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College of Humanities and Sciences
Virginia Commonwealth University

This is to certify that the thesis prepared by Peter Milton Sturke entitled GROWTH OF AGE-0 ATLANTIC MENHADEN (*Brevoortia tyrannus*) IN TWO TIDAL FRESHWATER TRIBUTARIES OF CHESAPEAKE BAY has been approved by his committee as satisfactory completion of the thesis requirement for the degree of Master's of Science in Environmental Science

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July 2011

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GROWTH OF AGE-0 ATLANTIC MENHADEN (*Brevoortia tyrannus*) IN TWO TIDAL
FRESHWATER TRIBUTARIES OF CHESAPEAKE BAY

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

By

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July, 2011

Dedication

To the memory of my grandmothers, Nola P. Sturke (1910-2010) and Helen D. Johnson (1925-2011), for their strength and wisdom as constant sources of inspiration.

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ABSTRACT

GROWTH OF AGE-0 ATLANTIC MENHADEN (*Brevoortia tyrannus*) IN TWO TIDAL FRESHWATER TRIBUTARIES OF CHESAPEAKE BAY

By Peter Milton Sturke

A thesis submitted in partial fulfillment of the requirements of the degree of Master of Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2011

Major Advisor: Dr. Gregory C. Garman, Ph.D.
Director, Center for Environmental Studies and
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Few studies have described growth rates of age-0 Atlantic menhaden (*Brevoortia tyrannus*). Growth rates from tidal freshwater habitats of the Mattaponi and James Rivers, Virginia in 2009 were described and compared using otolith microstructural analyses. Larval tidal freshwater growth rates were significantly faster in the culturally eutrophic James River when compared to those collected from the Mattaponi River (p -value < 0.001). Elevated primary production within tidal freshwater habitats promotes favorable conditions for larval Atlantic menhaden growth. No differences between river habitats for juvenile growth rates were evident.

Comparisons of age-0 growth rates to higher salinity habitats indicate that tidal freshwater habitats should be considered essential habitat for age-0 Atlantic menhaden.

Keywords: Mattaponi River, James River, tidal freshwater, Atlantic menhaden, *Brevoortia tyrannus*, growth, primary productivity, salinity.

INTRODUCTION

Atlantic menhaden (*Brevoortia tyrannus*; Clupeidae) is an economically valuable and ecologically important marine species native to the North American Atlantic slope (Hildebrand, 1963; Hale et al., 1991). Atlantic menhaden range from Nova Scotia to Florida (Reintjes, 1969) with older individuals concentrated in the northernmost parts of the range and younger age-classes farther south (Ahrenholz, 1991). The species serves a vital role in the ecology of marine systems by converting primary production into biomass available for apex-predators, making Atlantic menhaden an important forage species in the Chesapeake Bay (Ahrenholz, 1991; Vaughan, 1991; Jenkins and Burkhead, 1994;). Many aquatic and avian predators such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), Brown Pelican (*Pelecanus occidentalis*), and Osprey (*Pandion haliaetus*) feed extensively on Atlantic menhaden (Griffin and Margraf, 2003; Uphoff, 2003; Viverette et al., 2007). During the 1980s, abundance of Atlantic menhaden in the Chesapeake Bay sharply declined, coincident with evidence of food abundance-related stress in Osprey, weakfish (*Cynosion regalis*), and striped bass (McClellan and Byrd, 1991; Uphoff, 2003,2006;). Commercial landings of Atlantic menhaden declined to an average of 155,000 metric tons from a peak harvest of 712,000 metric tons over the last 50 years (ASMFC, 2010). Recent research conducted on the status of the Chesapeake Bay population resulted in new regulations that limit the annual commercial harvest to 109,000 metric tons (Blomo et al., 1988; Luo et al., 2001; ASFMC, 2010). Despite these management actions, the fishery has become increasingly reliant on younger age-classes (Vaughan and Smith, 1988; ASMFC, 2010). Atlantic menhaden are currently not overfished; however overfishing occurred during the 2008 season (Fishing mortality above threshold of 2.2; ASMFC, 2010).

Atlantic menhaden migrate between coastal marine waters and adjacent estuaries to spawn (Ahrenholz, 1991; Murdy et al., 1997). Two distinct spawning events -- March to May and September to October, occur in offshore waters surrounding the Chesapeake Bay (Murdy et al., 1997). Pelagic eggs drift and are advected into Chesapeake Bay where temperature, salinity, and predation are highly variable (Cambalik et al., 1998; Quinlan et al., 1999). Spatial and temporal variation in abundance and distribution of planktonic prey may cause a delay in timing of first feeding and mortality for larvae of many teleost species, including Atlantic menhaden (Mackas et al., 1985; Miller et al., 1988; Ali et al., 2003). Atlantic menhaden larvae are transported passively upstream into oligohaline and tidal freshwaters, with suitable nursery habitats for larval development (June and Chamberlin, 1959; Ahrenholz, 1991). Larval vertical positional changes in the water column and various hydrographic forces encourage advection and horizontal transport of Atlantic menhaden from offshore and estuarine waters (Forward et al., 1996). Larval and juvenile Atlantic menhaden nursery grounds vary spatially and temporally depending upon changes in plankton availability (Friedland et al., 1989; Friedland et al., 1996). Age-0 Atlantic menhaden frequently occur in areas of freshwater or low salinity (Massman et al., 1954; Rogers et al., 1984; Rozas and Hackney, 1984). Atlantic menhaden are one of the most abundant pelagic fish in Chesapeake Bay and postlarvae have been observed in tidal fresh water reaches of the James and Mattaponi Rivers, Virginia (Massmann et al., 1954; Friedland, 1988; Murdy et al., 1997; Seelig, 2010).

Advection of larval Atlantic menhaden into the estuarine turbidity and chlorophyll-a maximum of tidal freshwater habitats may benefit recruitment and survivorship significantly because of favorable conditions and food abundance (Houde, 1994; Buckaveckas et al., 2011). A cohort of a freshwater fish species is 40 times more likely to survive past the juvenile stage

metamorphosis than a typical cohort of a marine fish because of decreased stage duration (Houde, 1994). Jung and Houde (2003) demonstrated that the amount of freshwater delivered to Chesapeake Bay has a direct positive relationship with bay-wide fish biomass, potentially a response to increased availability of tidal freshwater habitats and a resulting strong year-class of Atlantic menhaden (Houde, 2009; Kimmel et al., 2009). Atlantic menhaden larvae documented within the Chesapeake Bay range between 30 and 100 days of age 14 and 34 mm fork length (Reintjes and Pacheco, 1966; Warlen, 1994; Warlen et al., 2002; Light and Able, 2003). The capacity for Atlantic menhaden to increase consumption of phytoplankton in addition to zooplankton is facilitated by substantial increases in complexity and efficiency of the alimentary tract and gill rakers (June and Carlson, 1971; Friedland et al., 2006). Atlantic menhaden residing in tidal freshwaters grow until approximately age-1 before emigrating to pelagic habitats; emigration occurs synchronously with increased concentrations of plankton, thereby reducing the stress on juvenile fish during out migration (Cushing, 1975; Friedland, 1988; Houde and Harding, 2009). Growth and development of age-0 Atlantic menhaden in tidal freshwater habitats remains unknown with no published study investigating potential benefits.

Estuarine and riverine nursery grounds are essential habitats for age-0 Atlantic menhaden and recruitment to the fishery (Friedland et al., 1996). Larval survival is a major regulator of recruitment to the adult population ('critical period' Hjort, 1914; 'match-mismatch' Cushing, 1975). Larval fish may experience enhanced recruitment success in tidal freshwater ecosystems particularly because of the nursery habitats which provide shelter from predators and foraging habitats (North and Houde 2001). Although larvae metamorphose into juveniles at varying salinities, those developing in low salinity waters are less prone to structural abnormalities, suggesting low salinity waters are advantageous for development (Lewis, 1966).

During residency, age-0 Atlantic menhaden have the potential to consume approximately 1-119 percent of the total annual primary productivity in Chesapeake Bay (Gottlieb, 1998; Luo et al., 2001). Juvenile menhaden consume 6-9% of the annual phytoplankton production in various estuaries on the Atlantic Slope and up to 100% of daily primary production (Peters and Schaaf, 1981). Although these publications illustrate the prospective water quality benefits supplied by Atlantic menhaden; Lynch et al. (2010) suggested age-0 Atlantic menhaden in Chesapeake Bay play a minor role in regards to eutrophication reduction. There is a significant abundance of primary productivity in the tidal freshwater portion of the James River (Bukaveckas et al., 2011), potentially enhancing food availability for age-0 Atlantic menhaden. However, there are no published studies linking importance of the tidal freshwater habitats to improved somatic growth of Atlantic menhaden larvae and juveniles.

Somatic growth of age-0 Atlantic menhaden is a function of density, recruitment timing, temperature, and food availability (Ahrenholz, 1991; Keller et al., 1990). The growth rate potential (GRP) of Atlantic menhaden is positively correlated with the concentration of phytoplankton, and the amount of nutrient loading affecting Chesapeake Bay waters because growth rates are highest in early June and late summer when nutrient loading may be greatest (Brandt and Mason, 2003). The level of cultural (anthropogenic) and natural eutrophication can influence the growth and development of age-0 menhaden by increasing food availability during a critical stage of the life cycle (June and Carlson, 1971). A range of growth rates have been reported for larval Atlantic menhaden originating from assorted geographic locations with varying salinities using daily otolith microstructure incremental analysis from 0.22 to more than 0.48 mm d⁻¹ (Powell and Phonlor, 1986; Maillet and Checkley, 1991; Warlen, 1992; Warlen et al., 2002; Houde and Secor, 2009). Although many publications have attributed variation of age-

0 Atlantic menhaden growth rates to cohort density sampled, timing of recruitment, temperature, or food availability, there are no published literature investigating the potential advantage of tidal freshwater nursery habitats.

The primary objective of this study is to describe the somatic growth rates of age-0 Atlantic menhaden in two tidal freshwater rivers using otolith incremental analysis. A second objective determined if an increased state of eutrophy, due to anthropogenic nutrient inputs, affects growth rates. Specifically, the hypothesis that age-0 Atlantic menhaden have a higher growth rate in the culturally eutrophic James River than in the naturally pristine Mattaponi River was tested. The final objective of this study was to determine if tidal freshwater habitats are beneficial to larval and juvenile Atlantic menhaden growth rates compared to growth rates from higher salinities. Specifically, the hypothesis that age-0 Atlantic menhaden will exhibit a higher rate of growth in tidal freshwater when compared to other published studies from high salinity habitats was tested.

MATERIALS AND METHODS

Study Area

Age-0 Atlantic menhaden were sampled in tidal freshwater reaches of the James and Mattaponi Rivers, Virginia. For the purposes of this study, tidal freshwater was defined as salinity less than 1 ppt at time of sampling (Odum, 1988). The James River is one of the largest rivers of the Southeastern United States, flowing east from the mountains of Virginia at the confluence of the Jackson and Cowpasture Rivers for about 540 km before draining into the Chesapeake Bay (Benke and Cushing, 2005). The headwaters of the Mattaponi River begin in Caroline County as a small non-tidal stream and increases in width into a tidal river with numerous wetlands by West Point where it combines with the Pamunkey River to form the York River (Benke and Cushing, 2005). The James River is used for commerce, navigation and industry (point source and non-point source pollution) enhancing productivity and the state of eutrophy. The absence of significant anthropogenic inputs to the Mattaponi River watershed reduces the level of eutrophy.

Field collection

Larval and juvenile Atlantic menhaden were collected using equipment in progression as the fish became increasingly mobile: 0.5 m bongo nets with 505 μ m mesh fished approximately 0.5m from the surface, boat push-netting (1.0 x 1.2m net, 0.64 cm mesh), boat electrofishing (Smith Root, pulsed DC), and use of gill nets or trawls. Tidal freshwater reaches of the Mattaponi and James Rivers were sampled at least twice a month between 24 February and 20 July 2009. Sampling on the Mattaponi River occurred from Walkerton, Virginia downstream to

the Gleason marsh above West Point, Virginia. Samples from the James River were collected from various locations from the Hopewell, Virginia downstream to just below Claremont, Virginia. Specimens were placed in ice and frozen in river water upon arrival to the laboratory to reduce any error with fish length estimates prior to otolith extraction.

Otolith Preparation and Extraction

Otolith microstructure analysis has been used extensively in age and growth studies on many fish, as first introduced by Panella (1971). Validity of using otolith microstructural analysis is based upon two assumptions: initial increment formation takes place at a known time and that each increment thereafter is deposited at a known rate (Geffen, 1987). Atlantic menhaden deposit their initial otolith increment 3 days post-hatch, and the increments are deposited at a rate of one per day independent of food availability (Lewis et al. 1972; Nelson et al. 1977; Maillet and Checkley, 1989). Therefore, Atlantic menhaden are a suitable candidate for otolith microstructure analysis.

Atlantic menhaden were considered as larvae after reaching the prejuvenile stage when the fish have the minimum adult fin ray complement but have not assumed the adult body form (Jones, 1978; Reintjes 1969). Juveniles had the adult body form, hardened ventral scutes, and pigmented scales (Jones, 1978; Able and Fahey, 1998). Samples were thawed using cold water and total lengths (TL) were measured to the nearest 0.1mm using calipers and weight (W) was measured to the nearest 1mg. Sagittal otoliths were extracted from each fish using a dissection microscope (Nikon SMZ 800) following Secor et al.(1991). Up to 20 larvae were selected randomly from each collection. Otoliths were cleaned, polished, and mounted on slides using thermoplastic mounting media (crystal bond) and viewed under a compound light microscope at 200 x magnification. The otoliths from juvenile fish were ground, polished using 0.3 micron

alumina powder, and read in the sagittal plane (Secor et al., 1991). Digital images of each whole otolith or plane were recorded using a Nikon D70 SLR camera to enhance precision in reading the otoliths with increased contrast (using Microsoft Picture Manager).

Otolith Increment Count Precision

A complete daily increment on the otolith is a bipartite structure composed of a translucent and a discontinuous (opaque) zone (Campana and Neilson, 1985). Otolith daily increments were enumerated by a single reader and as a measure of precision, a second experienced reader examined a randomly selected subsample of each collection (James and Mattaponi River). Precision was measured by comparing the capability of the readers to consistently reach the same count estimation on the same otolith. Precision was assessed with the coefficient of variation and a paired t-test between readers (CV; Zar, 1999).

Growth Analysis

Age estimates of larval and juvenile Atlantic menhaden were calculated as increment count plus three days (Maillet and Checkley, 1991). Separate linear regressions were fit to the Atlantic menhaden length-at-age data from each river for larval and juvenile fish. A Gompertz non-linear equation has often been used to describe the entirety of larval growth of Atlantic menhaden from 4mm to ~40mm (Warlen, 1992; Warlen et al., 2002; Houde and Secor, 2009). However, linear regression is commonly applied to express age and growth at specific lengths and ages (Warlen, 1992). Growth rate for the range of lengths is represented by the slopes of regression lines and are expressed in mm day^{-1} . Linear regressions were performed using the software package R version 2.8.1 (*lm* function, R Core Development Team 2010, Vienna, Austria). Slopes of the linear regressions between rivers were compared independently using the Student's t-test for both larval and juvenile samples. Growth rates were deemed significantly

different for $p < 0.05$. If not significantly different, slopes (growth rates) of the two rivers were combined and regressed to compare the growth rate of tidal freshwater populations to higher salinities.

Average growth rate was also calculated for each fish to represent the entire range of growth for each fish (Maillet, 1991):

$$\text{Average Growth Rate} = (TL - 5.0^*)/Age$$

where 5.0 is the total length at which the yolk is completely absorbed post-hatch (Jones, 1978; Ahrenholz 1991; Able, 1998), TL is the length of fish at collection, and Age is the estimated age of the individual. Individuals were grouped into monthly cohorts based on hatch date estimates and an analysis of variance was used to compare the mean absolute growth rates for each month.

RESULTS

Collections

A total of 697 larval and juvenile Atlantic menhaden were collected from various tidal freshwater locations on the James and Mattaponi River in 2009 (Figures 1 and 2). Water temperatures from sample reaches on the Mattaponi and James rivers increased from ~6°C in February to ~27°C in July. Salinity ranged from 0.1—7ppt during the sampling period, but fish were not collected from river locations above 1 ppt. As a function of eutrophication, Chlorophyll-A concentrations were considerably higher in the James River when than the Mattaponi River (Table 1). Fish were captured in both rivers from February to July of 2009 using various methods of collection (Table 2). All larval fish were captured using bongo nets from February to April, 2009. Juvenile menhaden were most effectively captured by boat push netting (57%) and boat electrofishing (36%) during July sampling collections. Otoliths were extracted from 252 specimens for microstructural age estimation.

Larval Growth

A total of 164 larval fish were aged from the tidal freshwater; Mattaponi (n=95) and James Rivers (n=69). Individual larval menhaden otolith samples were consistently aged to within ± 5 days (range 70- 141 days, n=41, Figure 3). The coefficient of variation was 3.9%. Paired t-tests indicate that sagittal otolith increment counts did not differ significantly between the first and second readers ($t=-0.67$, $p\text{-value}=0.51$, Figure 4).

Slopes of the regression lines from scatter plots of larval fish aged from the James and Mattaponi Rivers represent the tidal freshwater residence growth rate (mm d^{-1}). The growth

rates for larval fish during tidal freshwater residency (mm d^{-1}) differed significantly between Mattaponi and James Rivers ($t= 4.35$, $p<0.001$; Figure 5). Larval fish collected from the James River exhibited a significantly higher growth rate (0.1 mm d^{-1}) compared to those from the Mattaponi River (0.07 mm d^{-1}).

Larval fish aged by reader 1 were placed into monthly hatch date cohorts and individual growth rates were calculated. Individual growth rates were averaged based on hatch months and increased from October 2008 to January 2009 (Figure 6). Pooled averaged individual growth rates from the James and Mattaponi River larval fish, representing tidal freshwater averaged growth rates, were between 0.25 and 0.34 mm d^{-1} , respectively. Averaged monthly cohort growth rates increased from 0.29 mm d^{-1} during November 2008 to 0.34 mm d^{-1} from those fish hatched in January of 2009.

Juvenile Growth

A total of 88 juvenile fish were aged from the tidal freshwater Mattaponi ($n=52$) and James Rivers ($n=36$). Otoliths from several fish were either fractured, overground, or deemed unreadable and were removed from the study. Individual juvenile menhaden otolith samples were consistently aged by both readers to within ± 42 days (range 139-310 days, $n=21$; Figure 7). The coefficient of variation was 15.4%. Paired t-tests indicate that sagittal otolith whole structure increment counts differed significantly between the first and second readers ($t=3.73$, $p\text{-value}=0.009$, Figure 7).

Individuals ($n=88$) were placed into 5mm length bins to stabilize variation and the growth rate was calculated based on the linear regression of average age and average length within each bin. James River juvenile fish exhibited a significantly higher growth rate (0.96 mm d^{-1}) when

compared to that of the Mattaponi River fish (0.56 mm d^{-1} ; Figure 8; $p\text{-value} < 0.01$). Size ranges of juvenile menhaden collections from each river were not equally distributed posing a weakness for comparisons between river growth rates. However, the discrepancy in size and age classes between rivers suggest that juveniles from the James River collections were hatched earlier (Hatch range: 13 September 2008 to 22 December 2008) than those captured from the Mattaponi (Hatch range: 21 December 2008 – 14 February 2009; Table 4). A collective range of growth rates during tidal freshwater residency was created for juveniles from the Mattaponi and James River because the collections represent identical salinity regimes. This range is intended for comparisons to published literature from higher salinity habitats ($0.56 - 0.96 \text{ mm d}^{-1}$).

Due to a lack of precision when estimating ages of juvenile fish, average monthly growth rates were not calculated because the error weakens any potential conclusions.

DISCUSSION

Introduction

This is the first published study to describe age-0 growth rates of Atlantic menhaden during residency in tidal freshwater habitats of Virginia and one of a few published descriptions of growth utilizing whole-structure otolith microstructural analysis. Previous studies have described most of larval and juvenile growth from varying salinities and geographic locations (Lewis et al., 1972; Maillet and Checkley, 1991; Warlen, 1992; Ahrenholz et al., 1995; Houde and Secor, 2009). This study also represents a preliminary study investigating primary production as a potential factor affecting age-0 growth rates during tidal freshwater residency. Growth rates of larvae and juveniles in tidal freshwaters were comparable to those previously found in higher salinities (Maillet and Checkley, 1991; Warlen, 1992; Houde and Secor, 2009).

For comparison purposes, the present study describes growth rates from individuals captured during the late-larval (pre-juvenile) and juvenile stanzas of early life history as per Lewis et al. (1972). Lewis et al. (1972) collected Atlantic menhaden from various locations in the White Oak River estuary, North Carolina and described age-0 growth as three separate stanzas with inflection points corresponding to larval (30 mm), pre-juvenile (38 mm), and juvenile growth (above 40 mm). During the late-larval stage, length increases slowly because the fish are developing adult characteristics (Lewis et al, 1972; Warlen, 1992). Here pre-juvenile and late-larvae will be considered larvae growth.

Eutrophication and Primary Production

To address the primary hypothesis that age-0 growth rates are higher in the James River than those of the Mattaponi River due to increased nutrient inputs, larval growth rates from the James River (0.10 mm d^{-1}) were significantly higher than those found from the Mattaponi River (0.07 mm d^{-1} ; $p\text{-value} < 0.001$). Juvenile growth rates from the James River (0.96 mm d^{-1}) were significantly higher than those found from the Mattaponi River (0.56 mm d^{-1} ; $p\text{-value} < 0.01$).

The tidal freshwater reach of the James River exhibits an abundance of primary production (Buckaveckas et al., 2011) substantially higher in comparison to the Mattaponi River during sampling months (Chl-a, Table 1). Higher primary productivity (Chl-A, Table 1) evident in the sampling reach of the James River may have increased the growth rates of age-0 Atlantic menhaden by providing an abundance of food. These areas have been identified as the spatial extent of hydrographic features that retain larval fish within tidal freshwater regions known as the Chlorophyll-A maximum and estuarine turbidity maximum (North and Houde, 2001, 2003; Buckaveckas et al., 2011). During development, the gill raker apparatus becomes more complex and increases efficiency of grazing on planktonic organisms (June and Carlson, 1971; Friedland et al., 2006). The organic matter (planktonic organisms) of the James River has been quantified as being more abundant than nutritious (Buckaveckas, 2010); potentially indicating that food availability and not quality may be a controlling factor for age-0 growth. These results support the hypothesis that elevated primary production within the tidal freshwater portion of a system is advantageous to age-0 growth rates.

Salinity

Salinity is a factor in age-0 development of Atlantic menhaden (June and Chamberlin, 1959; Lewis, 1966; Wilkens and Lewis, 1971; Hettler, 1976; Ahrenholz, 2000). Ahrenholz (2000) reported that age-0 growth rates in low salinity treatments (0.2-0.8 mm d⁻¹) were significantly faster than those from the high salinity treatment (< 0.2 mm d⁻¹). Other laboratory experiments show that age-0 Atlantic menhaden are expected to exhibit behavior (increased activity) favorable for a faster metabolism and growth rate while inhabiting salinities less than 10ppt (Hettler, 1976). While low salinity waters are not critical for development (June and Chamberlin, 1959), low salinity habitats provide optimal conditions for successful development of larvae into the juvenile stage (Lewis, 1966; Wilkens and Lewis, 1971).

The effect of salinity on larval and juvenile growth rates of Atlantic menhaden from tributaries of Chesapeake Bay was unknown. Several studies have investigated larval and juvenile growth in higher salinity waters (Maillet and Checkley, 1991; Warlen, 1992; Ahrenholz et al., 1995; Houde and Secor, 2009). Growth rates reported by Warlen (1992) for larval Atlantic menhaden between ages 61-100 days (0.03-0.07 mm d⁻¹) were lower than those found from tidal freshwater habitats of the current study (0.07-0.10 mm d⁻¹), suggesting that tidal freshwaters are advantageous nursery grounds for this interval of larval growth. However, the averaged larval growth rate range from the current study (0.25 – 0.34 mm d⁻¹) are within the range (0.22 – 0.36 mm d⁻¹) reported by Warlen (1992) and Houde and Secor (2009) from higher salinities. These comparisons and findings substantiate the advantage of tidal freshwater nursery grounds for larval growth rates

Growth during the juvenile stage has been characterized as the third stanza in age-0 growth (Lewis et al., 1972) where growth accelerates after metamorphosis. No description exists

of juvenile Atlantic menhaden growth rates while inhabiting the tidal freshwater reaches of Virginia. The growth rate calculated by this study is comparable methodologically to the work by Houde and Secor (2009). Despite a decreased amount of precision in the current study on juvenile age estimations, the range of juvenile growth rate during tidal freshwater residency ($0.56 - 0.96 \text{ mm d}^{-1}$) encompasses the growth rate (0.73 mm d^{-1}) described by Houde and Secor (2009) from higher salinity habitats in Chesapeake Bay. However, this overlap or potential disparity could be an artifact of differing juvenile age estimation techniques and low precision from the current study which may be caused by less frequent and smaller sampling collections. Also, from the hatch date ranges of juvenile collections from each river suggests that the sampled fish represent separate individuals from different spawning efforts. An overlap of other growth rates for juveniles collected during tidal freshwater residency suggests that lower salinity waters are not detrimental to age-0 growth and development of Atlantic menhaden.

These findings do not provide strong evidence for a reduced or elevated growth rate in lower salinity waters. However, this does demonstrate that tidal freshwater habitats are exceptional nursery grounds for age-0 growth and development. The extent and cause of advantageous conditions could be an artifact of decreased predation in tidal freshwater habitats (Able, 2005), a preferable salinity regime for development into juveniles (June and Chamberlin, 1959; Lewis, 1966; Wilkens and Lewis, 1976), or founded entirely on quantity of food made available by increased eutrophication in the tidal freshwater systems at the chlorophyll-a and estuarine turbidity maximums (North and Houde, 2001, 2003; Buckaveckas et al, 2011).

Conclusion

The data collected, measured and analyzed from this study support the stated hypotheses and agree with previously published age-0 Atlantic menhaden growth rate studies. This study also contributes information that was previously undefined. Upstream transport to the tidal freshwater habitats is advantageous for age-0 Atlantic menhaden growth and development. This importance is exemplified by a higher growth rate of the larval stage for which any minor variability in marine species larval growth has the potential to register more pronounced effects on recruitment to the adult population (Houde, 1994). Quinlan and Crowder (1999) found that late larval and juvenile growth is fundamental for successful recruitment to the overall population. An increased understanding of age-0 growth and development facilitates more accurate future decisions regarding the Chesapeake Bay population and fishery. The importance of larval stage dynamics and recruitment to the fishery can be attributed to various environmental factors which influence distribution, abundance, and year class strength of Atlantic menhaden (Ali et al., 2003). The findings of this study corroborate the importance of tidal freshwater habitats for age-0 recruitment to the adult Atlantic menhaden population. The Atlantic menhaden is a crucial link in the trophic system of Chesapeake Bay and has the potential to reduce the amount of resident eutrophy. The gulf menhaden, *B. patronus*, has showed an increased removal of nitrogen and phosphorous relative to carbon from the Gulf of Mexico (Deegan, 1993). Considering the recent overfished status of the Atlantic menhaden population in 2008 (ASMFC, 2010), future research should be directed towards identifying specific limiting factors for age-0 recruitment and survival to the adult Chesapeake Bay population. To address management decisions investigations should include compensatory growth and year class strength variability.

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Table 1. Summary of water quality constituents of the Mattaponi and James Rivers from range of collections, 2009. Chlorophyll-A concentrations are extracted values and represent concentrations from the river channels. Data is courtesy of DEQ river monitoring data, NOAA CBIBS, and VCU Rice Center.

	Feb	March	April	May	June	July
Water Temperature (°C)						
James	6.3 — 7.2	9.3 — 10.8	15.6 — 16.8	22.2 — 22.5	26.3 — 27	27.2 — 28.1
Mattaponi	5.2	9	16	22	26	27
Chlorophyll-A (ug/L)						
James	7.42 ± 1.15	13.03 ± 4.10	7.22 ± 0.70	12.44 ± 7.17	13.53 ± 4.42	22.2 ± 5.40
Mattaponi	4.11 ± 4.35	5.71 ± 8.87	2.73 ± 2.01	4.95 ± 1.42	7.93 ± 6.73	4.11 ± 1.47
Salinity (ppt)						
James	0.1 — 2.7	0.1 — 2.4	0.1 — 0.5	0.1 — 0.3	0.1 — 0.4	0.1 — 0.4
Mattaponi	0.1 — 7.2	0.1 — 4.9	0.1 — 3.0	0.1 — 2.5	0.1 — 2.4	0.1 — 2.0

Table 2. Summary of successful 2009 age-0 collections of larval and juvenile Atlantic menhaden from the Mattaponi and James Rivers, Virginia, 2009 (n=697). Listed are the gear types used during sampling events, river ranged sampled (distance is from confluence with Chesapeake Bay), total length of fishes collected, and quantity of fishes collected.

Date	River	Gear Type	River range upstream from CB (km)	TL range (mm)	No. Collected
24-Feb-09	James	Bongo Net	86	31.5 — 32.1	2
4-Mar-09	Mattaponi	Bongo Net	56.1 — 75.6	32.2 — 36.6	9
5-Mar-09	James	Bongo Net	81 — 86	31.6 — 38.0	132
10-Mar-09	Mattaponi	Bongo Net	122	35.5 — 36.1	2
12-Mar-09	Mattaponi	Bongo Net	57.6 — 82.4	30.9 — 38.4	400
25-Mar-09	Mattaponi	Bongo Net	79.1 — 94.3	32.0 — 37.9	30
2-Apr-09	James	Bongo Net	106 — 112.5	28.0 — 38.2	17
8-Jul-09	James	Push Net	119	108.3 — 127	2
9-Jul-09	Mattaponi	Push Net	79 — 95	41.9 — 80.7	61
16-Jul-09	James	Push Net	119	123.1 — 180.5	6
20-Jul-09	James	Boat Electrofishing	118 — 122	104.5 — 150.0	38

Table 3. Summary of larval Atlantic menhaden collections from the James and Mattaponi Rivers in Virginia, 2009. Listed are range of collection dates, sample size, total length (TL), age (days), and hatch dates. SE = ± 1 standard error of the mean.

River	Mattaponi	James
Collection Date Range	4 Mar - 25 Mar 09	24 Feb - 2 Apr 09
n	95	69
TL (mm)	Range	30.9 — 38.4
	Mean \pm SE	35.6 \pm 0.2
Age (days)	Range	72 — 131
	Mean \pm SE	98 \pm 1
Hatch Date (Julian)	Range	305 — 376 (1 Nov 08 — 11 Jan 09)
	Mean \pm SE	339 \pm 1 (5 Dec 08 \pm 1)
		302 — 386 (29 Oct 08 — 21 Jan 09)
		331 \pm 2 (27 Nov 08 \pm 2)

Table 4. Summary of juvenile Atlantic menhaden collections from the James and Mattaponi Rivers in Virginia, 2009. Listed are range of collection dates, sample size, total length (TL), age (days), and hatch dates (Julian). SE = ± 1 standard error of the mean.

River		Mattaponi	James
Collection Date Range		9 July 09	8 July - 20 July 09
n		52	36
TL (mm)	Range	41.9 — 80.7	104.5 — 180.5
	Mean \pm SE	58.9 \pm 1.2	127.6 \pm 2.4
Age (days)	Range	114 — 199	207 — 310
	Mean \pm SE	158 \pm 3	261 \pm 4
Hatch Date (Julian)	Range	355 — 410 (21 Dec 08 — 14 Feb 09)	256 — 356 (13 Sept 08 — 22 Dec 08)
	Mean \pm SE	396 \pm 3 (30 Jan 09 \pm 3)	303 \pm 4 (30 Oct 08 \pm 4)

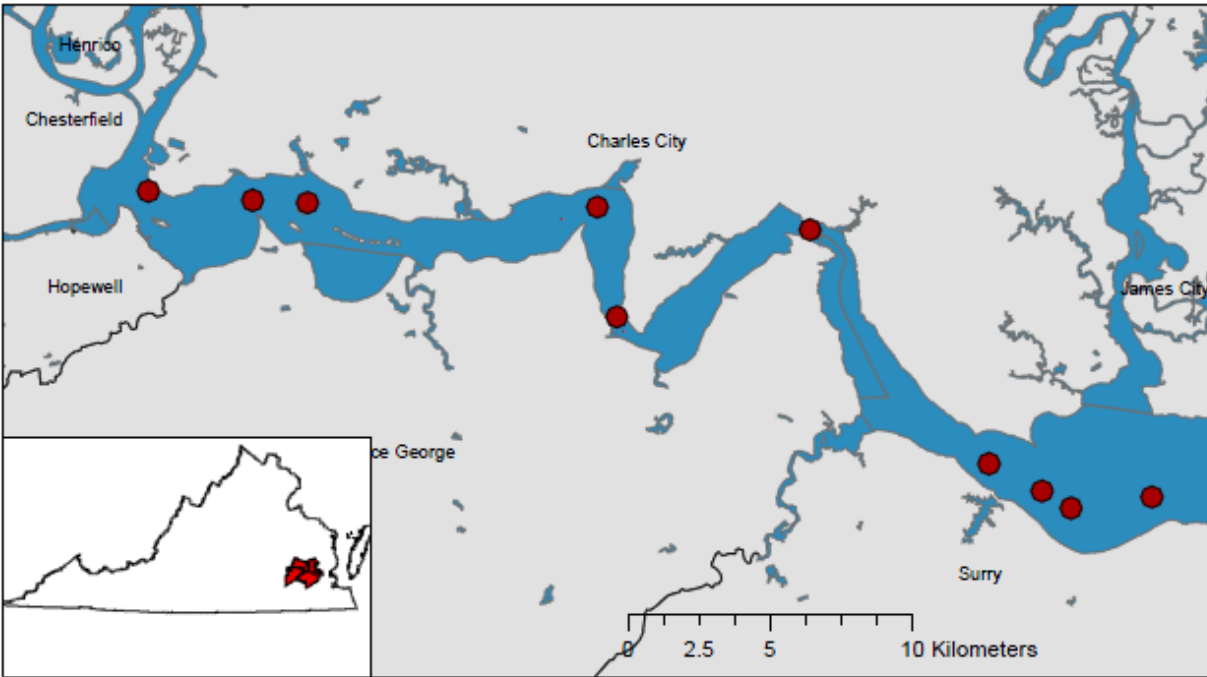


Figure 1. Age-0 Atlantic menhaden collections from the James River, Virginia, 2009. Symbols indicate sampling locations.

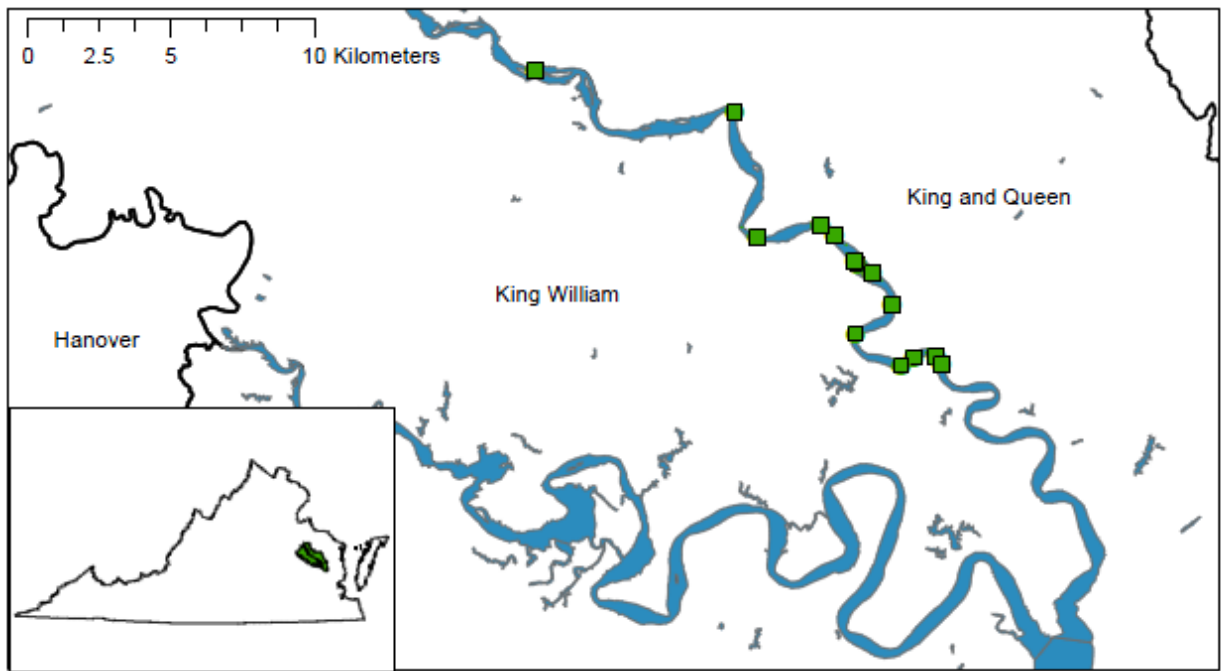


Figure 2. Age-0 Atlantic menhaden collections from the Mattaponi River in Virginia, 2009.

Symbols indicate sampling locations.

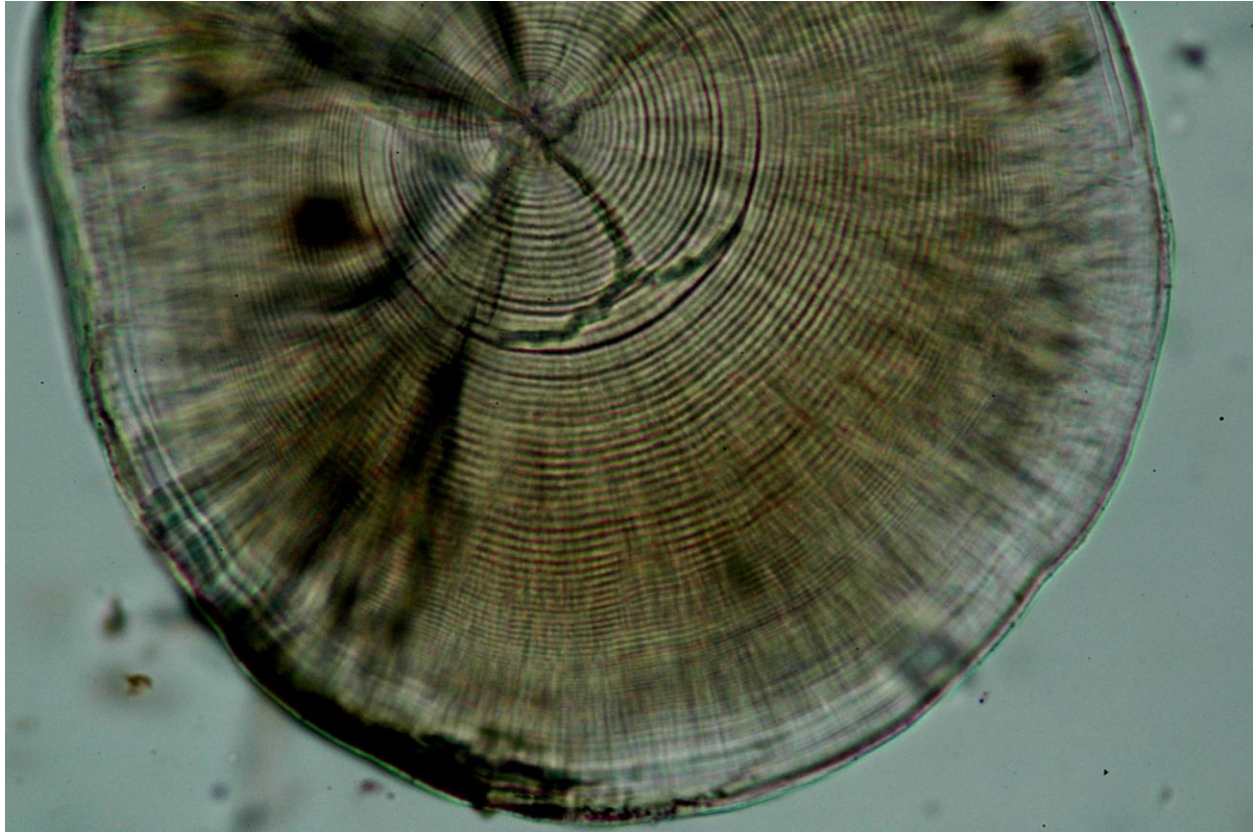


Figure 3. Otolith from Atlantic menhaden larvae collected from the Mattaponi River of Virginia, 21 March 2009; 99 days post-hatch; 36.7 mm TL.

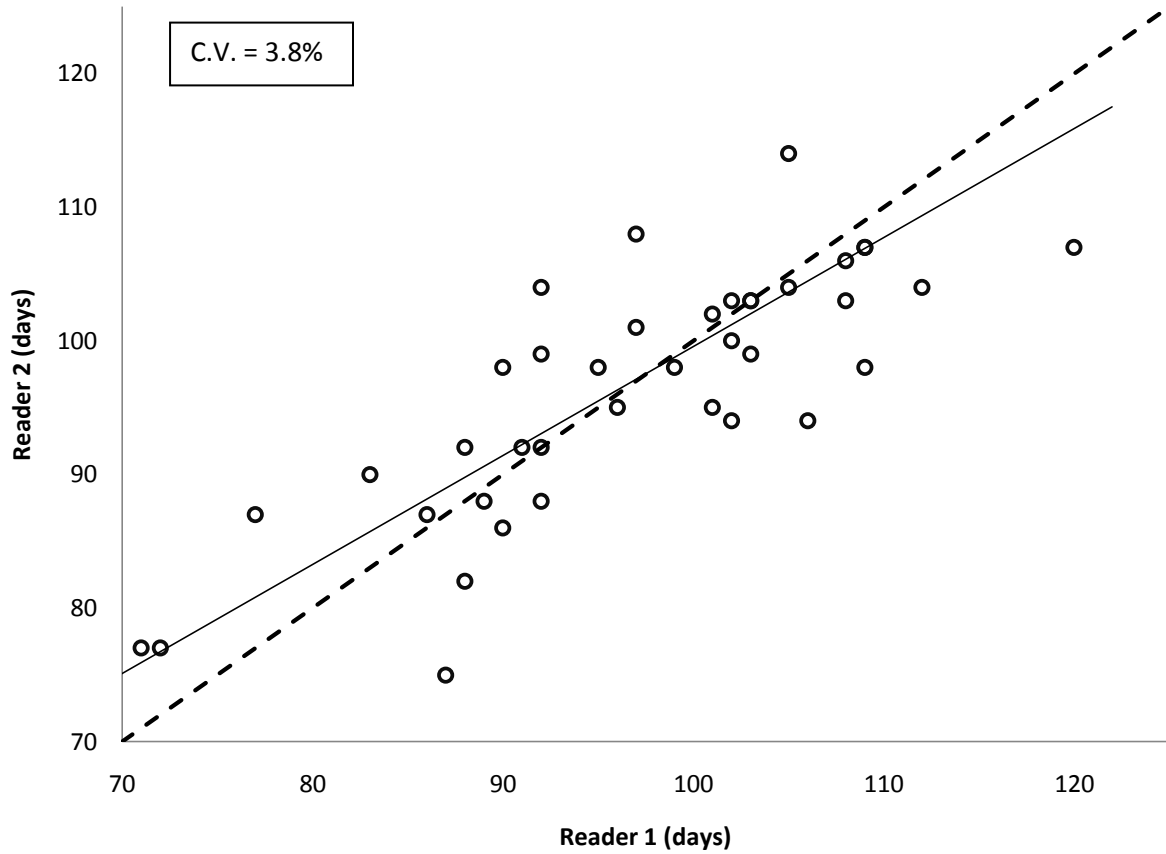


Figure 4. Bias plot of whole structure otolith increment blind reads made by both readers of larval Atlantic menhaden collected in 2009 (n=41). Dashed line represents 1:1 agreement between counts made by both readers. Solid line is the regression line of reads.

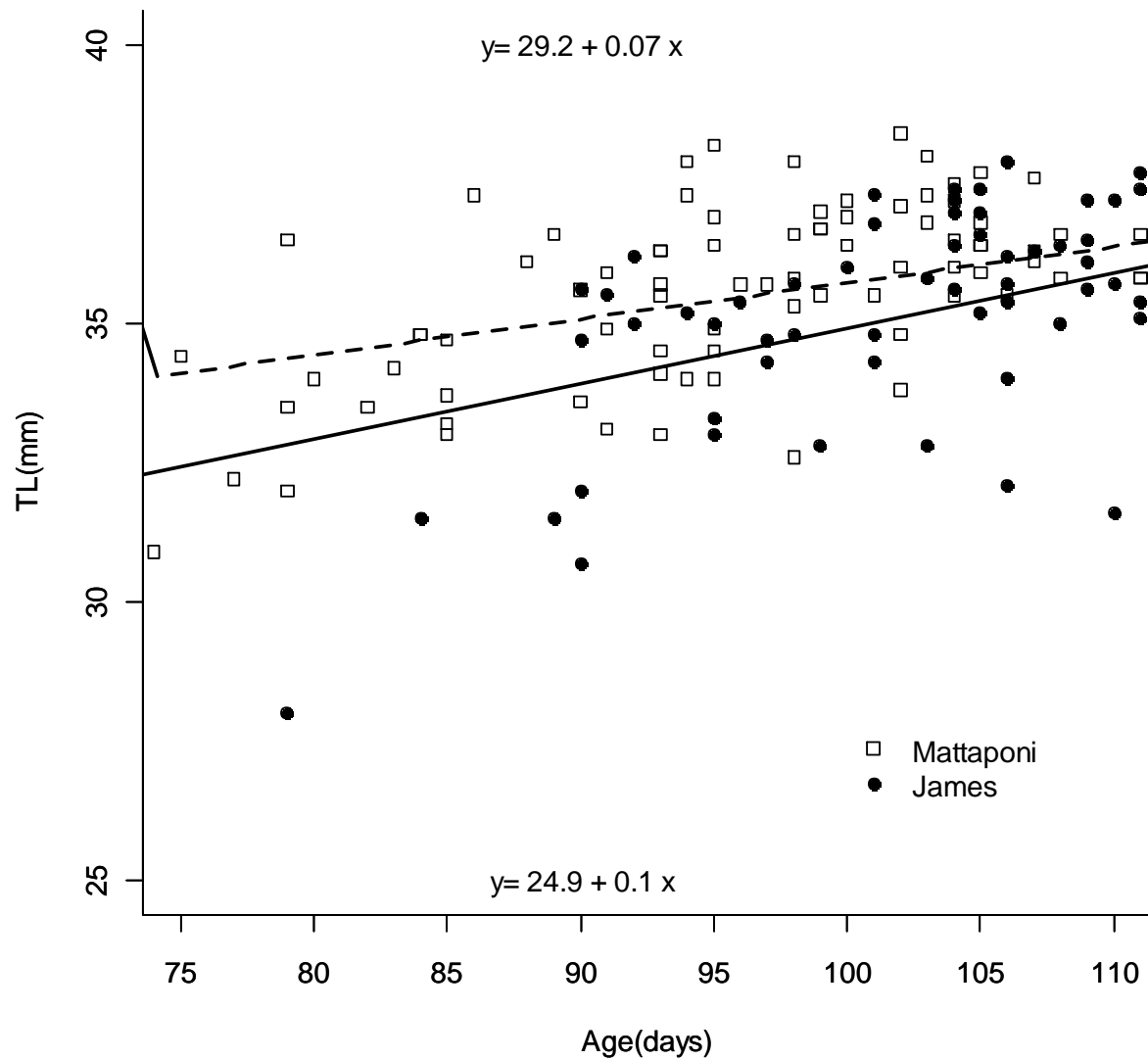


Figure 5. Total length (mm) versus Age (days) relationship for larval Atlantic menhaden collected from the Mattaponi and James Rivers of Virginia, 2009. The slopes of the lines are representative of the growth rate during residency in tidal freshwater reaches (mm d^{-1}).

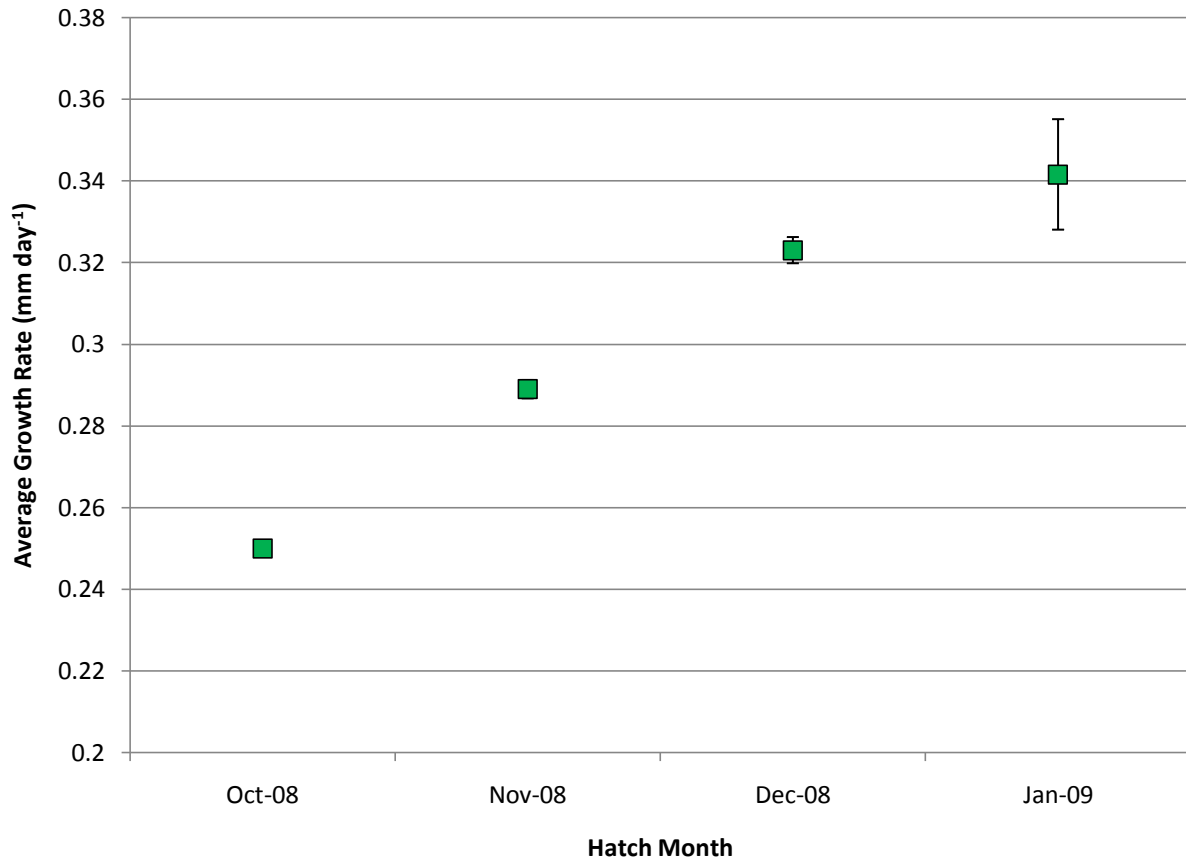


Figure 6. Average growth rates (mm d⁻¹) from individual larval Atlantic menhaden cohorts as designated by hatch date calculation.

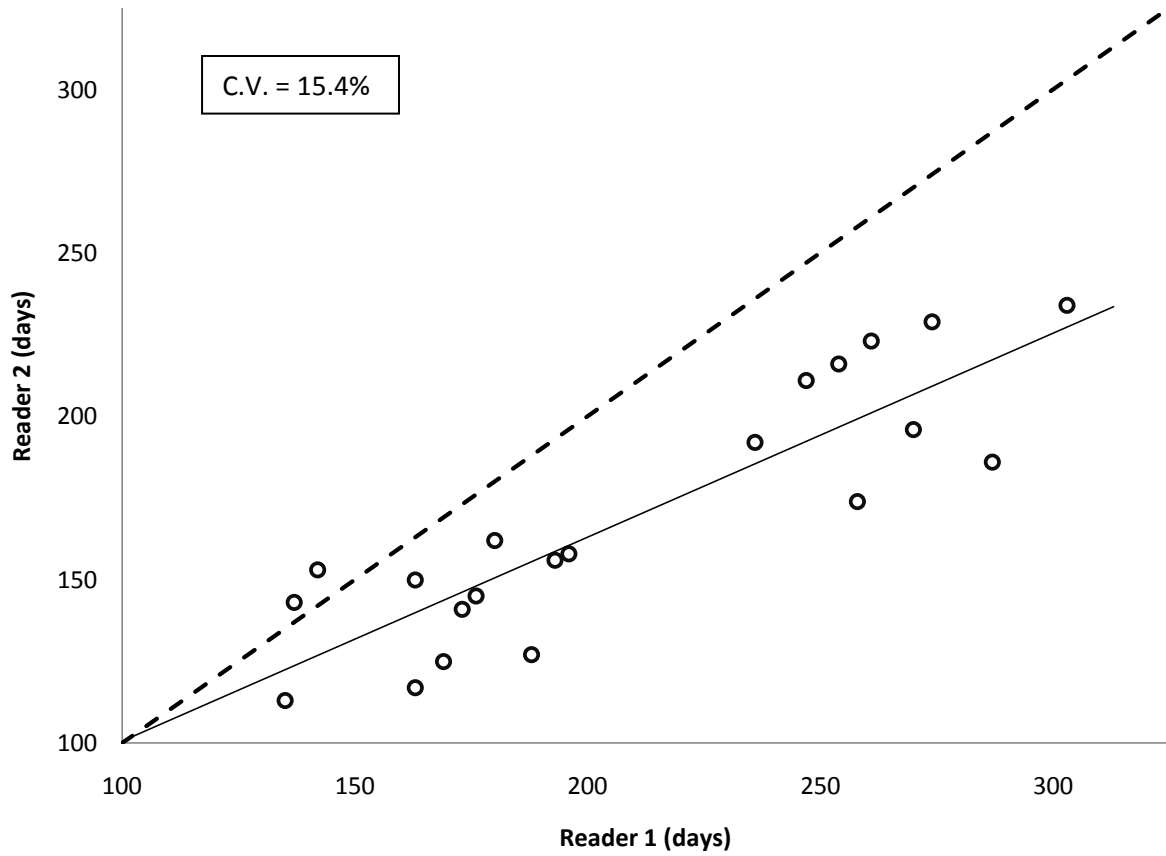


Figure 7. Bias plot of whole structure otolith increment counts made by two readers on juvenile Atlantic menhaden collected in 2009 (n=21). Dashed line indicates 1:1 agreement between incremental counts made by both readers. Solid line is the regression line.

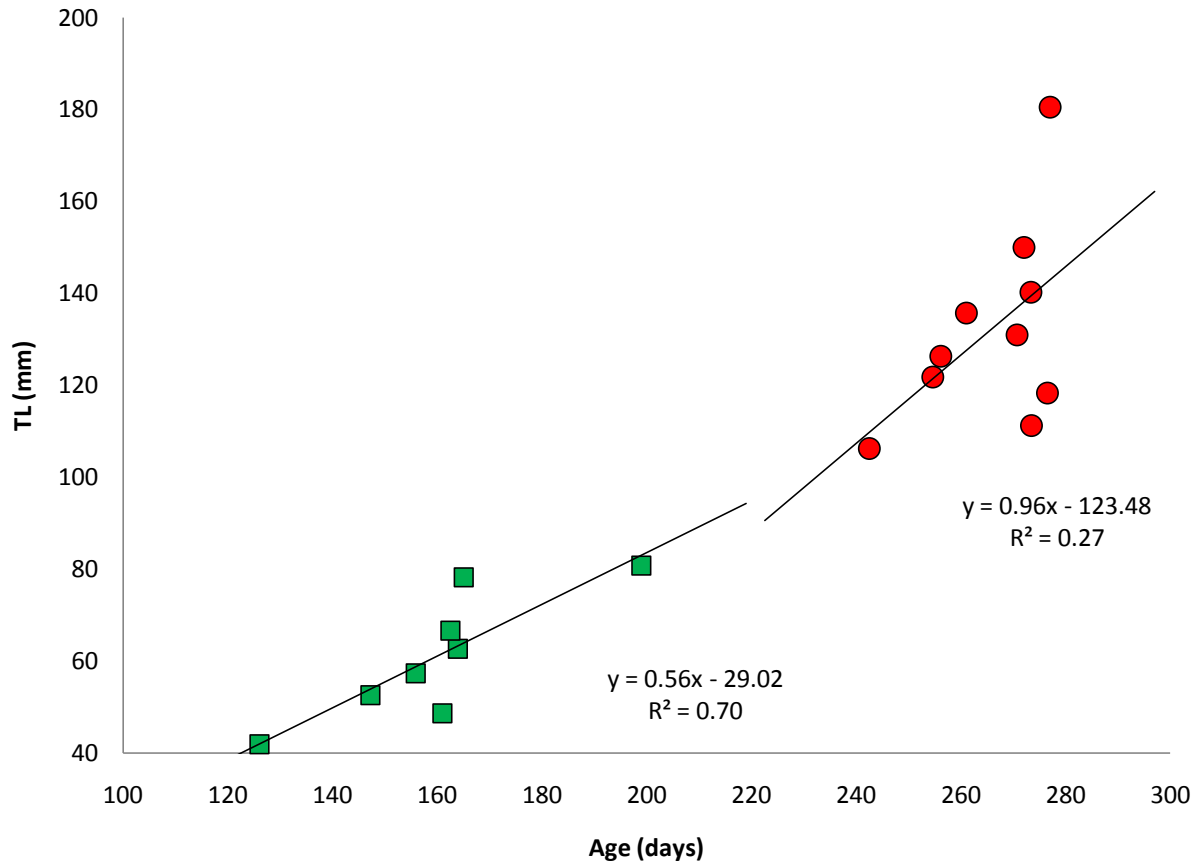


Figure 8: Total length (mm) versus Age (days) relationship for juvenile Atlantic menhaden collected from the Mattaponi and James Rivers of Virginia, 2009. Individual menhaden were placed into 5 mm length bins and regressions were calculated using average age and length within each bin. The slopes of the lines represent the growth rate during residency in tidal freshwater reaches (mm d^{-1}).

VITA

Peter Milton Sturke was born in Worcester, Massachusetts on his father's birthday December 8, 1985. He lived in Grafton, Massachusetts until 1995 when the family moved to Sterling, Virginia. The author received a Bachelors of Science in Biology from the University of Mary Washington in Fredericksburg, Virginia in May of 2008. Peter and his beautiful soon-to-be wife Kate will reside in Richmond, Virginia after completion of this thesis and look to move north in the future.