTION

Maturity schedules are a fundamental component of stock assessment. Restoration and exploitation targets are often based on maintaining a portion of the spawning stock biomass in reserve to facilitate continued recruitment and a viable fishery. In addition to estimates of vital rates (e.g., growth, natural mortality, and fishing mortality), projections of adult biomass require knowledge about year class strength and the maturation process, or the proportion of fish mature at a particular age. Changes in age at maturity can occur when strong year classes enter the spawning stock and may affect stock assessment models and management decisions (Maki et al. 2002). Maturity schedules may also change due to fishing or other factors such as hatchery inputs, genetics, or environmental conditions that affect growth. For example, lengths of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from different watersheds were found to be inversely related to age at maturity with larger juveniles maturing earlier than smaller juveniles (Scheuerell 2005). The effects of length on the proportion maturing at age also varied by watershed providing evidence that local environmental conditions and genetics were involved with controlling growth and maturation. Therefore, investigating the potential influence of genetic and environmental conditions on maturation should be performed at appropriate management scales (i.e. stock).

American shad is an anadromous clupeid that spawns in natal rivers from the St. John's River, Florida to the St. Lawrence River in Canada and is undergoing rigorous management efforts or restoration throughout much of its native range (Talbot and Sykes 1958; Walburg 1960; Carscadden and Leggett 1975b; Limburg et al. 2003). Populations of American shad from major rivers throughout North America are managed as separate stocks. Discrete stocks have been demonstrated through tagging studies (Dadswell et al. 1987), meristic investigations (Carscadden and Leggett 1975a), and genetic techniques (Bentzen et al. 1989; Waters et al. 2000) with evidence that reproductive isolation maintains stock-specific characteristics. Reproductive strategies of American shad include semelparous populations in rivers south of latitude 32° N, and varying degrees of iteroparity in more northern populations (Leggett and Carscadden 1978). Tagging studies (Dadswell et al. 1987) have also revealed that American shad stocks mix in the coastal ocean and likely encounter similar feeding conditions, and differences in reproductive characteristics resulting from food availability or quality are unlikely with observed differences believed to have a genetic basis (Leggett and Carscadden 1978).

Estimated proportion mature at age varies throughout the range of American shad. In New England, 25% of American shad are mature at age 5 and this proportion increases with decreasing latitude with 63% mature in the Hudson River, NY, 68% mature in the York River, VA, and 70% mature in Albemarle Sound, SC (Hattala et al. 2007). Recent assessments have used maturity schedules in biomass-per-recruit models to establish benchmark total mortality rates for management. These models require river-specific maturity schedules since each stock is managed separately (ASMFC 2007).

If stock-specific maturity patterns exist, then identical fishery regulations could have different impacts on neighboring stocks. For example, most American shad are harvested for roe and the fishery focuses on mature females (the immature component of the population is at sea and therefore unavailable to the fishing gear). If a shad fishery has knife-edge selectivity (fish become fully vulnerable at a particular age), the result may be differential harvest of an early maturing population that has yet to fully recruit to the gear compared with a late maturing population. For the early maturing population, most individuals mature and spawn at least once prior to becoming fully vulnerable to the fishery. However, in a late maturing population, in which most individuals mature at the fully vulnerable age, reduced reproductive output might occur because most of the spawning biomass consists of virgins that are harvested during the first spawning migration. In depleted stocks, persistent differences in maturation schedules may also affect stock recovery.

When American shad enter freshwater to spawn, it is thought that their scales begin to erode producing a mark or spawning check (Cating 1953; Judy 1961). Scale characteristics, including ages and spawning marks, may be used to determine age at maturity and the number of spawning migrations an individual has undertaken (Cating 1953; Judy 1961). Using this information, Maki et al. (2001) developed a model to estimate maturity schedules for American shad from the York River, Virginia. Resulting maturity estimates for the three years examined were consistent and the average maturity schedule for the combined dataset was 2.1, 32.5, 44.5, 16.8, and 4.1% for ages 3 through 7 (Maki et al. 2001). Cumulative maturity estimates showed that most individuals (79.1%) were mature by age 5.

The purpose of this study was to update these maturity data and to extend coverage to other rivers and year classes. We used the methodology developed by Maki et al. (2001), following their recommendation to examine maturity schedules on a year-class specific basis (longitudinal approach), as well as to use the cross-sectional approach originally proposed to compare maturity schedules from neighboring stocks of American shad from the James, York, and Rappahannock rivers.

The fishery for American shad in Virginia closed in 1994 before individuals of the year classes examined in this study were sexually mature and vulnerable to the fishery. This provided an opportunity to examine three stocks that experienced similar management histories. However, fishing mortality was not zero for these year classes because there was a mixed-stock, ocean-intercept fishery operating from the early 1980's to 2005 that resulted in an unknown harvest of Virginia shad (ASMFC 2007). Furthermore, Native American tribal communities are allowed to harvest American shad as part of a treaty dating back to Colonial times. In addition, a small bycatch fishery was permitted beginning in 2005 as part of the commercial striped bass fishery in Virginia and American shad are captured and released as bycatch in pound net fisheries throughout Chesapeake Bay with unknown effects on survival or migration.

There is concern with estimating maturity schedules for exploited stocks because of the differential survival between mature and immature individuals. Maki et al. (2001) examined the possible impact of differential survival rates and found that small departures in the ratio of mature to immature fish due to fishing mortality did not greatly affect maturation estimates.

METHODS

The spawning migration of adult American shad in the Rappahannock, York, and James rivers has been monitored annually since 1998 following a closure of the fishery (Olney and Hoenig 2001; ASMFC 2007). Migrating adults are captured using staked gill nets to produce an index of adult abundance based on catch rate of maturing females. The monitoring program mimics a fishery that was prosecuted in the 1980s in the York and James rivers and consists of a 273-m gill-net, constructed of 12.4 cm stretched-mesh, monofilament netting that is strung between poles driven into the riverbed at approximately 9.14 m intervals. The commercial fishery in the Rappahannock River used a slightly different design with 12.7 cm stretched-mesh monofilament netting placed between poles spaced every 14.6 m. Shad fisheries prosecuted during the 1950s used multifilament netting and conversion factors have been derived by Maki et al. (2006), to relate current catch rates from the monitoring program to historical catches in the York River (ASMFC 2007). In the monitoring program, nets are fished for two consecutive days each week during the spawning run from late February to May in all three rivers. All American shad are brought to the lab and processed (weighed, measured, sexed, and staged for maturity), and scales are removed for age determination and spawning history (Cating 1953). Data from only the pre-spawning females captured in 1998 – 2006 are used in this study because spent or partially-spent females would have different catchabilities relative to pre-spawn females and further would not be comparable to the commercial fishery since it was primarily targeting developing roe.

Because accuracy and precision in age determination from the scales of American shad is related to the experience of the scale reader (McBride et al. 2005), all ages used in this study were assigned by a single experienced individual. This individual participated in the McBride et al. (2005) age determination workshop and scored high in their evaluation of age determinations. Thus any bias associated with that individual in determining ages and spawning history would be consistent across years (cohorts) and rivers. To achieve a consistent database of ages, the scale reader re-aged historic collections of American shad scales dating from 1998 through 2002 because those years had been aged by a different individual.

In Virginia, American shad make their first spawning run between ages 3 and 7, and may continue to spawn up to age 10 or 11 (these maximum ages are estimated during a period of severe stock depletion). The model developed by Maki et al. (2001) estimated proportion mature at age using a cross-sectional approach because only three years of data were available and most cohorts had not completed a full life cycle, which would have allowed a longitudinal investigation. Currently, sufficient years of data are available to perform a longitudinal investigation and evaluate an assumption of the cross-sectional methodology that there is no change in maturation among year classes.

Maturation parameters (proportion mature at each age) are estimated assuming a multinomial distribution using the method of maximum likelihood. For year-class specific estimates, the equations are identical to those used in the cross-sectional methodology developed by Maki et al. (2001). Because the proportion mature at age is estimated for each age separately, there is no need to account for effort, as is typically required in longitudinal studies. Also, annual effort does not change appreciably in the monitoring program. For example, all of the age 8 fish captured in 2004 are from the 1996 year class and the spawning history obtained from their scales provides information to estimate the proportion of the population that matured at each age from ages 3 to 8. The following year, all age 9 fish captured are from the same 1996 year class and the spawning history obtained from their scales provides additional information to estimate the proportion of the population that matured at each age from ages 3 to 8. The amount of effort used to capture the fish at age 8 and age 9 (or any other age) can vary as long as catchability is not affected by spawning history (Maki et al. 2001). By combining all the data for a cohort into a single maximum likelihood, all of the available information for the year class is used simultaneously to estimate proportion mature at age. In addition to the longitudinal analysis, the cross-sectional method was also performed to compare the two approaches. The cross-sectional approach only requires a single year of maturation data to estimate proportion mature at age and assumes no variability in maturation among year classes.

RESULTS

Nine years of data were available from the Rappahannock River (n= 1,581 females), the York River (n= 3,398 females), and the James River (n= 2,220 females). Seven year classes had completed the maturation process to at least age 7 during the study and were used in the longitudinal investigation (1993 – 1999; Tables 1, 2 and 3). The greatest proportion of females matured at age 5 and this pattern was consistent for all three rivers and all years except for the 1994 year class from the Rappahannock and York rivers (Figure 1). Almost all females were mature by age 7, however there were four American shad that first matured at age 8. All four specimens were collected in 2002, two from the York River and two from the Rappahannock River. Two specimens were virgins from the 1994 year class; the other two were captured at age 9 and had one spawning mark (1993 year class).

The cumulative proportion mature at age was examined for each river to investigate patterns of maturity for each stock (Figure 2). For the Rappahannock River stock, the cumulative proportion mature by age 5 ranged from 0.59 (1995 year class) to 0.79 (1996 year class), the York River stock ranged from 0.60 (1995 year class) to 0.87 (1997 year class) and the James River stock ranged from 0.50 (1995 year class) to 0.85 (1993 year class). The average cumulative proportion mature by age 5 (combined year classes 1993 - 1999) within a stock was 0.70 for the Rappahannock River, 0.72 for the York River, and 0.60 for the James River (Figure 3). Estimates of the proportion mature at age from the combined dataset from the James River stock were consistently below estimates from the York river stock for ages 4 to 6, and also below estimates from the Rappahannock River stock for ages 5 and 6 resulting in an apparent delay in maturity for the James River stock that is split between ages 5 and 6 (Figures 1 and 2).

Variability in proportion mature at age was observed among stocks and among years. In some years, temporal patterns were consistent with lowest estimates observed for the proportion maturing at age 4 coinciding with the 1995 year class, age 5 for the 1994 year class, and age 6 for the 1993 year class in all three stocks (Figure 4). The female American shad contributing to those year classes were all captured in 1999. However, peaks in the proportion maturing at age did not coincide with any particular year class. The proportion maturing at age 5 varied from 0.31 (1994) to 0.56 (1998) for the Rappahannock River stock, 0.30 (1994) to 0.54 (1993 and 1997) for the York River stock and 0.33 (1994) to 0.59 (1993) for the James River stock.

One use of maturity schedules is to forecast spawning runs, but because the longitudinal method requires that all members of a year class reach maturity, it is not useful in this instance. Therefore maturity schedules were also estimated using the cross-sectional approach (Table 4; Figure 5). A temporal pattern in proportion mature at age was most evident for the 2002 spawning run. The high proportion of fish maturing at ages 6 to 8 resulted in lower proportions for ages 4 and 5 (because the sum of all ages must be equal to one). Estimates from 2002 for fish ages 4 and 5 were low indicating that the cross-sectional method may provide inaccurate estimates in some years. The age-4 fish captured during the 2002 spawning run would have been from the 1998 year class and estimates of the proportion mature at age 4 from the longitudinal analysis for this year class in each river were 0.12 (Rappahannock), 0.29 (York), and 0.16 (James). Similarly, for fish age 5 (1997 year class) captured during the 2002 spawning run, estimates from the longitudinal analysis were 0.55 (Rappahannock), 0.54 (York) and 0.41 (James). Compared with the longitudinal approach, the cross-sectional approach consistently underestimated the proportion mature at age for ages 4 and 5 during 2002.

A comparison of differences in estimated maturity schedules between the James River and York River stocks was performed under equilibrium conditions. By assuming constant and equivalent recruitment and mortality for the two stocks, and using the maturity schedules for the combined year classes (1993 – 1999) observed in this study for each system, the delayed maturation in the James River stock results in consistently lower numbers of mature females in the population (Figure 1.6).

DISCUSSION

Differences in maturity schedules between the James and York rivers, and to a lesser extent with those from the Rappahannock River, show that neighboring stocks experiencing similar climate regimes can have stock-specific maturity patterns that persist through time. Results of the longitudinal approach show that year-class specific age at maturity estimates are grossly similar; most fish mature between ages 4 and 6 in each of the three systems, and maturity peaks at age 5. However, there is sufficient inter-annual variability in the proportion maturing at age in the three rivers to evaluate maturity schedules for the stocks separately. The lowest proportion that matured at age 5 in each river were all from the 1995 year class, indicating a year effect, but highest estimates did not align with specific year classes. Therefore, estimates of the contribution from a particular year class to the spawning run in any given year could vary greatly among stocks.

The estimated proportion mature at age using the cross-sectional methodology in all three rivers suggests a regional similarity with respect to the demographics of the spawning run. However, results from the longitudinal analysis, which follows the same year classes in each river, did not show a common pattern among rivers when examined by age. There are years and ages that are in agreement, but other ages varied widely and without pattern. Year class size could have an effect on maturation schedules assuming competition for resources at large population sizes. However, when juvenile recruitment indices (available from the York and Rappahannock rivers) were examined, there was no correlation between the index value and age at maturity for any ages for either river. For example, the highest proportion of American shad maturing at age 6 in the cross-sectional analysis was observed in 2002. These fish would have been from the 1996 year class, which was the highest recruitment ever observed in the York River (Wilhite et al. 2003) and supports the hypothesis of a delay in maturity due to resource competition. However, when the 1996 year class is examined longitudinally, the estimated proportion maturing at age 6 is similar to that observed for the 1995 and 1999 year classes, two years of relatively low recruitment. Unfortunately, there is no interpretable juvenile index of abundance available for the James River, but numbers of hatchery released larvae that are available show no pattern in relation to age at maturity. Therefore, year class sizes at depleted stock levels observed during this study do not seem to affect the maturation process in predictable ways. Alternatively, dynamics in the coastal ocean may regulate maturity patterns independent of recruitment levels. For example, if abundance of a competitor increased relative to that of American shad then interspecific competition for resources may overwhelm observed changes in year class production of American shad (Trippel 1995). Thus our ability to evaluate expected changes in maturity schedules resulting from recruitment variability at low population sizes (i.e., early maturation for small year classes and later maturation for large year classes) would be obscured.

Another possibility is that maturation probability may be related to previous growth history and not to a particular size or age as found in chum salmon (*Oncorhynchus keta;* Morita and Fukuawaka 2006). Slow growth during a critical period (e.g., development and secretion of hormones) may delay maturation until more favorable conditions are encountered and these critical periods in development have not been observed in American shad because the immature component of the population is in the coastal ocean.

Why the cross-sectional approach, which spans multiple year classes, shows a higher degree of temporal agreement compared with year-class specific estimates is not clear. Annual variation in sampling effort does not explain the results since neither method requires information on effort, only the numbers of fish at age and the corresponding number of spawning marks. Furthermore, annual effort was similar in the sampling program from 1999 to 2006. A possible explanation is that catchability (due to selectivity or vulnerability) is not constant, but is similar among the rivers in any given year resulting in the observed patterns. Perhaps the timing of the spawning run is such that fish maturing at age 3 (regardless of their current age) tend to migrate up-river in a group and those maturing at age 4 follow at a different time, and so on. If this is the case, then results obtained from the monitoring program would depend on what portion of the population is caught relative to the demographics of the spawning run. However, age-specific patterns in catch have not been observed. Another explanation for potential catchability differences may be related to size and the swimming capabilities of similarly sized fish regardless of age.

As might be expected, maturity estimates for a particular age and year class obtained using the cross-sectional approach do not necessarily agree with the maturity estimates from the corresponding year class and age obtained using the longitudinal approach. Most likely, the additional members of a year class captured during subsequent years are incorporated into the longitudinal analysis and the proportion mature at age shifts compared with estimates obtained from the cross-sectional method. In some instances the two estimates match, but in others it is different and it will not be known until after the year class has reached its terminal spawning age whether there is agreement.

It has been shown that migrating American shad may abandon the spawning run after capture or handling, which may indicate more plasticity in spawning behavior than previously thought (Olney et al. 2006). Furthermore, pre-spawning American shad caught as bycatch in other fisheries, such as pound net fisheries in Chesapeake Bay, may alter their migration as result of handling stress. Perhaps other natural triggers such as abrupt changes in river temperature may cause maturing females to abandon the spawning run. Quinn and Adams (1996) showed that time of migration of American shad has shifted with warming of the Columbia River. If handling stress or changes in water temperature alter migration behavior, the result could be a shift in estimated age at maturity to older ages for virgin migrants that abandon the spawning run (i.e. fish that matured at age 5, but spawned at age 6 would appear as though they matured at age 6) and skipped years for fish that had previously spawned. While evidence of skipped years of spawning has not been found in scale analysis in

Virginia stocks, results from stable isotope analysis of otoliths suggest that skipping may occur (Secor and Rooker 2000).

Because evaluation of spawning history relies on scales, the underlying processes that result in spawning marks are important to understand. If spawning marks in scales are the result of metabolic processes, then abandoned migrations should still appear as marks in scales of fish that did not actually participate in the spawning event because ovaries begin maturing before the fish enter the river to spawn (Olney et al. 2001). However, if spawning marks are the result of erosion and absorption processes on the freshwater spawning grounds (Cating 1953), then spawning marks would not appear in scales of fish that abandoned the migration early (prior to entering freshwater). Differentiating among the possibilities is not possible at this point as we do not have a clear understanding of spawning mark formation.

The observed differences in age at maturity for the James River stock compared with stocks from the York and Rappahannock rivers may delay stock recovery in the James River. Assuming the only difference between James and York river stocks is the maturity schedule (i.e. assuming equilibrium conditions: identical recruitment and identical mortality rates for the York and James river stocks) the James River stock would produce 78% of the number of spawning females each year compared with the York River stock due to differences in maturity schedules. Delayed recovery of the James River stock would need to be accounted for in management considerations as neighboring stocks may meet target threshold values at different points in time. Because the James River stock has been at a low level of abundance, releases of hatchery-reared larvae have been conducted in the James River since 1992 to augment natural production of juveniles. In addition, a vertical slot fishway was constructed in Bosher's Dam, located near Richmond, VA in 1999 to allow access to more than 220 km of historic spawning and rearing areas (Weaver et al. 2003). An assessment of the contribution of hatchery-released larvae of American shad to the spawning run in the James River shows an increase in the catch rate resulting from the influx of mature hatchery-origin fish, a promising sign of recovery (Olney et al. 2003). However, despite the efforts to rebuild the James River stock, current levels remain below expectations and very low compared with historic levels. It is possible that the observed delay in maturity (and additional mortality incurred prior to maturation) is acting in concert with restricted access to spawning habitats to retard recovery of the James River stock. An additional factor that may slow recovery of the James River stock is the apparent consistent failure (near-zero) of wild juvenile recruitment as measured by the Virginia Institute of Marine Science striped bass seine survey.

Maki et al. (2002) found that American shad captured from the commercial fishery during the 1950's matured at later ages compared with estimates from the current monitoring program (based on data from 1998 – 2000). Shifts to an earlier age at maturity due to fishing has been found in Atlantic cod (*Gadus morhua*) and haddock stocks (*Melanogrammus aeglefinus*) among others, and demonstrates a compensatory response to population declines (Trippel 1995). Results from our study suggest that 13 years after the in-river moratorium, American shad stocks continue to mature at earlier ages relative to the 1950's. Based on current monitoring, the age of full recruitment to the staked gillnet fishery is age 5, corresponding to the age when the largest proportion of the population reaches maturity. The historical fishery targeted age-5 females and this was probably a contributing factor to its collapse during the 1980s. It is unknown whether the apparent shift in age at maturity since the collapse is due to harvest pressure or some other unknown factor. However, it does appear that the stocks are fixed at the current maturity schedule. If the Virginia fishery is to reopen in the future, the most risk adverse strategy would be to regulate the fishery to target American shad at older ages and allow a large portion of the spawning stock biomass the opportunity to spawn at least once.

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Table 1.1. The number of American shad females collected by age at capture and age at maturity for seven year classes from 1993 to 1999 in the Rappahannock River, Virginia. Table entries are numbers of females. Ages are based on scale analysis.

	Age at	Age at maturity					
Year class	capture	3	4	5	6	7	8
1993	3	NA					
	4	NA	NA				
	5	0	24	21			
	6	1	12	20	3		
	7	0	1	4	1	0	
	8	0	2	0	0	0	0
	9	0	0	0	0	1	1
	10	0	0	0	0	0	0
1994	3	NA					
	4	4	11				
	5	2	10	13			
	6	0	3	4	4		
	7	0	6	5	2	0	
	8	0	0	2	6	0	1
	9	0	2	2	1	0	0
	10	0	0	0	1	0	0
1995	3	0					
	4	0	7				
	5	0	12	47			
	6	0	4	26	11		
	7	0	1	9	22	0	
	8	0	2	9	1	0	0
	9	0	1	0	1	0	0
	10	0	0	0	1	0	0
1996	3	0					
	4	1	54				
	5	1	44	82			
	6	0	3	27	13		
	7	0	11	16	4	0	
	8	0	9	4	2	0	0
	9	0	1	1	0	0	0
	10	0	0	1	0	0	0
1997	3	1					
	4	6	41				
	5	0	3	21			
	6	0	19	36	18		
	7	1	2	13	9	0	
	8	0	3	7	1	0	0
	9	0	0	0	0	0	0
1998	3	0					
	4	0	4				
	5	0	28	146			
	6	0	17	52	23		
	7	0	2	11	8	2	
	8	0	0	4	0	0	0
1999	3	1					
	4	0	35				
	5	1	34	87			
	6	0	13	31	18		
	7	0	4	1	1	0	

Table 1.2. The number of American shad females collected by age at capture and age at maturity for seven year classes from 1993 to 1999 in the York River, Virginia. Table entries are numbers of females. Ages are based on scale analysis.

	Age at	Age at maturity					
Year class	capture	3	4	5	6	7	8
1993	3	NA					
	4	NA	NA				
	5	6	108	230			
	6	1	31	40	9		
	7	0	1	12	2	0	
	8	0	6	5	0	0	0
	9	0	0	0	3	0	1
	10	0	0	1	0	0	0
1994	3	NA					
	4	14	151				
	5	7	58	49			
	6	0	31	18	10		
	7	1	15	9	1	0	
	8	0	0	2	7	1	1
	9	0	1	1	1	0	0
	10	0	0	0	0	0	0
1995	3	8					
	4	10	23				
	5	1	21	99			
	6	5	23	38	8		
	7	0	0	13	34	8	
	8	0	5	7	6	0	0
	9	0	1	1	0	0	0
	10	0	0	2	0	0	0
1996	3	2					
	4	2	114				
	5	3	121	143			
	6	0	7	101	60		
	7	0	12	26	12	0	
	8	0	7	13	4	0	0
	9	0	1	3	0	2	0
	10	0	0	1	0	0	0
1997	3	12					
	4	11	182				
	5	0	25	91			
	6	1	45	55	13		
	7	0	38	35	17	0	
	8	0	8	10	2	1	0
	9	0	1	0	0	0	0
1998	3	6					
	4	0	17				
	5	0	50	100			
	6	0	32	52	29		
	7	0	8	11	7	1	
	8	0	1	1	0	0	0
1999	3	0					
	4	0	27				
	5	1	62	88			
	6	1	13	22	20		
	7	0	2	4	0	0	

Table 1.3. The number of American shad females collected by age at capture and age at maturity for seven year classes from 1993 to 1999 in the James River, Virginia. Table entries are numbers of females. Ages are based on scale analysis.

Year class	Age at capture	Age at maturity					
		3	4	5	6	7	8
1993	3	NA					
	4	NA	NA				
	5	1	13	44			
	6	0	9	19	5		
	7	0	0	2	1	0	
	8	0	1	1	2	0	0
	9	0	0	1	0	0	0
	10	0	0	0	0	0	0
1994	3	NA					
	4	3	53				
	5	2	18	55			
	6	0	16	10	5		
	7	0	4	5	7	0	
	8	0	0	3	7	7	0
	9	0	0	0	2	0	0
	10	0	0	0	0	0	0
1995	3	2					
	4	2	17				
	5	3	36	103			
	6	0	5	23	9		
	7	0	0	8	28	8	
	8	0	1	7	2	0	0
	9	0	0	2	0	1	0
	10	0	0	0	0	0	0
1996	3	0					
	4	2	125				
	5	0	44	58			
	6	0	5	46	44		
	7	0	8	19	5	1	
	8	0	3	4	3	0	0
	9	0	0	2	0	0	0
	10	0	0	0	0	0	0
1997	3	15					
	4	0	77				
	5	0	24	73			
	6	0	28	48	37		
	7	0	7	7	7	2	
	8	0	5	3	5	1	0
	9	0	0	0	0	0	0
1998	3	2					
	4	0	12				
	5	0	47	177			
	6	0	24	27	24		
	7	0	6	14	7	4	
	8	0	0	1	0	0	0
1999	3	1					
	4	0	52				
	5	1	39	127			
	6	0	11	55	41		
	7	0	1	1	0	0	

Table 1.4. Comparisons of the proportion maturing at age among stocks of American shad from the Rappahannock, York, and James rivers. Correlations are based on ranks using maturity estimates from the cross-sectional analysis.

Comparison	Age	Kendall's τ	*P* - value
Rappahannock - York	3	0.82	0.003
	4	0.40	0.140
	5	0.31	0.250
	6	0.67	0.012
	7	0.73	0.025
Rappahannock - James	3	0.43	0.127
	4	0.37	0.173
	5	0.54	0.046
	6	0.67	0.013
	7	0.66	0.038
York - James	3	0.52	0.063
	4	0.42	0.126
	5	0.50	0.075
	6	0.67	0.013
	7	0.56	0.073

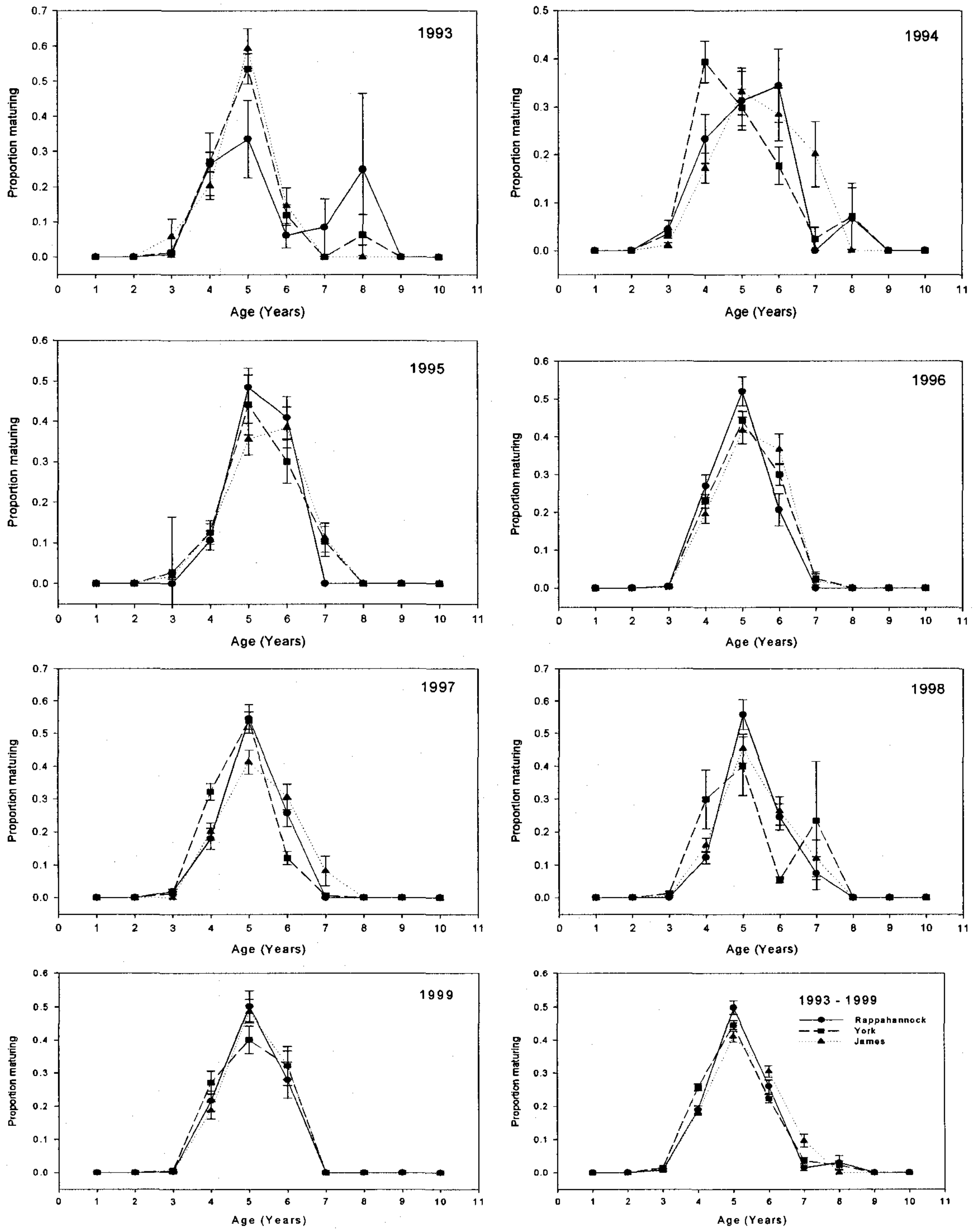

Figure 1.1. Proportion mature at age (±SE) for seven year classes based on longitudinal analyses for the Rappahannock, York and James river stocks of American shad.

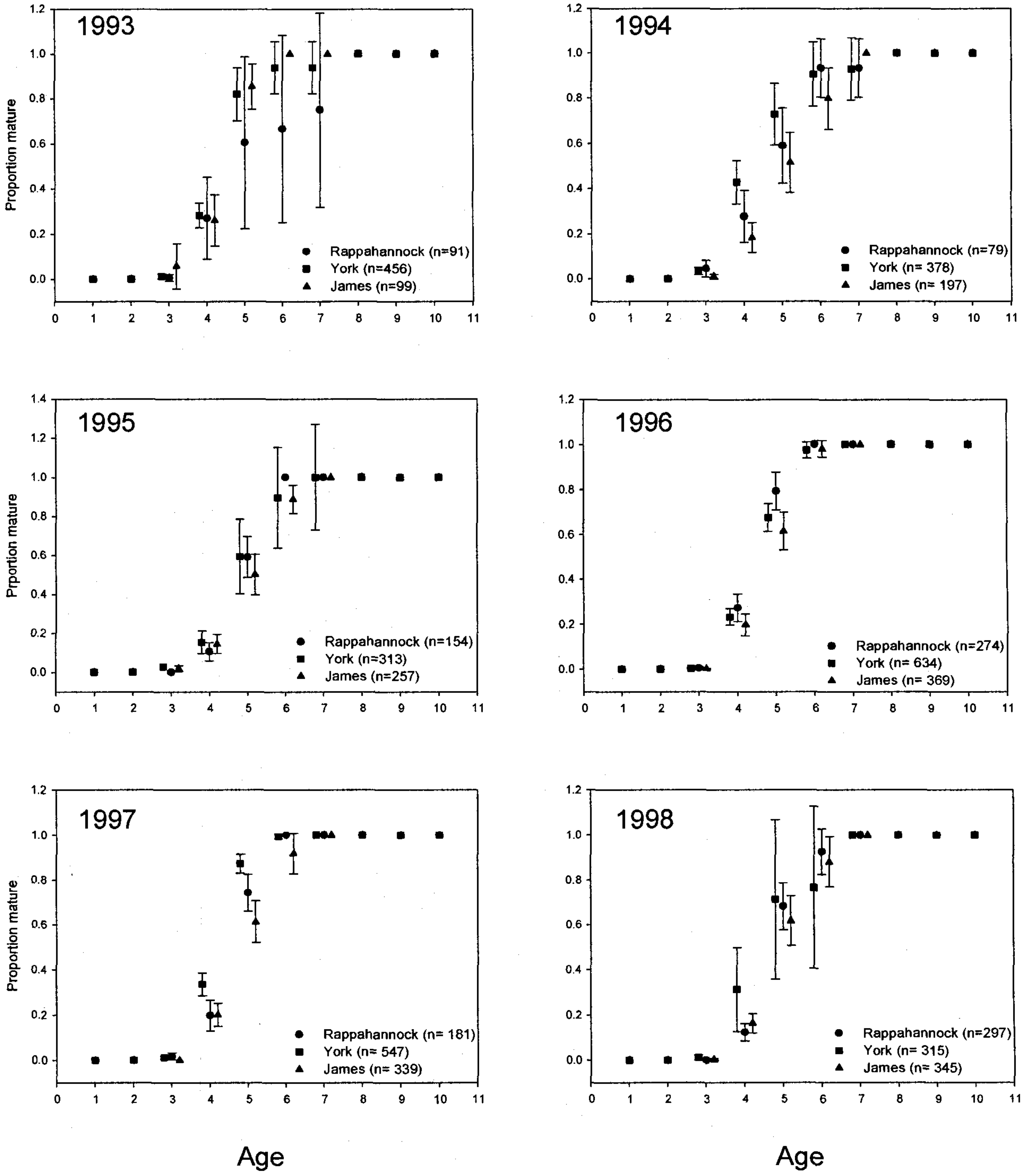

Figure 1.2. Proportion of American shad maturing by a given age and approximate 95% confidence intervals for seven year classes (1993 – 1999) from the Rappahannock, York, and James rivers.

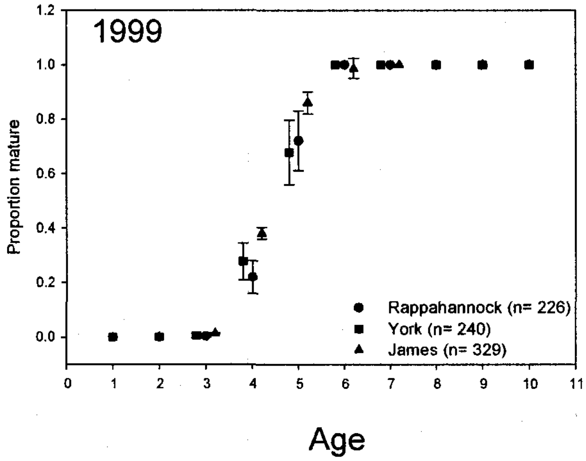

Figure 1.2. continued. Proportion of American shad maturing by a given age and approximate 95% confidence intervals for seven year-classes (1993 – 1999) from the Rappahannock, York, and James rivers.

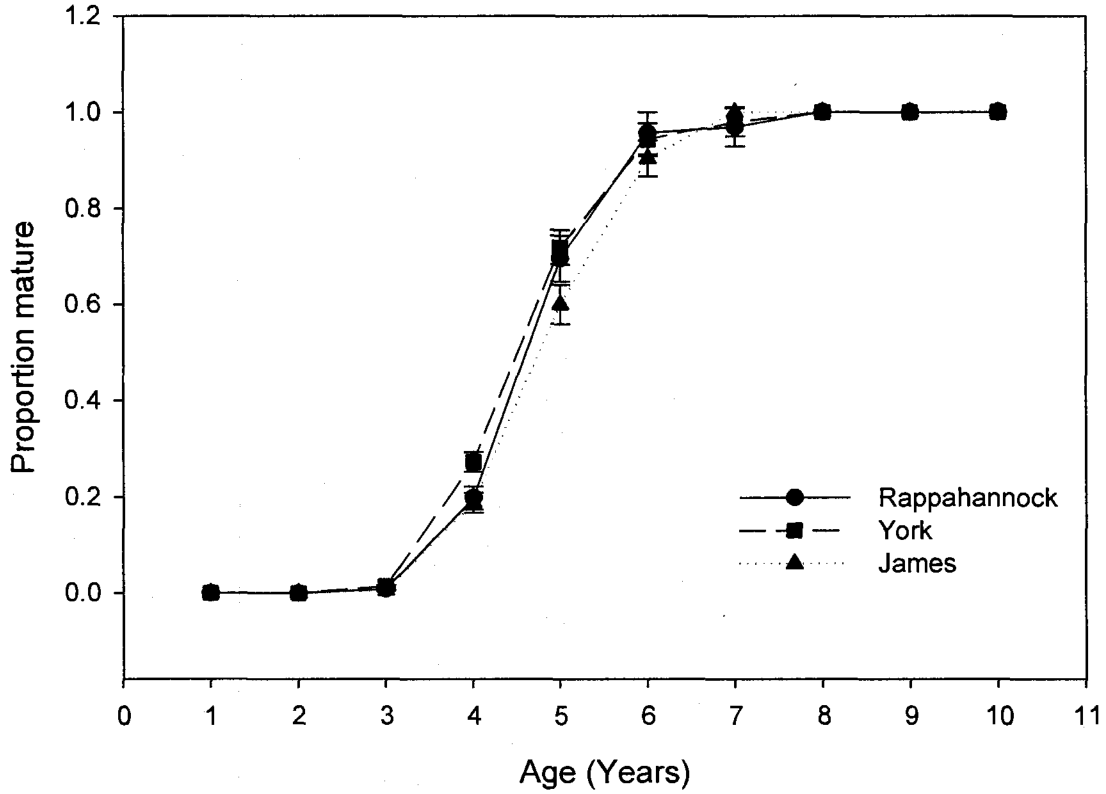

Figure 1.3. Proportion of American shad maturing by a given age and approximate 95% confidence intervals for seven year classes combined (1993 – 1999) from the Rappahannock, York, and James rivers.

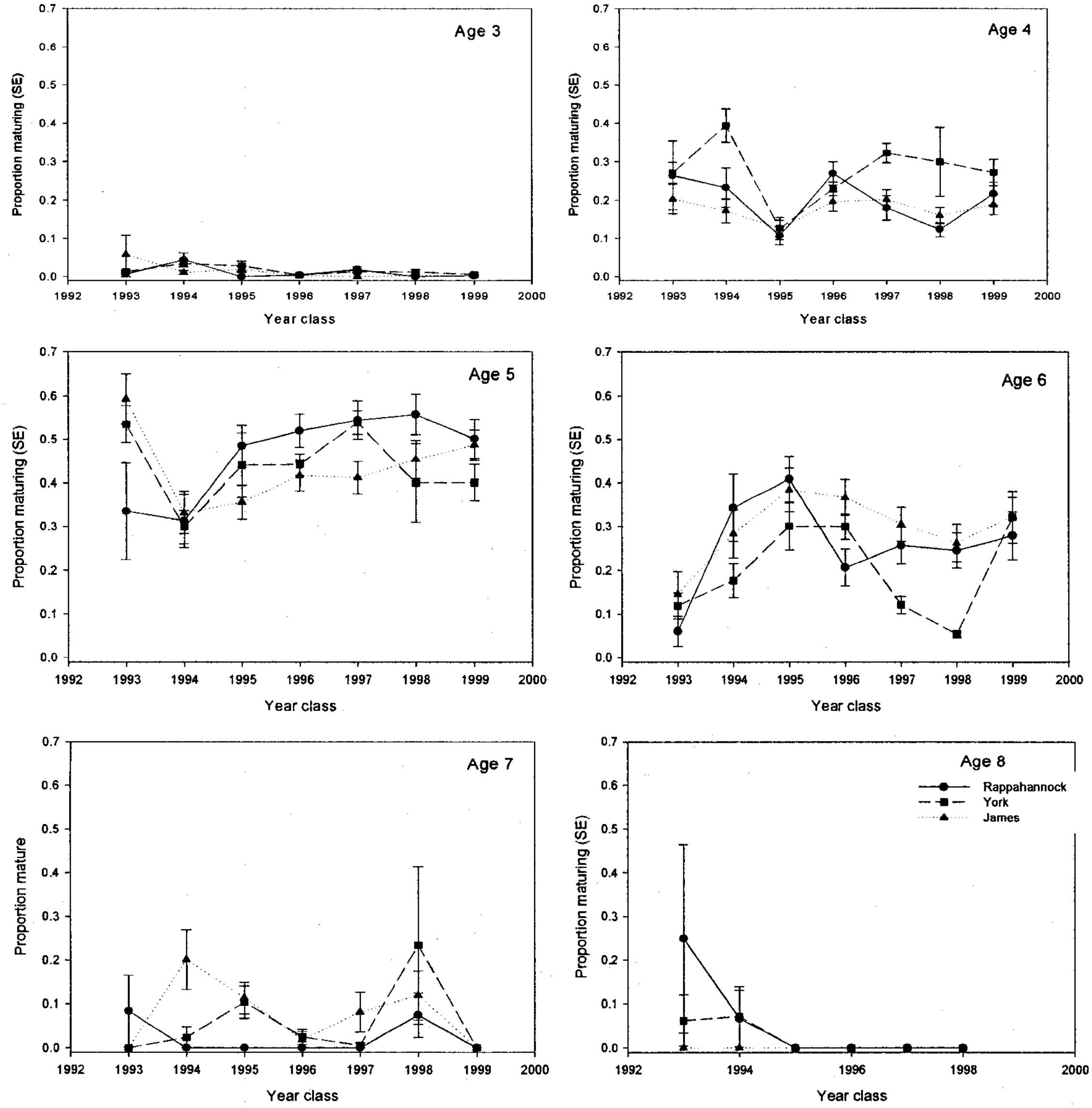

Figure 1.4. Comparison of age-specific maximum likelihood estimates for seven year classes of American shad from the Rappahannock, York, and James rivers. Shown are the proportion maturing at age (±SE).

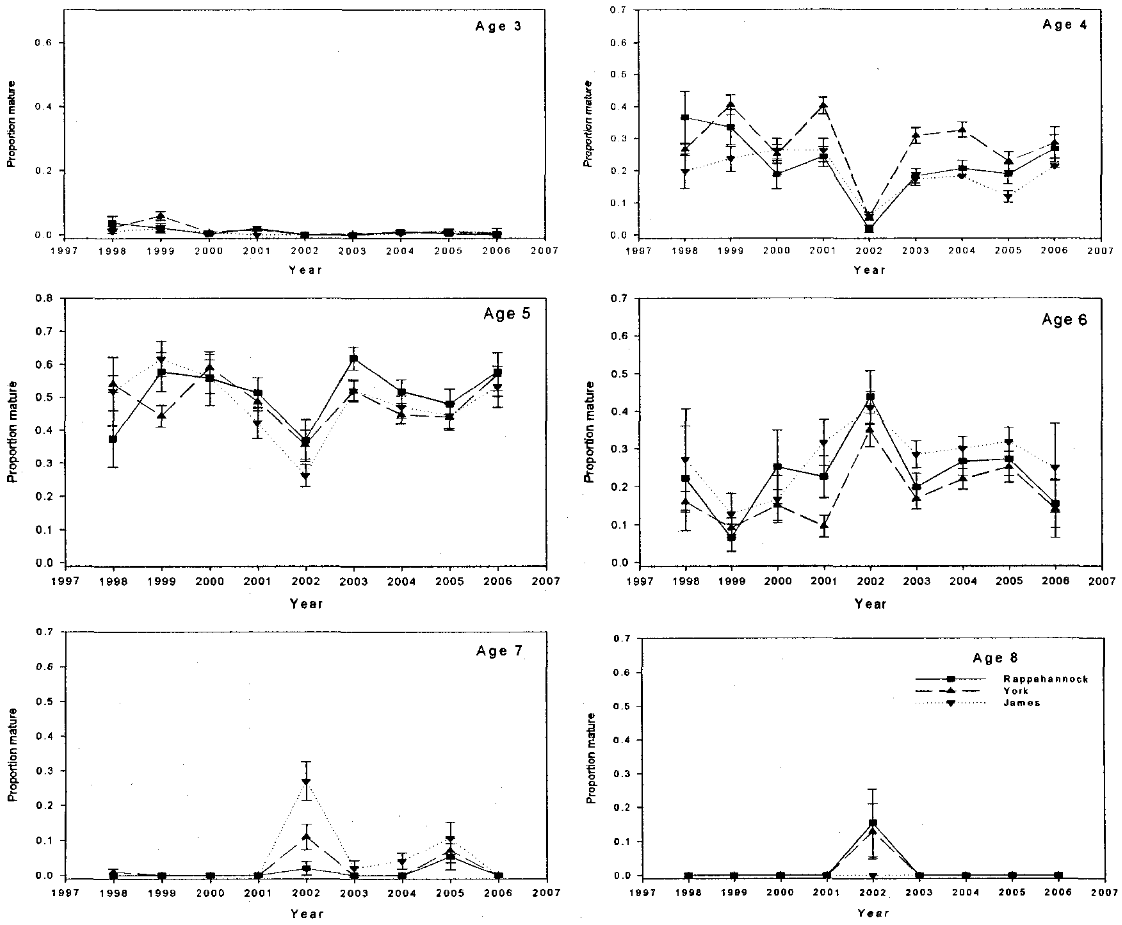

Figure 1.5. Comparison of age-specific maximum likelihood estimates for the proportion maturing by age for American shad from the Rappahannock, York, and James rivers using the cross-sectional approach (1998 – 2006). Shown are the proportion maturing at age (±SE).

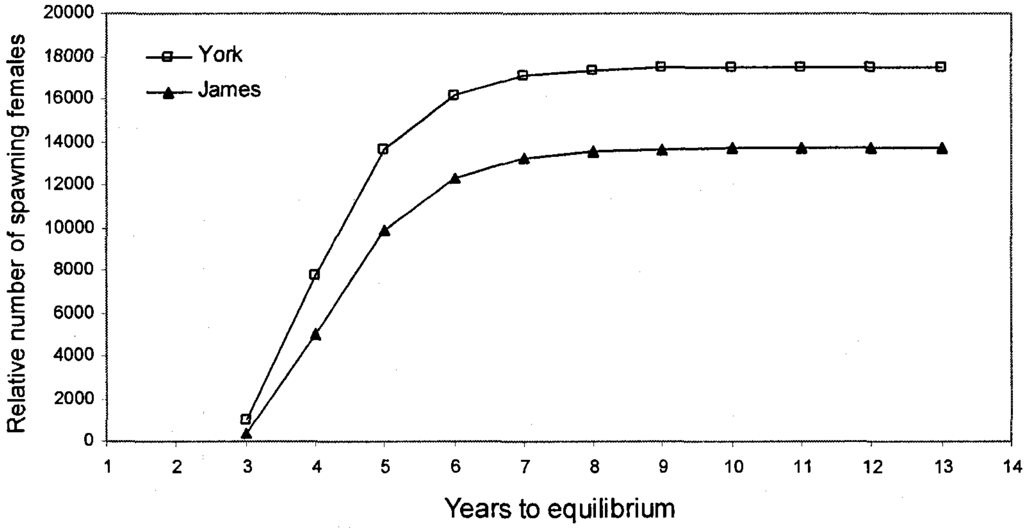

Figure 1.6. Effect of delayed maturity in female American shad from the James River compared with those from the York River assuming equivalent and constant recruitment and mortality between the two stocks.

Chapter Two

Growth, Mortality, and Recruitment Variability of Young-of-Year American Shad Cohorts in Lower Chesapeake Bay Nurseries

ABSTRACT

Understanding population dynamics of early-life stages of fishes can facilitate improved forecasting of year-class abundance and inter-annual variability in year-class strength. For depleted stocks under restoration or suffering overfishing, recruitment dynamics can be a significant factor affecting stock recovery and effectiveness of existing management strategies. American shad (*Alosa sapidissima*) populations have been reduced to low levels and attempts are being made to rebuild stocks throughout their range. This study investigates spatial and temporal variation of growth and mortality in young-of-year American shad by evaluating intra- and inter-annual cohort production in the Rappahannock, Mattaponi, Pamunkey and James rivers. Despite the close proximity of these four river systems, persistent differences in growth and mortality rates help to explain trends in year-class strength. High mortality rates among juveniles observed in the James River support the observation of almost complete recruitment failure of wild American shad in this system. Low mortality rates of young-of-year shad in the Rappahannock River are consistent with a trend of increasing recruitment of maturing females. Finally, lower mortality rates but similar growth rates in juvenile fish from the Mattaponi River compared with the Pamunkey River support the long-term record of greater juvenile production of American shad in the Mattaponi River.

INTRODUCTION

The early life history of fishes, including the egg-larvae and pre-recruit juvenile stages, is a dynamic period characterized by varying growth and mortality rates that ultimately determine year-class strength (Sissenwine 1984; Houde 1989, 1997a; Sogard 1997). Numerous theories have been developed to explain the causative processes of recruitment variability including environmental and biological phenomena that influence survival (for reviews see Anderson 1988; Houde 2008). Whereas processes acting during the egg and larval stages usually determine year class strength, the influence of post-metamorphic processes (i.e. those affecting juvenile growth and mortality) have gained support as important sources of recruitment variation or conversely, act as mitigating factors that dampen variability (Sissenwine 1984; Bradford 1992; Bradford and Cabana 1997).

Variability in both mortality (M) and growth (G) can have strong effects on year class strength when acting during the larval stage, acting to cause recruitment to vary by an order of magnitude or more (Houde 1987; Houde 1997a). Studying the dynamics of M and G in early stages of fish along with environmental conditions in nurseries can facilitate improved understanding of year class formation and annual variability in year class strength that are often observed. For species that are at historic lows in abundance or are suffering overfishing, recruitment dynamics can be a dominant factor affecting stock recovery and effectiveness of existing management strategies.

American shad (*Alosa sapidissima*) populations have been reduced to low levels since peak landings in the late 1800's and attempts have been made to rebuild stocks throughout their range (Limburg et al. 2003). The elimination of large reaches of spawning habitat through the construction of dams, and intense fishing pressure are believed to be among causes of population declines (Limburg et al. 2003). Efforts at rebuilding American shad stocks in Virginia include fishing moratoria, dam bypass structures that allow access to up-river spawning grounds, and stock enhancement projects through release of hatchery-raised larvae. Despite these efforts, Virginia stocks remain at low levels (ASMFC 2007).

In Virginia, annual production of young-of-year (YOY) American shad varies in space and time and recent estimates of year class strength can vary 16-fold in some instances. Among Virginia rivers, the Mattaponi River (a tributary of the York River) consistently produces higher juvenile abundance indices (JAIs; Virginia Institute of Marine Science, VIMS, striped bass survey) compared with the neighboring Pamunkey River, however processes that produce this pattern are not clearly understood (Wilhite et al. 2003). Higher JAIs may be related to greater abundance of spawning females, higher survival at some stage of development, faster growth, or a combination of these factors. My research investigated spatial and temporal variation of growth and mortality in YOY American shad by examining intra- and inter-annual cohort production in the Pamunkey and Mattaponi rivers. Population comparisons provide an opportunity to identify patterns in hatching, M, and G that may explain persistent differences in production of juveniles. The specific hypotheses that growth and mortality rates do not differ between the Mattaponi and Pamunkey rivers were tested. Furthermore, a time series of catch and length records of YOY American shad, along with associated environmental variables from these two rivers, allowed an investigation of factors contributing to year class strength. Faster growth and lower mortality of American shad in the Mattaponi River compared with the Pamunkey River would provide evidence of river-specific conditions that promote recruitment of YOY American shad. Additional comparisons of YOY American shad from the nearby James and Rappahannock rivers from a separate monitoring program are also included to produce a detailed temporal and spatial investigation of juvenile population dynamics in the lower Chesapeake Bay.

METHODS

Study location

The Virginia portion of the lower Chesapeake Bay estuary consists of three major river systems that support distinct spawning populations of American shad and historically produced large landings during the commercial fishery (Fig. 2.1). The Rappahannock River is the most northern river with a watershed of approximately 7032 km^2 and an average spring river discharge rate of 46.6 m^3/s. The Rappahannock River was once dammed, blocking access to historic spawning sites for anadromous fishes, but was re-opened in 2004. Samples of YOY American shad in the Rappahannock River were collected in the tidal freshwater near the city of Fredericksburg, VA from approximately river kilometer (rkm) 157 to 170.

The Mattaponi River is south of the Rappahannock River and stretches for more than 139 km before joining the Pamunkey River (180 km long) at West Point where the two tributaries unite to form the York River (West Point is located at rkm 52). The two free-flowing tributaries function as primary spawning and nursery habitat for American shad and together support the York River stock. The Pamunkey River watershed (3768 km^2) is larger than the Mattaponi River watershed (2274 km^2) and the Pamunkey River has a greater average spring discharge rate (47.5 m^3/s) compared with the Mattaponi River (27.2 m^3/s; Bilkovic et al 2002). American shad YOY on the Pamunkey River were collected from rkm 98 to 128 and on the Mattaponi River shad were taken from rkm 83 to 109.

The largest river in Virginia is the James River with a watershed of approximately 25,921 km^2 and an average spring discharge of 294.2 m^3/s. Access to historic spawning sites on the James River was once blocked by numerous dams, but has been partially re-opened by dam removals and the installation of a fish passageway at Bosher's Dam in Richmond (rkm 182.3; Weaver et al. 2003). Young of year American shad from the James River were taken at Bosher's Pool, just above the dam at Richmond, and in the tidal James below the dam.

Fish collection

American shad YOY were collected from 2005 to 2007. Collections from the Mattaponi and Pamunkey rivers were conducted on alternate weeks (beginning in June and continuing until no American shad are caught, typically August) using a bow-mounted pushnet consisting of a 5.2-m body, four-panel, 1.5-m x 1.5-m Cobb trawl modified to fit a square frame with 1.9-cm stretch mesh in the body and 1.27-cm stretch mesh in the cod end (Kriete and Loesch 1980). Because juvenile *Alosa* spp. are more vulnerable to collection at night, sampling was initiated 30 min after sunset and proceeded from the upper-most river station downriver (Loesch et al. 1982). Station selection followed a stratified random design and rivers were subdivided into four subunits (each 6.5 rkm long) with three random stations chosen within each subunit prior to each cruise resulting in 12 samples per cruise. Samples consisted of 5 min pushes resulting in sampling an average water volume of 600 m^3.

Collections on the James and Rappahannock rivers were obtained from the Virginia Department of Game and Inland Fisheries (VDGIF). The VDGIF uses a bow-mounted push net (0.75 m diameter with 3.18 mm mesh early in the spring and a 6.35 mm mesh later in the year) and electrofishing to collect juvenile American shad for evaluation of hatchery releases. Push net catches were standardized based on net dimensions and flow meter readings from 5 min tows to number captured per 300 m^3.

Hydrographic data

Daily water discharge rates and water temperatures from April to October were obtained from the U.S. Geologic Survey gauge stations (#01668000 – Rappahannock River, #1674500 - Mattaponi River, #01673000 – Pamunkey River, and #02037500 – James River). Because gauge stations on the Mattaponi and Pamunkey rivers did not record water temperature each year, additional water temperature data were obtained from continuous monitoring stations operated by the VIMS Virginia Estuarine and Coastal Observing System for 2005 (both rivers) and 2006 (Pamunkey River). Mean water temperatures during months of hatching and early larval growth occur were compared among years using ANOVA ($\alpha = 0.05$, unless otherwise noted) to analyze the influence of hydrographic conditions on hatch date distributions.

Sample processing

All American shad captured were weighed and measured to the nearest 0.01g and 0.1 mm total length (TL). A sub-sample of American shad juveniles was randomly chosen for age analysis from each cruise for development of a cruise-specific age-length key (Kimura 1977). The age-length key developed for each cruise was expanded to the total catch for that cruise by assigning ages proportional to their occurrence in the age-length key for each 4-mm length interval through the program AGEKEY (Isermann and Knight 2005). Data from American shad captured during 2005 in the Rappahannock River were used to evaluate potential length categories (from 3- to 6-mm length bins) to obtain optimal age-length keys (accurate age distribution with fewest number of otoliths processed). Length bins that are too narrow (e.g. 3 mm) increase the number of fish necessary to represent the catch with many bins having a single or only a few fish and length bins that are too wide (e.g. 6 mm) examine too few fish resulting in inaccurate estimates. The trade-off between the two extremes that optimize the number of fish required to properly characterize the age distribution but also limit the time required to process samples was determined to be 4-mm length bins. At least 50 fish from each cruise were sampled proportional to abundance at length and aged unless fewer than 50 fish were caught, then all were aged. Extremely high catches (> 2000) in a single cruise resulted in an increase in the number of fish that were aged (n=100) for that cruise.

Sagittal otoliths were removed and mounted with the sulcal groove facing up on slides using thermoplastic glue. Depending on the size of the otolith and clarity of the increments, otoliths were aged either whole at 337.5x under immersion oil or were ground using fine-grit sandpaper on both sides and viewed at 600x under immersion oil. Blind readings were conducted twice on each otolith and the final age assigned was the average of the two readings if the difference between readings was less than 10% of the average age. If the difference was greater than 10%, the sample was discarded and a replacement was randomly chosen from the appropriate length bin. In addition to ages, otoliths from the James and Rappahannock rivers were scanned for hatchery marks under ultraviolet light after ages were assigned. Hatchery fish with marked otoliths can be identified by fluorescent rings resulting from immersion in oxytetracycline (Hendricks et al. 1991).

Age validation

Daily deposition of increments in otoliths of young American shad has been documented (Crecco and Savoy 1985) and the assignment of correct daily ages in this investigation was validated through the use of 30 hatchery specimens that were obtained from a separate tag-retention study. The U.S. Fish and Wildlife Service, Harrison Lake National Fish Hatchery releases otolith-marked American shad larvae in the James and Rappahannock rivers as part of Virginia's stock restoration program. To validate mark retention, known age (+/- 1d) American shad larvae hatched in spring 2007 were raised in a hatchery pond until October 2007. Thirty specimens from the hatchery study were obtained and otoliths were processed in the same manner described previously. The prepared hatchery fish otoliths were mixed with otoliths from the Pamunkey and Mattaponi rivers collected during 2007 by another individual to avoid bias associated with knowing specimen origin. An additional set (n=10) of otoliths from juvenile American shad obtained from the VIMS juvenile fish and blue crab trawl survey were included in the age validation study to investigate increment formation during winter as well as to reduce bias due to otolith size since most of the shad from the Mattaponi and Pamunkey rivers were smaller than the hatchery specimens.

A total of 312 American shad were used for the age validation study. Collection date and location remained unknown throughout the aging process. After ages were assigned, the actual age of hatchery specimens was obtained from the hatchery manager. The average age assigned to the hatchery specimens under blind otolith readings was 151 d (range 138 – 159 d) while the actual age of those specimens was 161 d. There were five individuals (17%) that did not meet the 10% error criteria in the age validation study resulting in 83% agreement among age assignments. While most ages met the 10% error criteria, ages were not within 5 d of the known hatch date and therefore were incorrectly assigned to 5-d cohorts used in this study. The first 7 d of growth occurred in the hatchery under cool water temperatures and suboptimal diet (Michael Odom, pers comm.), which may have resulted in some age error due to poor ring formation at these early ages. If 7 d are added to each assigned age, 70 % of the ages fall within the 5 d cohort age bin used in this study. As a result of this known bias, American shad collected after 30 October were not used in growth or mortality estimates because of uncertainty in cohort assignment.

Additional age validation was conducted by comparing ages of hatchery fish from known hatch dates (typically 3 d prior to marking) with ages estimated from otoliths of recaptured hatchery fish. All hatchery fish released in VA have similar hatchery marks, either a single 3-d mark or two marks, one at day 3 and another at day 6. Because there are multiple releases of hatchery fish throughout spring, ages of recaptured hatchery fish could not be assigned to the true hatch date obtained from hatchery logs. However, age ranges of hatchery fish are known and otolith-based ages of hatchery fish would have to be between the first hatch date released by the hatchery and the last hatch date released. Therefore, ages of marked hatchery shad that exceeded the known age range of released fish were omitted (66 fish out of 634 from the James River,10.4% and 5 fish out of 228, 2.2% from the Rappahannock River). The result is an estimated 10% error rate for wild American shad.

Hatch date distributions

Hatch dates of American shad juveniles were obtained by subtracting otolith age from the date of capture for each river. Because older cohorts experienced longer periods of mortality compared with younger cohorts, hatch date distributions were adjusted for mortality (Limburg 1996; Hoffman and Olney 2005). Cohort-specific mortality rates were used if available, otherwise average mortality rates from the entire year class were used to adjust hatch dates.

Growth

A candidate set of three growth models was initially considered to model juvenile growth for all rivers and years combined: von Bertalanffy, $L_t = L_\infty*(1 - e^{-k(t-t_o)})$, Gompertz, $L_t = L_\infty e^{(-1/k*e^\wedge-k(t-t_o))}$, and Richards, $L_t = L_\infty*(1 - d*e^{-k(t-t_o)})^{1/d}$; where L_t is length at age t, L_∞ is the asymptotic maximum length, t is age in days, t_0 is the theoretic length at age zero, and d is a dimensionless scaling parameter. Model parameters were estimated using maximum likelihood and models were compared using Akaike's Information Criterion (AIC; Burnham and Anderson

2002). Once the best growth model was identified, non-linear mixed models were used to compare three a priori hypotheses about processes controlling growth of American shad juveniles in Virginia. Proposed models included random effects due to river, year, and the combined effects of river and year. The candidate set of three models was evaluated using AIC.

Cohort-specific (5-d age bins) and year-class growth rates were estimated from back-calculated hatch dates and measured lengths for each river population following Crecco and Savoy (1985 and 1987). Instantaneous growth, G, was calculated by taking the derivative of the growth model with respect to time and calculating G at specific ages (40, 60, 80, and 100 d) for comparison. Because the Rappahannock River contained both hatchery-origin and wild American shad juveniles, a comparison of growth between groups was also performed.

Mortality

Cohort-specific (5-d age bins) and annual (year class) natural mortality rates were estimated by assigning ages to entire catch based on observed length and predicted age from the age-length-key and conducting linear regression analysis on the resulting catch-at-age data. The decline in abundance was assumed to be exponential and was described by: $N_t = N_0e^{-M*t}$ where N_t is abundance at time t, N_0 is initial abundance, and M is the instantaneous natural mortality rate (d^{-1}). Regressions were run using age of peak abundance as the starting point for the regressions for each cohort and only for those cohorts collected in three or more cruises. Age bins with fewer than 5 fish per bin were not used in regression analysis because of known bias with small sample sizes.

Historic data

Long-term data for a JAI for American shad were available from the Mattaponi and Pamunkey rivers by the VIMS juvenile striped bass survey. A continuous time series of catch and length records, as well as river flow and water temperature from each river, were available from 1985 to 2007. The survey sampling design consists of a series of 5 rounds (approximately every two weeks) from July to September where fixed stations were sampled using a minnow seine. Fixed stations include index stations (n=4 in the Mattaponi River and n=3 in the Pamunkey River) that are sampled every year and auxiliary stations (2 each in the Mattaponi and Pamunkey rivers) were sampled depending on stream flow conditions to ensure proper coverage of striped bass habitat. Collections were made by deploying a 30.5 m long, 1.2 m deep, 6.4 mm mesh seine perpendicular to the shoreline until either the net was fully extended or a depth of about 1.22 m was encountered. The offshore end of the seine was then pulled down-current and back to the shore. Although duplicate hauls were made at each index station during each round, and a single haul was made at each auxiliary station during most rounds, only YOY American shad taken in the first haul were used in analyses. All American shad collected were identified and counted and all individuals or a sub-sample of at least 25 individuals were measured to the nearest mm fork length. Annual JAIs were calculated as the geometric mean catch per haul and were based only on the first haul at each site. Mean daily water temperature and mean daily water flow were taken from the same USGS gauging stations on each river as described above.

Cowan et al. (2000) discuss the influence of critical weight in the establishment of successful year classes of fishes arguing that density-dependent decreases in growth and recruitment are likely to occur during the juvenile stage. To test the hypothesis that strong year classes of American shad in Virginia are comprised of small fishes due to density-dependent limitations on growth, a candidate set of models was developed to relate mean lengths of American shad near the end of the growing season (September) to water flow, water temperature, and annual abundance estimates. Mean water temperature was calculated using data from March to May since peak hatch of American shad larvae typically occurs during this time period and water temperature is likely to have the strongest influence on early growth. Water flow data from February to May was used to calculate mean flow as it has been demonstrated that flow can effect recruitment of larval American shad (Crecco and Savoy 1984).

The candidate model set consisted of seven competing hypotheses about the relationship between mean length of YOY shad and additional variables including water flow, water temperature, and annual JAIs in the Mattaponi and Pamunkey rivers (Table 2.1). Model parameters were estimated using maximum likelihood methods assuming a normal distribution of errors, which is appropriate for mean lengths. Strength of evidence for competing models was evaluated using the Information-Theoretic approach (Burnham and Anderson 2002).

RESULTS

Hydrography

Seasonal patterns in water discharge (m^3/s) were evident with high flow during spring and periods of low flow during summer months (Table 2.2). Annual discharge was below long-terms averages in 2005 and 2007 and slightly above average in 2006. There was a delay in springtime discharge in 2006 compared with the other two years. Mean discharge in all four rivers from April to October was lowest in 2007. The James River had the highest mean discharge rate, which was 3 to 4 times the rate observed in the Rappahannock River (Table 2.2). Mean discharge in the Pamunkey River was half of the flow observed in the Rappahannock River, but 1.5 times that observed in the Mattaponi River (Table 2.2).

Mean daily water temperature increased from April to August and decreased during September and October (Table 2.2). Mean water temperatures were lowest during 2006 in the Rappahannock, Mattaponi, and James rivers, while the lowest mean temperature in the Pamunkey River was in 2007. Warmest temperatures occurred during 2007 in the Rappahannock and James rivers and during 2005 in the Mattaponi River and 2006 in the Pamunkey River. Significant differences in water temperatures were observed during some months when hatching typically occurs (from April to June) with lowest water temperatures during April 2007 in all four rivers (Table 2.2).

American shad lengths and weights

A total of 14,140 YOY American shad were collected in push nets from 2005 to 2007 in the Rappahannock, Mattaponi, Pamunkey, and James rivers (Table 2.3). Highest abundance in each river occurred in 2005 followed by 2007 except for the Pamunkey River which suffered recruitment failure during 2007. The majority of American shad (81.5%) were captured in the Mattaponi River with more than 52% of those collected during 2005.

A mixture of wild and hatchery origin American shad were captured in the Rappahannock River. Releases of hatchery shad as larvae totaled more than 3 million in 2005, increased to 6 million in 2006, and decreased to 4 million in 2007. Re-captures of hatchery-origin fish comprised 59.4% of the catch in the Rappahannock in 2005, 28.6% in 2006, and 37.3% in 2007. Mean TLs of wild American shad from the Rappahannock River were larger than hatchery American shad and ranged from 59.1 to 59.9 mm (Table 2.3). Hatchery fish mean TLs ranged from 38.6 to 53.3 mm. Mean weights of wild American shad were greater than hatchery fish and ranged between 1.90 and 2.79 g. Mean weights of hatchery shad were about half the weights of wild shad, ranging from 0.86 to 1.43 g.

Length and weight distributions of YOY American shad from the Mattaponi River differed from those in the Pamunkey River from 2005 to 2007 (Kolmogorov-Smirnov, $P < 0.05$). Mean TLs from the Mattaponi River ranged from 47.8 to 57.7 mm and in the Pamunkey River ranged from 47.5 to 71.3 mm. Mean weights of American shad in the Mattaponi River were less than those in the Pamunkey and were between 1.30 and 2.12 g, whereas they were between 1.34 and 3.70 g in the Pamunkey River.

Almost all of the YOY American shad captured in the James River were of hatchery origin. Mean TLs ranged from 45.0 to 54.3 mm and mean weights ranged from 0.94 to 2.85 g (Table 2.3). A few otoliths did not show clear hatchery marks because the entire otolith fluoresced under ultraviolet light making mark discrimination difficult. There were eight wild American shad collected above Bosher's Dam, and all were collected in 2007. Releases of hatchery-origin shad in the James River were relatively consistent with 6 million larvae released in 2005, about 7 million in 2006, and 6 million in 2007.

Age determination

A total of 2,927 YOY American shad (20.7 % of total number caught) were aged. Mean ages of hatchery fish in the Rappahannock River ranged from 49.7 to 57.4 d, whereas mean ages of wild American shad ranged from 59.5 to 77.3 d (Table 2.3). In the Mattaponi River, mean ages ranged from 53.3 to 57.6 d and in the Pamunkey River mean ages ranged from 49.4 to 63.2 d. Mean ages of hatchery fish in the James River ranged from 43.5 to 70.5 d.

Hatch dates

Hatch dates of American shad appeared to follow peak flow events in spring. In the Rappahannock River, observed hatch dates of wild American shad occurred after peak discharge events in April when flows were ≤100 m^3/s and when water temperatures increased to 15 °C (Fig. 2.2). In the Mattaponi River, where flow is much lower, hatch occurred at flows $\leq$ 60 m^3/s, and at temperatures as low as 11 °C (Fig. 2.3). Hatch in the Pamunkey River occurred at flows $\leq$100 m^3/s and at temperatures similar to those in the Mattaponi River (11 °C; Fig. 2.4).

Hatchery-reared American shad were released in the Rappahannock River from 7 April to 16 May during 2005, from 30 April to 30 May during 2006, and from 3 May to 30 May during 2007 (Fig. 2.2). Hatch dates from recaptures of hatchery marked juveniles varied each year. In 2005 and 2006, ages of recaptured hatchery fish spanned the dates of releases indicating that most releases were producing YOY American shad. In 2007, however, recaptures were only from releases that occurred later in the spring (12 May to 27 May). Wild American shad hatch dates ranged from 2 April to 25 June in 2005, from 26 April to 3 June in 2006, and from 25 April to 20 May in 2007.

Hatch dates in the Mattaponi River during 2005 and 2006 were similar and ranged from approximately mid-April to late-June with peak hatch occurring on 21 May (Fig. 2.3). In 2007, hatch dates ranged from 13 April to 7 June with peak hatch occurring three weeks earlier (30 April) than in the other two years.

In the Pamunkey River hatch dates were more variable than in the Mattaponi River and peak hatch typically occurred earlier in the Pamunkey River. Hatching ranged from 17 April to 12 June with peak hatch occurring on 11 May in 2005 (Fig 2.4). In 2006 hatch occurred earlier from 7 April to 12 June with peak hatch on 14 April. In 2007 hatch dates ranged from 10 April to 31 May.

American shad captured in the James River were nearly all hatchery fish. Releases of hatchery fish occurred from 9 April to 11 May in 2005, from 10 April to 12 May in 2006 and from 5 April to 7 May in 2007 (Fig. 2.5). Recaptures of hatchery fish in 2005 and 2006 occurred from 22 April to 17 May and in 2007 from 14 April to 4 May. The eight wild American shad captured above Bosher's Dam hatched between 28 April and 3 May, 2007.

Mortality

Instantaneous mortality of American shad increased from 2005 to 2007 in all rivers with the James River having the highest mortality rates and the Rappahannock River the lowest rates (Fig. 2.6). In 2005, M of American shad in the James River was 8 times higher than the estimate for wild American shad from the Rappahannock River, and twice that for hatchery American shad from the Rappahannock River. Similarly, M of American shad from the James River in 2005 was twice the observed rates for wild American shad in the Mattaponi and Pamunkey rivers (Table 2.4). Mortality increased in 2006 among rivers with American shad in the James River experiencing nearly 8 times the mortality rate found in the Rappahannock River and 2.5 times the rates observed for the Mattaponi and Pamunkey populations. The highest values of M were observed in 2007 with the James River population experiencing 8.5 times the rates observed for hatchery fish and 3.4 times the rate of wild American shad in the Rappahannock. Mortality rate in the James River was 2.4 times higher than in the Mattaponi River.

Within the Rappahannock River, instantaneous mortality for wild YOY American shad was four times lower than that of hatchery-origin fish during 2005. But in 2007, mortality of wild shad was 2.5 times higher (0.05 d^{-1}) than that of hatchery fish (0.02 d^{-1}). However, the standard errors of the estimated M's were wide making it difficult to compare years. Too few hatchery American shad were captured in 2006 to estimate mortality (Table 2.4).

Cohort specific mortality rates of YOY American shad from the Mattaponi River were 1.5 times higher in 2006 than in 2005; highest mortality rates in the Mattaponi River were observed in 2007, with an average M for all cohorts combined of 0.07 d^{-1} (Table 2.4).

Mortality rates of cohorts from the Pamunkey River were higher than those in the Mattaponi River and ranged from 0.02 to 0.09 d^{-1} (Table 2.4). Nevertheless, the estimate for all cohorts combined was the same as that for all Mattaponi River cohorts (0.04 d^{-1}). In 2006, M from the Pamunkey River was similar to that in the Mattaponi River and ranged from 0.03 to 0.08 d^{-1}. Cohort-specific mortality estimates in the James River, which could only be estimated in 2005, ranged from 0.04 to 0.07 d^{-1} (Table 2.4).

Growth

Growth of YOY American shad slowed in late summer and the von Bertalanffy growth equation was superior to the other models in characterizing growth (Table 2.5). Because of model convergence issues related to the negative correlation between L_∞ and k, the von Bertalanffy model was re-parameterized by substituting $\varpi = L_\infty * k$ (Gallucci and Quinn 1979). Asymptotic length was calculated from model results using the formula $L_\infty = \varpi / k$ and the variance of L_∞ was estimated using the Delta method.

The non-linear mixed model with a river*year interaction term for random effects, that also included a variance inflation factor to account for increasing length with increasing age, was the best model in the candidate set (Table 2.6). Standardized residuals for the selected model were random and show that the variance inflation factor in the model properly accounted for increasing lengths with increasing age (Fig. 2.7). Furthermore, residuals were plotted against the random effects for Year (Fig. 2.8) and River (Fig. 2.9) and results are centered near zero and show that there is no bias for the best model.

Maximum length by the end of summer for juvenile American shad was 112.86 mm TL (SE 1.658) and varied by river and year (Fig. 2.10). Deviations from estimated L_∞ due to random effects from each river and year are shown in Table 2.7. Parameter estimates for maximum length ($L_\infty = \omega / k$) of juvenile American shad in the James River were always above average, whereas those same estimates were below average for the Mattaponi River. The individual effects of River (Table 2.8) and Year (Table 2.9) on parameter estimates show that there were significant differences in L_∞ between the James and Mattaponi rivers compared with the average estimate and that L_∞ during 2005 was significantly different from the other two years. The growth coefficient, k, was significantly different in the Mattaponi River from the average compared with the other rivers and differed significantly during 2005 versus the average.

Cohort-specific growth

Growth of wild and hatchery-origin American shad from the Rappahannock River showed similar patterns among years. However, G was faster for wild American shad (Table 2.10; Fig. 2.7). Instantaneous growth rates of wild shad at 40 d (G_{40}) were 1.2 times higher during 2005 than in 2007. Although, growth rates of wild American shad decreased by 100d, rates in 2005 remained 1.5 times those observed in 2007.

Instantaneous growth in the Mattaponi River at 40 d in 2005 was 74% of that observed in 2006, and 68% of that observed in 2007. In the Pamunkey River, G_{40} during 2006 was 85% of that observed in 2005. Comparisons of G_{40} between rivers showed that American shad from the Pamunkey River grew nearly 1.5 times faster than those from the Mattaponi River in 2005, but slower in 2006. Instantaneous growth at 100 d (G_{100}) slowed in each river relative to G_{40}, with the Mattaponi River having higher rates than the Pamunkey River.

Cohort specific G_{40} in the Mattaponi River was slower during 2005 compared with 2006 and 2007 (Table 2.11). Instantaneous G_{40} ranged from 0.77 to 1.14 mm d^{-1} in 2005, from 1.02 to 2.06 mm d^{-1} in 2006 and from 0.87 to 1.29 mm d^{-1} in 2007. Growth rates declined with age and at 100 d, ranged from 0.20 to 0.34 mm d^{-1} in 2005, from 0.14 to 0.39 mm d^{-1} in 2006, and from 0.10 to 0.30 mm d^{-1} in 2007. Cohort-specific K's for Mattaponi shad in 2006 were negatively correlated with water temperature (Pearson's correlation, r= -0.73, p=0.039) and positively correlated with flow (r = 0.77, P=0.026).

In the Pamunkey River, cohort specific G_{40} during 2005 was 0.3 to 0.4 mm d^{-1} faster than in 2006 (Table 2.12). Instantaneous growth estimates at 40 d ranged from 1.16 to 1.46 mm d^{-1} in 2005 and from 0.77 to 1.19 mm d^{-1} in 2006. At 100 d, growth slowed and ranged from 0.08 to 0.50 mm d^{-1} in 2005 and from 0.24 to 0.43 mm d^{-1} in 2006. Growth coefficients were negatively correlated with water flow during 2005 with higher growth rates at lower flow levels (Pearson's correlation, $r = -0.922$, $P=0.026$).

Young-of-year shad in the James River reached smaller asymptotic lengths during 2005 compared with 2006 (Table 2.10; Fig. 2.10). Growth of American shad at 40 d was similar between 2005 and 2007, but was about 10% lower than that observed during 2006 (Table 2.10). Cohort specific instantaneous growth rates at 40 d ranged from 0.74 to 1.12 mm d^{-1} in 2005. Growth rates at 100 d slowed to 0.29 to 0.39 mm d^{-1} for cohorts in 2005. Growth rates at 100 d during 2005 and 2007 were 0.10 mm d^{-1} lower than in 2006.

Changes in relative biomass of year classes from the Mattaponi and Pamunkey rivers were estimated by combining growth and mortality models after converting lengths to weights by applying an allometric relationship between length and weight: $W_t = a*L_t^{\wedge b}$. Results show annual differences in YOY shad biomass, with peak relative biomass differing >2-fold in the Mattaponi River among years and about 1.75-fold in the Pamunkey (Fig. 2.11). Age at which peak relative biomass occurred also differed among years, ranging from 40 d to 60 d post-hatch (Fig. 2.11). By 100 d, estimated year-class relative biomass was consistent with patterns of recruitment observed through JAI estimates from the

VIMS striped bass seine survey with relatively strong year-classes during 2005, and weaker year-classes during 2006 and 2007 (Table 2.13). Year-classes that reached peak relative biomass later in the year resulted in higher JAI estimates.

Historic records of shad abundance

Evidence supports the hypothesis that water flow, water temperature, and abundance have an effect mean length (FL) of YOY American shad at the end of summer. There was no support for including all three variables together to predict mean length, but considerable support for including abundance and either water flow or water temperature (Table 2.1). Comparing the best fit model with observed fork lengths of American shad from the striped bass seine survey shows a strong congruence for the Mattaponi and Pamunkey river systems (Fig. 2.12). Furthermore, there is a decline in mean fork length versus abundance for both river populations (Fig. 2.13).

DISCUSSION

Age validation

Young of year American shad deposit daily increments in otoliths through early fall with sufficient visibility to provide accurate ages to about 160 d. A previous age validation study demonstrated daily deposition of increments in larval American shad, but assumed that daily deposition continued throughout the juvenile stage (Crecco and Savoy 1985). Limburg (1994) also demonstrated that otolith ring counts were possible for YOY American shad using pond-reared specimens and was able to correctly assign ages up to 152 d. Because the basis of many growth and mortality models is the assumption of known ages, validation is a critical aspect of research (Beamish and McFarlane 1983). The use of known-age fish reared in outdoor ponds provides a suitable method for such age validation (Campana 2001).

Potential sources of error in age assignment in this study were most likely due to hatchery origin and two specific regions in the otolith. The first corresponds to the core region and difficulty in determining daily increments during the first few days in the hatchery. Further examination of wild and hatchery American shad otoliths showed that increments near the core of wild American shad were more visible than those from hatchery fish verifying the influence of hatchery conditions on early growth. The second region resulting in errors was the miscount of increments along the outer posterior edge of the otolith from either the close proximity of the increments to one another or poor slide preparation. After about 70 d there is a decrease in increment width and after 100 d, individual growth increments are difficult to discern. Otoliths must be ground to the very edge for all daily increments to be clearly visible. If the otoliths are ground too much, several increments could easily be removed and the loss would be difficult to detect. Conversely, not grinding otoliths enough causes the increments at the edge to blur into one another under transmitted light and increases the chances of incorrect increments counts. During winter, increment width becomes a significant source of error as increments in otoliths of wild American shad collected in January (age 270+ d, assuming a hatch date of 15

April) were extremely difficult to detect at the outer edge of the otoliths. Ages assigned to American shad captured in January were biased low and indicated that hatch would have been during August, a phenomenon never observed in Virginia. The difficulty in counting increments for American shad after growth slows suggests an upper limit to effective daily ageing of YOY American shad using visible light microscopes.

Hatch dates and hydrography

The timing of spawning for American shad is considered to be temperature dependent and typically occurs when water temperatures are between 15 and 25 ^{o}C (Bilkovic et al. 2002). Therefore, it was not unexpected that hatch date distributions among neighboring rivers showed strong synchrony related to flow and water temperature given the small range of latitude (1^{o}) of the four populations of American shad. The exception was the Pamunkey River during 2006 with peak hatch occurring 35 d prior to peak hatch in the Mattaponi River and 16 d prior to the peak for wild American shad in the Rappahannock River. Differences in observed hatch date distributions could be related to water flow as the spring freshet was delayed in 2006 compared with the other two years. Why the hatch date distribution in the Pamunkey River would vary from the observed patterns in the Mattaponi and Rappahannock rivers is unknown. Perhaps differences are the result of differing spawning activity, different age distribution of adult spawners, or differential survival of early stages.

Duration of hatch is not directly related to year class strength. Hatch of American shad was variable and lasted longer in the Mattaponi River than in the Pamunkey River in some years. During 2005, hatching occurred an additional 21 d on the Mattaponi compared with hatch dates from the Pamunkey River, while during 2006 and 2007 there was little difference (< 5 d). If spawning lasted longer on the Mattaponi River, then that could explain the larger year class size observed in 2005. However, that does not account for larger year classes observed in the Mattaponi River during 2006 or 2007. Furthermore, hatch of wild American shad in 2005 in the Rappahannock River lasted for 84 d, yet the JAI value for the Rappahannock River was nine times lower than in the Mattaponi River for that year. The period during which hatching occurred, as inferred from otolith analysis, only accounts for those cohorts that survived to be caught as juveniles. In addition, there is limited information on spawning stock size and demographics, both critical components in estimating egg production.

Growth and mortality

Growth of YOY American shad slowed with corresponding decreases in seasonal water temperature. Previous work on early stages of American shad also found growth to slow towards the end of summer (Chittenden 1969; Crecco et al. 1983; Limburg 1996). However, one study found growth to be exponential (Hoffman and Olney 2005). Hoffman and Olney (2005) examined otoliths of juvenile American shad in the Pamunkey River during a period of high recruitment (JAIs of 0.8 and 1.1) compared with this study and found similar hatch dates and mortality rates, but different growth rates. Early growth rate estimates (age = 40 d) were similar between studies (about 0.8 to 0.9 mm d^{-1}), but late stage growth was drastically slower during 2005 to 2007 (this study). Daily growth rate of YOY American shad at 80 d was estimated from data provided in Hoffman and Olney (2005) and was two to four times faster than rates observed in this study (approximately 0.725 mm d^{-1} during 1998 and 1999 versus 0.17 to 0.48 mm d^{-1} from 2005 to 2007). Growth rates of YOY American shad reported from the Connecticut River also were higher than I observed in this study. The Connecticut River rates ranged from 1.2 to 1.4 mm d^{-1} between age 30 and 60 days and from 0.8 to 0.9 mm d^{-1} between age 60 and 90 days (Crecco et al. 1983; Crecco and Savoy 1985). Higher growth rates in northern rivers compared with rivers in VA is consistent with counter-gradient growth with similar sizes reached by the end of the growing season independent of latitude (Conover 1990). If there are differences in size at the end of the first year and stocks of juvenile American shad mix in the coastal ocean, as is currently believed (Talbot and Sykes 1956), then size-dependent mortality can play a significant role in structuring coastal population dynamics of YOY American shad. Smaller YOY American shad from Virginia stocks may experience higher predation pressure compared with larger-sized northern American shad. Savoy and Crecco (2004) found that increased abundance of predatory striped bass (*Morone saxatilis*) provided a plausible explanation for recent and severe declines of American shad and blueback herring (*Alosa aestivalis*) in the Connecticut River and this hypothesis could easily be extended to include other stocks as well. However, counter gradient growth does not explain differences observed between Hoffman and Olney (2005) and mine. If there has been a reduction in growth of YOY American shad in VA nurseries in recent years, then the result would be smaller sizes at the time if emigration and a likely increase in mortality due to predation. In any case, the increased abundance of striped bass in recent years could be slowing recovery of American shad stocks independent of regulatory changes in American shad fisheries due to dynamics during the juvenile stage that could occur in the freshwater tributaries or in the coastal ocean.

Average mortality rates of YOY American shad year-classes increased in all four rivers during the period from 2005 to 2007. Rates observed in the James and Rappahannock rivers should be considered with caution since the sampling design did not cover the entire juvenile nursery, but only the portion where catches of hatchery fish were expected. Estimated mortality rates from the Mattaponi and Pamunkey rivers. Where sampling covered the entire nursery, are similar to rates reported in Hoffman and Olney (2005), but higher than rates from the Connecticut River (Crecco et al. 1983). In the Connecticut River, Crecco et al. (1983) found that juvenile mortality rates were relatively low (0.018 to 0.020 d^{-1}) and remained consistent among years, while Hoffman and Olney (2005) found that mortality rates in the Pamunkey River varied and ranged from 0.078 to 0.096 d^{-1}. It is apparent that mortality of YOY American shad from Virginia rivers is more variable and higher than that of more northern populations and likely contributes to poor year class strength.

Lower and less variable mortality rates for YOY American shad in the Mattaponi River compared with that of the Pamunkey River likely contributes to the greater production of American shad in the Mattaponi River. Only small variability in mortality is sufficient to alter year-class strength by an order of magnitude or more (Houde 1987; Houde 1997a). Cohort-specific mortality rates of American shad in the Mattaponi River were low and relatively constant in 2005, but were higher and more variable during 2006 and 2007. A similar pattern was observed for growth rates indicating that production of biomass was highly variable in the Mattaponi River. Juvenile abundance indices for 2006 and 2007 from the Mattaponi River were similar (0.29 and 0.24), while the JAI in 2005 was >6 times higher (1.66), suggesting that variable rates in growth and mortality limited cohort production during 2006 and 2007. A comparison of M/G for the Mattaponi River showed the lowest M/G during 2005 relative to 2006 and 2007 indicating a greater possibility for recruitment success. In the Pamunkey River, higher growth rates in 2005 and similar mortality rates compared with 2006 resulted in a lower M/G ratio and coincided with a higher JAI in 2005.

Evidence supports a positive relationship between length at the end of the first summer and water flow or water temperature, and a negative relationship with con-specific abundance. It has been proposed that high water discharge increases production of YOY American shad through subsidies of terrestrially derived allochthonous material, which stimulates zooplankton production thereby increasing the food-base available for feeding (Hoffman et al. 2007). Furthermore, decreased size due to high abundance of siblings provides some evidence that YOY American shad in Virginia are food-limited and indicates that growth is density dependent. The linkage between high flow that stimulates production of prey and promotes growth versus high flow that reduces growth through increased turbidity and poor feeding or short residence time of nutrients may be a fertile area of study.

Cohort dynamics of YOY American shad in Virginia are highly variable as a result of complex interactions with the environment and density-dependent processes. Despite the close proximity of four river systems studied, there were persistent differences in growth and mortality rates that support observed trends in year-class strength and status of stocks. Inferences are limited on the James and Rappahannock rivers because the scope of sampling did not encompass the entire nursery habitat. However, the high mortality rates observed in the James River may be the reason for almost complete recruitment failure of wild American shad in this system. Furthermore, the low mortality rates in the Rappahannock River are consistent with an increasing trend in recruitment of maturing adult females (ASMFC 2007). Lower mortality rates and similar growth rates of YOY American shad observed in the Mattaponi River compared with the Pamunkey River support observations of greater juvenile production in the Mattaponi River (Wilhite et al. 2003). Because populations from the Mattaponi and Pamunkey rivers are considered a single stock for management (York River stock), and there is evidence that female American shad hatched in the Mattaponi River spawn in the Pamunkey River, observed differences in growth and mortality are likely driven by river-specific processes and not genetically derived from local adaptations at the tributary level (Walther et al. 2008). Differences in population dynamics of YOY American shad observed between rivers in VA demonstrates the level of variation in annual rates that exists at a relatively small spatial scale and the potential impacts those rates may have on year-class strength.

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Table 2.1. Summary of a priori models examining variables (water temperature, water flow, American shad JAI) that may influence mean fork length in September in the Mattaponi and Pamunkey rivers. Shown are the log-likelihood values, number of parameters (K), corrected Akaike Information Criterion values (AIC_c), AIC differences (Δi), model likelihood, and Akaike weights (ωi).

Species	River	Model	Variables	log(*L*)	K	AIC_c	Δi	Model likelihood	ωi
American shad	Mattaponi	1	Flow, temperature, abundance (linear)	-41.58	5	97.45	5.42	0.07	0.04
		2	**Flow, abundance (linear)**	**-41.61**	**4**	**93.88**	**1.85**	**0.40**	**0.22**
		3	Temperature, abundance (linear)	-42.16	4	94.98	2.95	0.23	0.12
		4	Flow, temperature (linear)	-51.68	4	114.03	22.00	0.00	0.00
		5	Flow, temperature, abundance (exponential)	-40.85	5	95.99	3.96	0.14	0.08
		6	**Flow, abundance (exponential)**	**-40.68**	**4**	**92.03**	**0.00**	**1.00**	**0.54**
		7	Temperature, abundance (exponential)	-41.36	6	101.19	9.16	0.01	0.01
	Pamunkey	1	Flow, temperature, abundance (linear)	-32.13	5	84.25	6.24	0.04	0.02
		2	**Flow, abundance (linear)**	**-32.26**	**4**	**78.23**	**0.22**	**0.90**	**0.32**
		3	**Temperature, abundance (linear)**	**-32.57**	**4**	**78.86**	**0.85**	**0.65**	**0.23**
		4	Flow, temperature (linear)	-33.90	4	81.52	3.51	0.17	0.06
		5	Flow, temperature, abundance (exponential)	-32.36	5	84.72	6.71	0.03	0.01
		6	**Flow, abundance (exponential)**	**-32.15**	**4**	**78.01**	**0.00**	**1.00**	**0.36**
		7	Temperature, abundance (exponential)	-29.99	6	88.77	10.76	0.00	0.00

Table 2.2. Mean monthly water temperature and discharge rate from April to October and the average for the time period from the Rappahannock, Mattaponi, Pamunkey and James rivers (2005 - 2007). Significant differences (ANOVA, Tukey HSD, a =0.05) among years for months when hatch typically occurs (April to June) are indicated by different superscript letters.

		Water temperature (^{o}C)			Water discharge (m^3/s)		
River	Month	2005	2006	2007	2005	2006	2007
Rappahannock	Apr	14.4 ^{a}	16.5 ^{b}	13.6 ^{a}	103.9	39.3	62.0
	May	18.0 ^{a}	19.7 ^{ab}	21.4 ^{b}	49.5	28.1	23.2
	Jun	26.1 ^{a}	25.4 ^{a}	26.7 ^{a}	19.1	35.1	9.7
	Jul	28.2	27.5	27.6	28.9	31.9	3.3
	Aug	28.1	29.0	28.2	11.7	5.0	6.5
	Sep	24.6	21.1	25.1	5.3	29.4	3.3
	Oct	15.0	14.2	21.0	67.0	54.6	6.5
	Average	24.0	23.0	25.5	40.8	31.9	16.3
Mattaponi	Apr	15.7 ^{a}	16.1 ^{a}	15.0 ^{a}	29.2	12.6	24.8
	May	19.1 ^{a}	17.8 ^{a}	19.6 ^{a}	16.4	10.4	13.6
	Jun	26.5 ^{a}	22.6 ^{b}	23.4 ^{b}	5.5	8.1	4.8
	Jul	29.6	25.4	24.6	6.3	12.3	1.8
	Aug	29.7	25.8	25.3	2.9	1.2	2.0
	Sep	26.2	19.8	21.6	0.9	16.2	0.9
	Oct	18.4	14.2	17.9	9.0	19.3	2.5
	Average	26.0	21.3	22.4	10.0	11.4	7.2
Pamunkey	Apr	15.4 ^{a}	17.4 ^{a}	14.0 ^{b}	51.8	17.1	36.0
	May	19.2 ^{a}	20.9 ^{a}	20.2 ^{a}	26.1	14.8	12.1
	Jun	27.4 ^{a}	26.2 ^{ab}	24.5 ^{b}	10.1	16.0	6.9
	Jul	30.0	28.8	26.1	8.5	7.9	4.1
	Aug	28.3	29.4	26.7	5.5	2.9	4.5
	Sep	25.0	22.9	23.0	2.7	15.6	2.4
	Oct	17.8	21.3	18.4	18.5	44.6	4.2
	Average	25.3	25.6	23.5	17.6	17.0	10.0
James	Apr	15.1 ^{a}	17.9 ^{b}	14.4 ^{a}	355.6	155.2	356.7
	May	18.9 ^{a}	20.4 ^{ab}	21.8 ^{b}	185.0	94.6	154.4
	Jun	26.4 ^{a}	25.8 ^{a}	26.9 ^{a}	94.0	227.2	86.8
	Jul	29.1	28.7	28.3	95.2	122.6	54.4
	Aug	29.1	30.1	29.7	58.6	31.2	41.6
	Sep	26.4	22.0	26.5	39.4	134.9	29.7
	Oct	17.7	15.2	21.0	121.0	306.4	51.0
	Average	25.6	24.0	26.4	135.5	153.2	110.7

Table 2.3. Length, wet weight, and age of American shad from the Rappahannock, Mattaponi, Pamunkey, and James rivers (2005 - 2007). The number of American shad (N), minimum (Min), maximum (Max), and SD of total length, wet weight, and daily age are shown.

			Total length (mm)				Wet weight (g)				Age (d)			
River	Year	N	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Rappahannock (Wild)	2005	125	20.0	104.9	59.9	22.0	0.19	9.65	2.79	2.5	25	168	77.3	33.8
	2006	35	36.6	104.2	59.7	14.6	0.39	7.95	2.07	1.6	34	157	59.5	23.2
	2007	52	33.0	74.8	59.1	8.8	0.39	3.87	1.90	0.8	37	93	60.0	13.5
Rappahannock (Hatchery)	2005	183	27.0	93.8	38.6	13.6	0.26	7.05	0.86	1.1	34	139	49.7	20.2
	2006	14	31.8	62.2	50.8	7.8	0.21	2.11	1.15	0.5	32	66	51.9	9.6
	2007	31	37.0	73.8	53.3	9.5	0.47	3.67	1.43	0.7	38	90	57.4	15.1
Mattaponi	2005	7362	18.1	93.3	47.8	15.5	0.05	6.93	1.30	1.1	19	167	57.6	28.1
	2006	1424	25.3	104.5	55.6	18.5	0.14	9.23	2.12	1.8	26	152	53.3	22.4
	2007	2738	28.4	96.9	57.7	10.9	0.24	7.53	2.01	1.0	26	130	54.8	14.6
Pamunkey	2005	806	22.1	97.8	53.2	14.1	0.09	7.82	1.62	1.2	25	151	54.9	17.3
	2006	666	28.1	102.6	47.5	14.8	0.04	9.97	1.34	1.5	28	114	49.4	14.4
	2007	70	38.1	99.3	71.3	10.1	0.49	8.74	3.70	1.4	37	82	63.2	8.3
James (Hatchery)	2005	308	27.3	132.1	54.3	27.9	0.30	20.04	2.85	4.2	30	186	70.5	48.8
	2006	142	34.4	110.5	51.1	12.1	0.40	10.26	1.41	1.4	34	128	51.7	14.9
	2007	184	33.5	65.7	45.0	6.1	0.41	2.52	0.94	0.3	31	69	43.5	5.6

Table 2.4. Instantaneous total mortality rates for the Rappahannock, Mattaponi, Pamunkey, and James rivers from 2005 to 2007 by year class (All) and cohort. M is the mortality rate, se is the standard error and N are the number of American shad.

	2005					2006					2007				
River	Cohort	Hatch date	M	se	N	Cohort	Hatch date	M	se	N	Cohort	Hatch date	M	se	N
Rappahannock															
Hatchery	All		0.04	0.037	113					14	All		0.02	0.015	26
Wild	All		0.01	0.013	57	All		0.02	0.011	35	All		0.05	0.026	52
Mattaponi	3	28-Apr	0.04	0.018	290	3	3-May	0.04	0.021	100	3	1-May	0.10	0.025	180
	4	3-May	0.04	0.008	381	4	8-May	0.05	0.019	280	4	6-May	0.07	0.003	499
	5	8-May	0.01	0.020	264	5	13-May	0.05	0.016	227	5	11-May	0.07	0.009	532
	6	13-May	0.05	0.013	1561	6	18-May	0.02	0.024	213	6	16-May	0.04	0.009	559
	7	18-May	0.03	0.012	995	7	23-May	0.09	0.019	88	7	21-May	0.03	0.012	192
	8	23-May	0.04	0.009	573	8	28-May	0.09	0.004	91	8	26-May	0.21	0.006	84
	9	28-May	0.03	0.008	1370	9	2-Jun	0.05	0.028	46	9	31-May	0.06	0.050	91
	10	2-Jun	0.01	0.009	540	10	7-Jun	0.02	0.011	18	10	5-Jun	0.06	0.012	74
	11	7-Jun	0.02	0.011	135										
	12	12-Jun	0.02	0.012	78										
	All		0.04	0.003	5948	All		0.06	0.006	1073	All		0.07	0.003	2362
Pamunkey	3	3-May	0.03	0.002	65										
	4	8-May	0.08	0.069	62	4	28-Apr	0.08	0.017	225					
	5	13-May	0.09	0.075	85	5	3-May	0.08	0.026	137					
	6	18-May	0.04	0.012	88	6	8-May	0.04	0.011	65					
	7	23-May	0.03	0.012	107	7	13-May	0.02	0.031	33					
	8	28-May	0.02	0.007	78										
	All		0.04	0.008	583	All		0.07	0.009	537					70
James	4	9-May	0.04	0.011	49										
	5	14-May	0.07	0.030	59										
	All		0.08	0.019	194	All		0.15	0.044	78	All		0.17	0.020	154

Table 2.5. Comparisons of growth models for juvenile American shad during the first year of growth. K is the number of paramters estimated, AIC is Akaiki's Information Criterion, and ΔAIC is the difference between the best model and the others.

Model	loglik	K	AIC	ΔAIC
von Bertalanffy	-48135.20	4	96278.40	0.00
Gompertz	-48389.46	4	96786.91	508.51
Richards	-48142.63	5	96295.26	16.86

Table 2.6. The estimates of fixed-effects parameters for $L_t=\omega/k*(1-e^{-k*(age-t0)})$; $\omega = L_\infty*k$, and the logliklihood, AIC, and ΔAIC values. Total observations = 14,151, number of groups for the best model (bold) = 12.

Model	ϖ ±SE(ω)	k ±SE(k)	t0 ±SE(t0)	L_∞ ±SE(L_∞)	LogLik	AIC	ΔAIC
River	1.57 (0.11)	0.0145 (0.0027)	8.705 (0.978)	108.27 (0.82)	-46960.63	93943.27	6770.95
Year	1.88 (0.32)	0.0198 (0.0047)	8.254 (3.38)	94.95 (1.54)	-44972.96	89967.91	2795.59
River*year	**1.58 (0.21)**	**0.0140 (0.0036)**	**4.289 (2.79)**	**112.86 (1.66)**	**-43575.16**	**87172.32**	**0**

Table 2.7. Deviation of parameter estimates (random effects) from fixed-effects by river and year.

River	Year	ω	k	t0
James	2005	-0.56	-0.0078	-4.76
	2006	-0.42	-0.0077	-5.16
	2007	-0.36	-0.0052	-5.57
Mattaponi	2005	-0.27	0.0001	-2.99
	2006	0.99	0.0133	10.90
	2007	1.08	0.0186	9.93
Pamunkey	2005	0.52	0.0096	8.71
	2006	-0.90	-0.0184	-15.20
	2007	-0.31	-0.0094	-6.00
Rappahannock	2005	-0.50	-0.0071	1.72
	2006	-0.18	-0.0031	-3.02
	2007	0.90	0.0172	11.45

Table 2.8. Effects of River on parameter estimates in the fixed effects model for growth of American shad juveniles relative to the James River.

Parameter	River	Value	Std.Error	DF	t-value	p-value
ω	James	1.0870	0.32333	14128	3.362	0.0008
	Mattaponi	1.0921	0.43831	14128	2.492	0.0127
	Pamunkey	0.2505	0.45141	14128	0.555	0.5789
	Rappahannock	0.5037	0.46546	14128	1.082	0.2792
k	James	0.0064	0.00562	14128	1.134	0.2569
	Mattaponi	0.0183	0.00752	14128	2.433	0.0150
	Pamunkey	0.0013	0.00776	14128	0.165	0.8689
	Rappahannock	0.0087	0.00796	14128	1.092	0.2750
t_0	James	-2.1318	5.29875	14128	-0.402	0.6875
	Mattaponi	12.3819	6.61928	14128	1.871	0.0614
	Pamunkey	2.2742	7.07218	14128	0.322	0.7478
	Rappahannock	9.9423	7.02429	14128	1.415	0.1570

Table 2.9. Effects of Year on parameter estimates in the fixed effects model for growth of American shad juveniles realtive to 2005.

Parameter	Year	Value	Std.Error	DF	t-value	p-value
ω	2005	1.3704	0.34980	14131	3.918	0.0001
	2006	0.0098	0.49727	14131	0.020	0.9843
	2007	0.6598	0.50831	14131	1.298	0.1943
k	2005	0.0126	0.00611	14131	2.058	0.0396
	2006	-0.0037	0.00868	14131	-0.422	0.6729
	2007	0.0087	0.00890	14131	0.972	0.3311
t_0	2005	4.9367	4.60396	14131	1.072	0.2836
	2006	-5.6628	6.74257	14131	-0.840	0.4010
	2007	2.2096	6.80502	14131	0.325	0.7454

Table 2.10. Cohort specific growth estimates of American shad from the James and Rappahannock river from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_o and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm d^{-1}) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided. Separate estimates of growth for hatchery (James and Rappahannock) and wild (Rappahannock only) American shad were performed.

River	Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_0 (SE)	N	G_{40}	G_{60}	G_{80}	G_{100}
James	2005	2	29-Apr	93.89 (16.511)	0.0157 (0.007)	11.76 (8.792)	13	0.95	0.69	0.50	0.37
		3	4-May	88.45 (9.974)	0.0203 (0.006)	16.90 (5.795)	39	1.12	0.75	0.50	0.33
		4	9-May	99.42 (8.747)	0.0157 (0.003)	11.66 (2.792)	83	1.00	0.73	0.53	0.39
		5	14-May	88.65 (4.704)	0.0218 (0.003)	14.61 (1.920)	96	1.11	0.72	0.46	0.30
		6	19-May	87.64 (6.567)	0.0158 (0.004)	3.04 (5.607)	13	0.74	0.54	0.39	0.29
		All		96.04 (4.506)	0.0156 (0.002)	9.32 (1.772)	247	0.93	0.68	0.50	0.36
	2006	All		116.03 (6.917)	0.0136 (0.002)	8.05 (2.421)	140	1.02	0.78	0.59	0.45
	2007	All		99.98 (8.595)	0.0157 (0.002)	5.23 (2.220)	184	0.91	0.66	0.49	0.35
Rappahannock Wild	2005	All		113.07 (4.735)	0.0132 (0.001)	13.41 (1.957)	125	1.05	0.81	0.62	0.48
	2006	All		111.39 (7.419)	0.0154 (0.002)	6.45 (3.632)	35	1.02	0.75	0.55	0.41
	2007	All		95.88 (9.306)	0.017 (0.005)	3.37 (6.004)	52	0.88	0.62	0.44	0.31
Hatchery	2005	All		112.43 (4.736)	0.0114 (0.001)	10.87 (1.193)	183	0.92	0.73	0.58	0.46
	2006	All		92.60 (11.655)	0.0178 (0.004)	6.306 (3.920)	14	0.90	0.63	0.44	0.31
	2007	All		90.19 (8.616)	0.0169 (0.004)	2.70 (5.258)	31	0.81	0.58	0.41	0.29

Table 2.11. Cohort specific growth estimates of American shad from the Mattaponi River from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_0 and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm d^{-1}) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_0	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	3	28-Apr	68.49 (1.244)	0.027 (0.002)	17.21 (1.246)	309	0.99	0.58	0.34	0.20
	4	3-May	86.00 (3.273)	0.016 (0.001)	8.78 (1.423)	390	0.84	0.61	0.44	0.32
	5	8-May	80.05 (1.188)	0.022 (0.001)	11.33 (0.640)	719	0.93	0.60	0.39	0.25
	6	13-May	77.04 (1.022)	0.023 (0.001)	8.69 (0.455)	1129	0.86	0.54	0.34	0.22
	7	18-May	82.49 (0.850)	0.018 (0.000)	2.35 (0.490)	1230	0.75	0.53	0.37	0.26
	8	23-May	78.23 (0.817)	0.022 (0.001)	5.81 (0.619)	1398	0.81	0.52	0.33	0.21
	9	28-May	83.24 (0.935)	0.019 (0.001)	2.48 (0.686)	1077	0.77	0.53	0.37	0.25
	10	2-Jun	88.68 (1.441)	0.016 (0.001)	4.09 (1.975)	405	0.80	0.58	0.42	0.30
	11	7-Jun	91.26 (1.736)	0.016 (0.001)	5.74 (2.457)	256	0.83	0.61	0.45	0.33
	12	12-Jun	89.81 (2.564)	0.020 (0.003)	17.19 (5.827)	106	1.14	0.76	0.51	0.34
	All		90.44 (0.489)	0.015 (0.000)	2.42 (0.258)	7362	0.77	0.57	0.42	0.31
2006	3	3-May	88.39 (1.257)	0.040 (0.003)	26.54 (1.002)	21	2.06	0.93	0.42	0.19
	4	8-May	89.74 (2.985)	0.041 (0.004)	24.71 (0.808)	143	1.97	0.87	0.38	0.17
	5	13-May	84.63 (1.699)	0.044 (0.003)	22.00 (0.594)	319	1.69	0.70	0.29	0.12
	6	18-May	91.14 (1.920)	0.030 (0.002)	14.68 (0.807)	304	1.28	0.70	0.38	0.21
	7	23-May	85.73 (1.831)	0.036 (0.003)	15.64 (1.432)	255	1.29	0.62	0.30	0.14
	8	28-May	97.09 (3.556)	0.022 (0.002)	6.61 (2.562)	150	1.02	0.66	0.43	0.28
	9	2-Jun	90.22 (2.821)	0.034 (0.005)	19.20 (2.878)	119	1.51	0.77	0.39	0.20
	10	7-Jun	108.41 (6.243)	0.017 (0.003)	9.77 (4.246)	60	1.11	0.79	0.56	0.39
	All		127.00 (3.820)	0.013 (0.001)	5.055 (0.939)	1424	1.04	0.80	0.62	0.48
2007	3	1-May	90.51 (2.628)	0.023 (0.002)	9.08 (3.202)	181	1.03	0.64	0.40	0.25
	4	6-May	90.71 (2.347)	0.021 (0.002)	2.77 (2.285)	504	0.87	0.57	0.38	0.25
	5	11-May	85.53 (2.013)	0.027 (0.002)	8.37 (1.904)	721	0.98	0.58	0.34	0.20
	6	16-May	81.94 (1.652)	0.031 (0.002)	13.52 (1.257)	578	1.12	0.60	0.32	0.17
	7	21-May	77.66 (1.844)	0.039 (0.004)	18.15 (1.316)	176	1.29	0.59	0.27	0.12
	8	26-May	96.69 (3.743)	0.023 (0.002)	12.00 (1.316)	148	1.17	0.74	0.47	0.30
	9	31-May	77.85 (2.329)	0.041 (0.006)	16.17 (2.142)	110	1.20	0.53	0.24	0.10
	All		81.92 (0.842)	0.032 (0.001)	13.86 (0.678)	2738	1.14	0.60	0.32	0.17

Table 2.12. Cohort specific growth estimates of American shad from the Pamunkey River from 2005 and 2006 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_o and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm d^{-1}) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_0	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	3	3-May	119.74 (8.239)	0.014 (0.002)	13.38 (1.438)	99	1.16	0.87	0.66	0.50
	4	8-May	89.01 (4.468)	0.029 (0.003)	19.07 (1.293)	138	1.40	0.79	0.44	0.25
	5	13-May	79.41 (2.238)	0.040 (0.004)	20.51 (0.958)	135	1.46	0.66	0.30	0.13
	6	18-May	83.11 (2.746)	0.032 (0.003)	15.72 (1.157)	115	1.22	0.64	0.34	0.18
	7	23-May	72.97 (2.324)	0.046 (0.009)	18.00 (3.703)	88	1.22	0.49	0.20	0.08
	All		85.94 (1.866)	0.026 (0.002)	14.31 (0.898)	805	1.15	0.68	0.41	0.24
2006	4	28-Apr	94.25 (6.850)	0.021 (0.003)	16.11 (1.381)	224	1.19	0.79	0.52	0.34
	5	3-May	98.29 (11.441)	0.017 (0.003)	8.40 (2.043)	135	0.97	0.69	0.50	0.35
	6	8-May	100.61 (12.786)	0.015 (0.003)	3.40 (3.960)	69	0.86	0.64	0.48	0.36
	7	13-May	87.50 (5.639)	0.019 (0.004)	-0.78 (4.003)	33	0.77	0.52	0.36	0.24
	All		110.19 (4.963)	0.014 (0.001)	7.67 (1.019)	629	0.97	0.74	0.56	0.43

Table 2.13. The juvenile abundance index (JAI) for American shad collected in beach seines on the Rappahannock, Mattaponi, Pamunkey, and James rivers. The index is is the geometric mean catch per haul. SD, standard deviation and N, number of seine hauls are shown.

	2005			2006			2007		
River	JAI	SD	N	JAI	SD	N	JAI	SD	N
Rappahannock	0.18	0.592	33	0.08	0.245	34	0.16	0.354	35
Mattaponi	1.66	1.351	50	0.29	0.554	48	0.24	0.487	47
Pamunkey	0.02	0.11	40	0	0	37	0	0	36
James	0	0	20	0.11	0.254	20	0.04	0.155	20

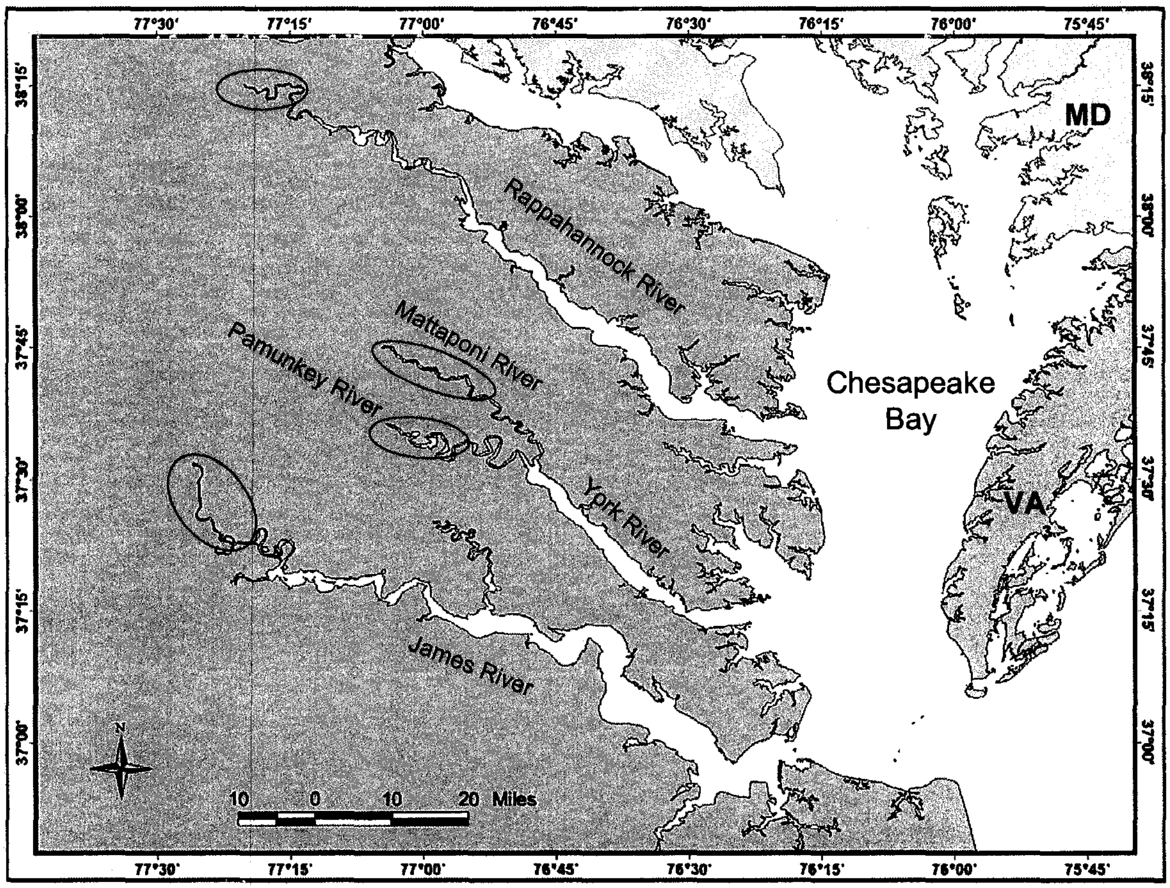
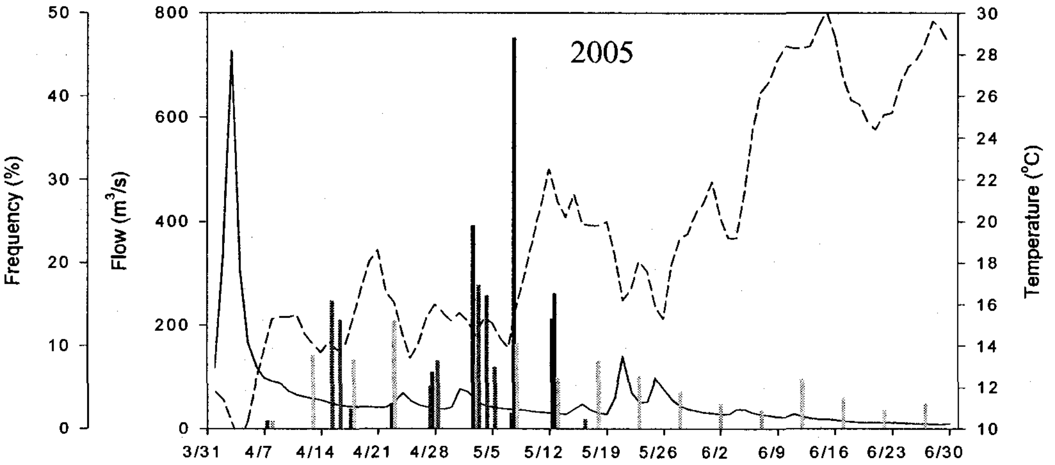
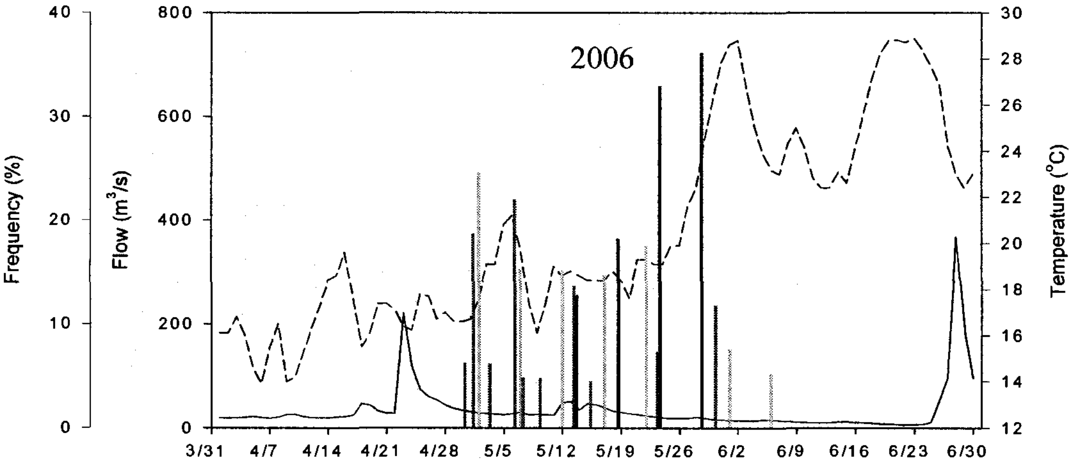


Figure 2.1. Virginia rivers and sampling locations (circled regions) for juvenile American shad, 2005 - 2007.

Figure 2.2. Adjusted hatch date distributions of hatchery (black bars) and wild (light bars) American shad collected in the Rappahannock River along with water discharge (solid line) and temperature (dashed line) during 2005, 2006 and 2007. Dark gray bars represent proportion of hatchery fish and the release date.


2005
Frequency (%)
50
40
30
20
10
0
Flow (m³/s)
800
600
400
200
0
Temperature (°C)
30
28
26
24
22
20
18
16
14
12
10
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30


2006
Frequency (%)
40
30
20
10
0
Flow (m³/s)
800
600
400
200
0
Temperature (°C)
30
28
26
24
22
20
18
16
14
12
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30

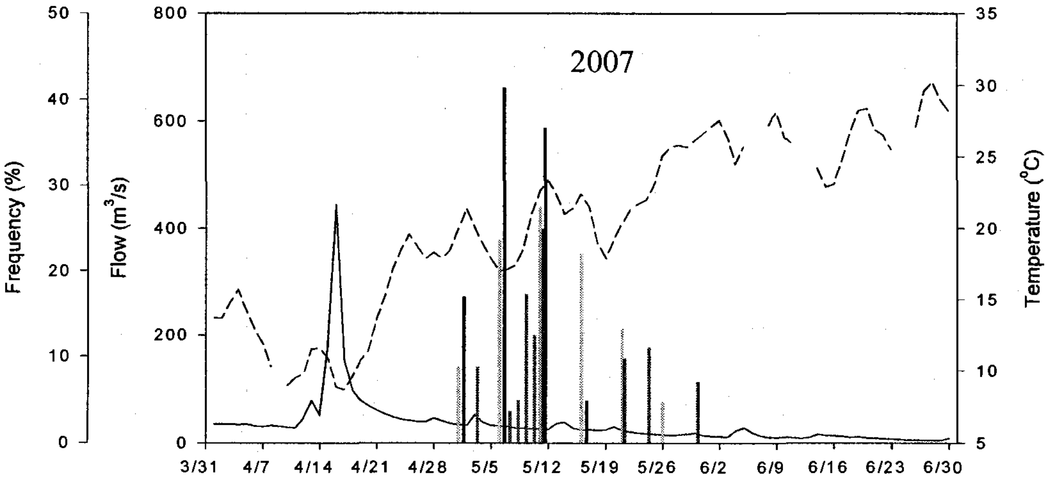
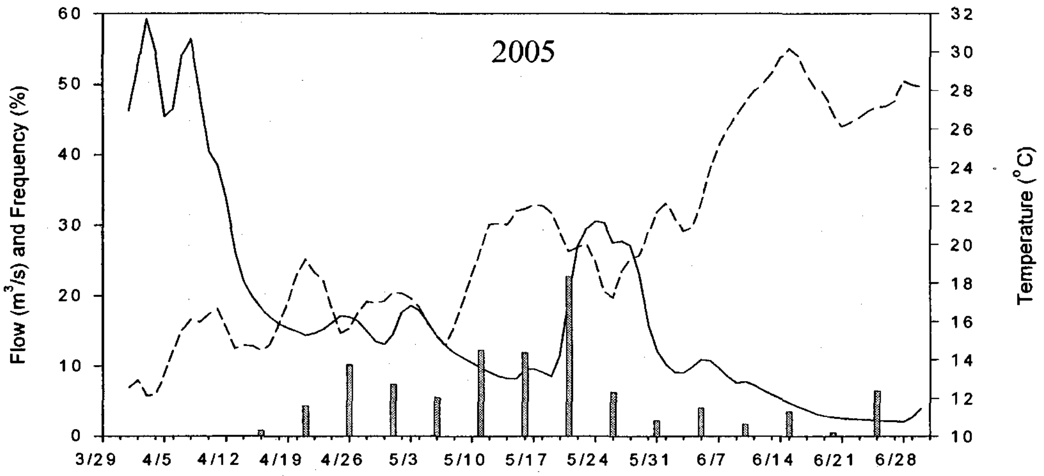
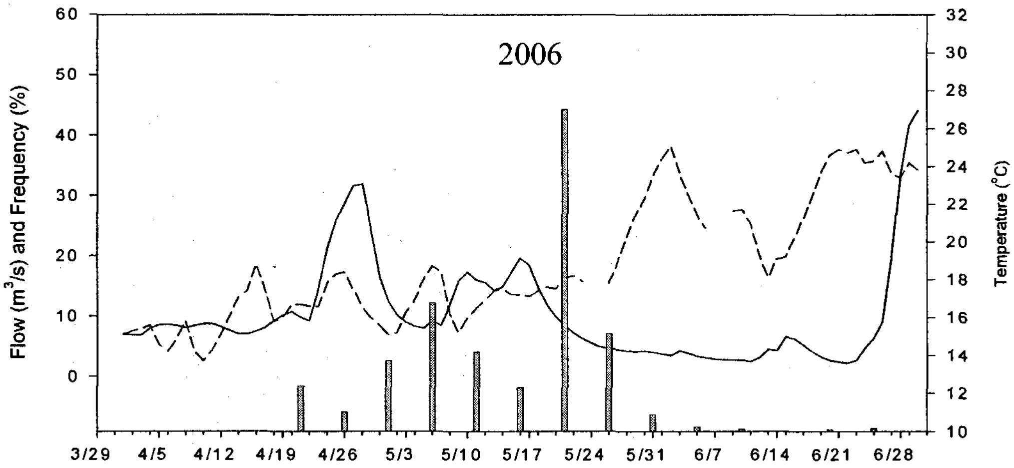

2007
Frequency (%)
50
40
30
20
10
0
Flow (m³/s)
800
600
400
200
0
Temperature (°C)
35
30
25
20
15
10
5
3/31
4/7
4/14
4/21
4/28
5/5
5/12
5/19
5/26
6/2
6/9
6/16
6/23
6/30

Figure 2.3. Adjusted hatch date distributions of American shad (bars) collected in the Mattaponi River and water discharge (solid line) and temperature (dashed line) during 2005, 2006 and 2007.


2005
Flow (m^3/s) and Frequency (%)
Temperature (°C)
60
50
40
30
20
10
0
32
30
28
26
24
22
20
18
16
14
12
10
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28


2006
Flow (m^3/s) and Frequency (%)
Temperature (°C)
60
50
40
30
20
10
0
32
30
28
26
24
22
20
18
16
14
12
10
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28

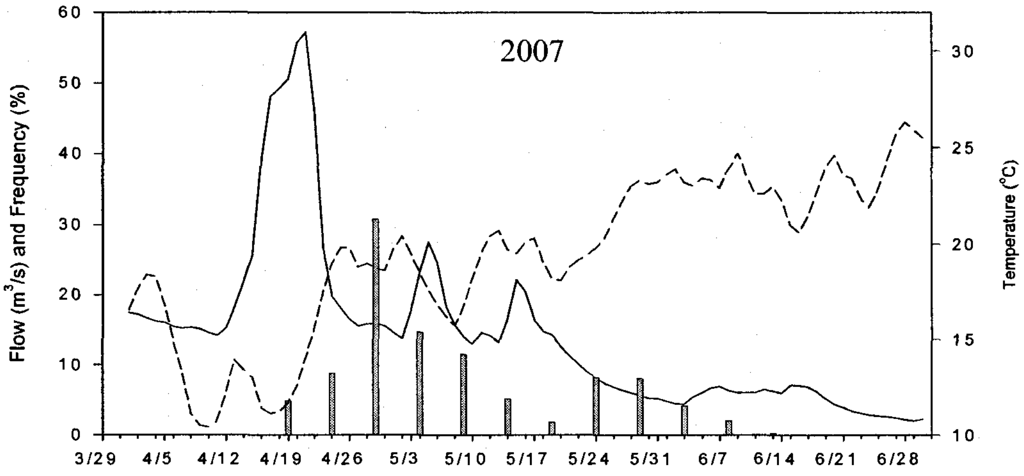
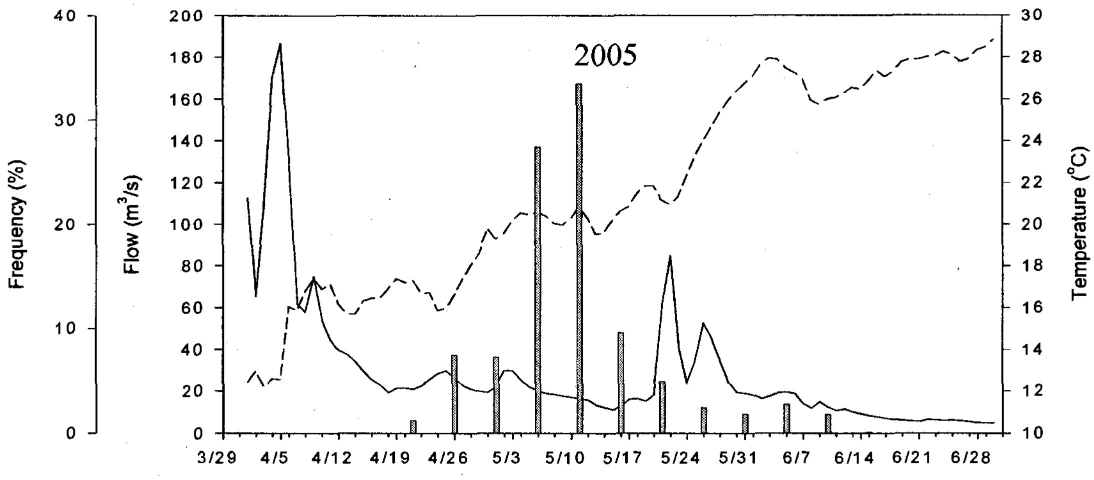
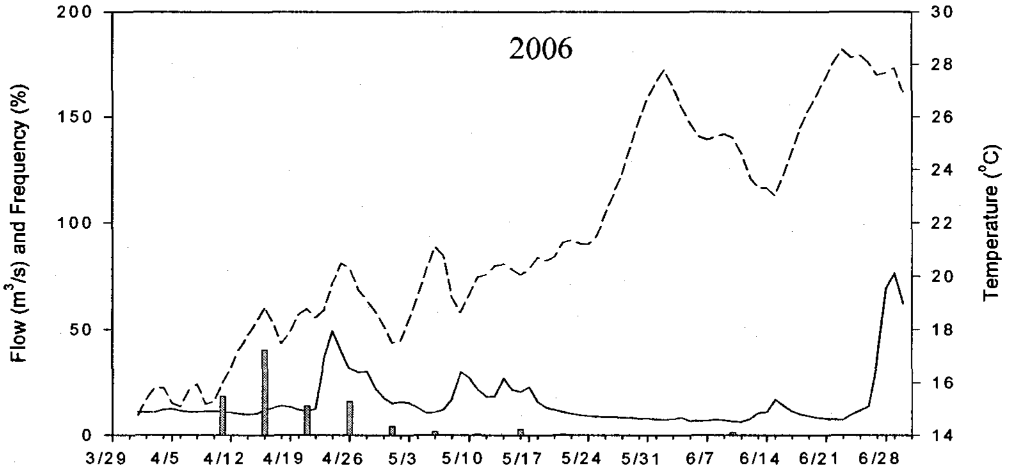

2007
Flow (m^3/s) and Frequency (%)
Temperature (°C)
60
50
40
30
20
10
0
30
25
20
15
10
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28

Figure 2.4. Adjusted hatch date distributions of American shad (bars) collected in the Pamunkey River and water discharge (solid line) and temperature (dashed line) during 2005, 2006 and 2007.


2005
Frequency (%)
Flow (m^3/s)
Temperature (°C)
0
10
20
30
40
0
20
40
60
80
100
120
140
160
180
200
10
12
14
16
18
20
22
24
26
28
30
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28


2006
Flow (m^3/s) and Frequency (%)
Temperature (°C)
0
50
100
150
200
14
16
18
20
22
24
26
28
30
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28

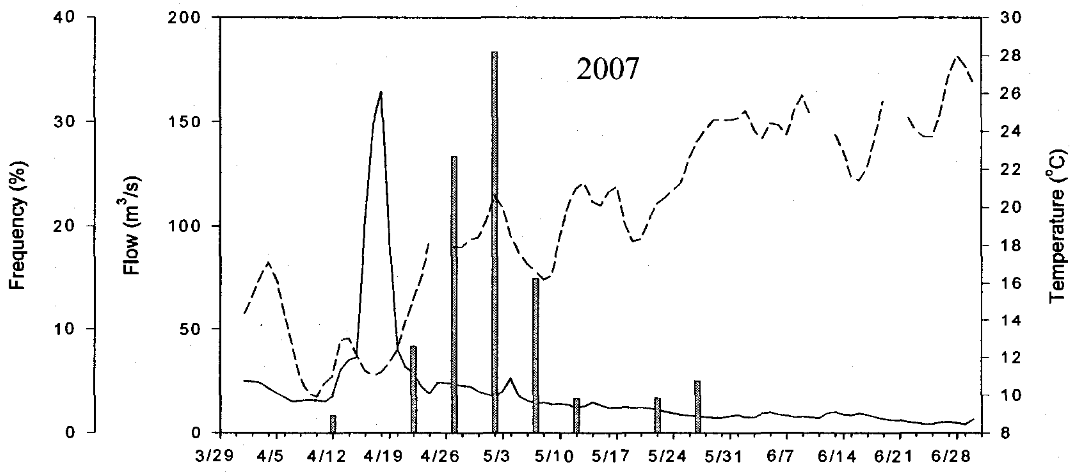
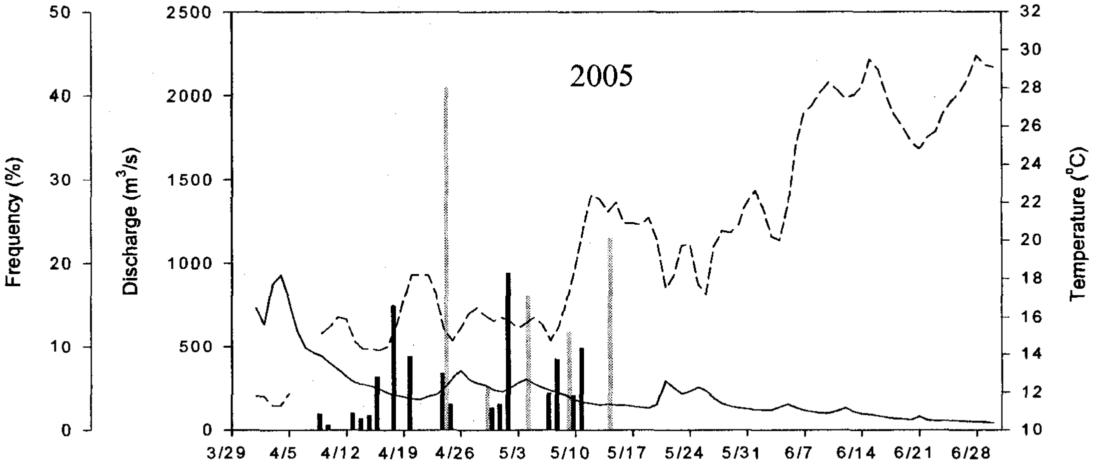
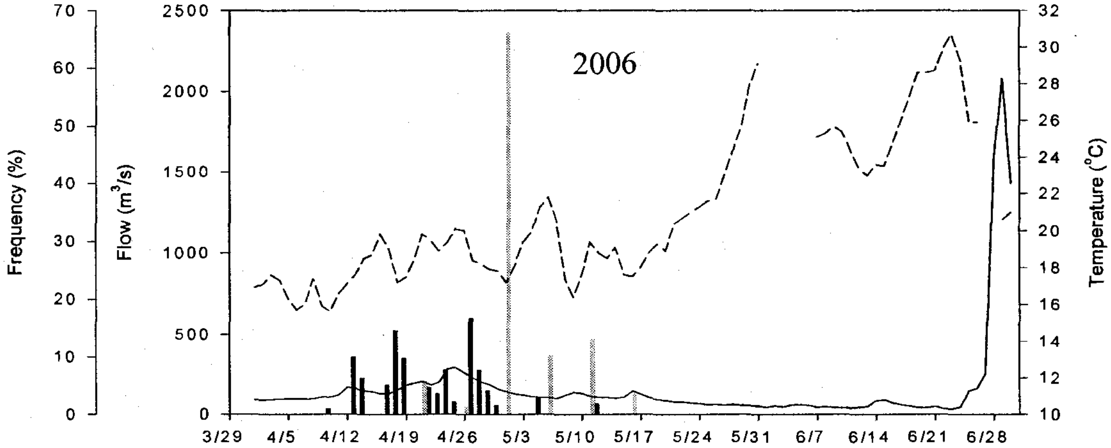
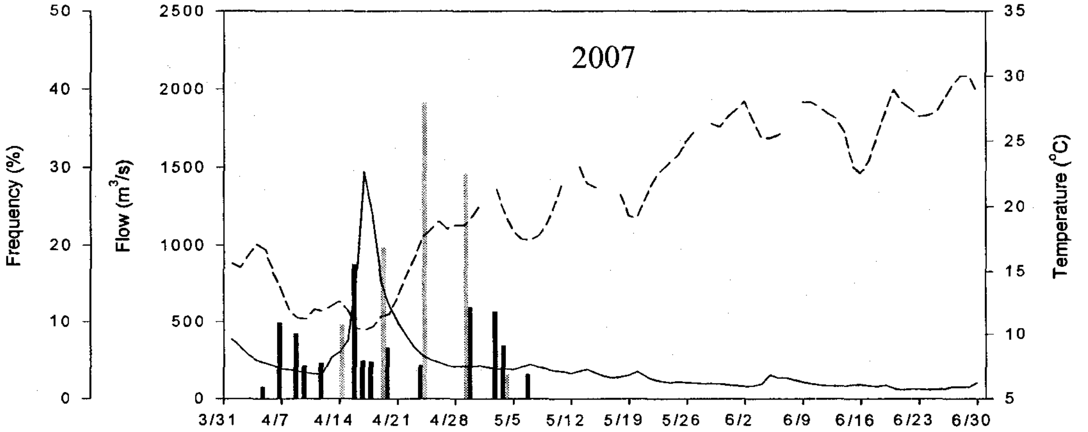

2007
Frequency (%)
Flow (m^3/s)
Temperature (°C)
0
10
20
30
40
0
50
100
150
200
8
10
12
14
16
18
20
22
24
26
28
30
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28

Figure 2.5. Adjusted hatch date distributions of hatchery reared American shad (gray bars) collected in the James River and water discharge (solid line) and temperature (dashed line) during A. 2005, B. 2006, and C. 2007. Black bars represent proportion of hatchery fish and release date.


2005
Frequency (%)
Discharge (m^3/s)
Temperature (^{o}C)
0
10
20
30
40
50
0
500
1000
1500
2000
2500
10
12
14
16
18
20
22
24
26
28
30
32
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28


2006
Frequency (%)
Flow (m^3/s)
Temperature (^{o}C)
0
10
20
30
40
50
60
70
0
500
1000
1500
2000
2500
10
12
14
16
18
20
22
24
26
28
30
32
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28


2007
Frequency (%)
Flow (m^3/s)
Temperature (^{o}C)
0
10
20
30
40
50
0
500
1000
1500
2000
2500
5
10
15
20
25
30
35
3/31
4/7
4/14
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5/5
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6/9
6/16
6/23
6/30

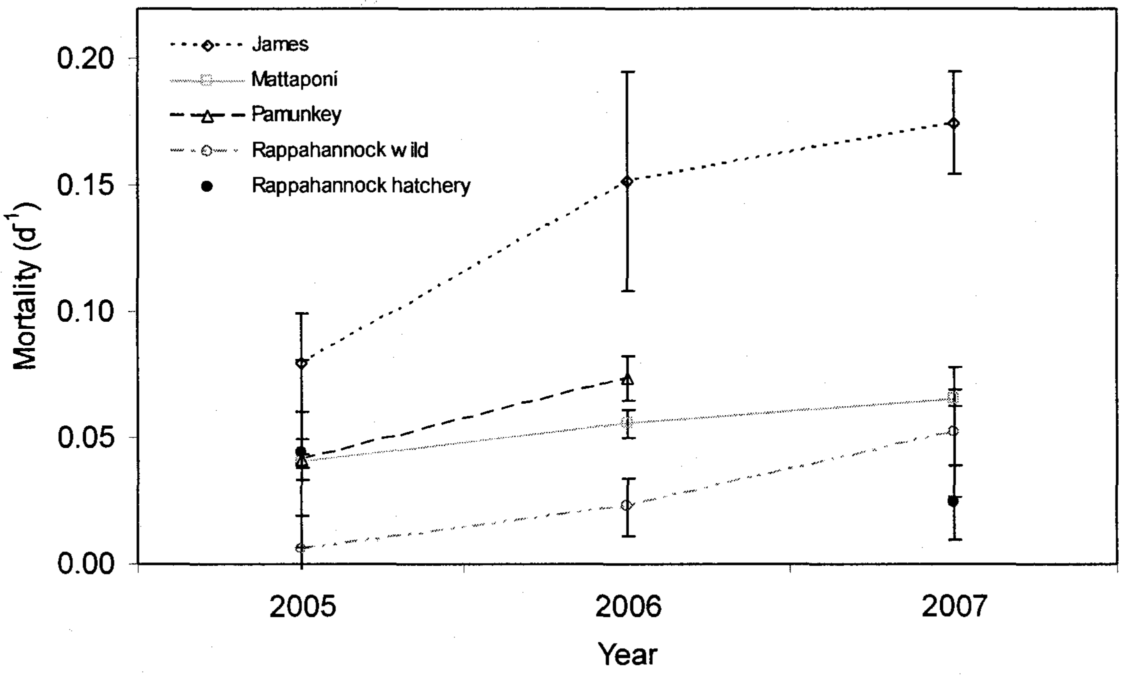


Figure 2.6. Instantaneous total mortality rates (se) of juvenile American shad from the Rappahannock, Mattaponi, Pamunkey, and James rivers (2005 – 2007).

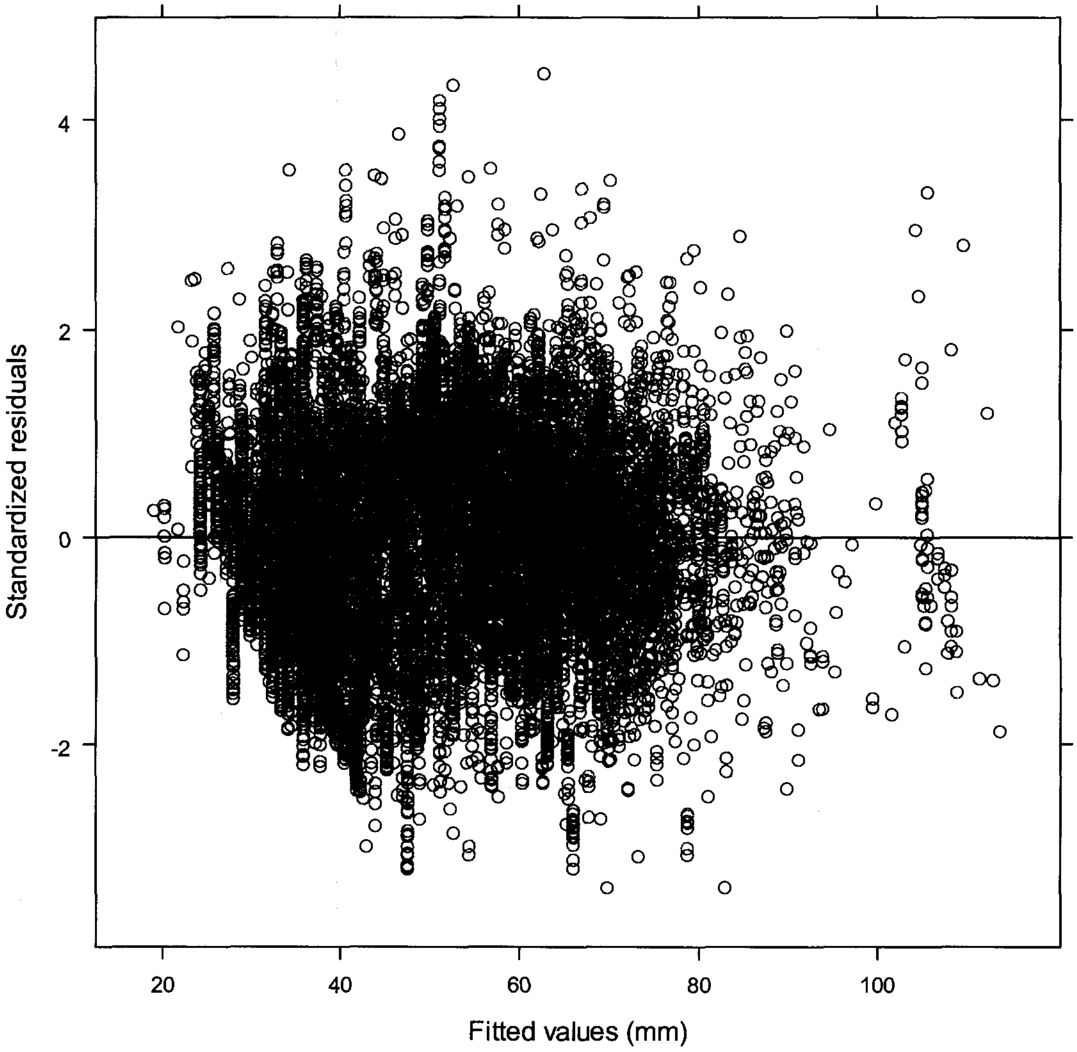


Figure 2.7. Standardized residuals vs. fitted values for the von Bertalanffy mixed effects model.

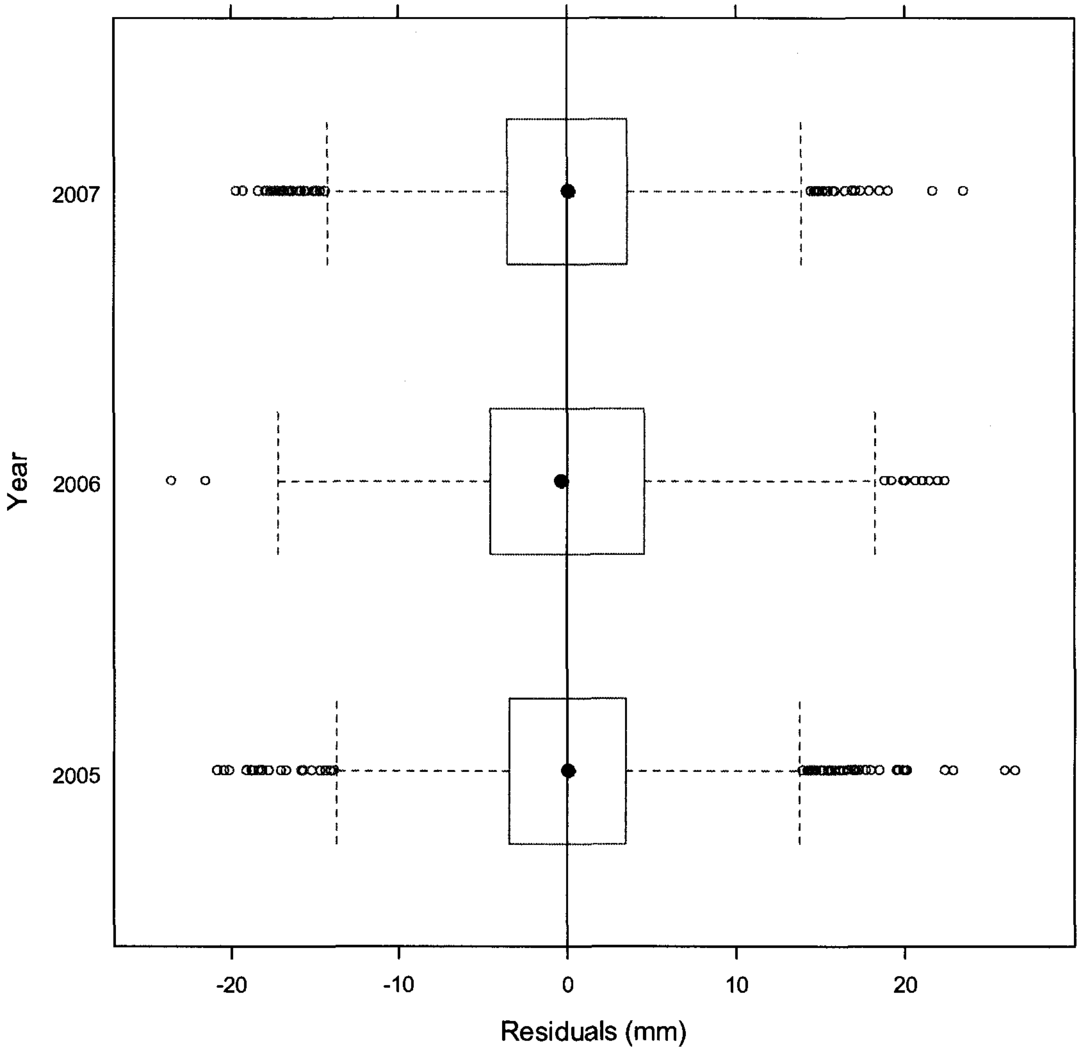


Figure 2.8. Standardized residuals vs. Year for the von Bertalanffy mixed effects model.

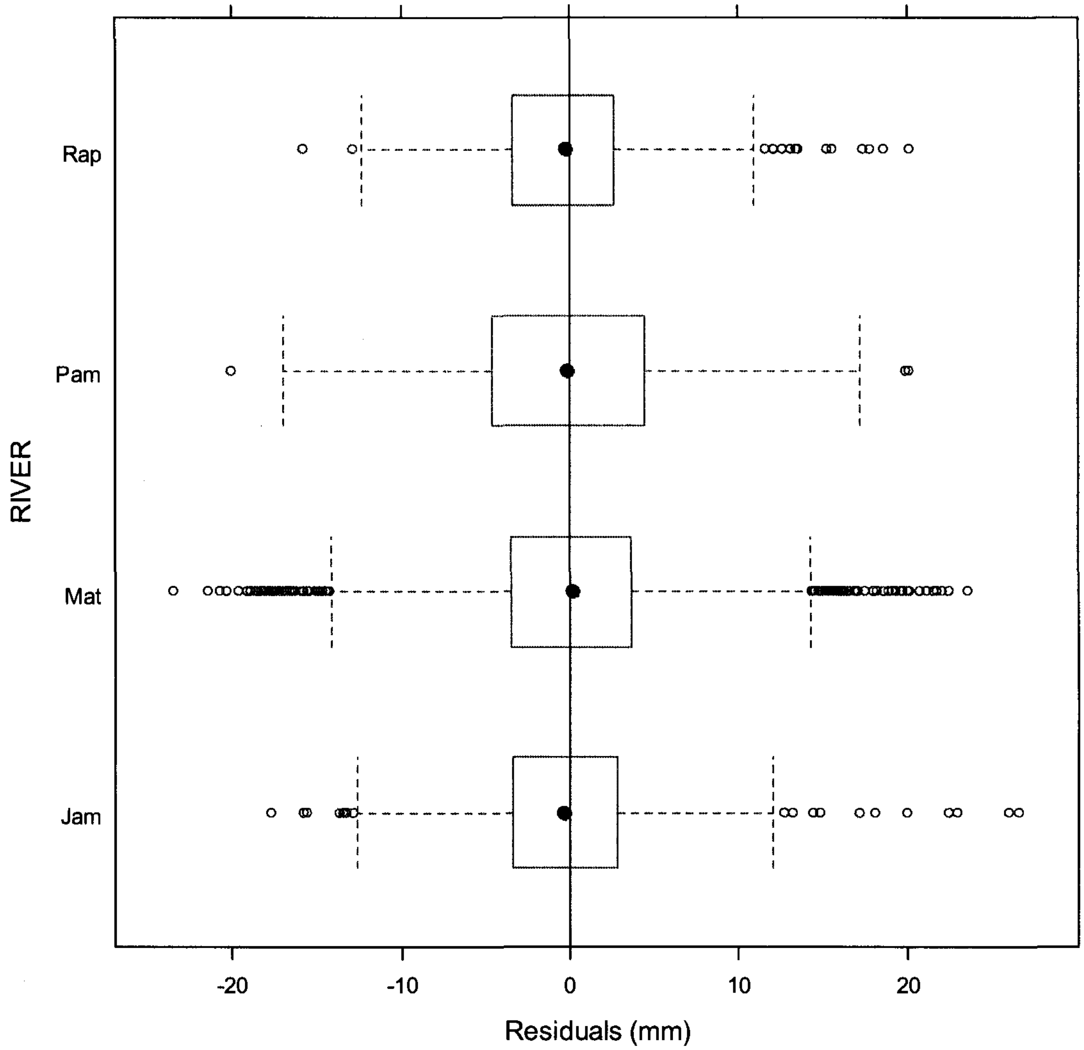


Figure 2.9. Standardized residuals vs. River for the von Bertalanffy mixed effects model.

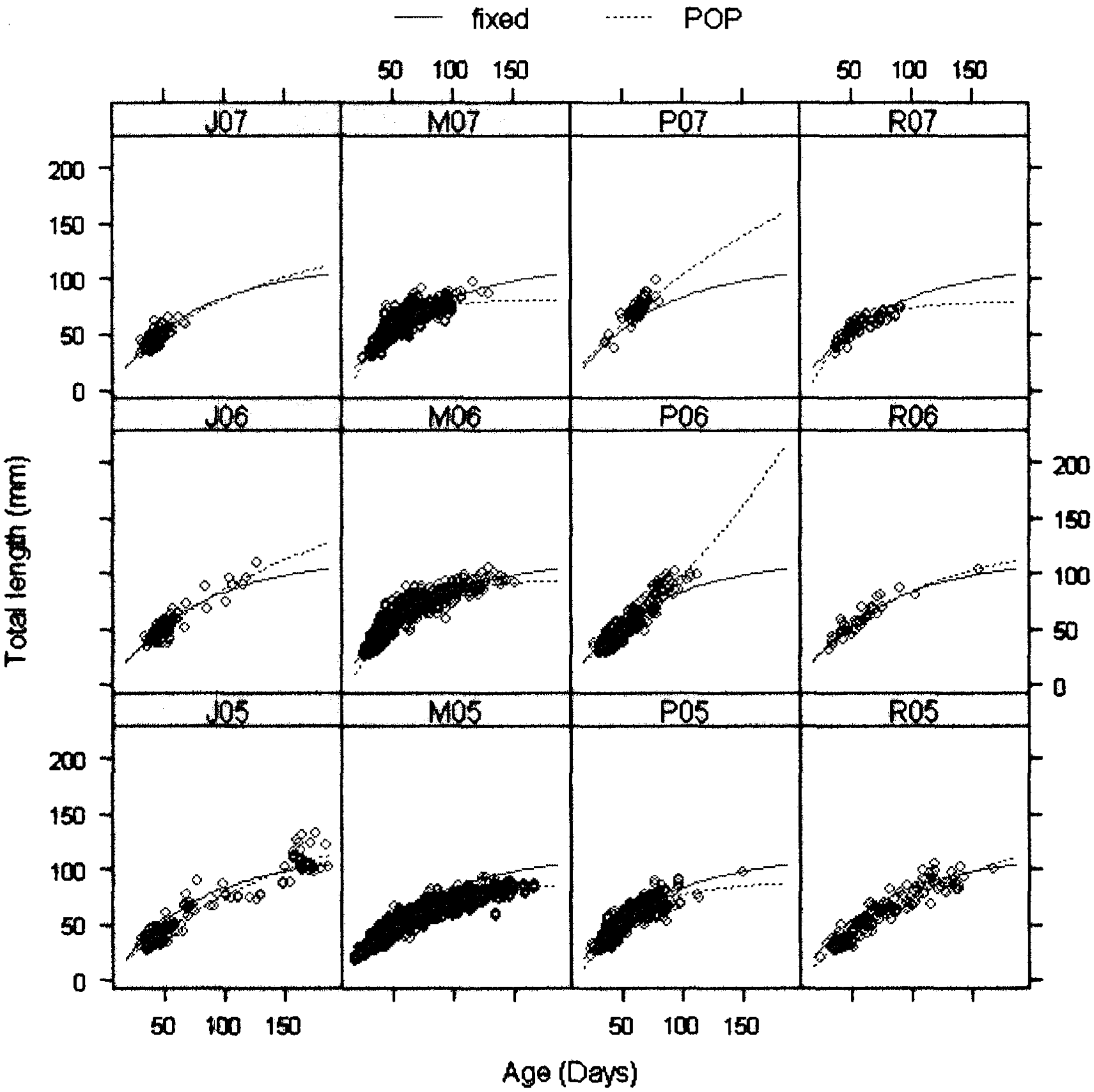


Figure 2.10. Global predictions (fixed) of juvenile American shad growth and within population level predictions (POP) for year classes in the Rappahannock (R) , Mattaponi (M), Pamunkey (P), and James (J) rivers from 2005 to 2007 (05, 06, 07).

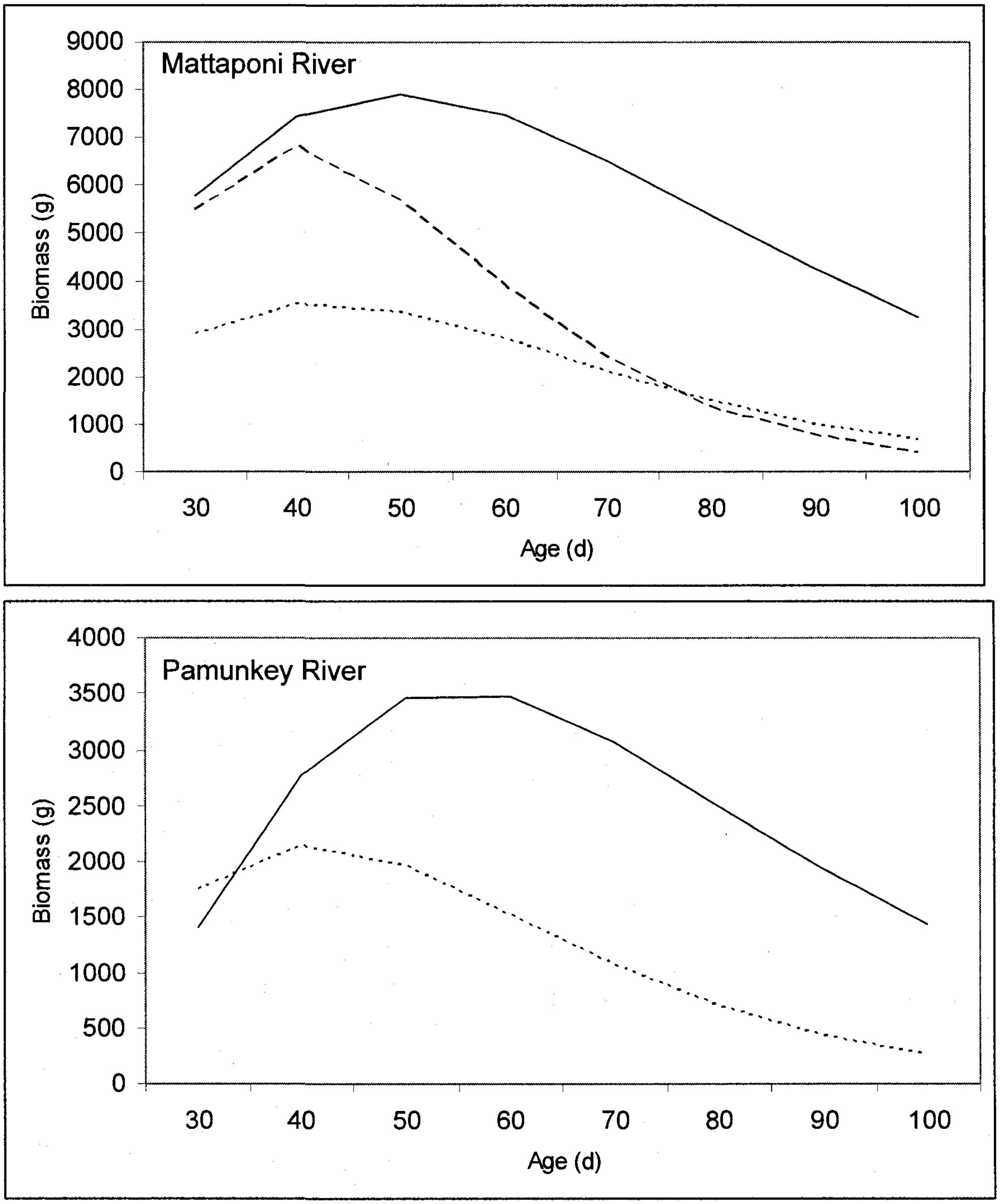
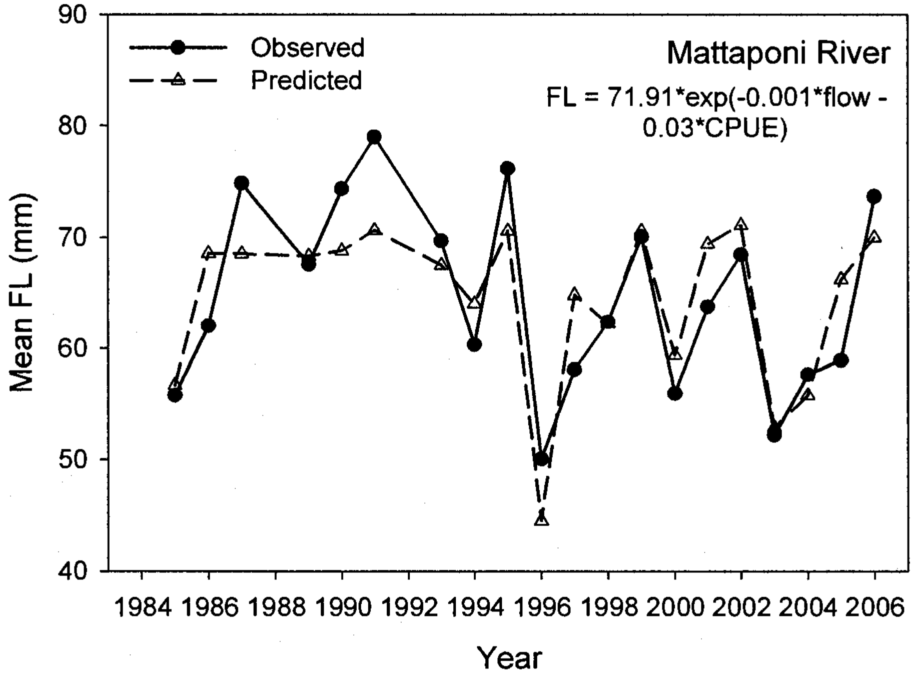


Figure 2.11. Change in biomass for American shad in the Mattaponi and Pamunkey Rivers in 2005 (solid line), 2006 (dotted line), and 2007 (dashed line). Biomass was calculated using year class parameter estimates from models for growth (von Bertalanffy) and mortality (exponential decay) and the allometric relationship between length and weight.



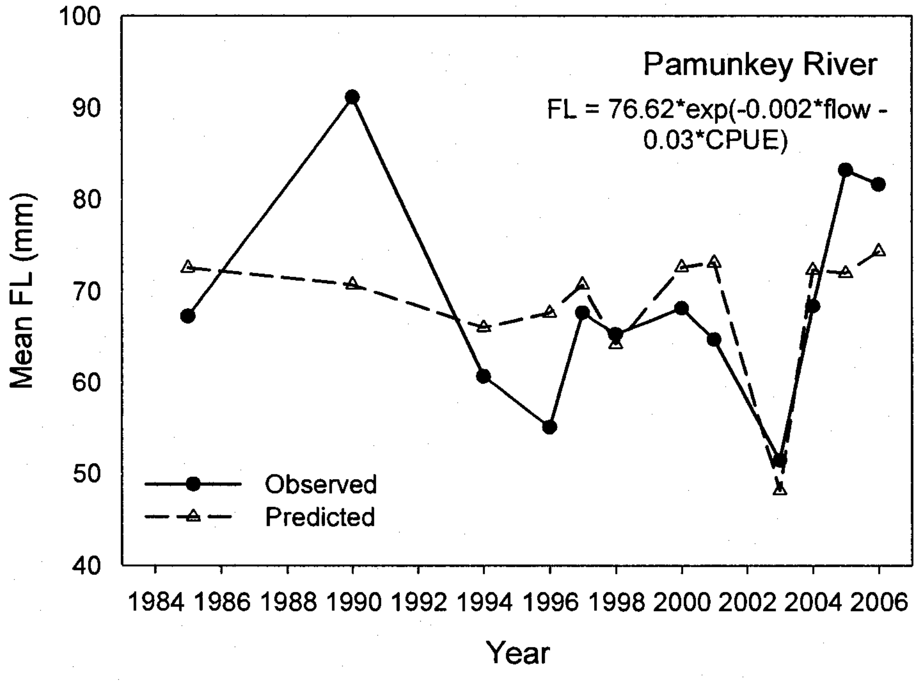


Figure 2.12. Comparison of best-fit model estimates of mean fork length with observed mean fork length during September from the VIMS striped bass seines survey in the Mattaponi and Pamunkey rivers, 1985 to 2004

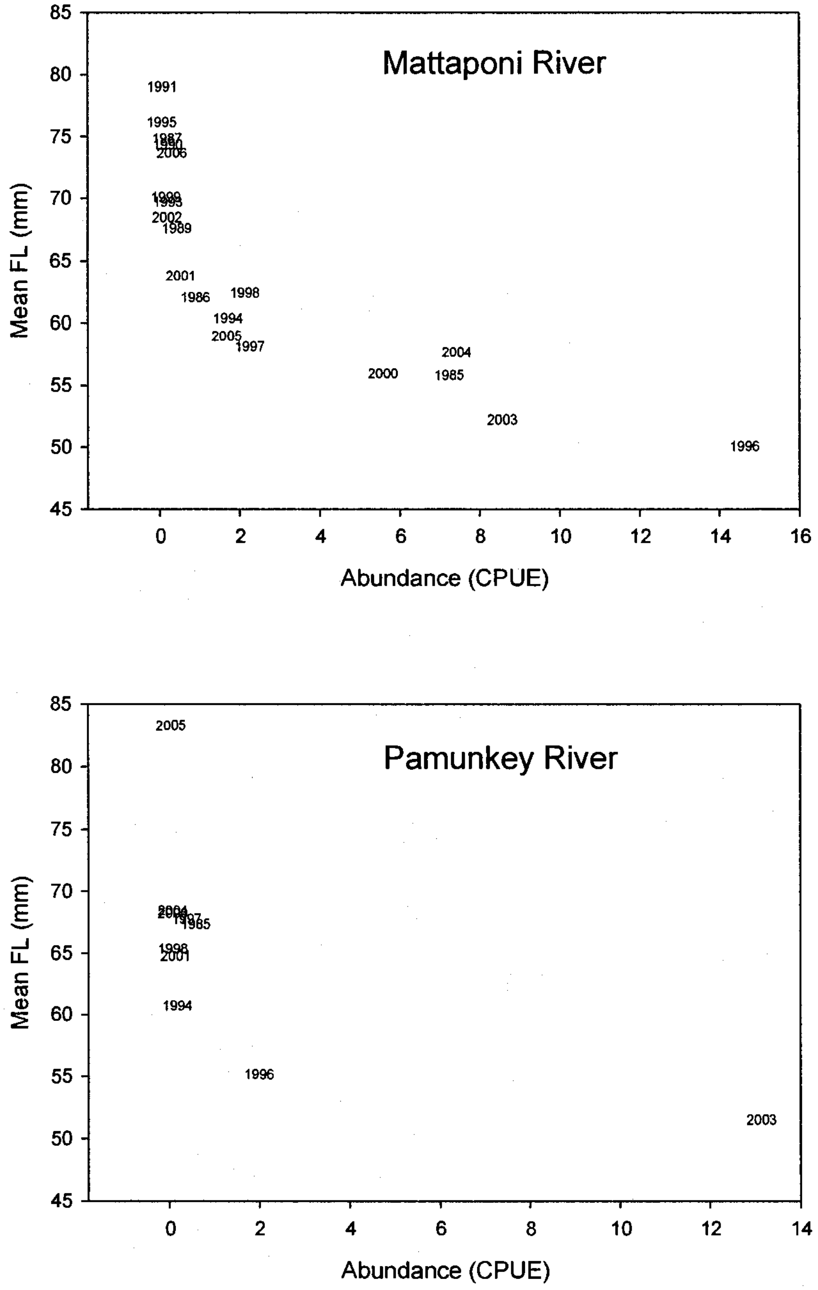


Figure 2.13. Relationship between the geometric mean catch per unit effort and mean fork length in September from the Virginia Institute of Marine Science striped bass seine survey for the Mattaponi and Pamunkey rivers, 1985 – 2007. Missing years in the figures are years no American shad were collected in September.

Chapter Three

Population Dynamics of Young-of-Year Blueback Herring in Lower Chesapeake Bay Nurseries

ABSTRACT

A decline in stocks of anadromous river herring (blueback herring and alewife) throughout the Atlantic coast of the U.S. and Canada has resulted in harvest restrictions in portions of their range and the consideration of management actions in other regions. Possible causes of the declines have been attributed to loss of habitat, overexploitation, and increased predation. Objectives of this study were to examine temporal and spatial variability in growth and mortality rates of young-of-year blueback herring in Virginia rivers and examine year-class production in relation to water flow, water temperature, and conspecific abundance. Young-of-year blueback herring recruitment in Virginia rivers is an episodic process with multiple peaks observed throughout summer. Cohorts were captured throughout the sampling period at larger sizes and similar abundances indicating that cohorts were not fully vulnerable possibly due to movement into the sampling area from adjacent habitats. Patterns in observed growth and mortality rates indicate that river-specific processes regulate year-class production. Furthermore, conspecific abundance was an important predictor of size at the end of summer, indicating density-dependent regulation of growth. Large year-classes that are smaller in size prior to emigration into the coastal ocean may experience higher mortality rates resulting in recruitment regulation (i.e., compensatory mortality).

INTRODUCTION

Stocks of anadromous river herrings (blueback herring, *Alosa aestivalis* and alewife, *A. pseudoharengus*) are in decline throughout the Atlantic coast of the U.S. and Canada (Schmidt et al. 2003). A survey of long-term data from large rivers encompassing the range of river herring shows that both species are overexploited and declining trends in juvenile abundance indices (JAIs) have been evident since the 1980's (Schmidt et al. 2003). Unfortunately, reported commercial landings of blueback herring and alewife are often combined, thus limiting our understanding of stock dynamics for the two species. In the Connecticut River, recent declines in anadromous blueback herring and American shad (*A. sapidissima*) have been attributed to predation resulting from an increase in striped bass (*Morone saxatilis*) stocks (Savoy and Crecco 2004). In Chesapeake Bay, striped bass is at historic high levels of abundance and the potential for increased mortality of anadromous *Alosa* due to predation is a plausible hypothesis. However, juvenile abundance indices of blueback herring in Virginia have been in decline since the late 1960's and 1970's to low levels that persist today (VIMS unpublished data). Consistently low JAIs of blueback herring during the 1980's, when stocks of striped bass were at historic lows, indicates that additional factors are operating to reduce potential recruitment of blueback herring. The low abundance of blueback herring and alewife stocks has resulted in harvest closures in Massachusetts, Rhode Island, Connecticut, and North Carolina, and additional management options are currently under consideration throughout their range (ASMFC 2007).

In Chesapeake Bay, adult blueback herring ascend fast-flowing streams and rivers to spawn in spring when water temperatures are between 14 and 26 °C, typically from April to June (Loesch and Lund 1977; O'Connell and Angermeier 1999). Spawning of blueback herring occurs in nearly all available habitats including swamps, oxbows, canals, streams, and main river channels (Walsh et al. 2005). Developing juveniles remain in tidal freshwater nurseries until water temperatures decline in fall, then migrate to the lower estuary or coastal waters until sexually mature, approximately three to four years later. Evidence from trawl surveys conducted along the Atlantic coast show similar migratory patterns as that of American shad, with movements of blueback herring stocks northward along the coast during summer and southward in winter (Neves 1981).

Population dynamics of early-life stages of fishes vary in space and time resulting in order of magnitude changes in year-class strength (Houde 1987). This study examines growth and mortality rates of young-of-year blueback herring in four rivers in lower Chesapeake Bay to test the hypothesis that environmental factors control growth and mortality. Data were collected for three seasons to compare trends in growth and mortality among rivers and years along with associated environmental conditions to better understand year-class production. The close proximity of the populations (about 1° latitude) was expected to result in similar growth and mortality rates among rivers and years assuming environmental conditions are the primary driver of population dynamics. Furthermore, historical collections of blueback herring were examined for relationships between production of blueback herring (i.e. mean length in September) with water flow, water temperature, and conspecific abundance.

METHODS

Methods of fish collection and analysis used in the investigation of blueback herring population dynamics are identical to those used for American shad (Chapter 2, this study). However, there were no hatchery-origin blueback herring available to validate ages. Because the same aging methodology was applied to juvenile American shad and blueback herring otoliths, and the fact that both species overlap in space and time for spawning and juvenile growth, it is assumed that blueback herring ages had similar error rates reported for American shad juveniles. Validation of daily deposition of increments in blueback herring otoliths was conducted by Sismour (1994).

RESULTS

Hydrography

Seasonal patterns in water discharge (m^3/s) were evident with high flow during spring and periods of lowest flow occurring during summer months (Table 3.1). Annual discharge was below average in 2005 and 2007 and slightly above average in 2006. Mean discharge in all four rivers from April to October was lowest in 2007. The James River had the highest mean discharge rate, followed by the Rappahannock River, Pamunkey River and the Mattaponi River.

Mean daily water temperature increased from April to August and decreased during September and October (Table 3.1). Mean water temperatures were lowest during 2006 in the Rappahannock, Mattaponi and James rivers, while the lowest mean temperature in the Pamunkey River was observed in 2007. Warmest mean temperatures for the study period occurred during 2007 in the Rappahannock and James rivers and during 2005 in the Mattaponi River and 2006 in the Pamunkey River.

Significant differences were observed during months when hatching typically occurs (April to June) with lowest water temperatures during April 2007 in all four rivers. Mean water temperature during April in the Rappahannock (16.5 °C) and James rivers (17.9 °C) was significantly warmer in 2006 than in 2005 and 2007 (ANOVA, $p<0.05$). In the Pamunkey River, April water temperatures were significantly colder (14.0 °C) in 2007 and significantly warmer (17.4 °C) in 2006 (ANOVA, $p<0.05$). Water temperatures increased in May, but were significantly colder during 2005 in the Rappahannock and James rivers. There were no significant differences in mean temperatures ($p>0.05$) among years for the month of April or May in the Mattaponi River or for the month of May in the Pamunkey River. No significant differences ($p>0.05$) in water temperature were found during June for the Rappahannock and James rivers. However June was significantly warmer during 2005 in the Mattaponi River compared with 2006 and 2007 (ANOVA, $p<0.001$). In the Pamunkey River, June was significantly warmer in 2005 than in 2007 (ANOVA, $p<0.001$).

Blueback herring catches

A total of 13,358 blueback herring were captured and 2371 (17.7%) were aged (Table 3.2). Hatch of blueback herring occurred from April through July. The earliest 5-d cohort hatched 19 April 2006 in the Pamunkey River, where mean April water temperatures were significantly higher than in other years in this river, and the latest hatched cohort was 11 July 2005 from the Rappahannock River, though hatching typically occurred during May and June (Fig. 3.2).

The Rappahannock River had the highest number of blueback herring collected (N=7921) and the greatest number of 5-d cohorts, with 14 cohorts in 2005, 11 cohorts in 2006 and 9 cohorts in 2007. Highest catch of blueback herring occurred in 2006. Mean TL ranged from 45.8 mm in 2007 to 53.1 mm in 2006, and mean weight ranged from 0.91 g in 2007 to 1.43 g in 2006 (Table 3.2). Mean age was 54.9 d in 2005, 78.8 d in 2006 and 54.2 d in 2007. The greatest range in ages was from 17 to 179 d and occurred in 2006.

A total of 2096 blueback herring were collected in the Mattaponi River with the highest catch occurring in 2005. The number of cohorts decreased from 13 in 2005 to 9 cohorts in 2007. Mean TL ranged from 46.7 mm in 2007 to 53.2 mm in 2005 and mean weight ranged from 1.09 g in 2007 to 1.55 g in 2005 (Table 3.2). Mean age was 73.9 d in 2005, 60.0 d in 2006 and 52.4 d in 2007.

Greatest catch of blueback herring in the Pamunkey River occurred in 2005 and decreased in 2006 and 2007. Mean TL was 47.9 mm in 2005, 42.3 mm in 2006, and 51.2 mm in 2007 (Table 3.2). Mean weight followed a similar pattern among years. Mean age was 54.9 d in 2005, 78.8 d in 2006 and 54.2 d in 2007.

The James River produced the second highest number of blueback herring (2781) with peak catch occurring in 2007. Mean TL ranged from 51.0 mm in 2007 to 60.1 mm in 2006 and mean weight ranged from 1.24 g in 2007 to 2.25 g in 2006 (Table 3). Mean age was 65.7 d in 2005, increased to 70.6 d in 2006 and was 60.5 d in 2007. Most of the blueback herring were collected below Bosher's Dam in the tidal James River.

Growth

Growth of blueback herring slowed in fall with maximum lengths typically less than 100 mm TL. Model comparisons for length-at-age data for all rivers and years combined indicated that the von Bertalanffy model best characterized growth compared with Gompertz and Richards models (Table 3.3). The combination of river and year in mixed model analysis of the von Bertalanffy growth model resulted in the best model compared with the fixed effects of just river or year (Table 3.4). A variance inflation factor to account for increasing length with increasing age was included in the best model. Standardized residuals for the selected model were random and show that the variance inflation factor in the model properly accounted for increasing lengths with increasing age (Fig. 3.3). Furthermore, residuals were plotted against the random effects for Year (Fig. 3.4) and River (Fig. 3.5) and results are centered near zero and show that there is no bias for the best model indicating a good fit to the data.

Maximum length of blueback herring in Virginia was 84.94 mm TL. The deviation of parameter estimates due to random river and year effects exhibited mixed results with estimates of growth of blueback herring in the Mattaponi and Pamunkey rivers always above average (Table 3.5; Figure 3.6). There were significant effects of river (relative to the James River; Table 3.6) and year (relative to 2005; Table 3.7) on estimates of growth parameters that resulted in inclusion of both effects in the final model. Growth estimates in the Pamunkey River for 2006 and 2007 were unrealistic due to small sample sizes and the age range of specimens that were collected. All other estimates of growth fit well for each river and year combination (Fig. 3.6).

Instantaneous growth rates (G, obtained from the derivative of the von Bertalanffy growth model) of blueback herring at age 40 d (G_{40}) were variable among rivers and years. In the Rappahannock River, G_{40} during 2005 was 1.25 times greater than in 2006 (Table 3.8). In the Mattaponi River, G_{40} for all cohorts was similar between 2005 and 2006 (about 0.70 mm d^{-1}) and increased by about 20% in 2007 (Table 3.9), and in the Pamunkey River G_{40} increased each year from 0.76 mm d^{-1} in 2005 to the fastest observed rate in the study (1.17 mm d^{-1} in 2007; Table 3.10). Growth of blueback herring in the James River showed the only decreasing trend among years and ranged from 0.82 mm d^{-1} in 2005 to 0.56 mm d^{-1} in 2007 (Table 3.11). Growth rate at 40 d had a significant negative relationship with the number of fish caught each year in the James River (linear regression, $r^2=0.40$, $P=0.028$). Growth at 100 d ranged from 0.1 to 0.3 mm d^{-1} in all rivers, with highest G_{100} in the Pamunkey and Mattaponi rivers and lower rates observed in the Rappahannock and James rivers.

There were consistent patterns in growth among rivers and cohorts (excluding the James River) that show increasing growth rates at 40 d corresponding with increasing water temperature at hatch. Cohort-specific growth in the Rappahannock River in 2006 increased from cohort 1 to 6 then decreased with the exception of cohort 9 (Table 3.8). Water temperature followed a similar trend with an increase from the date of hatch for cohorts 1 to 6 and then a slight decrease during hatch of subsequent cohorts. The opposite pattern was observed in the Rappahannock River during 2007, with highest growth rates observed for the earliest hatched cohorts even though those cohorts experiences the coolest seasonal water temperatures. In the Mattaponi River, growth (G_{40}) of cohorts generally increased with increases in water temperature each year, although G_{40} during 2007 was relatively high and constant among cohorts (Table 3.9). Growth of cohorts in the Pamunkey River was relatively consistent (Table 10) for most cohorts (G_{40} between 0.70 to 0.79 mm d^{-1}), although G_{40} for cohort 9 = 0.68 mm d^{-1} and Cohort 11 = 0.90 mm d^{-1}. There was much greater variability of growth among cohorts of blueback herring in the James River than observed in the other populations (Table 3.11). Furthermore, in 2007, patterns in growth of blueback herring at 40 d in the James did not follow changes in water temperature and decreased with increasing water temperature.

Mortality

Instantaneous mortality rates (M) varied by river and year with no consistent pattern among rivers. In the Rappahannock and Pamunkey rivers, M was high in 2005, decreased in 2006 and increased again in 2007 (Fig. 3.7). Estimated rates were the same for 2006 and 2007, but during 2005 the rate in the Rappahannock River was almost twice has high as that observed in the Pamunkey River. Mortality of blueback herring in the Mattaponi River was nearly constant throughout the study and ranged from 0.012 to 0.023 d^{-1} (Table 3.12). The James River showed a different pattern with increasing mortality from a low of 0.037 in 2005 to 0.146 d^{-1} in 2007. Cohort-specific mortality rates were problematic in this study. Catch-at-age distributions showed blueback herring were not captured in proportion to their true abundance on some dates, presumably because they were unavailable to the gear, resulting in no clearly defined ascending and descending limb in the catch curve (Fig. 3.8). Therefore, cohort-specific mortality rates were not estimated.

Historic records of blueback herring abundance

In the Mattaponi River, there was support for two of the candidate models as plausible hypotheses for factors influencing mean length of blueback herring. There was a linear relationship between mean length and water temperature and abundance and a linear relationship between mean length and water temperature, abundance, and water flow. A similar result was found for the Pamunkey River with the addition of an exponential model that includes water flow and abundance. The best fit model (Fig. 3.9) for each river shows a significant relationship between observed and predicted mean lengths. Mean length in both rivers show density-dependence with a decline in mean length with increasing abundance. However, there was less support for density-dependent growth in the Mattaponi River (Fig. 3.10). Too few blueback herring were captured in the James and Rappahannock rivers in September to examine possible relationships between length and environmental variables.

DISCUSSION

Young-of-year blueback herring recruitment in the Mattaponi and Pamunkey rivers is an episodic process with multiple peaks observed throughout summer each year. Burbidge (1974) also noted an increase in blueback herring abundance in late summer and attributed the increases to movements of blueback herring out of nearby tributaries and oxbows along the James River. Both this study and Burbidge (1974) sampled in the main channel and cannot address spatial distribution of blueback herring among different habitats although it is known that oxbows, flooded swamps, streams and shorelines serve as suitable habitats for YOY blueback herring (O'Connell and Angermeier 1997; Kosa and Mather 2001; Walsh et al. 2005). Multiple peaks in abundance observed throughout summer in this study were not the result of prolonged spawning as ages were determined to be from the same cohorts captured earlier in the season. Furthermore, the influx of new recruits observed in this study was not related to gear avoidance because new recruits were from the same hatch dates as cohorts captured previously, but now at larger sizes. Gear avoidance behavior would be expected to be greater for larger individuals and would result in a reduction in the number captured, not an increase. Therefore, availability of blueback herring varied during the summer.

Walsh et al. (2005) observed spawning of blueback herring in nearly all available habitats in North Carolina rivers, including flooded swamp areas. And they observed increases in abundance of larval blueback herring in the river as the nearby swamps drained. There are backwater areas that are accessible in the Mattaponi and Pamunkey rivers that could be important nursery habitat, and movement of YOY blueback herring out of these areas could have served as a source of new recruits from established cohorts. Spatially separated cohorts of blueback herring that maintain cohesion during residence in the nursery is consistent with the contingent hypothesis (Clark 1968; Secor and Piccoli 1996; Kraus and Secor 2004). Additional work to characterize contingents either through increased sampling or stable isotope analysis of otoliths would provide additional support for this possibility. For example, Hoffman et al. (2007b) were able to discern habitat use of juvenile American shad using turnover rates of stable isotopes as shad moved from one habitat to another. They found that YOY American shad occupied discrete sections of river for up to a month at a time. A similar study that also incorporates age could elucidate blueback herring population dynamics on a spatial scale resulting in detailed understanding of important habitats.

Continuous recruitment of blueback herring to the sampling gear violates one of the assumptions necessary for estimation of mortality rates using catch curves. Catch curves typically have an ascending limb for ages of fish that have not fully recruited to the gear and a descending limb when they are assumed to be fully recruited, with the slope of the regression line for the descending limb being and estimate of the total instantaneous mortality rate. The pulses of recruits to the main river channel (where sampling was conducted) resulted in multiple peaks that showed that the entire population of blueback herring from a particular cohort was not vulnerable to capture. Therefore, estimated cohort-specific mortality rates would be biased, because estimates would only be for those fish captured in the main river channel. Furthermore, mortality would only be estimated for the largest recruitment pulse and would not account for losses incurred prior to the peak from smaller contingents. As a result, combining all cohorts into a single group provides better estimates of mortality for blueback herring under the sampling regime used in this study. More frequent sampling may have allowed for the estimation of mortality for each recruitment pulse of a particular cohort. Future investigations that examine cohort specific mortality of blueback herring will have to account for recruitment pulses either by increased sampling frequency or through a sample design that encompasses the range of habitats available to YOY blueback herring.

Production of YOY blueback herring

Stock-specific patterns of growth were evident in the Mattaponi and Pamunkey rivers with growth of blueback herring consistently higher in the Pamunkey River than in the Mattaponi River. Growth rates of YOY blueback herring in the James and Rappahannock rivers were lower than that observed in the Mattaponi and Pamunkey rivers, at least at the limited spatial scale that was sampled. However abundance of blueback herring was greater in the James and Rappahannock rivers than in the Mattaponi or Pamunkey rivers, suggesting density-dependent growth limitation. Furthermore, when examining historic collections of blueback herring from the Mattaponi and Pamunkey rivers, conspecific abundance was identified as an important variable in the candidate model set that had a negative effect on predicted length at the end of summer. Length at the end of summer was used as a proxy for mass under the assumption that larger blueback herring are better able to avoid predation than smaller blueback herring. If there is food limitation in these systems, strong year classes that grow slowly may be subject to higher predation rates thus acting to regulate and stabilize recruitment. Evidence of food limitation was found for YOY American shad in a previous study in the Mattaponi River that may be related to water flow (Hoffman et al. 2007a). Increased water flow altered the food web base by introducing terrestrially derived carbon, which stimulated secondary production. The shift was subsequently observed in an isotopic shift in American shad tissue indicating that juveniles were feeding on new sources of carbon and perhaps increasing growth because of it (Hoffman et al. 2007).

The amount of variation in growth of YOY blueback herring observed in the James River compared with the other three systems could be related to available habitat. The James River has two additional river systems (the Appomattox River and the Chickahominy River) that feed into it below Bosher's Dam. The origin of the blueback herring captured is not known, however most were collected in this study from below the dam. It is possible that the variability in growth observed in this study represents a homogenization of YOY blueback herring from each of the three rivers (and associated habitats within these systems) as they migrate out of primary nurseries and into the tidal estuary before moving into Chesapeake Bay in fall. In the Rappahannock River there are approximately 125 tributaries available to anadromous alosines (O'Connell and Angermeier 1997), and similar variability in growth could be expected in the Rappahannock River if the entire nursery was sampled, however the majority of these additional systems were well downstream from the area sampled during this study.

Mortality of blueback herring varied by year and river population with lowest rates observed in the Mattaponi River and highest rates observed in the James and Rappahannock rivers. The high mortality rates observed in the James and Rappahannock rivers may be due to limited sampling design as blueback herring were collected from limited reaches of these rivers near Bosher's Dam on the James River and near the city of Fredericksburg on the Rappahannock River. Nonetheless, Dixon (1996) examined mortality rates of blueback herring in the Rappahannock River and found similar instantaneous mortality rates of 0.03 to

$0.07\ d^{-1}$ in 1991 and 0.13 to $0.14\ d^{-1}$ in 1992. These rates are high and can have significant impacts on year class strength (Houde 1989 and 1997). The relatively low M observed in the Mattaponi River suggests the possibility of strong recruitment from this system. Comparing M/G in each river indicates that the Mattaponi River has the lowest ratio further supporting strong recruitment potential from this system, however the Pamunkey River typically produces higher JAI values.

Population dynamics of YOY blueback herring is highly variable in Virginia. In the Pamunkey River, faster growth and higher mortality rates were observed compared with the Mattaponi River, where growth and mortality rates were relatively constant among years. Blueback herring from strong year-classes experience lower growth due to density-dependent processes and are smaller on average compared to weaker year-classes. Length of YOY blueback herring at the time of emigration may vary by a factor of 1.5 (42 mm Fl versus 64 mm Fl), while weight may vary by more than three (0.77 g versus 2.52 g) in strong versus weak year-classes. If predation pressure on migrating blueback herring is size-selective, a smaller mean length at the end of summer could increase mortality and reduce the contribution of a strong year class to the spawning stock. This is particularly important since blueback herring reside in shallow coastal waters where species such as striped bass also overwinter (Milstein 1981; Savoy and Crecco 2004). For species that are at low levels of abundance, recruitment stabilization may act to slow recovery.

Despite the close proximity of stocks and relatively consistent climatic regime among rivers, there is sufficient variability to affect YOY blueback herring population dynamics on a river-specific basis. The diverse array of habitats available to blueback herring as nurseries and the unknown contribution of these habitats to juvenile production remains an important area of research. Also critical to understanding the status of blueback herring stocks are species specific effort and landings data and independent assessments of adult abundance. Changes in growth and mortality of YOY stages can help to identify processes and sources of recruitment variation, but without data on adult dynamics, little inference can be made about how these dynamics may affect fisheries.

LITERATURE CITED

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Table 3.1. Mean monthly water temperature and discharge rate from April to October and the average for the time period from the Rappahannock, Mattaponi, Pamunkey and James rivers (2005 - 2007). Significant differences (ANOVA, Tukey HSD, a =0.05) among years for months when hatch typically occurs (April to June) are indicated by different superscript letters.

		Water temperature ($^{\circ}$C)			Water discharge (m^{3}/s)		
River	Month	2005	2006	2007	2005	2006	2007
Rappahannock	Apr	14.4 ^{a}	16.5 ^{b}	13.6 ^{a}	103.9	39.3	62.0
	May	18.0 ^{a}	19.7 ^{ab}	21.4 ^{b}	49.5	28.1	23.2
	Jun	26.1 ^{a}	25.4 ^{a}	26.7 ^{a}	19.1	35.1	9.7
	Jul	28.2	27.5	27.6	28.9	31.9	3.3
	Aug	28.1	29.0	28.2	11.7	5.0	6.5
	Sep	24.6	21.1	25.1	5.3	29.4	3.3
	Oct	15.0	14.2	21.0	67.0	54.6	6.5
	Average	24.0	23.0	25.5	40.8	31.9	16.3
Mattaponi	Apr	15.7 ^{a}	16.1 ^{a}	15.0 ^{a}	29.2	12.6	24.8
	May	19.1 ^{a}	17.8 ^{a}	19.6 ^{a}	16.4	10.4	13.6
	Jun	26.5 ^{a}	22.6 ^{b}	23.4 ^{b}	5.5	8.1	4.8
	Jul	29.6	25.4	24.6	6.3	12.3	1.8
	Aug	29.7	25.8	25.3	2.9	1.2	2.0
	Sep	26.2	19.8	21.6	0.9	16.2	0.9
	Oct	18.4	14.2	17.9	9.0	19.3	2.5
	Average	26.0	21.3	22.4	10.0	11.4	7.2
Pamunkey	Apr	15.4 ^{a}	17.4 ^{a}	14.0 ^{b}	51.8	17.1	36.0
	May	19.2 ^{a}	20.9 ^{a}	20.2 ^{a}	26.1	14.8	12.1
	Jun	27.4 ^{a}	26.2 ^{ab}	24.5 ^{b}	10.1	16.0	6.9
	Jul	30.0	28.8	26.1	8.5	7.9	4.1
	Aug	28.3	29.4	26.7	5.5	2.9	4.5
	Sep	25.0	22.9	23.0	2.7	15.6	2.4
	Oct	17.8	21.3	18.4	18.5	44.6	4.2
	Average	25.3	25.6	23.5	17.6	17.0	10.0
James	Apr	15.1 ^{a}	17.9 ^{b}	14.4 ^{a}	355.6	155.2	356.7
	May	18.9 ^{a}	20.4 ^{ab}	21.8 ^{b}	185.0	94.6	154.4
	Jun	26.4 ^{a}	25.8 ^{a}	26.9 ^{a}	94.0	227.2	86.8
	Jul	29.1	28.7	28.3	95.2	122.6	54.4
	Aug	29.1	30.1	29.7	58.6	31.2	41.6
	Sep	26.4	22.0	26.5	39.4	134.9	29.7
	Oct	17.7	15.2	21.0	121.0	306.4	51.0
	Average	25.6	24.0	26.4	135.5	153.2	110.7

Table 3.2. Length, wet weight, and age of blueback herring from the James, Mattaponi, Pamunkey, and Rappahannock rivers (2005 - 2007). The number of blueback herring (N), minimum (Min), maximum (Max), and SD of total length, wet weight, and daily age are shown.

			Total length (mm)				Wet weight (g)				Age (d)			
River	Year	N	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
James	2005	744	35.4	74.6	54.3	7.8	0.47	3.95	1.58	0.7	40	108	65.7	16.4
	2006	435	47.1	74.7	60.1	4.9	0.74	4.35	2.25	0.6	52	96	70.6	8.6
	2007	1602	33.6	68.5	51.0	6	0.37	2.80	1.24	0.4	33	94	60.5	12.7
Mattaponi	2005	1625	21.9	85.6	53.2	15.1	0.10	4.66	1.55	1.0	20	151	73.9	32.6
	2006	225	24.6	83.5	51.6	13.2	0.12	4.30	1.44	1.0	17	135	60.0	24.4
	2007	246	23.9	83.5	46.7	12.5	0.23	4.45	1.09	0.8	24	121	52.4	18.9
Pamunkey	2005	399	24.7	90.2	47.9	11.3	0.12	4.64	1.07	0.8	25	149	60.9	21.1
	2006	53	27.9	67.7	42.3	10.9	0.16	2.86	0.80	0.7	27	80	45.7	13.6
	2007	108	24.0	72.8	51.2	11.9	0.10	3.34	1.43	0.9	29	72	50.0	10.7
Rappahannock	2005	422	29.1	63.1	50.4	5.1	0.31	2.30	1.20	0.3	26	96	54.9	8.7
	2006	4284	21.0	86.1	53.1	7.0	0.14	4.90	1.43	0.5	17	179	78.8	19.4
	2007	3215	21.5	63.0	45.8	5.8	0.19	2.07	0.91	0.3	19	78	54.2	11.2

Table 3.3. Comparisons of growth models for juvenile blueback herring during the first year of growth. K is the number of paramters estimated, AIC is Akaiki's Information Criterion, and ΔAIC is the difference between the best model and the others.

Model	loglik	K	AIC	ΔAIC
von Bertalanffy	-39698.58	4	79405.16	0.00
Gompertz	-440371.37	4	80750.73	1345.57
Richards	DNC	5		

Table 3.4. The estimates of fixed-effects parameters for $L_t=\omega/k*(1-e^{-k*(age-t0)})$; $\omega = L_\infty*k$, and the logliklihood, AIC, and ΔAIC values. Total observations = 13,368, number of groups for the best model (bold) = 12.

Model	ϖ ±SE(ω)	k ±SE(k)	t0 ±SE(t0)	L_∞ ±SE(L_∞)	LogLik	AIC	ΔAIC
River	1.07 (0.072)	0.0122 (0.0020)	-10.06 (3.81)	87.81 (4.47)	-37605.66	75231.32	2404.64
Year	1.35 (0.066)	0.018 (0.002)	-2.48 (0.566)	73.15 (7.13)	-38702.86	77425.71	4599.03
River*year	**1.30 (0.149)**	**0.0153 (0.0037)**	**-4.35 (2.284)**	**84.94 (6.2)**	**-36402.34**	**72826.68**	**0**

Table 3.5. Deviation of parameter estimates (random effects) from fixed-effects by river and year.

River	Year	ω	k	t0
James	2005	-0.203	-0.003	-6.094
	2006	0.323	0.006	1.392
	2007	0.024	0.004	-5.663
Mattaponi	2005	-0.266	-0.005	-0.970
	2006	-0.273	-0.006	-5.456
	2007	-0.170	-0.006	2.568
Pamunkey	2005	-0.450	-0.009	-6.021
	2006	-0.480	-0.014	-4.046
	2007	-0.347	-0.016	2.361
Rappahannock	2005	0.980	0.022	12.026
	2006	-0.103	0.002	-1.991
	2007	0.965	0.026	11.895

Table 3.6. Effects of River on parameter estimates in the fixed effects model for growth of blueback herring juveniles relative to the James River.

Parameter	River	Value	Std.Error	DF	t-value	p-value
ω	James	1.017	0.198	13345	5.149	0.000
	Mattaponi	0.056	0.253	13345	0.221	0.825
	Pamunkey	-0.145	0.266	13345	-0.545	0.586
	Rappahannock	0.884	0.261	13345	3.383	0.001
k	James	0.012	0.004	13345	2.845	0.004
	Mattaponi	-0.002	0.005	13345	-0.316	0.752
	Pamunkey	-0.009	0.006	13345	-1.652	0.099
	Rappahannock	0.020	0.006	13345	3.604	0.000
t_0	James	-21.372	6.486	13345	-3.295	0.001
	Mattaponi	16.163	6.976	13345	2.317	0.021
	Pamunkey	14.623	7.448	13345	1.963	0.050
	Rappahannock	24.325	6.965	13345	3.493	0.001

Table 3.7. Effects of Year on parameter estimates in the fixed effects model for growth of blueback herring juveniles relative to 2005.

Parameter	Year	Value	Std.Error	DF	t-value	p-value
ω	2005	1.311	0.241	13348	5.430	0.000
	2006	-0.180	0.343	13348	-0.526	0.599
	2007	0.145	0.343	13348	0.424	0.671
k	2005	0.016	0.006	13348	2.620	0.009
	2006	-0.005	0.009	13348	-0.541	0.589
	2007	0.002	0.009	13348	0.180	0.857
t_0	2005	-4.385	3.197	13348	-1.372	0.170
	2006	-3.712	4.856	13348	-0.764	0.445
	2007	3.892	4.622	13348	0.842	0.400

Table 3.8. Cohort-specific growth estimates of blueback herring from the Rappahannock River from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_0 and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm/d) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_0 (SE)	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	All		61.58 (1.231)	0.037 (0.004)	18.96 (2.058)	422	1.05	0.50	0.24	0.11
2006	1	30-Apr	61.36 (2.352)	0.020 (0.003)	-7.28 (4.725)	57	0.48	0.32	0.22	0.15
	2	5-May	70.31 (1.166)	0.014 (0.001)	-14.42 (1.614)	302	0.46	0.35	0.26	0.20
	3	10-May	72.61 (0.989)	0.015 (0.001)	-4.65 (1.362)	319	0.56	0.41	0.30	0.22
	4	15-May	68.73 (1.066)	0.018 (0.001)	-0.40 (1.744)	435	0.59	0.42	0.29	0.21
	5	20-May	72.54 (0.876)	0.017 (0.001)	0.55 (1.229)	696	0.63	0.45	0.32	0.23
	6	25-May	70.51 (1.107)	0.019 (0.001)	3.81 (2.081)	488	0.68	0.46	0.31	0.21
	7	30-May	65.93 (0.558)	0.022 (0.001)	1.09 (1.688)	862	0.62	0.39	0.25	0.16
	8	4-Jun	63.70 (0.894)	0.025 (0.002)	-1.27 (3.771)	568	0.57	0.34	0.21	0.13
	9	9-Jun	77.28 (1.366)	0.017 (0.001)	-0.81 (2.699)	335	0.66	0.47	0.33	0.23
	10	14-Jun	62.32 (1.225)	0.023 (0.002)	-12.14 (4.446)	218	0.43	0.27	0.17	0.11
	All		70.83 (0.366)	0.017 (0.000)	4.94 (0.647)	4284	0.66	0.47	0.34	0.24
2007	1	7-May	67.37 (4.574)	0.026 (0.004)	5.33 (3.346)	128	0.71	0.42	0.25	0.15
	2	12-May	54.71 (0.704)	0.055 (0.005)	13.54 (1.600)	268	0.70	0.24	0.08	0.03
	3	17-May	50.78 (0.378)	0.077 (0.006)	17.11 (0.941)	541	0.67	0.15	0.03	0.01
	4	22-May	58.41 (0.918)	0.029 (0.002)	0.06 (1.299)	762	0.53	0.30	0.17	0.10
	5	27-May	59.52 (1.993)	0.029 (0.003)	2.72 (2.293)	410	0.59	0.33	0.18	0.10
	6	1-Jun	63.99 (1.886)	0.024 (0.002)	0.90 (2.160)	620	0.60	0.37	0.23	0.14
	All		54.61 (0.366)	0.041 (0.001)	18.83 (0.631)	3215	0.94	0.41	0.18	0.08

Table 3.9. Cohort specific growth estimates of blueback herring from the Mattaponi River from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_0 and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm/d) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_0 (SE)	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	3	8-May	84.95 (4.490)	0.012 (0.001)	-5.41 (2.451)	45	0.59	0.47	0.37	0.29
	4	13-May	78.64 (1.787)	0.014 (0.001)	-4.12 (1.438)	103	0.60	0.45	0.34	0.25
	5	18-May	81.37 (1.622)	0.015 (0.001)	0.16 (1.062)	304	0.67	0.50	0.37	0.27
	6	23-May	77.79 (1.337)	0.017 (0.001)	1.06 (0.979)	390	0.69	0.49	0.34	0.24
	7	28-May	79.84 (1.234)	0.019 (0.001)	7.96 (1.695)	326	0.83	0.56	0.38	0.26
	8	2-Jun	91.94 (1.706)	0.014 (0.001)	3.84 (1.457)	176	0.78	0.59	0.44	0.34
	9	7-Jun	88.28 (1.980)	0.016 (0.001)	7.33 (2.340)	126	0.84	0.61	0.44	0.32
	10	12-Jun	92.12 (2.043)	0.016 (0.001)	12.91 (1.996)	93	0.97	0.70	0.50	0.36
	11	17-Jun	92.93 (2.559)	0.014 (0.001)	6.10 (2.539)	44	0.82	0.62	0.46	0.35
	All		98.57 (0.692)	0.012 (0.004)	5.96 (2.283)	1625	0.70	0.57	0.47	0.38
2006	3	11-May	91.28 (8.787)	0.013 (0.003)	-5.80 (4.351)	12	0.66	0.51	0.39	0.30
	4	16-May	84.53 (5.870)	0.016 (0.003)	-5.27 (4.887)	22	0.66	0.48	0.34	0.25
	5	21-May	92.84 (5.696)	0.012 (0.002)	-10.49 (3.615)	33	0.61	0.48	0.38	0.30
	6	26-May	86.83 (4.610)	0.016 (0.002)	0.08 (2.669)	57	0.73	0.53	0.39	0.28
	7	31-May	96.74 (4.458)	0.013 (0.001)	-3.91 (2.482)	56	0.70	0.54	0.42	0.33
	8	5-Jun	90.25 (6.814)	0.017 (0.003)	3.59 (4.839)	24	0.82	0.59	0.42	0.30
	9	10-Jun	92.69 (10.708)	0.015 (0.005)	-0.96 (13.044)	11	0.75	0.56	0.41	0.31
	All		112.12 (2.252)	0.009 (0.001)	1.48 (1.291)	225	0.72	0.60	0.50	0.42
2007	3	11-May	94.13 (15.340)	0.015 (0.004)	4.57 (3.454)	29	0.84	0.62	0.45	0.34
	4	16-May	76.80 (4.058)	0.024 (0.003)	8.547 (1.742)	55	0.86	0.54	0.34	0.21
	5	21-May	78.88 (37.836)	0.015 (0.022)	-9.33 (64.380)	71	0.56	0.42	0.31	0.23
	6	26-May	92.38 (4.817)	0.016 (0.002)	5.28 (2.666)	57	0.85	0.62	0.45	0.33
	7	31-May	84.79 (11.851)	0.018 (0.006)	4.78 (7.308)	18	0.81	0.56	0.40	0.28
	All		118.35 (2.378)	0.096 (0.001)	9.50 (0.864)	246	0.84	0.70	0.58	0.48

Table 3.10. Cohort specific growth estimates of blueback herring from the Pamunkey River from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_o and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm/d) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_o (SE)	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	3	7-May	91.86 (10.619)	0.014 (0.003)	4.02 (4.743)	23	0.78	0.59	0.44	0.33
	4	12-May	71.18 (3.416)	0.023 (0.003)	5.51 (2.939)	60	0.74	0.47	0.29	0.18
	5	17-May	66.17 (3.262)	0.027 (0.005)	8.25 (3.384)	66	0.76	0.44	0.26	0.15
	6	22-May	78.42 (4.675)	0.017 (0.002)	2.27 (2.936)	70	0.70	0.50	0.36	0.26
	7	27-May	86.37 (7.047)	0.015 (0.003)	5.74 (5.274)	63	0.77	0.57	0.43	0.32
	8	1-Jun	91.83 (7.218)	0.014 (0.002)	8.31 (4.044)	42	0.83	0.63	0.47	0.35
	9	6-Jun	103.09 (7.633)	0.010 (0.001)	-2.08 (3.846)	24	0.68	0.56	0.45	0.37
	10	11-Jun	110.79 (8.052)	0.010 (0.001)	6.04 (3.208)	21	0.79	0.65	0.53	0.43
	11	16-Jun	108.43 (8.697)	0.012 (0.002)	10.89 (5.327)	12	0.90	0.71	0.56	0.45
	All		131.63 (2.085)	0.006 (0.001)	0.91 (1.280)	399	0.66	0.58	0.51	0.45

Table 3.11. Cohort-specific growth estimates of blueback herring from the James River from 2005 to 2007 including cohort number, hatch date (mid-point of the 5-d range), asymptotic length (L_∞), K, t_o and N. Growth parameters were estimated from the von Bertalanffy growth function. Instantaneous daily growth (G mm/d) estimates from the derivative of the VBGF at ages 40, 60, 80 and 100 d are provided.

Year	Cohort	Hatch date	L_∞ (SE)	K (SE)	t_o (SE)	N	G_{40}	G_{60}	G_{80}	G_{100}
2005	2	11-May	51.19 (2.937)	0.081 (0.118)	6.84 (66.603)	104	0.28	0.06	0.01	0.00
	4	21-May	75.54 (3.454)	0.023 (0.004)	5.57 (5.435)	46	0.79	0.49	0.31	0.19
	5	26-May	75.41 (2.582)	0.021 (0.002)	4.28 (3.996)	146	0.74	0.49	0.33	0.22
	7	5-Jun	76.97 (3.046)	0.024 (0.004)	14.13 (4.226)	79	1.00	0.61	0.38	0.23
	9	15-Jun	72.03 (1.924)	0.028 (0.004)	7.16 (3.290)	35	0.80	0.46	0.26	0.15
	All		92.38 (1.048)	0.012 (0.001)	0.84 (1.488)	744	0.69	0.54	0.43	0.34
2006	1	4-May	76.81 (4.094)	0.028 (0.008)	10.06 (17.987)	15	0.93	0.53	0.30	0.17
	3	14-May	68.77 (4.058)	0.030 (0.014)	2.48 (21.338)	46	0.67	0.37	0.20	0.11
	4	19-May	67.16 (2.697)	0.033 (0.011)	2.87 (13.132)	72	0.65	0.33	0.17	0.09
	5	24-May	71.12 (3.898)	0.030 (0.008)	6.55 (9.325)	87	0.78	0.43	0.24	0.13
	6	29-May	61.13 (3.838)	0.073 (0.218)	11.65 (199.076)	113	0.56	0.13	0.03	0.01
	All		76.31 (1.446)	0.021 (0.002)	8.32 (3.972)	435	0.83	0.54	0.35	0.23
2007	1	4-May	68.85 (3.581)	0.025 (0.008)	0.57 (10.899)	43	0.64	0.39	0.23	0.14
	2	9-May	64.55 (2.677)	0.029 (0.004)	3.27 (3.791)	201	0.65	0.36	0.21	0.12
	3	14-May	61.23 (0.701)	0.053 (0.005)	19.24 (1.829)	326	1.08	0.38	0.13	0.05
	4	19-May	70.78 (2.222)	0.024 (0.003)	1.58 (3.196)	327	0.67	0.42	0.26	0.16
	5	24-May	63.00 (1.673)	0.025 (0.003)	-4.32 (4.038)	296	0.52	0.31	0.19	0.11
	6	29-May	58.83 (1.634)	0.029 (0.004)	-5.93 (7.656)	276	0.45	0.26	0.14	0.08
	7	3-Jun	57.76 (3.042)	0.032 (0.011)	-5.58 (14.308)	71	0.43	0.23	0.12	0.06
	All		69.98 (0.803)	0.019 (0.001)	1.27 (1.614)	1602	0.64	0.44	0.30	0.20

Table 3.12. Blueback herring total instantaneous mortlaity rate (d^{-1}) and standard error (SE) from the Rappahannock, Mattaponi, Pamunkey, and James rivers, 2005 - 2007.

	2005			2006			2007		
River	M	se	N	M	se	N	M	se	N
Rappahannock	0.144	0.020	307	0.056	0.006	2950	0.120	0.034	1613
Mattaponi	0.016	0.007	1119	0.023	0.005	146	0.012	0.009	215
Pamunkey	0.079	0.016	135	0.049	0.018	53	0.119	0.054	108
James	0.037	0.008	679	0.114	0.018	319	0.146	0.032	561

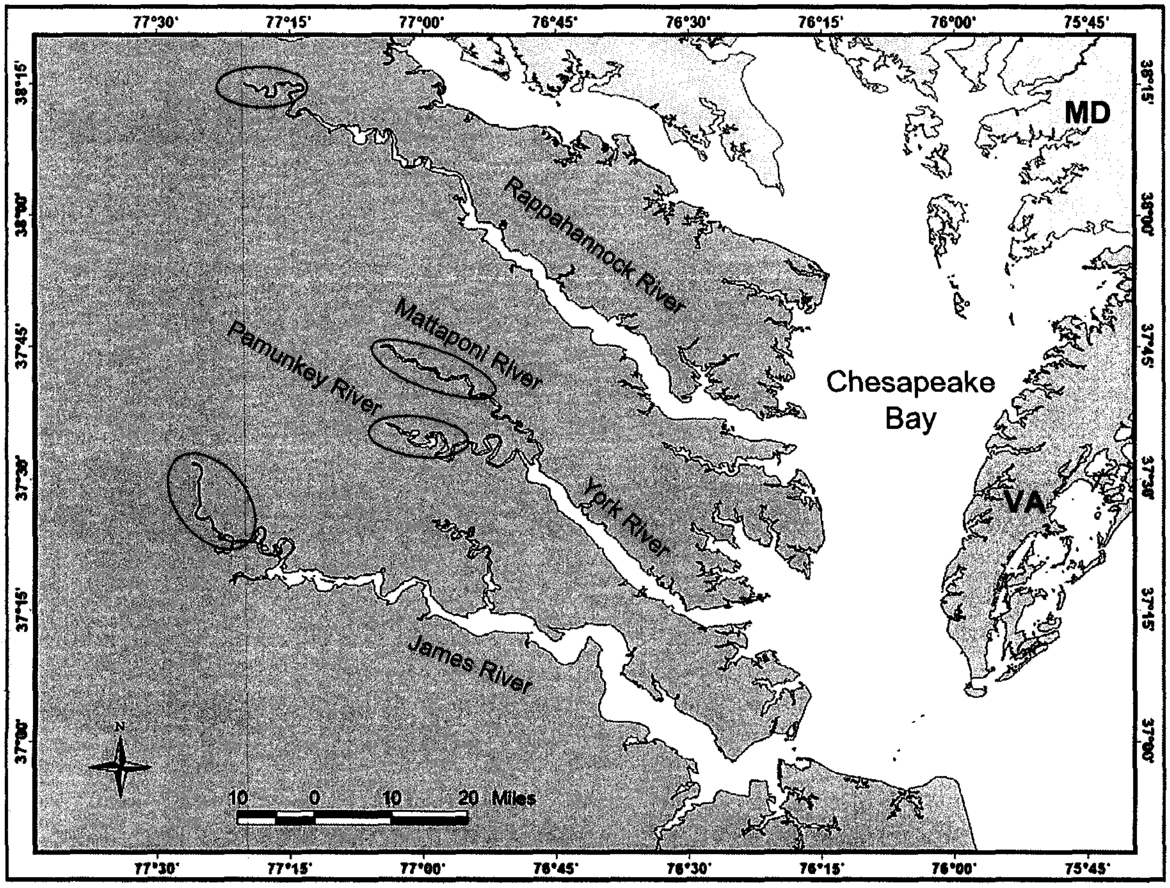
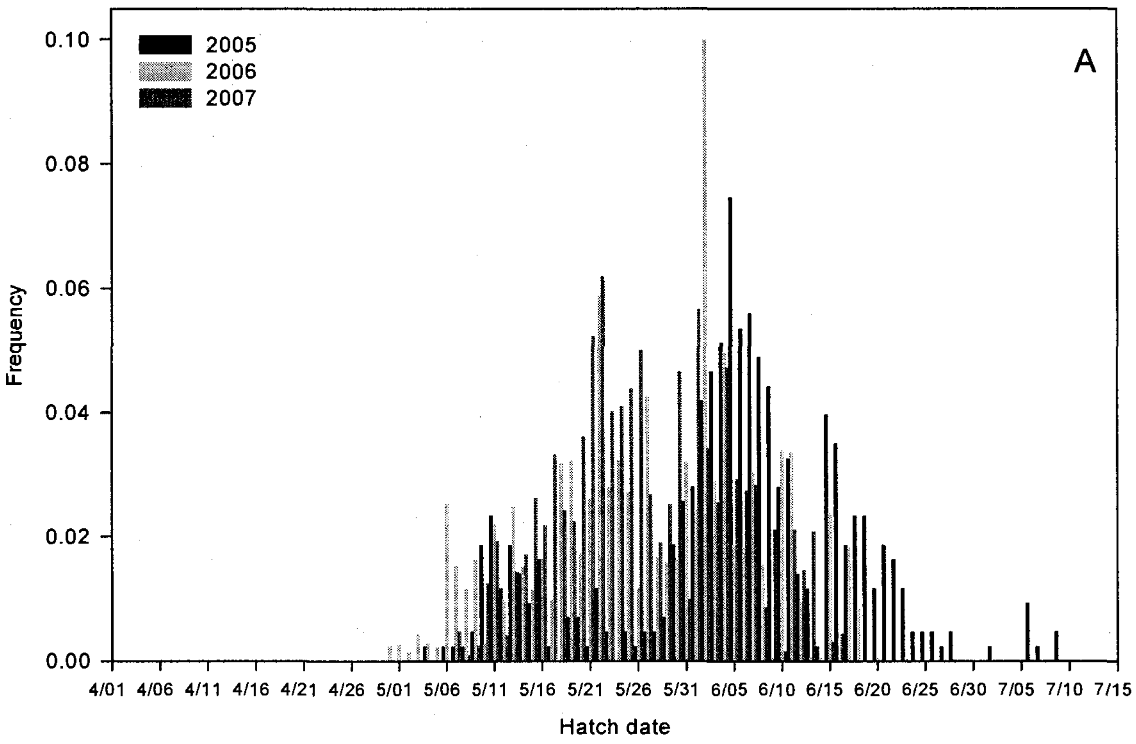


Figure 3.1. Virginia rivers and sampling locations (circled regions) for juvenile blueback herring, 2005 - 2007.



0.10
0.08
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0.04
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Frequency
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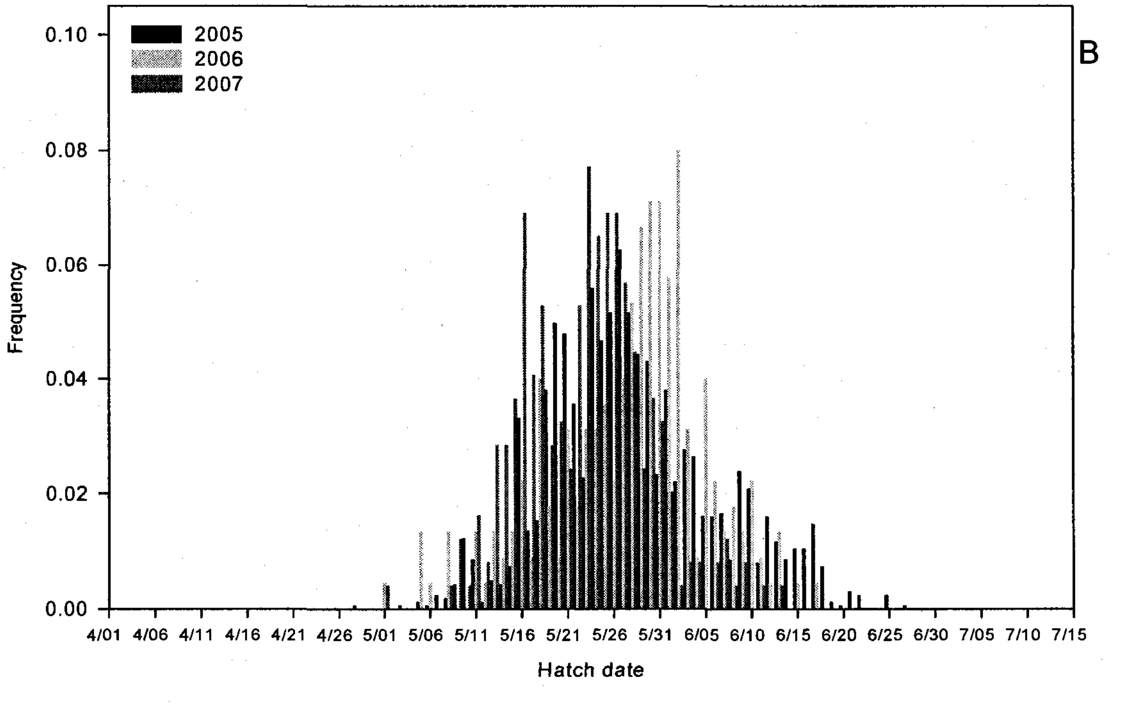
2006
2007
A
4/01 4/06 4/11 4/16 4/21 4/26 5/01 5/06 5/11 5/16 5/21 5/26 5/31 6/05 6/10 6/15 6/20 6/25 6/30 7/05 7/10 7/15
Hatch date



0.10
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Frequency
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4/01 4/06 4/11 4/16 4/21 4/26 5/01 5/06 5/11 5/16 5/21 5/26 5/31 6/05 6/10 6/15 6/20 6/25 6/30 7/05 7/10 7/15
Hatch date

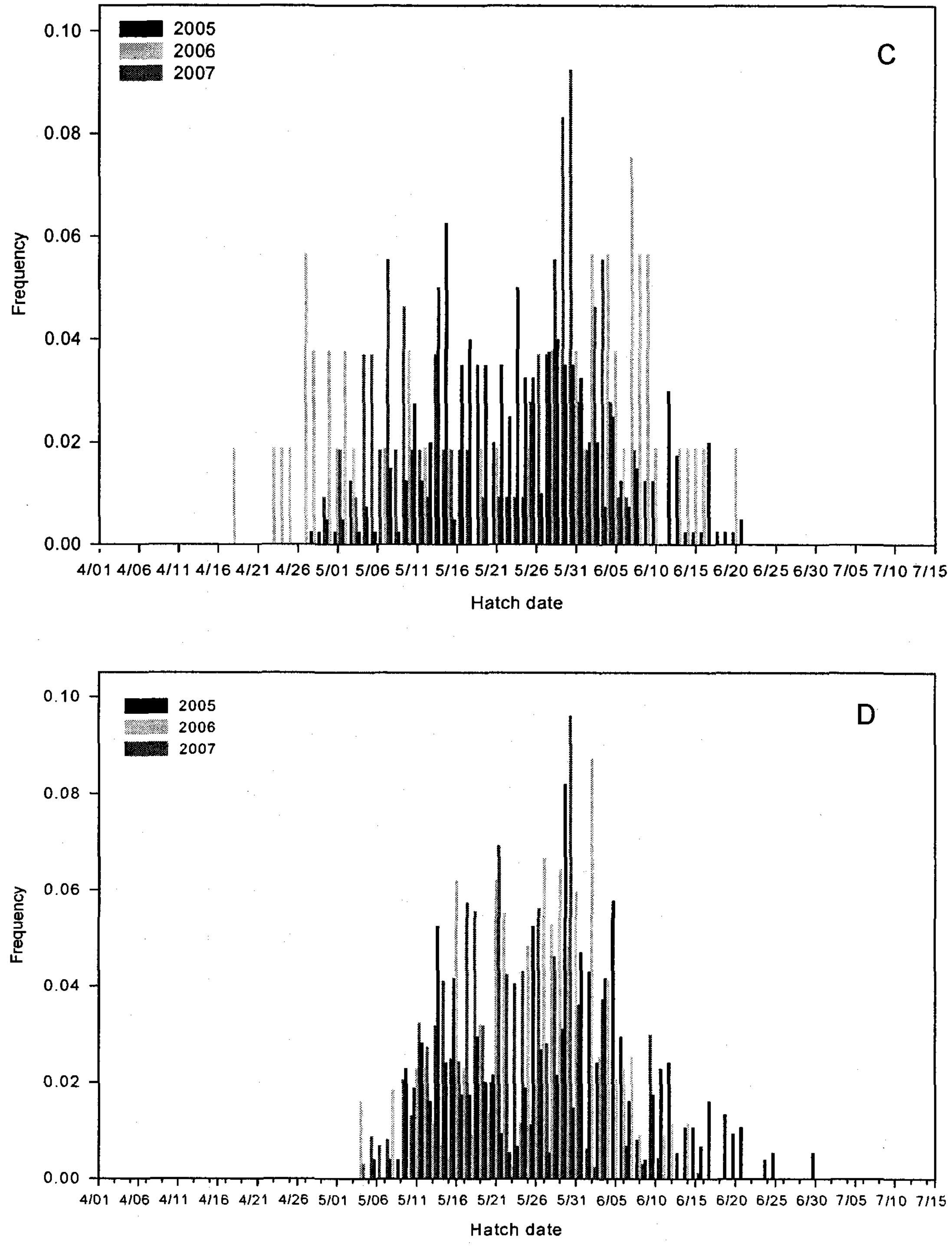


Figure 3.2. Hatch date distributions of young-of-year blueback herring from the Rappahannock (A), Mattaponi (B), Pamunkey (C), and James (D) rivers from 2005 to 2007.

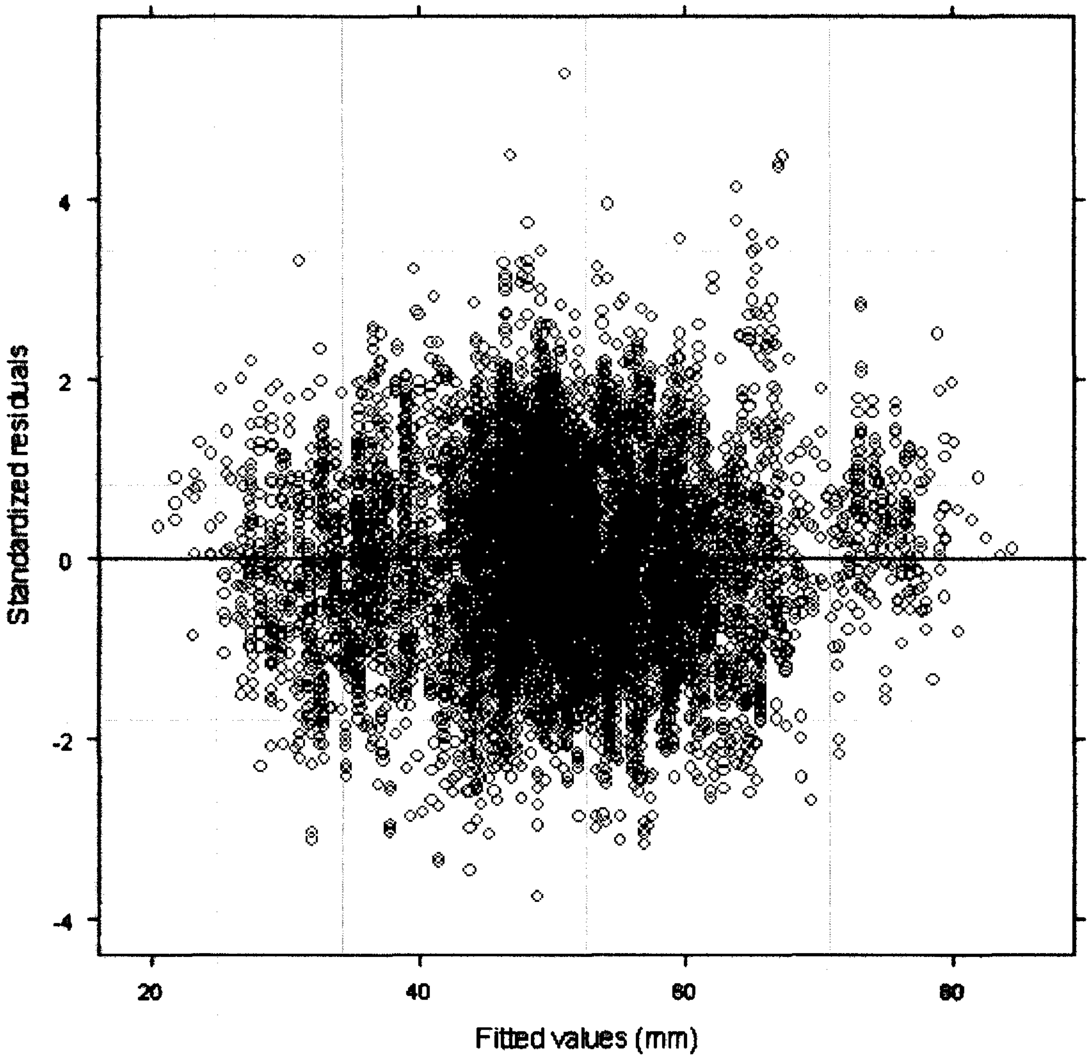


Figure 3.3. Standardized residuals vs. fitted values for the von Bertalanffy mixed effects model.

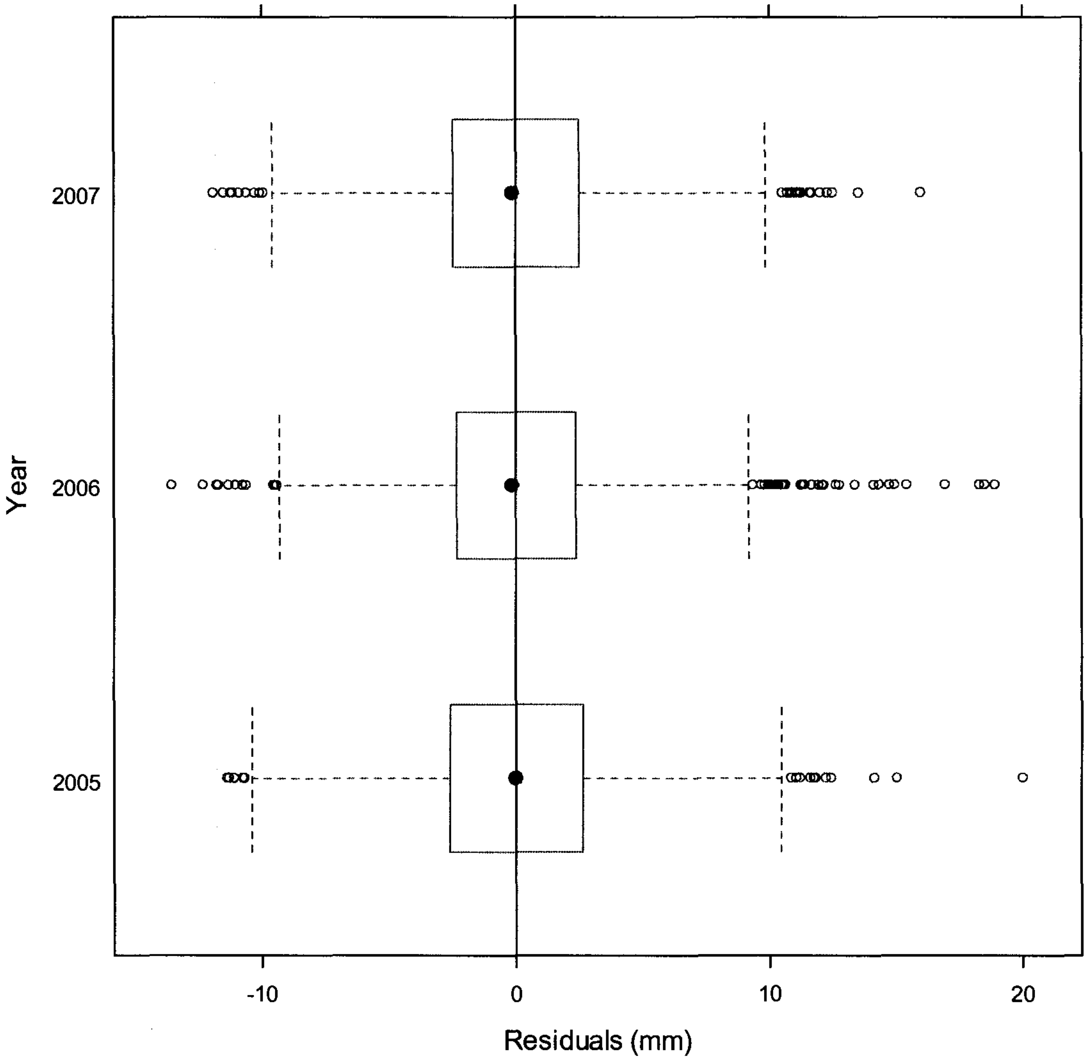


Figure 3.4. Standardized residuals vs. Year for the von Bertalanffy mixed effects model.

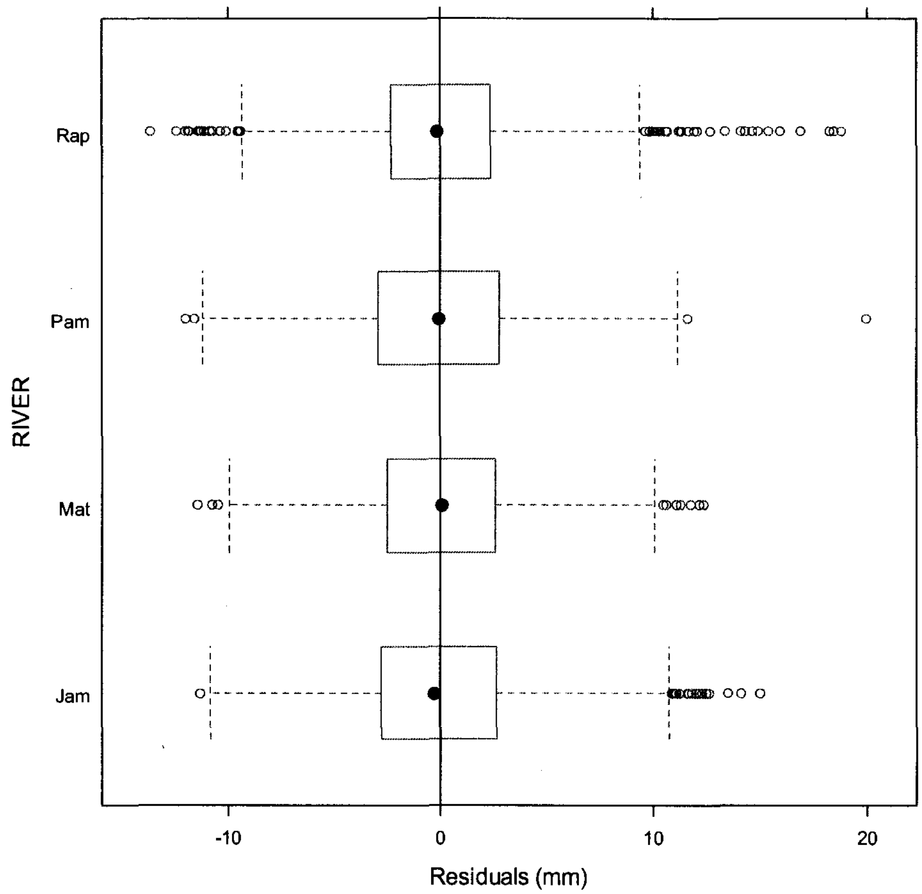


Figure 3.5. Standardized residuals vs. River for the von Bertalanffy mixed effects model.

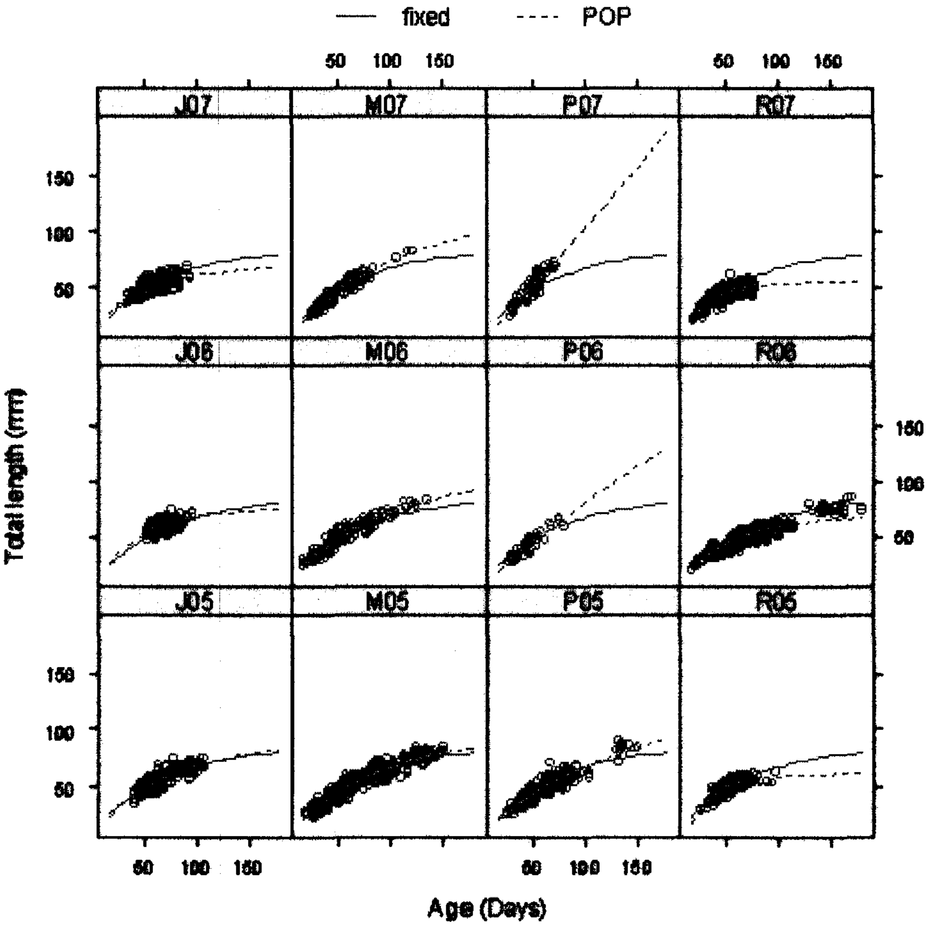


Figure 3.6. Global predictions (fixed) of juvenile blueback herring growth and within population predictions (POP) for year classes in the Rappahannock (R) , Mattaponi (M), Pamunkey (P), and James (J) rivers from 2005 to 2007 (05, 06, 07).

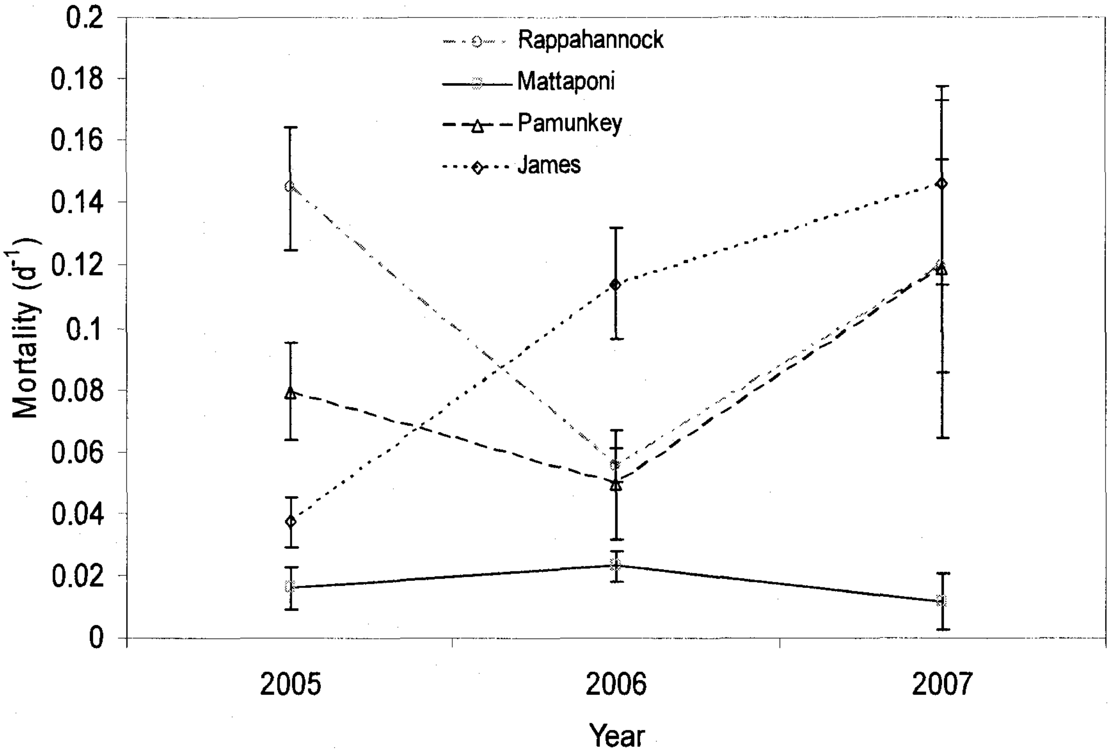


Figure 3.7. Total instantaneous mortality rates for the Rappahannock, Mattaponi, Pamunkey and James rivers, 2005-2007.

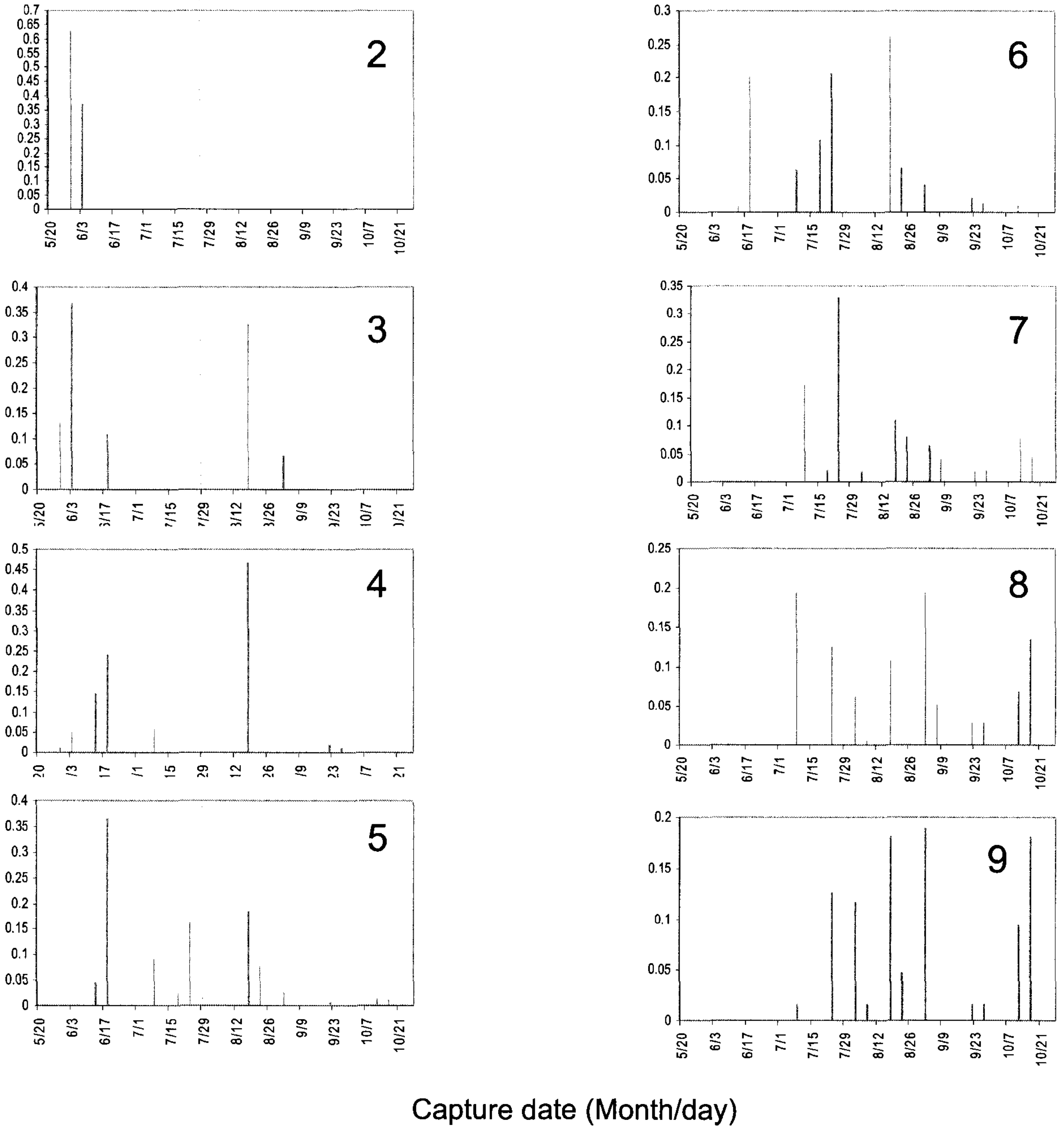
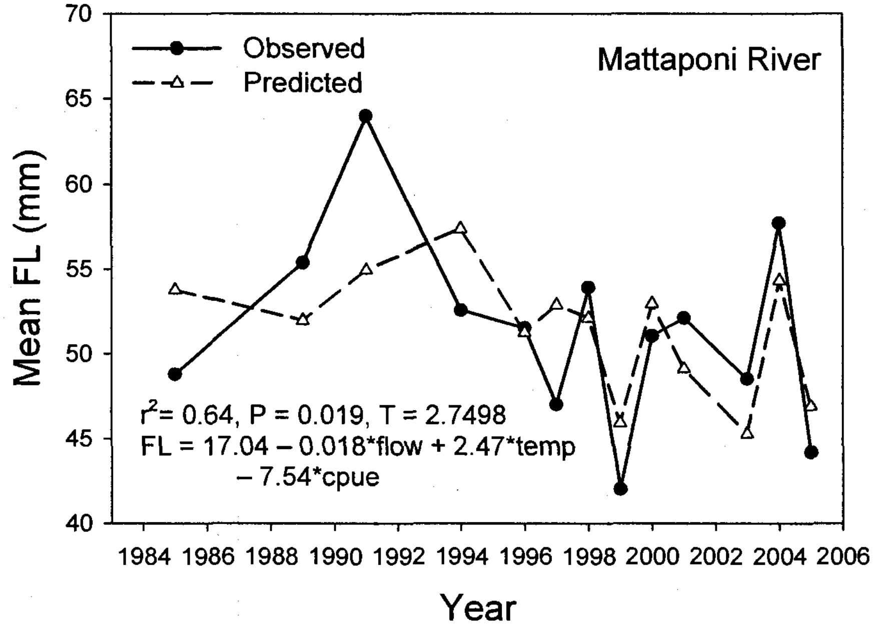


Figure 3.8. Catch (frequency) of blueback herring cohorts (2 – 9) captured in the Mattaponi River during 2005.



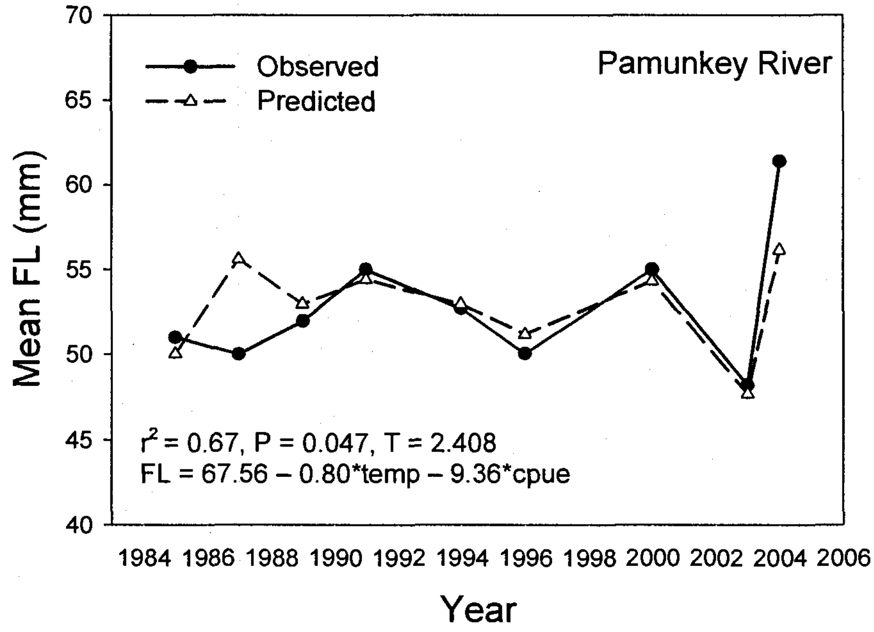


Figure 3.9. Predicted mean fork length from best-fit model and Pearson correlation test results for young-of-year blueback herring from VIMS striped bass seine survey from the Mattaponi and Pamunkey rivers, 1985 to 2007.

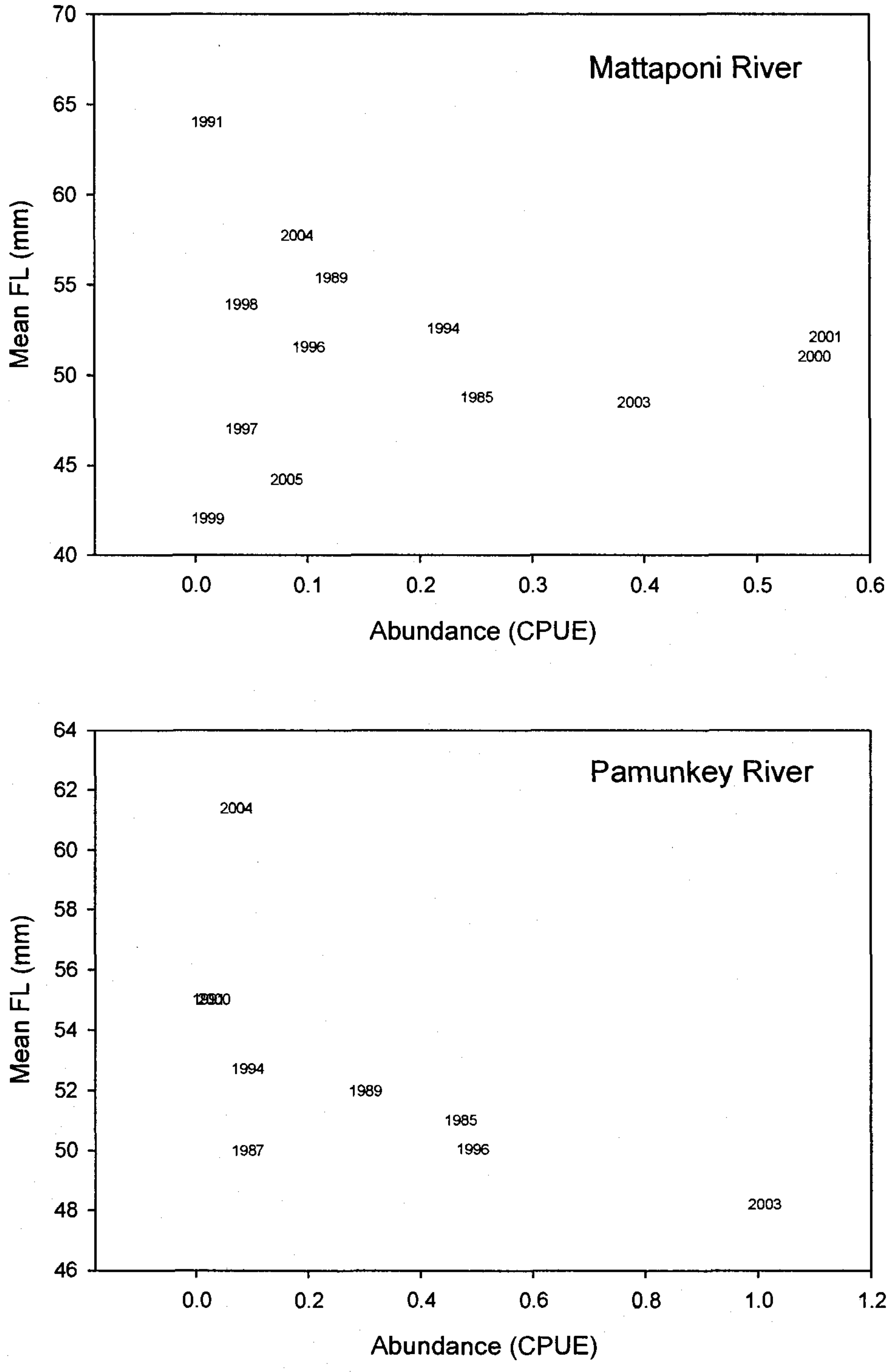


Figure 3.10. Comparison of annual geometric mean catch per unit effort and mean fork length in September from the Mattaponi and Pamunkey rivers, 1985-2007. Missing years in the figures indicates years no blueback herring were collected in September.

Chapter Four

Abundance of Juvenile American Shad may be Used to Assess the Future Strength of the Spawning Run in Chesapeake Bay

ABSTRACT

Predicting spawning stock biomass from juvenile abundance has been a focal point of fisheries research. Natural variability in abundance, unknown sources of mortality on immature fish and survey error have resulted in limited success, especially for anadromous fishes. However, the prediction of relative strength of adult spawning runs from juvenile indices holds promise for American shad in Chesapeake Bay. Cohort-specific catch-at-age data from an adult monitoring program in Virginia were used to estimate the annual total instantaneous mortality rate for available year classes. The analysis used maturity schedules (see Chapter 1) estimated to determine the proportion mature between ages 3 and 7 that would be expected to spawn (all shad are mature after age 8). Juvenile indices of abundance obtained from a seine survey were incorporated into an additive model that used estimated mortality rates and maturity schedules to adjust cohorts comprising the spawning for years they were at large prior to making the spawning run. The sum of the indices for spawning age-classes (ages 3 to 10 or 11) resulted in a predicted index that matched observed trends from 1998 to 2006 for three stocks of American shad in Virginia. Furthermore, the model can be used to forecast the spawning index three years into the future.

INTRODUCTION

American shad is an anadromous clupeid that returns to natal rivers to spawn along the eastern seaboard of North America from northern Florida to New Brunswick (Talbot and Sykes 1958; Walburg 1960; Carscadden and Leggett 1975). The American shad fishery was once the most lucrative fishery in the U.S. with peak landings in the late 1800's and declining catches thereafter to levels that remain extremely low by comparison (Limburg et al. 2003). Many factors contributed to the collapse of the fishery including overfishing, dam construction, poor water quality, and loss of nursery habitat. Efforts to rebuild stocks began with hatchery operations in the 1800's and early 1900's and have continued with the addition of fishing regulations and moratoria, construction of dam bypass structures and breaches or complete removal of dams (ASMFC 2007; Hendricks et al. 2003; Weaver et al. 2003). Despite these efforts, most stocks show little evidence of recovery (ASMFC 2007). Spawning runs of American shad are monitored in various ways, from counts of fish lifted over dams to surveys of spawning adults in natal rivers to provide catch rate estimates or relative abundance indices.

Factors that affect distribution and survival (e.g. water temperature, oceanic currents, predation, fishing) of migratory species span wide geographic ranges making it difficult to assess impacts on all life stages without costly surveys. Furthermore, other processes such as stock structure and mixing add complexity that is difficult to account for in models often forcing simplifying assumptions that may not be realistic. In some cases, unique aspects of the biology and ecology of the species under investigation may allow for the removal of some assumptions from models. For example, because of the homing nature of American shad and apparent low rates of in-river stock mixing (Hendricks et al. 2003), immigration and emigration can be neglected in models and population dynamics can focus on discreet stocks with reasonable confidence. In addition, because each river supports a separate stock, a population dynamics model developed for one river can be tested in other rivers to explore its applicability in a broader context.

Two relative abundance indices of American shad often provide data for stock assessments: an index of abundance for juveniles (JAI) and an adult index obtained by multiple methods (sentinel fisheries, electrofishing, passage counts, etc.) during the in-river spawning migration. These data sources were widely used in the recent coast-wide survey of stock status (ASMFC 2007). In Virginia, an assessment using an adult index determined that Virginia stocks are currently stable, but at levels that are insufficient to lift a ban on fishing established in 1994. The assessment did not account for recent juvenile production and future recruitment into the spawning population although qualitative inferences about recruitment failure or success were considered. Therefore, new insights and methods that relate juvenile abundance to adult biomass in a predictive capacity could strengthen the assessment process.

To examine the relationship between juveniles and adult American shad, an additive model was developed that incorporates available juvenile abundance indices, estimated maturity schedules, and adult mortality rates and compares them with observed catches of female American shad from a staked gill net fishery (SGN). The model was used to predict spawning indices for three rivers: Rappahannock, York, and James rivers. The SGN monitoring program is a sentinel fishery using traditional gear fished at historical locations in each river. The program was initiated to assess American shad stocks in Virginia (Olney and Hoenig 2001). Index values are compared with historical catches in the 1950's and 1980's and the values obtained comprise the principle assessment data on current adult abundance.

METHODS

Relative abundance Indices

The Virginia Institute of Marine Science has been monitoring the spawning migration of adult American shad in the York, James, and Rappahannock rivers since 1998 (Fig. 4.1). Migrating adults are captured using staked gill nets, a gear that was used when the fishery was in operation, to produce an index of abundance (Olney and Hoenig 2001). The same gear design is used in the York and James rivers, which consists of a 273 m long stand of 12.4 cm stretched-mesh, monofilament netting that is strung between poles driven into the riverbed at 9.14 m intervals. The Rappahannock River fishery used a slightly different design with 12.7 cm stretched-mesh monofilament netting placed between poles spaced every 14.6 m. Historical gear designs were adhered to, as closely as possible, so that catch rates from current monitoring efforts could be directly related to historical catches from the same locations. Nets were fished weekly for two consecutive days during the spawning run from late February to May during 1998 to 2007 in all three rivers. All American shad were brought to the lab, weighed, measured, sexed, and staged for maturity. In addition, scales were removed and used for age determination (Cating 1953). Annual total instantaneous mortality rates were estimated using longitudinal catch-at-age data for year classes that had been caught during the SGN monitoring program over a sufficient number of reproductive years to yield a catch-curve regression. Cohort-specific mortality rates were estimated for year classes from 1994 to 1998 (Figs. 4.2 – 4.4). Because portions of American shad populations mature between ages three and seven, abundance-at-age data were adjusted by dividing by the predicted proportion mature to account for individuals that are still alive but immature and therefore unavailable to the gear (Maki et al. 2001; Olney and Hoenig 2001). More recent year-classes (1999 - 2003) were assumed to experience the mean mortality rate derived from the estimates for the 1994 to 1998 year classes. Although it should have been possible to estimate a mortality rate for the 1999 year class in theory, only three age classes with five or more fish per age was available and therefore regression analysis was not performed.

A time series of juvenile indices was obtained from the VIMS striped bass seine survey. The seine survey samples the James, York, and Rappahannock rivers, including tidal freshwater habitats, during five approximately biweekly sampling periods from July through mid-September. At each fixed station, the seine (30.5 m x 1.22 m x 6.4 mm bar mesh) is deployed perpendicular to the shoreline (either until the net is fully extended or a depth of approximately 1.2 m is reached) leaving one end in a fixed position onshore while the other end is hauled with the current until the seine is fully extended and then back to the shore. The geometric mean catch per haul from the seine survey has been shown to correlate with another independent survey in the York River that specifically targeted juvenile *Alosa* spp., and is therefore assumed to provide a JAI for the Rappahannock River as well (Wilhite et al. 2003). Catches of juvenile American shad in the seine survey on the James River are consistently low or zero. The spawning run of American shad on the James River is considered to be dependent on the release of hatchery-reared larvae (Olney et al. 2003; ASMFC 2007). As a result, the number of larvae released each year by the Virginia Department of Game and Inland Fisheries (VDGIF) was used as a proxy for juvenile abundance.

Model development

A predictive model that relates juvenile abundance to annual adult abundance across all ages was constructed by combining the proportion mature-at-age, year-class specific adult mortality rates and juvenile indices of abundance into an index of spawning adults (ISA) at time t is as follows:

$ISA_t = \Sigma^{x}_{a=3} (e^{-z_i * a})(y_i)(r_{i,a})$ where, a = age, x = maximum age of expected year-class in the spawning population, Z_i= year-class specific total instantaneous mortality rate, y_i = year-class specific juvenile index of abundance, $r_{i,a}$ = age- and year-class specific proportion mature (see Chapter 1). Least-squares estimation was used to derive a multiplier to adjust the ISA value to the same scale as the SGN index. The relationship between the adjusted ISA and the observed adult index resulting from the SGN monitoring program was examined using correlation analysis. Since the model is based on juvenile abundance indices, it can predict spawning indices beginning three years in the future – the year that a portion of the current year class will reach maturity and be available to the gillnet monitoring gear. Although the proportion mature at age 3 is low compared with older ages, strong year classes may make important contributions to the spawning run at age 3.

Age-specific catch rates were calculated in the same manner as annual catch rates to examine the relationship between JAI estimates and age-specific catch in a longitudinal approach and models were re-evaluated by year class. This was performed as a test of the model formulation and parameter estimates.

RESULTS

Female American shad catch rate indices from the SGN monitoring program from 1998 to 2007 were highest in the York River for most years followed by the James and Rappahannock rivers (Table 4.1). There was no correlation among indices for the time series between the York and James rivers (Kendall's tau= 0.156, p=0.601) or the York and Rappahannock rivers (Kendall's tau= 0.067, p=0.861), but there was a significant correlation between the James and Rappahannock rivers (Kendall's tau= 0.556, p=0.029).

Total instantaneous mortality estimates (Z) for adult American shad from longitudinal catch curves were highest in the James River and varied between 0.703 and 1.017. Estimates from the York River were from 0.556 to 1.032, and those from the Rappahannock River were from 0.489 to 0.898 (Table 4.2). There was insufficient data to estimate Z for all year classes that comprised the spawning run (typically ages 3 to 10). Therefore mean total instantaneous mortality rate estimates from each river were used for year classes without explicit estimates (1994 to 1999) and resulted in Z = 0.862 for the York River, Z = 0.699 for the Rappahannock River and Z = 0.814 for the James River.

Juvenile abundance indices for the York River had a wide range, but estimates were consistently higher in the York River than in the Rappahannock River (Table 4.3). Years with low abundance estimates in the York River coincided with low abundance estimates in the Rappahannock River (1991, 1992, 1995, 1999 and 2002). Hatchery production did not begin until 1992 in the James River and numbers released varied from 50,000 larvae in 1992 to the highest level of 10,000,000 larvae in 1998. Releases in recent years in the James River have been decreasing since annual hatchery production is now shared with a new restoration program in the Rappahannock River that began in 2004.

The ISA predicted from the model followed observed trends from the SGN in all three rivers. In the York River, aside from 1998, there was an increasing trend from 1999 to 2001 and a decreasing trend thereafter (Fig. 4.5A). However, the Pearson correlation coefficient was low (r =0.189). In the Rappahannock River, the model matched observed abundance estimates more closely with obvious deviations from 2002 to 2004 (r =0.4958; Fig. 4.5B). The James River model estimates were closest of all three rivers to observed trends (r =0.64) and closely matched in all years but 2006 (Fig. 4.5C).

The longitudinal analysis resulted in very strong positive relationship between observed and expected values for total number of females captured from a given year-class throughout the study (Fig. 4.6; Pearson's correlation, r=0.94). Regressions of age-specific catch rates on JAI estimates were not significant (α>0.05) indicating a disconnect between juvenile abundance estimates and adult indices.

DISCUSSION

Results obtained from the model followed observed values in all three rivers with some obvious deviations. The assumption that catch rates of juveniles (producing the JAI) are proportional to their actual abundance and similarly for adults captured through the SGN monitoring program is an important component of the model. The proportionality assumption of the JAI was tested by Wilhite et al. (2003) by comparing it with an independent evening push net survey designed to capture juvenile *Alosa* spp. (Kriete and Loesch 1980) on the Pamunkey and Mattaponi Rivers (both tributaries of the York River). The study demonstrated that the two surveys produced similar trends in abundance for both tributaries lending some support to the assumption that the JAI is a valid index of abundance. If the surveys had not shown similar trends then it could be assumed that one (but not necessarily both) were biased. As a result of the similarity in abundance trends between the two surveys, the evening push net survey was discontinued.

Catchability of female American shad in the SGN may change annually, resulting in deviations from the proportionality assumption. Unfortunately, without additional data, catchability cannot be evaluated directly in the program. However, the agreement between juvenile recruitment indices and adult abundance produced by the ISA model suggests that both monitoring programs are characterizing trends in abundance through time.

Total instantaneous mortality rates estimated through longitudinal catch curves were applied to juvenile and adult American shad from the time they were in the freshwater nursery to maturity. The application of this assumption is doubtful. The JAI is developed for juvenile American shad after the period of highest mortality, which occurs during larval and early juvenile stages and prior to emigration out of the nursery during November and December (Hoffman 2007). Juvenile American shad spend anywhere from three to seven years in the coastal ocean before returning to the natal river to spawn for the first time and little is known about mortality during this time period. It is possible that variable mortality rates during offshore residency result in deviations of observed abundance estimates from model predictions, but there is currently no way to evaluate this hypothesis. Another explanation for deviations between model results and observed indices is the use of mean mortality rates applied to year classes that survived known fishing activity, but unknown levels of harvest. Mortality rates for the 1994 to 2005 year classes could be highly variable depending on catches from fisheries that were persecuted during their residence in coastal waters. Unfortunately there is no other data available to estimate harvest levels or mortality rates for these year classes.

The close match of the predicted ISA to the James River SGN index supports the hypothesis of Olney et al. (2003) that the James River population is dependent on hatchery operations. Olney et al. (2003) showed that adult American shad from hatchery operations were contributing to the adult spawning run and that the proportion of hatchery fish was increasing. They interpreted this as a hopeful sign of recovery for the depleted James River population. The model results are in agreement with this assessment. The fact that the James River spawning index can be predicted from the number of hatchery-reared larvae also supports the observation of recruitment failure of wild fish in the system (ASMFC 2007). The JAI time-series for juvenile American shad in the James River from 1980 to 2006 shows no recruitment in 22 out of 26 years and very low recruitment for the other four years. Either the seine survey sampling design is insufficient to capture juvenile American shad in the James River or failed production and recruitment are persistent and hindering stock recovery.

Aside from forecasting spawning run strength, the predictive model of spawning adults also provides a framework to develop testable hypotheses that can examine factors affecting spawning runs. For example, water temperature strongly influences timing and migration of American shad spawning runs (Leggett and Whitney 1972; Quinn and Adams 1996) and could be used as a covariate in models to determine its influence on spawning run strength. Other hypotheses can be developed and incorporated into the model including fishing mortality and other removals and their effects on future spawning events. Refinements to the model can include evaluations of the mean mortality rate for more recent year classes and annual models can be updated with maturity schedules and mortality estimates as data becomes available. Until coastal populations of American shad are studied and stock-specific harvest can be tallied, inferences about coastal processes and effects on American shad stocks will have to rely on samples collected from natal rivers.

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Table 4.1. The SGN catch index for spawning female adult American shad from the York, James, and Rappahannock Rivers. The index is the area under the curve of daily catch rate (female kg/m/day) versus time of year.

Year	York	James	Rappahannock
1998	14.71	2.57	1.46
1999	5.42	2.99	1.30
2000	7.52	6.61	1.75
2001	12.97	5.01	5.77
2002	7.47	5.62	3.08
2003	8.98	9.34	7.10
2004	9.72	7.41	7.06
2005	4.64	7.16	3.69
2006	2.85	1.74	3.01
2007	5.01	4.45	2.60

Table 4.2. Total instantaneous mortality estimates, standard error, and sample size from longitudinal catch curves for adult American shad from the York, James, and Rappahannock Rivers. Catch-at-age data from the VIMS SGN monitoring program were adjsuted by dividing the catch for ages 3 to 6 by the proportion mature to account for immature individuals that are alive, but unavailable to the gear.

	York River			Rappahannock River			James River		
Year	Z	SE	n	Z	SE	n	Z	SE	n
1994	1.032	0.0910	482	0.734	0.0805	114			
1995	0.783	0.0697	422	0.489	0.1162	126	0.728	0.1871	83
1996	0.968	0.0929	639	0.835	0.1804	292	1.017	0.0775	120
1997	0.556	0.1248	847	0.539	0.1610	292	0.703	0.1983	144
1998	0.972	0.4495	405	0.898	0.2842	452	0.810	0.2888	82
Average	0.862	0.1949		0.699	0.1796		0.814	0.1424	

Table 4.3. Juvenile indices of abundance for American shad from the York, James, and Rappahannock Rivers. The York and Rappahannock River indices are the geometric mean catch per haul from the VIMS Striped Bass Seine Survey. The James River abundance index is the estimated number of hatchery released larval American shad from the Virginia Department of Game and Inland Fisheries. Hatchery releases did not begin until 1992 on the James River.

Year class	York	James	Rappahannock
2006	1.21	6,400,000	0.11
2005	1.83	6,000,000	0.27
2004	7.24	6,600,000	0.81
2003	21.45	8,700,000	0.72
2002	0.24	8,400,000	0.00
2001	0.70	9,300,000	0.34
2000	5.06	8,900,000	0.08
1999	0.28	7,300,000	0.02
1998	2.64	10,000,000	0.23
1997	2.21	5,900,000	0.30
1996	17.71	5,800,000	0.35
1995	0.36	5,300,000	0.00
1994	1.57	1,600,000	0.11
1993	0.40	500,000	0.25
1992	0.00	50,000	0.00
1991	0.28	na	0.00
1990	0.61	na	0.03

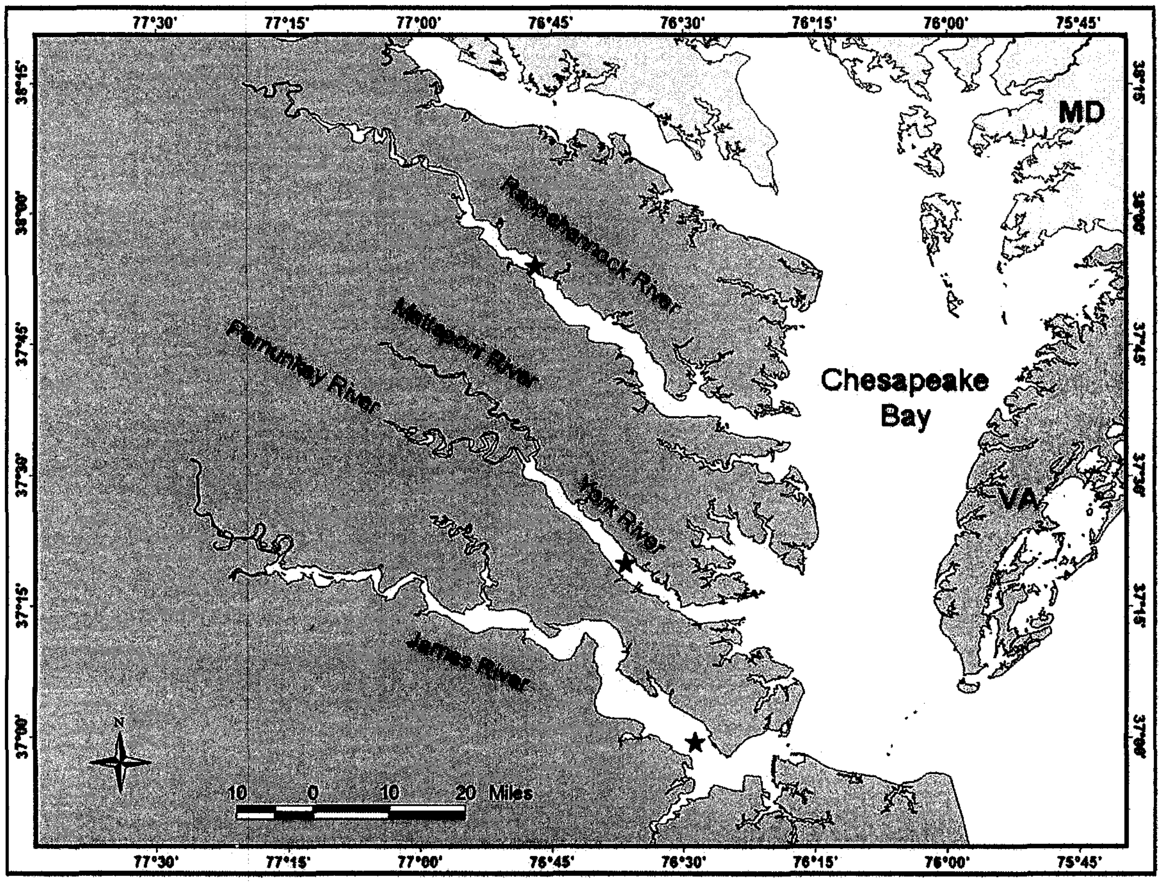

Figure 4.1. Map of Virginia showing the location of staked gill net stands (stars) used to capture female American shad on the migration to the spawning grounds in the Rappahannock, York, and James rivers.

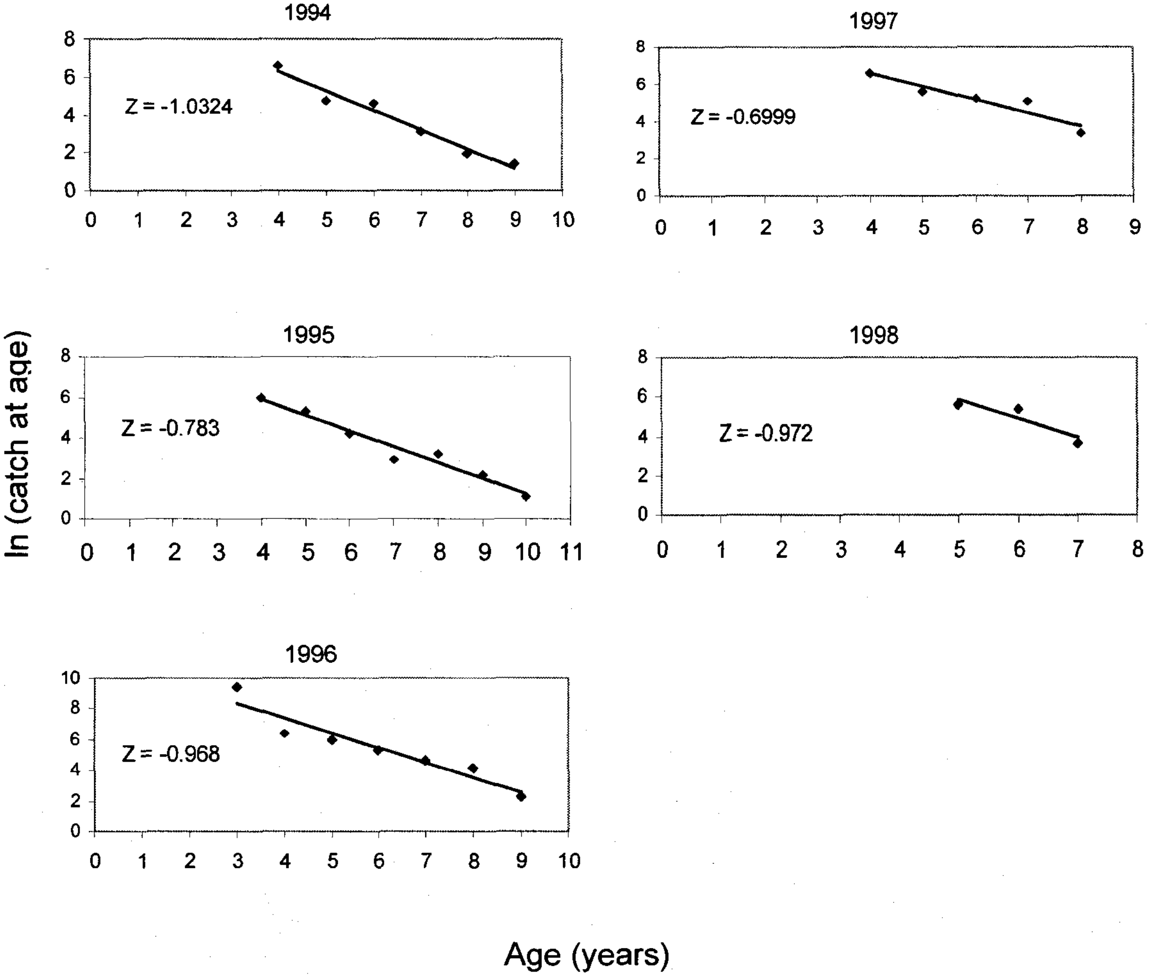

Figure 4.2. Year-class specific catch curves for female American shad from the York River from 1994 to 1998.

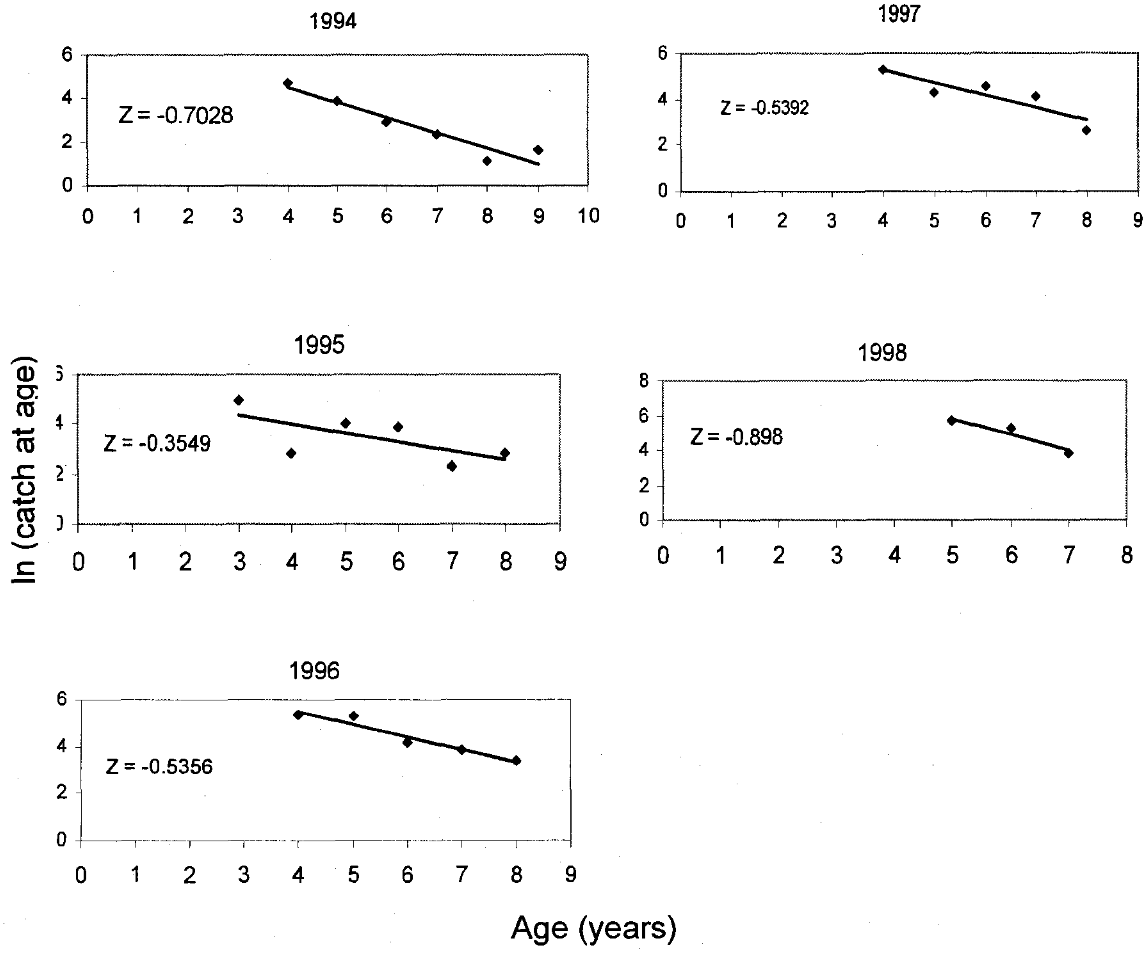

Figure 4.3. Year-class specific catch curves for female American shad from the Rappahannock River from 1994 to 1998.

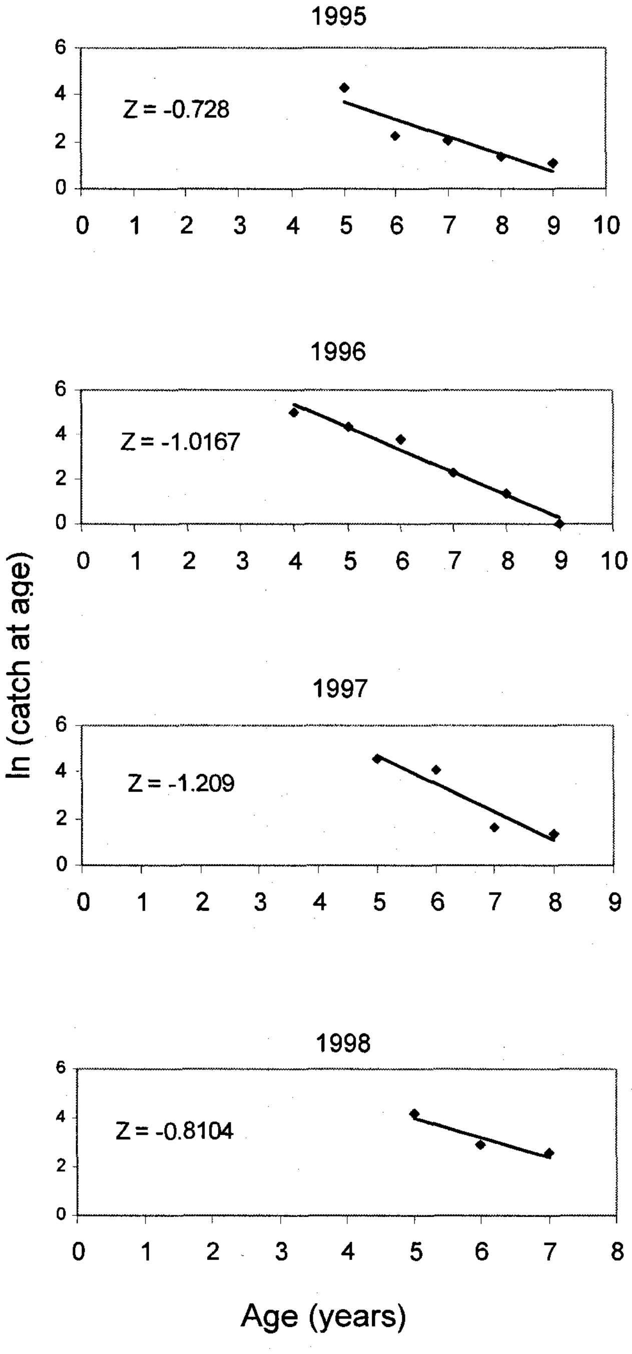

Figure 4.4. Year-class specific catch curves for female American shad from the James River from 1995 to 1998.

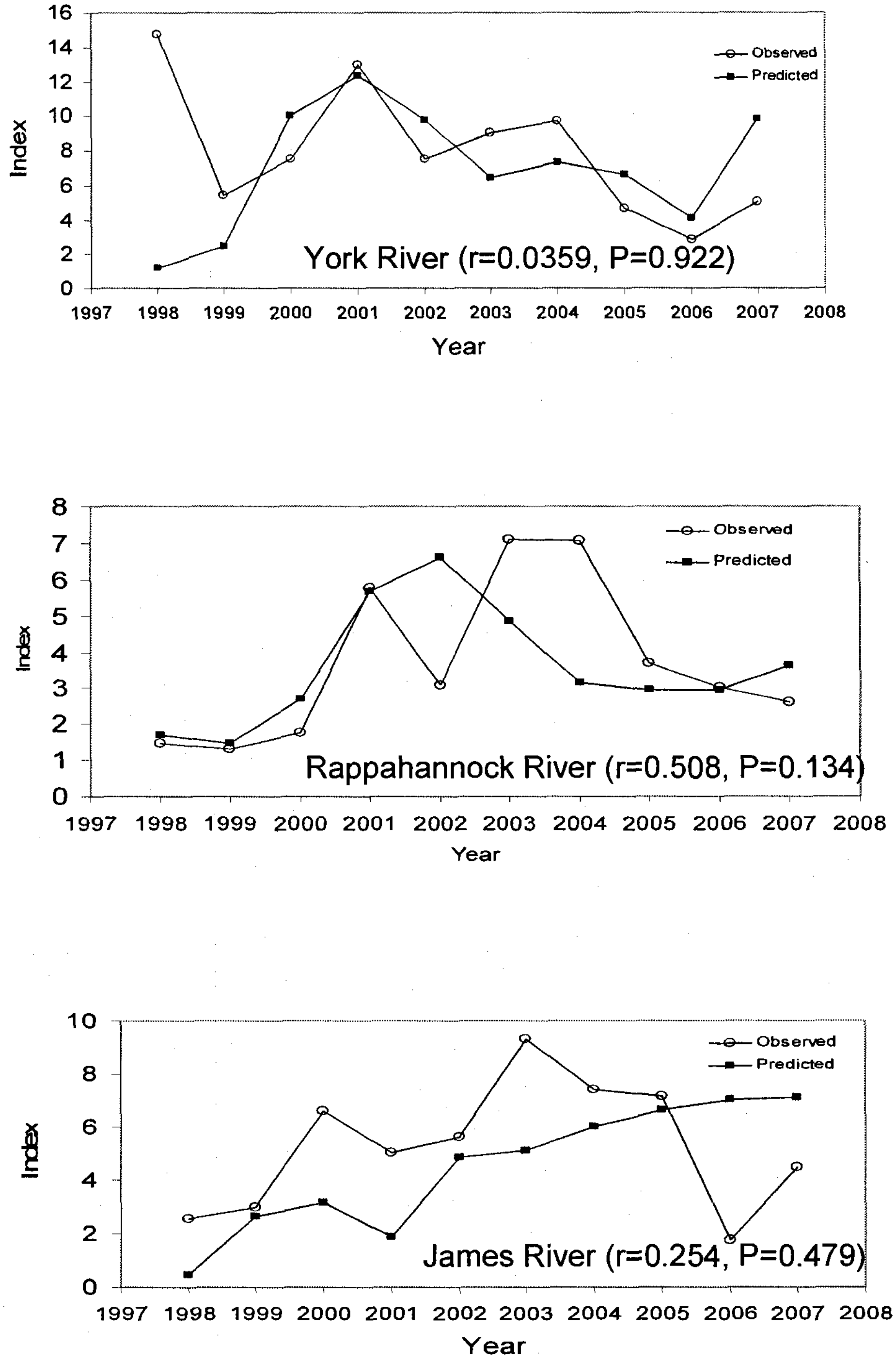

Figure 4.5. Observed (dotted line) and predicted (solid line) index of spawning adults in the York, Rappahannock, and James rivers.

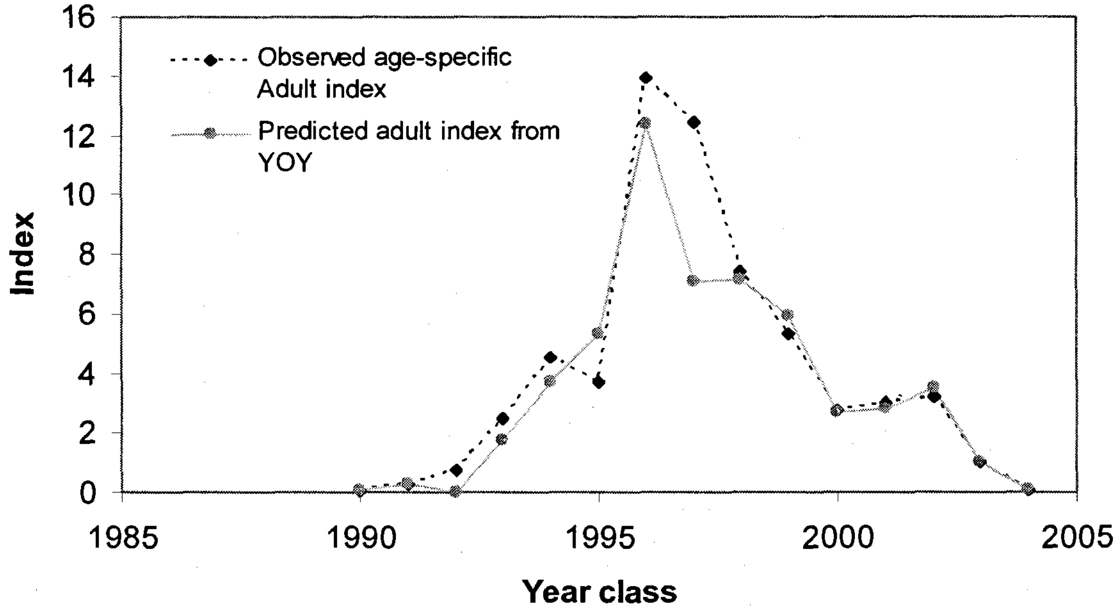

Figure 4.6. Observed catch rate (dotted line) and predicted (solid line) catch rate of female American shad by year-class from the York River. Index values are the total sum of females captured from ages 3 to 10 years or the maximum age possible given the age of the year-class. For example, the estimated index for the 2002 year-class can only consist of females ages 3 to 5 since sampling ended in 2007 for this study.

SUMMARY

It is has been established that year-class strength is cast during the earliest stages of life for most teleost fishes. Numerous hypotheses have been developed to explain potential causes of mortality as well as the great variability in abundance that is often observed for young fishes and these hypotheses include density-dependent and density–independent processes (Sissenwine 1984; Houde 1987, 1989, 2008; Anderson 1988; Houde 1989; Houde 2008). While year-class strength can be the result of factors acting during egg and larval stages, the influence of post-settlement processes (those affecting juvenile growth and mortality) on adult demographics has gained support as a significant source of recruitment variation or conversely, acting to compensate and dampen variability (Sissenwine 1984; Bradford 1992; Bradford and Cabana 1997).

Observed patterns in growth and mortality for YOY American shad and blueback herring in my research varied by species and by temporal and spatial scales. If regional-scale environmental conditions were the primary driver of population dynamics, then it was expected that the four river systems investigated would show similar temporal trends since their proximity to one another varies by < 1° of latitude. It appears however that river-specific and stock-specific attributes strongly influence population dynamics of YOY American shad and blueback herring.

In Virginia, juvenile abundance indices of American shad have shown varying recruitment patterns with up to 16-fold differences in estimated YOY year-class strength over the course of monitoring efforts (ASMFC 2007).

Though we have gained insight into some probable causes of recruitment variability in Virginia rivers, for example water flow (Hoffman et al. 2007), important characteristics in population biology, such as annual variability in growth and mortality rates between neighboring stocks, or annual differences within a single stock, are not fully understood. I determined that water flow and conspecific abundance alter production of juvenile American shad and blueback herring through processes that effect growth in Virginia rivers. For each species, lengths of individuals from strong year classes were, on average, smaller than lengths of fish from weaker year-classes at the end of summer due to density-dependent processes. Reduced size can have important consequences as year-classes leave the nursery habitat. Because both species are anadromous and spend the first winter in estuaries and along the coast, size-specific predation potentially can have significant effects on mortality (Rice et al. 1997). Potentially higher mortality rates on stronger YOY year classes tends to stabilize recruitment, which may act to slow recovery of stocks that are at historically low levels of abundance.

In addition to YOY population dynamics, maturation schedule is a potential source of variability that may affect stock recovery by altering the relationships between strong year classes and their subsequent recruitment into the spawning stock. Maki et al. (2001) evaluated age and spawning history of American shad in a cross-sectional study to estimate the maturity schedule for York River adults based on data from 1998 to 2000. I used the same procedure to examine maturity schedules of individual year classes in a longitudinal study, comparing maturity schedules among stocks from the neighboring James, York, and Rappahannock Rivers based in data from 1993 to 1999. While most American shad were mature by age 5, year-class-specific estimates of maturity at age 5 ranged from 50% to 85% mature on the James River, from 59% to 79% on the Rappahannock River, and from 60% to 87% on the York River. The lowest estimates for all rivers were all from the 1995 year class, suggesting that a common factor influenced maturation of this year class. However, the highest estimates of maturation at age 5 did not align with specific year classes. Therefore, estimates of the contribution from a particular year class to the spawning run could vary greatly among stocks. Furthermore, the differences observed between the James and York River maturity schedules, and to a lesser extent those from the Rappahannock River, show that neighboring stocks experiencing similar climate regimes can have stock-specific maturity patterns that persist through time.

The observed delay in maturity for the James River stock compared with stocks from the York and Rappahannock Rivers may have implications for stock recovery. Because the James River stock has been at a low level of abundance, releases of hatchery reared larvae have been conducted in the James since 1992 to augment natural production of juveniles. An assessment of the contribution of hatchery-released American shad to the spawning run in the James River showed an increase in catch rate resulting from the influx of mature hatchery-origin fish (Olney et al. 2003). However, despite efforts to rebuild the James River stock, current levels remain below expectations and very low relative to historic levels.

Because American shad stocks are at depressed levels, classic stock-recruitment models (i.e., Ricker, Beverton-Holt) are not useful for management since sufficient contrast in levels of spawning stock abundance has not been observed. Therefore a simple model based on adult mortality rates and maturity schedules, and juvenile indices of abundance was developed to predict adult catch rates in three rivers. The modeled results gave similar trends to observed trends in the adult monitoring program, with some obvious deviations that are not easily explained. One possible explanation is related to coastal water temperature and timing of spawning migrations, with higher catch rates occurring during colder years and lower catches in warmer years.

The close match of the predicted and observed catch rates of returning adults in the James River supports the hypothesis of Olney et al. (2003) that the James River population is dependent on hatchery operations. Olney et al. (2003) demonstrated that adult American shad of hatchery origin were contributing to the adult spawning run and that the proportion of hatchery fish was increasing. They interpreted this as a hopeful sign for recovery of the depleted James River population. My model results are in agreement with this assessment. The fact that the James River spawning index can be predicted from the number of hatchery-reared larvae also supports the observation of recruitment failure of wild fish in that system (ASMFC 2007). The JAI time series for juvenile American shad in the James River from 1980 to 2006 shows no recruitment for most years (22 out of 26) and very low recruitment for the remaining four years. If significant recruitment of wild American shad were occurring, predicted catch rates would vary since these additional recruits were not accounted for in the model.

Production of YOY American shad and blueback herring varies in time and space due to complexities within each river system. The expectation that population dynamics would be correlated in river systems sharing similar climate regimes in any given year was not supported. However, production of YOY American shad and predictions of adult spawning runs are possible within stocks providing new insights that may foster testable hypotheses about coastal processes affecting stock recovery.

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VITA

Troy Daryl Tuckey

Troy Tuckey was born to Carolyn and Daryl Tuckey in Baltimore, Maryland on July 26, 1971. He graduated from Perry Hall High School in 1989. In 1994, he earned his B.S. in Biology from the University of South Florida, and in 2000 his M.S. from the University of Charleston, South Carolina. Troy entered the doctoral program at the College of William and Mary School of Marine Science in 2004.