ABSTRACT

Title of Thesis: DYNAMICS OF INGRESS, HATCH DATES, GROWTH, AND FEEDING OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, LARVAE AT THE CHESAPEAKE BAY MOUTH

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Recruitment of Atlantic menhaden to Chesapeake Bay declined in the late 1980s. Although reasons are not understood, a decline in larval supply to the Bay is one hypothesized explanation. The objective of this thesis was to evaluate levels and variability in larval ingress by conducting 18 ichthyoplankton cruises at the Bay mouth during three years at monthly intervals from fall through spring (2005-06, 2006-07, and 2007-08). The concentrations of ingressing larvae were estimated for each year and also for months within each year. Larval spatial and temporal distributions at the Bay mouth were evaluated with respect to tides and day-night differences. Age, growth rates and hatch dates were determined from otolith-aged larvae and compared among years and months. Larvae were most abundant in 2007-08, but grew fastest in 2006-07. Most ingressing larvae hatched in the November to December period. Copepods were the dominant prey in diets of larval menhaden.

DYNAMICS OF INGRESS, HATCH DATES, GROWTH, AND FEEDING OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, LARVAE AT THE CHESAPEAKE BAY MOUTH

By

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DEDICATION

To my hardworking mother and father.

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Chapter 1: Background and Introduction

The Atlantic menhaden *Brevoortia tyrannus* is an abundant clupeid fish, distributed from Florida to Nova Scotia on the North American east coast (Hildebrand 1948; Hildebrand 1964; Reintjes 1960; Reintjes 1964; Reintjes 1969; MDSG 2009). It is both economically and ecologically important, supporting the largest commercial fishery on the east coast and also serving as a forage base for many piscivorous predators. Recruitment levels of Atlantic menhaden have fluctuated during the past 50 years. Recruitment was high in the 1970s and 1980s, but has been low for two decades, a cause of concern for fishery managers and ecologists who recognize the important ecological services provided by menhaden (MDSG 2009; ASMFC 2010). The causes of recent low recruitments are not known.

My thesis addresses larval ingress from offshore spawning grounds to Chesapeake Bay, which historically has been the major juvenile nursery for menhaden on the Atlantic coast (MDSG 2009). The objectives of my research are: 1) to quantify ingress and evaluate its inter-annual and seasonal variability, 2) describe spatial distribution of larvae at the Chesapeake Bay mouth during ingress and evaluate it with respect to hydrological and physical factors, 3) describe age and growth of ingressing larval menhaden at the Chesapeake Bay mouth, 4) determine hatch dates of ingressing larvae, 5) describe and characterize ontogenetic stages of Atlantic menhaden at ingress, 6) document the diet and feeding of Atlantic menhaden at the Chesapeake Bay mouth and evaluate temporal variability.

Atlantic Menhaden Early Life Stages

Atlantic menhaden spawns offshore on the continental shelf over a broad range from New England to the Carolinas (MDSG 2009). Larvae enter the Chesapeake Bay and other estuaries, which serve as nursery grounds for young-of-the-year Atlantic menhaden. The Chesapeake Bay is a major nursery. Chesapeake Bay and other estuaries provide physical, chemical, and biological conditions, including high productivity, that are favorable for young-of-the-year juvenile menhaden (Reintjes and Pacheco 1966). Atlantic menhaden are abundant in Chesapeake Bay, playing an important role in the Bay ecosystem as well as supporting its largest fishery.

Atlantic menhaden larvae begin their lives in the coastal ocean as visual zooplankter-feeding predators and later, after entering estuaries, shift to a filter-feeding diet (June and Carlson 1971). The shift comes after metamorphosis, in the transition from the larval to the juvenile stage when menhaden are approximately 38 to 40 mm in length (June and Carlson 1971; Lewis *et al*. 1972). During metamorphosis major morphological changes occur in the gill structure. The branchial baskets develop specialized gill rakers with filamentous branchiospinules. These structures act as a "sieve" to filter food particles from the water (June and Carlson 1971; Friedland 1985; Friedland *et al*. 2006).

Atlantic menhaden also is a key forage species in the Chesapeake Bay. Juvenile menhaden are seasonally abundant and important prey for numerous recreationally and commercially sought fishes in the Chesapeake Bay, including striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and Spanish mackerel (*Scomberomorus maculatus*) (Lippson 1991; Uphoff 2003). Along the Atlantic

coast menhaden is prey to additional species, including tunas and sharks (Rogers and Van Den Avyle 1989). Additionally, menhaden is important in diets of mammals and many birds (Reintjes 1969; Ahrenholz 1991; Lippson 1991; Viverette *et al*. 2007). The trophic position of filter-feeding Atlantic menhaden supports a direct energetic link from primary production to higher trophic levels (Rogers and Van den Avyle 1989).

Menhaden supports the single largest fishery in the Chesapeake Bay and accounts for as much as 87 percent of total commercial landings in Virginia (Kirkley 1997). Annual catches exceeded 100,000 tons from the 1980s through the 1990s (Smith 1999). Reedville, VA, is home-base to the single, industrial-scale purse-seine fishery for Atlantic menhaden on the east coast (MDSG 2009). Most of the fishing effort takes place in or near Chesapeake Bay, with historical annual catches averaging 154,980 tons (Blankenship 2010). Reduction of menhaden to meal and oil mostly produces various animal feeds and supplements, and the human health supplement, omega-3 fatty acids (Blankenship 2010). A pound net and small-boat purse-seine fishery in Chesapeake Bay lands menhaden for bait to be utilized in commercial and recreational fisheries (MDSG 2009).

Menhaden recruitment to Chesapeake Bay

A steep decline in age-0 menhaden recruitment level occurred in the Chesapeake Bay from the early 1990s to the present (MDSG 2009). The decline in recruitment levels continued despite evidence that the Atlantic coast-wide menhaden spawning stock population remained above or near target levels based on fisheries stock assessments (ASMFC 2010). Recruitment level of age-0 menhaden in the Chesapeake Bay appears to

have stabilized at a low level since 1992 (Figure 1.1). This present low level of menhaden recruitments in the Bay is not unique. Menhaden also experienced a period of low recruitments from 1959 through 1970.

There are concerns regarding localized depletion of Atlantic menhaden in Chesapeake Bay because recruitment remains low. Research on localized depletion and its causes, including intense localized fishing, is ongoing. There is potential for localized depletion but it has not been demonstrated with certainty (Haddon 2009; Maguire 2009). Responding to concerns, ASMFC placed a cap on annual menhaden landings from the Chesapeake Bay purse-seine reduction fishery (ASMFC 2006). The cap limits harvest of menhaden in the Bay to 109,020 metric tons for eight years from 2006 to 2013 (ASMFC 2009).

Proposed explanations for causes of the low recruitments in the Chesapeake Bay are not based on research results. One hypothesis is that predation-caused natural mortality of age-0 menhaden has increased in the Bay. The striped bass, a key predator of menhaden in the Bay and coastwide, has recovered since a decline in abundance in the 1970s-1980s (Richards and Rago 1999) and has reached historical population highs since the early 1990s. Increased predation on menhaden by striped bass may have increased the natural mortality rate of YOY menhaden, reducing recruitment potential (Vaughan *et al*. 2002; Uphoff 2003; MDSG 2009). Uphoff (2003) noted a decrease in supply of age 0-2 menhaden as early as 1998, following an increase in potential consumption by the recovered striped bass population. Another possible explanation for low YOY menhaden recruitment and localized depletion is an increase in disease mortality (Kane *et al*. 1998, 2007)

Recruitment levels in menhaden are thought to depend on environmental conditions and their variability (AMAC 2000; MDSG 2009). The early life stages in the Atlantic menhaden life cycle are vulnerable to physical, biological, and environmental conditions. Offshore mortality from predation, starvation, or hydrological stress may occur during the egg or early larval stages although there are no estimates of such mortality. Instantaneous mortality rates of late-staged menhaden larvae ranged from 0.038 to 0.056 d-1 in mesocosm experiments (Keller *et al*. 1990). In the laboratory, larval Atlantic menhaden experience high mortality rates at temperatures of ≤ 5 degrees Celsius (Lewis 1965). However, living late-stage larvae have been collected inside the Chesapeake Bay at temperatures ≤ 2 °C (Massmann *et al*. 1962; Houde *et al*. 2010).

It has been hypothesized that a decrease in the larval supply of Atlantic menhaden to Chesapeake Bay or a decline in survival of juveniles in the Bay are possible causes of recent low recruitments. Atlantic menhaden in the Chesapeake Bay are part of a single stock that ranges from Nova Scotia to Florida (Reintjes 1969; Ahrenholz 1991; Lynch 2010; MDSG 2009). Most spawning occurs offshore over the continental shelf, primarily during a 4-6 month period from fall through winter (Warlen 1994). In early fall adults begin a southward migration from waters in the northern part of the range that culminates in December south of Cape Hatteras (Roithmayr 1963; Nicholson 1971; Dryfoos *et al*. 1973; Kroger and Guthrie 1973; Ahernholz 1991; Warlen 1994). The population is believed to spawn as it migrates, with most spawning occurring from the Mid-Atlantic to the Carolinas. Hatching occurs offshore and larvae must be transported to estuarine habitats where they ingress before metamorphosing to the juvenile stage. Spawning temperatures generally must be ≥ 15 °C (Stegmann and Yoder 1996; Stegmann *et al*.

1999). In the laboratory, declines in temperature from 18 to 14 °C sharply reduce the ability of menhaden females to spawn (Fitzthugh and Hettler 1995).

Many estuarine-dependent species including Atlantic menhaden, Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and southern (*Paralichthys lethostigma*) and summer flounder (*P. dentatus*) spawn in the offshore environment, mostly during winter, relying on transport to deliver their larvae to estuaries (Miller *et al*. 1984). Miller *et al*. (1984) hypothesized that increased survival at low rations under cold temperatures and reduced predation pressure are potential benefits to winter spawning. More importantly, shoreward currents provide favorable conditions for estuarine transport in the winter (Miller *et al*. 1984). Tidal-stream transport (Arnold 1981; Beckley 1985; Forward and Tankersley 2001) and responses to passive buoyancy (Miller 1988; Epifanio and Garvine 2001) have been proposed as mechanisms for larval transport. Spring-spawned fishes such as bluefish rely on transport along the outer shelf associated with the Gulf Stream (Lee and Atkinson 1983; Hare and Cowen 1996) whereas winter-spawned fishes are more influenced by mid- to outer shelf processes (Epifanio and Garvine 2001). Larval transport has been reported as a two-phase process (Boehlert and Mundy 1988; Warlen 1992). Larvae are transported initially at a fast rate to the nearshore environment (Warlen 1992). Transport thereafter is at a slower rate and relies on estuarine flow dynamics.

Transport of larval menhaden and subsequent ingress into estuaries are thought to be dependent on physical processes that affect transport and survival. The offshore environment presents numerous obstacles that challenge successful transport to an estuary. Offshore feeding of larval menhaden has yet to be studied. However, in the

laboratory, temperature has been demonstrated to influence growth and survival of larvae (Powell and Phonlor 1986). Early-stage larvae have limited swimming capability and thus rely on water currents for transport. Hydrographic conditions and climate patterns likely govern the transport of larval menhaden. Wind regimes may be especially important when considering inter-annual and decadal scale variability in transport. Research results suggest that transport to estuary mouths is quite rapid. Larvae reportedly reached estuaries in about 45 to 60 days after hatching (Reintjes 1969; Ahrenholz 1991; Warlen 1992; Warlen *et al*. 2002).

Few studies have investigated the movement of larval menhaden into the Chesapeake Bay. Kendall and Reintjes (1975) reported inter-annual variability in the timing of menhaden ingress into mid-Atlantic estuaries. Hare *et al*. (2005) in a two-day survey evaluated larval ingress of three offshore spawned fishes, including Atlantic menhaden, with respect to physical processes near the Chesapeake Bay mouth. Their results suggested that ingress of Atlantic menhaden is mostly influenced by wind driven flux and tidal residual bottom inflow. However, they suggested that behavioral responses by larvae to physical forces, and not physical forces alone, influence transport into an estuary. Behavioral responses in vertical positioning of Atlantic menhaden larvae with respect to physical conditions at the mouths of estuaries have been observed in studies on ingress into North Carolina estuaries (Hettler and Hare 1998; Forward *et al*. 1999a; Forward *et al*. 1999b).

Thesis Chapters

My research focused on larval ingress of Atlantic menhaden at the mouth of the Chesapeake Bay. The thesis describes and quantifies important biological and ecological features associated with ingress. Chapters 2 and 3 are written as stand-alone chapters, anticipating eventual publication in peer-reviewed journals. Chapter 4 summarizes and synthesizes findings.

Chapter 1. Introduction

This chapter is primarily background information on Atlantic menhaden and recruitment variability. An introduction to menhaden early life history and issues related to larval ingress are provided.

Chapter 2. Larval Ingress and Ingress Variability

This chapter addresses larval ingress of Atlantic menhaden and ingress variability. It includes an evaluation and discussion of inter-annual and monthly ingress variability, based on 18 research cruises and surveys to the Chesapeake Bay mouth from December 2005 to April 2008. Abundances of ingressing larvae, variability in ingressing numbers and the distributions of ingressng larvae across the Chesapeake Bay mouth were analyzed with respect to hydrography and environmental factors.

Chapter 3. Age, growth, hatch dates, and feeding by ingressing Atlantic menhaden larvae

The third chapter has two components: the first is age and growth of Atlantic menhaden larvae and the second is foods and feeding of the larvae at the Bay mouth. In this chapter inter-annual and monthly age variability, indicators of the offshore-to-estuary transport period, is evaluated. In addition, inter-annual variability in hatch dates and hatch-date distributions are determined for research conducted from 2005-2008. Growth and growth variability of larval menhaden during the transport period are reported and discussed. Finally, diets of larval menhaden at the Chesapeake Bay mouth are reported and discussed in relation to available zooplankton prey.

Chapter 4. Summary and conclusions

The final chapter is a summary, providing conclusions and presenting a synthesis of findings and implications of the research. In this chapter, the supply of larval menhaden is discussed in relation to observed recruitment levels of young-of-the-year menhaden in Chesapeake Bay.

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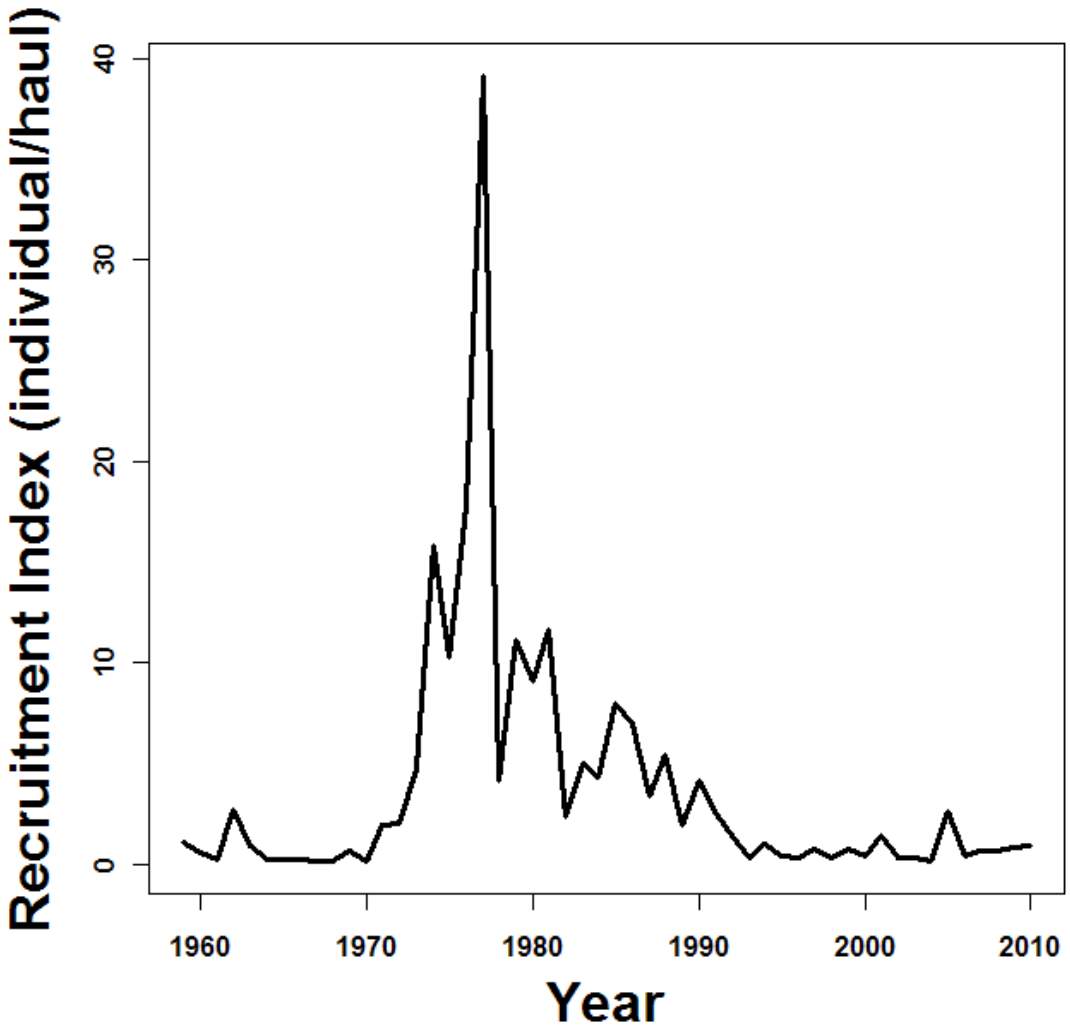

Figure 1.1. Maryland age-0 Atlantic menhaden recruitment index from MD DNR seine survey. Five river systems in the Maryland portion of the Bay were sampled by MD DNR during the survey (*http://dnr.maryland.gov/fisheries/juvindex/index.asp*). The metric was area-weighted by river system to produce this time series.

Chapter 2: Ingress of Atlantic menhaden *Brevoortia tyrannus* larvae into Chesapeake Bay

Abstract

Annual recruitment levels of young-of-the year (YOY) juvenile Atlantic menhaden to Chesapeake Bay have remained low following a decline that began in the 1980s. Although reasons are not yet understood, a decline in larval supply to the Bay is one hypothesized explanation. In a three-year survey, nine-fold variability in abundance of ingressing larvae was observed. Larvae were more abundant in 2007-08 (8.44 larvae/m^3 ± 2.08 se) than in 2005-06 (2.32 larvae/m^3 ± 0.42 se) or 2006-07 (0.90 larvae/m^3 ± 0.17 se). Variability in larval concentrations among months was higher than that among years. Mean larval concentrations did not differ significantly across the 20-km-wide Chesapeake Bay mouth. Mean lengths of larvae collected at the south side of the Bay mouth were larger than larvae at other sites. Mean concentrations of larvae were higher in night catches than day catches in 2006-07 and 2007-08, but not in 2005-06. Mean lengths of larvae collected at night were longer than larvae collected during the day. Larval concentrations differed significantly among tide stages but the patterns differed among years and among months within year. Larval concentrations at the Chesapeake Bay mouth in the three years were not concordant with subsequent age-0 juvenile recruitment indices.

Introduction

Atlantic menhaden spawns offshore on the continental shelf. Recruitment depends on successful transport of larval menhaden to estuaries where they spend the first year of juvenile life. Recruitment levels of age-0 menhaden in the Chesapeake Bay have remained low since a steep decline in the mid-1980s (ASMFC 2004; 2010; MDSG 2009). There are several hypotheses to explain low recruitments (ASMFC 2004). Among them is a decline in the supply of larval Atlantic menhaden from offshore waters where they begin their lives. Atlantic menhaden in the Chesapeake Bay are part of a single coastwide population that ranges from Nova Scotia to Florida (Hildebrand 1948; Hildebrand 1964; Reintjes 1960; Reintjes 1964; Reintjes 1969; MDSG 2009). The complexities of the Atlantic menhaden life cycle likely contribute to variability in early life survival, distribution, and recruitment of juveniles to Atlantic coast estuaries.

During summer the adult population is distributed throughout its range along the Atlantic coast from Florida to Nova Scotia, with older age classes predominating to the north and younger ages to the south (June and Reintjes 1960; June 1961; June and Nicholson 1964; Rogers and Van Den Avyle 1989). Higham and Nicholson (1964) noted that spawning occurs in every month of the year, mostly by age-3+ menhaden. These authors suggested that, because of the geographical age distribution, menhaden spawning occurs mostly in the northern reaches of its range during the summer, as proposed by Judy and Lewis (1983) based on their study of seasonal and spatial distributions of eggs and larvae along the Atlantic coast. By early fall the adult component of the population begins to migrate southward (Roithmayr 1963; Reintjes 1969; Nicholson 1971; Dryfoos

et al. 1973; Kroger and Guthrie 1973; Ahernholz 1991; Warlen 1994). Spawning intensifies along the mid-Atlantic coast and in the South Atlantic Bight during this migration and has been proposed to be at its peak when menhaden reach the waters south of Cape Hatteras in December (Higham and Nicholson 1964; Judy and Lewis 1983).

Larval menhaden are advected to the mouths of estuaries just prior to transformation to the juvenile stage (Reintjes 1969; Ahrenholz 1991; Warlen 1994). Menhaden eggs hatch offshore (Reintjes 1969; Maillet and Checkley 1991; Warlen 1992, 1994). In the offshore environment, larval fishes, including menhaden, have limited swimming capability (Shanks 1995) and thus are dependent on ocean circulation for transport to estuaries (Hare *et al*. 1999; Quinlan *et al*. 1999; Rice *et al*. 1999; Stegmann *et al*. 1999; Werner *et al*. 1999). Research on the duration of transport, based on estimated age-at-ingress, has indicated that most menhaden larvae that ingress into estuaries in North Carolina had transport periods of more than one month duration and a mean period of two months (Warlen 1992, 1994; Warlen *et al*. 2002). At ingress, menhaden larvae are > 20 mm total length (TL) and presumably have considerable horizontal swimming capability (Warlen 1992, 1994; Shanks 1995; Warlen *et al*. 2002). It is hypothesized that, under unfavorable environmental conditions, including extreme cold temperatures in winter, larval menhaden may grow slowly and mortality may increase, leading to variable offshore survival and supply to estuaries (Lewis 1965; Powell and Phonlor 1986).

Research conducted by the SABRE program investigated transport duration, transport trajectories, hydrographic influences, and the importance of larval behavior by developing linked, individual-based bio-physical models (Hare *et al*. 1999; Quinlan *et al*. 1999; Rice *et al*. 1999; Stegmann *et al*. 1999; Werner *et al*. 1999). The SABRE team

suggested that transport of menhaden larvae in the near-shore coastal ocean results in dispersal of larvae primarily along-shore and southward (Quinlan *et al*. 1999), implying that a substantial proportion of spawning and early larval development takes place in the Mid-Atlantic Bight. Massmann et al. (1962) reported menhaden larvae at distances > 40 miles offshore of the mouth of Chesapeake Bay. Based on increases in length of larvae in a shoreward direction, Massmann et al. suggested that larval movement is shoreward. Modeling results from SABRE, however, suggested that cross-shelf transport mechanisms are a secondary component of the transport process and that north to south along-shore transport predominates.

Understanding mechanisms that drive offshore larval transport has proven to be a difficult task. Water currents, winds and larval behavior are important components in modeling larval transport (Hare *et al*. 1999). Hoss et al. (1989) suggested that vertical movements in the water column may promote shoreward, cross-shelf transport of larvae and merit consideration for inclusion in transport models.

Ingress of menhaden larvae to estuaries has been monitored by programs in North Carolina and the Mid-Atlantic states, usually at fixed stations near the entrance to estuaries (Forward *et al*. 1999; Hare *et al*. 2005; Hettler and Hare 1998; Warlen 1992, 1994; Warlen *et al*. 2002). After menhaden larvae reach the entrance of an estuary factors that promote their ingress, while important, are poorly understood. Circulation, hydrography, winds, and tides all may play a role in determining if ingress will be successful. Olney and Boehlert (1988) suggested that ingressing fish larvae, including menhaden, in the Chesapeake Bay may utilize the non-tidal up-bay salt wedge intrusion for recruitment into the estuary based on an ichthyoplankton survey near the Bay mouth.

In a two-day study at the Chesapeake Bay mouth, Hare *et al*. (2005) reported that wind-driven, up-estuary flux and residual bottom tidal inflow, combined with vertical positioning behavior, appeared to be responsible for up-estuary movement of larval menhaden. Reiss and McConaugha (1999) considered event-scale upwelling and downwelling forces as cross-frontal mechanisms for transport of larval fishes into or away from the entrance of Chesapeake Bay. They explain that upwelling-favorable southwesterly winds divert the Chesapeake Bay plume front offshore possibly resulting in the advection of some larval fishes offshore. Subsequent rapid weakening of those winds allows the Chesapeake Bay plume flow to revert against the coast trapping low salinity water offshore and, in effect, retaining larvae offshore.

There is a need for information on variability in the inter- and intra-annual ingress patterns of Atlantic menhaden to the Chesapeake Bay to better understand how offshore supply influences recruitment patterns. The objective of this chapter is to describe inter-annual and monthly abundances and variability in patterns of ingress by menhaden larvae at the Chesapeake Bay mouth, with particular interest in identifying peak periods of ingress. Based on ichthyoplankton surveys, ingress of menhaden larvae at the Bay mouth and its annual and monthly variability are described and analyzed in relation to tide stages, time of day, depth distributions and location across the Bay mouth.

I hypothesized that ingress of Atlantic menhaden larvae and peak levels of ingress into the Chesapeake Bay would vary monthly and inter-annually. Variability may be attributable to shifts in spawning times and areas, both inter-annually and during a spawning season. Explaining the mechanisms that generate along-shore and cross-shelf

transport was beyond the scope of this study. Patterns of ingress are described based on a three-year sampling program conducted at the Chesapeake Bay mouth..

Methods

Study Area, Surveys, and Sample Collections:

The study area is located at the mouth of the Chesapeake Bay where ingress of ocean-spawned Atlantic menhaden larvae occurs. The Bay mouth is 20-km wide and has three shipping channels of different depths (Figure 2.1). The Chesapeake Channel is the deepest with depths of 17.7 m. The shallower North Channel is 14-m deep. Between these channels is a shallow flat, the Middle Grounds, with depths of 11.3 to 14.1m (Valle-Levinson *et al*. 2001). At the southern end of the Bay mouth is the Thimble Shoal Channel with depths of 8.0 to 11.8 m. Depths between Thimble Shoal Channel and Lynnhaven Inlet average 10 m (Valle-Levinson and Lwiza 1998).

A sampling transect was designated across the Chesapeake Bay mouth, located approximately 1-mile seaward of the Chesapeake Bay Bridge/Tunnel. Four stations were sampled on the transect in December 2005. Five fixed stations (Figure 2.1) were designated and sampled on all remaining survey cruises during the three-year program.

Eighteen cruises were conducted in the December 2005 to April 2008 period (Table 2.1). Cruises were conducted from November to April, the season when ingress was expected to occur. All except two of the cruises were on the University of Maryland Center for Environmental Science's 20.0-m R/V *Aquarius*. The remaining two cruises were on the University of Delaware's 44.5-m RV *Hugh Sharp*.

Ichthyoplankton and zooplankton samples were collected at each station on the RV *Aquarius* cruises with a 1-m^2 mouth-opening Tucker Trawl with 280-µm mesh nets. A Tucker trawl with 1-mm mesh nets was used in the two cruises conducted in early November 2007 and February 2008 on the R/V *Hugh Sharp*. Flowmeters were secured in the mouths of each Tucker-trawl net to allow calculation of volume filtered. The 280-µm mesh was suitable for collection of small fish larvae and mesozooplankton in the size range eaten by larval menhaden. The Tucker trawl with 1-mm meshes was sufficient to capture ingressing menhaden larvae, which are mostly > 20-mm length, but did not sample small ichthyoplankton of other taxa or mesozooplankton. Each Tucker Trawl had two nets. In a deployment, one net was fished obliquely from near-bottom to the pycnocline and the second was fished from the pycnocline to surface. On occasions when a pycnocline was not well defined the bottom net was towed from near bottom to mid-depth. On most deployments, tow durations for each net were four minutes (mean volume filtered = 216.31m^3 ± 60.39 se). On several cruises during 2006-07, tows were extended to six minutes to increase numbers of larval menhaden in catches (mean volume filtered = 463.96 m^3 ± 14.32 se). During each cruise, all stations on the transect were sampled at least twice and up to four times a day to encompass two photic periods (night and day) and a range of tide stages. Samples were preserved in 100% ethanol.

In addition to the sample collections, depth profiles of hydrographic conditions were measured at each station using a SeaBird CTD (conductivity, temperature, and depth). On occasions when the CTD was not available or malfunctioned (Days 2 and 3 in March 2007, all 21 stations in April 2007, and one station in November 2007) a YSI sonde was used to record those measurements at 1-m depth intervals. Tide stages and

predicted currents were obtained from tide charts using the "Capn Voyager" software Tides 32 (Star Technologies). The tide stage at the time of each sample collection was recorded.

Laboratory Procedures

Ichthyoplankton samples were processed in the laboratory. Menhaden larvae were identified, enumerated, and subsequently measured. The protocol for measuring menhaden larvae was to measure all larvae in samples containing fewer than 100 larvae and to measure a random subsample of 100 in samples with more than 100 larvae. Lengths of unmeasured larvae in samples with more than 100 menhaden larvae were estimated from the length-frequency distributions of measured larvae and proportional assignment of lengths to unmeasured larvae. The proportion of larvae in each 1-mm length bin was determined for each sample. Mean lengths from only the measured larvae (1,172 in 2005-06, 939 in 2006-07, and 3,342 in 2007-08) were compared among monthly cruises and among the three years in a nested ANOVA followed by the Tukey HSD multiple comparisons test to determine significance of individual means.

Larval Concentrations

Catches of menhaden larvae were expressed as concentrations (number per 100 m^3 of water filtered). This metric is an index of larval ingress into Chesapeake Bay and was used for all comparisons and analyses. Larval ingress into estuaries may occur in pulses (Warlen 1994). The standard deviations for the daily mean larval concentrations at the Bay mouth were compared to the respective means using simple linear regression

to ascertain if temporal patchiness increases with mean concentration of menhaden larvae.

The temporal (inter-annual and monthly), spatial (among stations, above vs below pycnocline), tide stage, and day vs. night variability in larval menhaden concentrations were analyzed using Analysis of Variance (ANOVA). The model chosen for the analysis was a nested ANOVA. It was selected because it allowed subgrouping the factors within different levels of other factors. The response variable in the model, larval concentration, was $\log_e$-transformed to achieve a more consistent and more homogeneous scale of variability. To include logarithmic values for larval concentrations of zero, a constant equal to half the lowest positive larval concentration value was added to all larval concentration data, including the zero values. This adjustment and approach have been debated but are used quite commonly in practice (Venables and Dichmont 2004). Geometric mean concentrations of larvae are reported based on the back-transformed $\log_e$ values. Significant differences in mean larval concentrations among the levels of each factor were identified using the Tukey Honestly Significant Difference (HSD) method of multiple comparisons.

Inter-Annual Variability in Larval Concentrations

Larvae were sampled over a three-year period during three consecutive ingress seasons (2005-06, 2006-07, 2007-08). The inter-annual differences in larval concentrations at the Bay mouth were analyzed using the nested ANOVA ($\alpha = 0.05$).

Among-Cruises Variability in Larval Concentrations

Differences among cruises in larval concentrations at the Bay mouth were included in the nested model to identify seasonal patterns. Because cruises were mostly conducted at monthly intervals, among-cruise differences in larval concentrations largely represent monthly (i.e., seasonal) differences. In the model, the among-cruise variability was nested within each level of year. This allowed testing for differences in larval concentrations among the five cruises (December-April) in 2005-06, six cruises (November through April) in 2006-07, and seven cruises (Early November, Late November-April) in 2007-08.

Among-Stations Variability in Larval Concentrations

Distributions of menhaden larvae across the mouth of Chesapeake Bay were evaluated by testing for differences in mean larval concentrations among the five stations sampled during the study. Note that in December 2005 only four stations were sampled. In the analysis, mean concentrations at each station were aggregated; these means do not include data from December 2005. The nested ANOVA was used for the analysis. Among-station differences in larval concentrations were nested within year and also nested within cruises (i.e., months) within year.

Tide-stage Variability in Larval Concentrations

Sampling for larval menhaden was conducted under different tide stages to determine if abundance or availability of larvae differed among stages. In most cruises, entire tidal cycles were included. Predicted tide stages were recorded from the software

"Capn Voyager". Four tide stages were designated based on the software: slack before ebb, ebb, slack before flood, and flood. The differences in mean larval concentrations among tide stages were tested in the nested ANOVA.

Between-Depths Variability in Larval Concentrations

Differences in mean larval concentrations between two depth zones in the water column (above and below pycnocline) were tested in the nested ANOVA. Larval concentrations in the two depth zones were nested within years and within cruises (i.e., months) within years.

Day-Night Variability in Larval Concentrations

Concentrations of menhaden larvae collected during the day and night were compared. The variability attributable to day and night differences in larval concentrations was analyzed in the nested ANOVA. Differences in larval concentrations between day and night were nested within years and also nested within cruises (i.e., months) nested within years.

The Nested Analysis of Variance and *F*-Tests

The model used to analyze differences in larval concentrations is:

$$C = y + m(y) + t(y) + v(y) + s(y) + p(y) + t(m(y)) + v(m(y)) + s(m(y)) + p(m(y))$$

Where C is larval menhaden concentration, y is year, t is tide stage, v is top vs. bottom, s is sampling station at the Bay mouth, p is day vs. night, and m is cruise.

Type III *F*-tests (Sokal and Rohlf 1969) were conducted to determine if the source of within-year variability in larval concentrations is greater than the source of variability in larval concentrations from the two-level nested term, months within year. This *F*-value and test were calculated by dividing the mean square from variability in larval concentrations due to year by the type III mean square of months within year. This approach tested the null hypothesis that among-year variability in larval concentrations is greater than the variability in larval concentrations attributable to months-within-year. In a similar way, *F*-tests were conducted to determine if the sources of variability from the two-level nested terms (tide within year, top vs. bottom within year, day vs. night within year, and stations within year) are greater than variability from the three-level nested terms (tide within month within year, etc.).

$$F = MS_{year} / MS_{months\text{-}within\text{-}year}$$

Larval Lengths

Differences in total length between top and bottom samples, day vs. night, among stations, and among tides were tested using ANOVA. In cases when differences were significant Tukey HSD was used to identify means that differed significantly.

Larval Ingress vs. Juvenile Index

Age-0 juvenile relative abundances of Atlantic menhaden are estimated annually in Chesapeake Bay by Maryland DNR from seine sampling in Maryland waters of Chesapeake Bay (*http://dnr.maryland.gov/fisheries/juvindex/index.asp*). The juvenile

abundance values for 2006-2008 were compared to mean annual ingress levels. The proportion of positive Tucker-trawl tows (the proportion of tows with at least 1 menhaden larva) was used as another metric to relate larval ingress to subsequent juvenile recruitments (Mangel and Smith 1990; Uphoff 1993).

Results

Hydrography at the Chesapeake Bay Mouth

Mean water-column temperatures ranged from 4.53 ^{o}C to 14.29 ^{o}C across cruises at the Bay mouth during the three-year study (Table 2.2). Mean water temperatures differed significantly ($p < 0.001$) among years. Multiple comparisons of mean temperatures among the three years were significantly different for all combinations. The mean water temperature was lowest in 2005-06 ($\bar{x} = 8.25\ ^{o}$C ± 0.16 se), intermediate in 2006-07 ($\bar{x} = 9.65\ ^{o}$C ± 0.19 se), and highest in 2007-08 ($\bar{x} = 10.31\ ^{o}$C ± 0.15 se) (Table 2.2). In each of the years, the within-year monthly (i.e., among cruises) differences in water temperatures also were significant ($p < 0.001$). Only in January and February 2008 were temperatures not significantly different. Mean temperatures were similar above and below pycnocline (Table 2.3).

Mean water-column salinities among cruises at the Bay mouth ranged from 22.98 to 29.47 units (Table 2.2). Mean salinity differed significantly among the three years ($p < 0.001$) and among months within each year ($p < 0.001$). The mean salinity was lowest in 2005-06 ($\bar{x} = 25.60 \pm 0.25$ se), intermediate in 2006-07 ($\bar{x} = 26.35 \pm 0.16$ se), and highest in 2007-08 ($\bar{x} = 27.68 \pm 0.12$ se). Mean salinity in 2005-06 was significantly lower than

in 2006-07 ($p = 0.006$) and 2007-08 ($p < 0.001$); and, mean salinity in 2006-07 differed significantly from 2005-06 and 2007-08 ($p < 0.001$). Mean salinities below the pycnocline were generally about 2 units higher than above the pycnocline (Table 2.3).

Catches of Larvae

A total of 9,840 larvae was collected at the Chesapeake Bay mouth. The highest catches occurred at different temperatures during the three years. In 2005-06 the highest catches occurred at temperatures between 5 and 10 ^{o}C (Figure 2.2a). In 2006-07, highest catches occurred at temperatures < 6 ^{o}C (Figure 2.2b) while in 2007-08 highest catches were made at > 9 ^{o}C (Figure 2.2c).

Larval Length

The aggregated length-frequency distributions of larval Atlantic menhaden were very similar in the three years (Figure 2.3). But, the mean total length (TL) of larval menhaden differed significantly among years ($p < 0.001$). Mean TL in 2005-06 ($\bar{x}$ = 26.88 mm ± 0.12 se) was significantly smaller than the mean TL in 2006-07 and 2007-08. The mean TL in 2006-07 ($\bar{x}$ = 27.94 mm ± 0.10 se) and 2007-08 ($\bar{x}$ = 28.13 mm ± 0.05 se) did not differ ($p = 0.178$) (Table 2.4).

The within-year differences of mean lengths of larval menhaden among cruises were significant ($p < 0.001$) (Table 2.5). Mean lengths were significantly smaller during the first cruise in each year: December 2005 ($\bar{x}$ = 22.66mm ± 0.54 se), November 2006 ($\bar{x}$ =22.90 mm ± 0.35 se), and early-November 2007 ($\bar{x}$ = 24.07 mm ± 0.19 se), than in all other months. Beyond this observation, there were no seasonal patterns in any of the

years. The largest mean length in 2005-06 occurred in April ($\bar{x}$ = 28.07 mm ± 0.41 se) but was only significantly longer than the mean length for the December cruise. In 2006-07, the mean length was longest in January ($\bar{x}$ = 33.60 mm ± 1.19 se), which was significantly longer than the mean length for all cruises except December ($\bar{x}$ = 30.97 mm ± 0.44 se). The longest mean length in 2007-08 occurred in January ($\bar{x}$ = 29.36 mm ± 0.26 se), which was significantly longer than the mean length in early November ($\bar{x}$ = 24.07 mm ± 0.19 se), late-November ($\bar{x}$ = 28.17 mm ± 0.13 se), and December ($\bar{x}$ = 28.58 mm ± 0.05 se) of that sampling year.

The length distributions of ingressing larval menhaden were similar among cruises (Figure 2.4). Most larvae were in the 15 to 35-mm TL range. There was clear bimodality in the length-frequency distribution of larvae collected during December 2005, but length distributions from all other cruises appear to be unimodal.

Mean lengths did not differ between the top ($\bar{x}$ = 26.93 mm ± 23 se) and bottom ($\bar{x}$ = 27.22 mm ± 0.26 se) tows (p = 0.402). Mean lengths of larvae were significantly longer at night ($\bar{x}$ = 27.48 mm ± 0.19 se) than during day ($\bar{x}$ = 26.50 mm ± 0.32 se) (p = 0.006). Mean length of larvae was significantly longer at the Lynnhaven station (south side of Bay mouth) than at the four other stations (p = 0.002) (Table 2.6). There were no differences in mean lengths among the four tide stages (p = 0.176) (Table 2.7).

Ingress Concentrations

The geometric mean of larval Atlantic menhaden concentrations differed approximately 4-fold among the three years of the study (Table 2.8). The differences were significant (p < 0.001). For comparison, the arithmetic means (not analyzed

statistically) in larval concentrations differed 9-fold. Concentrations of Atlantic menhaden larvae at the Chesapeake Bay mouth were highest in 2007-08 ($\bar{x}$ = 8.44 larvae/100m^3 ± 2.08) (*geometric mean* = 0.49 larvae/100m^3 ± 0.13 se) and lowest in 2006-07 ($\bar{x}$ = 0.90 larvae/100m^3 ± 0.17) (*geometric mean* = 0.11 larvae/100m^3 ± 0.08 se) (Figure 2.5). The mean concentration in 2005-06 ($\bar{x}$ = 2.32 larvae/100m^3 ± 0.42) (*geometric mean* = 0.31 larvae/100m^3 ± 0.16 se) was significantly higher than the mean concentration in 2006-07 ($p < 0.001$) and marginally lower than the mean concentration in 2007-08 ($p = 0.011$). The mean larval concentration in 2007-08 was higher than the mean concentration in 2006-07 ($p < 0.001$). Inter-annual variability in mean larval menhaden concentrations, although highly significant, was not greater than the within-year monthly variability (From Table 2.9; $p = 0.153$).

In 2005-06, larval menhaden concentrations at the Chesapeake Bay mouth were highest in January ($\bar{x}$ = 4.40 larvae/100m^3 ± 1.20) (*geometric mean* = 1.14 larvae/100m^3 ± 0.30 se) and February 2006 ($\bar{x}$ = 4.62 larvae/100m^3 ± 1.01) (*geometric mean* = 1.63 larvae/100m^3 ± 0.29 se) (Figure 2.6a; Table 2.10). In 2006-07, larval menhaden concentrations at the Bay mouth were consistently low (< 0.15 larvae/100 m^3) during all cruises except February 2007 ($\bar{x}$ = 3.72 larvae/100m^3 ± 0.72) (*geometric mean* = 1.04 larvae/100m^3 ± 0.21 se) when concentrations were significantly higher than in other months (Figure 2.6b). In contrast, in 2007-08 larval concentrations were consistently high, peaking in December 2007 ($\bar{x}$ = 23.07 larvae/100m^3 ± 7.33) (*geometric mean* = 1.36 larvae/100m^3 ± 0.32 se), and in March 2008 ($\bar{x}$ = 5.07 larvae/100m^3 ± 2.45) (*geometric mean* = 1.16 larvae/100m^3 ± 0.38 se) (Figure 2.6c). Larval concentrations peaked in

different cruise months among years. Peak ingress occurred in February of 2005-06 and 2006-07, but in December 2007-08 (Figure 2.6).

Catches of larvae were variable and variability increased with the mean concentration, indicating patchy occurrences of larvae at the Bay mouth (Figure 2.7). The standard deviation of the mean larval concentration for tows during each cruise was directly related to the mean ($p < 0.001$). Numbers of larvae per sample ranged from 0 to 92 in 2005-06, 0 to 99 in 2006-07, and 0 to 1481 in 2007-08 (Table 2.1).

Larval Distributions

Stations

The among-station variability in concentrations of Atlantic menhaden at the Bay mouth was remarkably and unexpectedly small (Figure 2.8). Within-year differences among the five stations were not significant (Table 2.7; $p = 0.093$). Within-month differences in mean larval concentrations among stations within years also were not significant (Table 2.7; $p = 0.161$).

Vertical Distributions

Mean larval menhaden concentrations above and below the pycnocline differed significantly within years (Table 2.8; $p = 0.002$). In 2005-06 the mean concentration was significantly higher ($p = 0.003$) above the pycnocline ($\bar{x} = 3.63$ larvae/100m^3 ± 0.79) (*geometric mean* = 0.48 larvae/100m^3 ± 0.23 se) compared to mean concentration below the pycnocline ($\bar{x} = 1.09$ larvae/100m^3 ± 0.26) (*geometric mean* = 0.17 larvae/100m^3 ± 0.19 se) (Figure 2.9; Table 2.9). However, in 2006-07 and 2007-08, the mean

concentrations did not differ significantly above and below pycnocline. For among-month comparisons, no significant differences in mean larval concentrations were detected above and below the pycnocline in any of the years (From Table 2.8; $p = 0.058$).

Tide Stage

Sampling had not been designed to take place on designated tide stages. The most frequently sampled tide stages were ebbing tide ($n = 347$ tows) and flooding tide ($n = 361$ tows) for the three years combined. Within-year patterns of larval menhaden concentrations among tide stages were not consistent but differences were highly significant (Table 2.8; $p < 0.001$). Multiple comparisons showed that mean larval concentrations did not differ significantly among tide stages in either 2005-06 or 2006-07 (Table 2.12). In 2007-08, larval concentrations were highest in the slack before ebb tide ($\bar{x} = 6.71$ larvae/100m^3 ± 2.41) (*geometric mean* = 0.95 larvae/100m^3 ± 0.23 se) and flood tide ($\bar{x} = 15.03$ larvae/100m^3 ± 3.68) (*geometric mean* = 2.30 larvae/100m^3 ± 0.56 se) (Figure 2.10). Within-month (= cruise) differences of mean larval concentrations among tide stages were significant (Table 2.8; $p = 0.011$). The within-year variability in larval concentrations among tide stages was significantly higher than the within month variability (Table 2.8; $p < 0.001$).

Day vs Night

Within-year differences in mean larval concentrations between day and night were significant (Table 2.8 $p < 0.001$). However, those differences were not consistent. Larval concentrations were higher during the day in 2005-06 (Figure 2.11; Table 2.13)

but significantly higher at night in the next two years (Table 2.11). Note that relatively few samples were taken at night in 2005-06 compared to the other years. In 2007-08, the difference in mean larval concentrations between night and day was 14.02 larvae/100m^3 (geometric mean difference = 0.84 larvae/100m^3). In December 2007, the mean concentration at night was higher by 35.83 larvae/100 m^3 (geometric mean difference = 9.22 larvae/100 m^3) than the daytime mean concentration. The within-month differences in larval concentrations between day and night were significant (Table 2.8; $p < 0.01$) but not consistent (Table 2.13). Within-year variability in larval concentrations between day and night was significantly higher than within-month variability (Table 2.9; $p = 0.014$).

Larval Ingress and Juvenile Index

Neither the levels (larval menhaden concentrations) of annual ingress nor the proportion of positive Tucker-trawl tows (tows that included one or more menhaden larvae) in the three years were concordant with annual young-of-the-year index levels in September of the three years (Figure 2.12).

Discussion

Success of Atlantic menhaden during the late-larval and juvenile stages potentially controls overall population growth rate (Quinlan and Crowder 1999). The concentrations and abundance of menhaden larvae at the mouths of estuaries is a measure of survival and success of the transport process from spawning ground to nursery. Spawning in the Mid-Atlantic Bight during fall-early winter months (Higham and

Nicholson 1964; Kendall and Reintjes 1975; Judy and Lewis 1983; Berrien and Sibunka 1999) and subsequent spawning in the South Atlantic Bight in late winter are potential major sources of ingressing larvae to the Atlantic coast (Reintjes 1961; Higham and Nicholson 1964; Kendall and Reintjes 1975). The complex life cycle of menhaden, combined with probable variable spawning areas and times, and variability in transport pathways, gives rise to many possible sources of variability in supply of larvae to estuaries. Direct relationships between larval supply, measured as abundance at ingress to estuaries, and estuarine juvenile abundance of spot (*Leiostomus xanthurus*), pinfish (*Lagodon rhomboides*), and southern flounder in North Carolina have been reported (Taylor *et al*. 2009). Long-term studies of ingress of menhaden and other fishes into the Chesapeake Bay are crucial to understanding inter-annual changes and patterns of offshore supply of larvae to the Bay. They also are important to evaluate causes of recruitment variability to the menhaden stock, which has declined dramatically since the 1980s (MDSG 2009). Long-term studies are especially needed to evaluate the relationship between larval ingress and subsequent young-of-the-year (YOY) recruitment. There was no evidence of concordance between larval ingress and YOY recruitment in my three-year study although it would be difficult to confirm such a relationship with so few years of data.

There was substantial inter-annual and seasonal variability in the supply of menhaden larvae to the Chesapeake Bay mouth in the three-year program. Based on the monthly age distributions of ingressing larvae (Chapter 3), the supply of larval menhaden to the Bay mouth was continuous from November through April in all years of the study.

Although my collections did not span other months, the observed patterns of abundance indicate that relatively few larvae ingress before October or after April.

Mean larval menhaden ingress at the Chesapeake Bay mouth experienced 9-fold inter-annual variability based on the arithmetic mean concentrations or 4-fold variability based on the geometric means. It is obvious that the year-to-year variability can be considerable. Similar levels of variability in ingress were observed for larvae of American eel *Anguilla rostrata*, summer flounder, and spot into coastal bays on the Eastern Shore of Maryland (Love *et al*. 2009). Additionally, I observed strong variability in monthly ingress patterns and the months of peak ingress differed among years. In the nested ANOVA, the month-within-year term accounted for more of the variability of larval abundance at the Chesapeake Bay mouth. The year of highest ingress, 2007-08, was characterized by high concentrations of menhaden larvae in November and December (Figure 2.6). Conversely, the year of lowest ingress, 2006-07, experienced low larval ingress in November and December. The magnitude of ingress in 2005-06 was intermediate with peaks in the December through February period. This pattern indicates that a large fraction of the year-to-year differences in ingress is attributable to numbers ingressing early in the season. Larvae ingressing from November through January were hatched prior to December (Chapter 3) when the spawning population reportedly is located offshore of the mid-Atlantic coast (Higham and Nicholson 1964; Judy and Lewis 1983).

Month-to-month differences in ingress may be a result of differences in spawning intensity or seasonal changes in transport trajectories. Modeling results have suggested that spawning from fall to early winter in the mid-Atlantic region accounts for most

ingress of Atlantic menhaden to Chesapeake Bay (Quinlan *et al*. 1999). In Chapter 3 of this thesis, I reported that > 90% of larval menhaden collected at the mouth of Chesapeake Bay had been hatched by December 15 in each of the three years. Ingress in 2006-07 was low but continuous from November through April except for a notable peak in larval concentrations during February 2007. In the other years, higher ingress levels were observed early in the season and could have resulted from increased abundance of larvae or more favorable transport toward Chesapeake Bay from late fall and early winter spawning activity in the mid-Atlantic.

It was expected that higher numbers of larvae would be encountered at the northern side of the Chesapeake Bay mouth because the net flow in that area is into the estuary (Valle-Levinson and Lwiza 1997; Valle-Levinson 2001). However, there was no evidence of significant differences in concentrations of ingressing menhaden larvae across the Chesapeake Bay mouth. Across-channel variability in larval menhaden concentrations in a small tidal inlet at Beaufort, North Carolina was reported (Churchill *et al*. 1999). The authors noted spatial differences in net water flow through Beaufort Inlet, with the eastern side dominated by net inflow and the western side net outflow. Ingress of menhaden larvae was predominantly on the eastern side of Beaufort Inlet. Although inflow to Chesapeake Bay is stronger at the north side of the Bay mouth (Valle-Levinson and Lwiza 1997; Valle-Levinson 2001), menhaden larvae were not concentrated there. In research on Atlantic croaker larvae near the mouth of Chesapeake Bay, Schaffler *et al*. (2009) reported a similar result and did not find any differences in larval abundance across the Bay mouth. Those authors also had expected to find a higher abundance of larvae near the northern side of the Bay mouth. Mechanisms other than bulk inflow may

be important in transporting larvae across the Bay mouth and into the estuary. For example, during southwesterly winds net inflow occurs at near-bottom depths across the mouth of Chesapeake Bay (Valle-Levinson *et al*. 2001). Also, wind-induced flux may be an important mechanism for ingress of larvae into Chesapeake Bay (Joyeux 2001; Valle-Levinson *et al*. 2001; Hare *et al*. 2005).

Despite lack of pattern in the larval distribution across the Bay mouth, mean lengths of menhaden larvae collected at the Lynnhaven station (southernmost station) were significantly longer than mean lengths at all other stations. The net flow of water at this station is seaward (Valle-Levinson and Lwiza 1997; Valle-Levinson 2001). The reason for the observed spatial distribution of sizes is not clear. Once larvae have entered Chesapeake Bay it is possible that they are re-circulated near the mouth of the Bay, possibly more commonly at the south side, due to flow conditions reported near the mouth (Valle-Levinson and Lwiza 1997; Valle-Levinson 2001).

There were no clear patterns in the vertical positioning of menhaden larvae in the water column during this study, nor were larvae more abundant (or available to the Tucker trawl) during flooding tides as had been reported in some studies (Hare *et al*. 2005). Movement and ingress of larvae of marine organisms often is controlled by vertical migrations cued to tides (Forward and Tankersley 2001). These behaviors have been reported for movement and ingress of larval fishes into estuaries, including weakfish, summer flounder, and spot (Weinstein *et al*. 1980; Boehlert and Mundy 1988; Rowe and Epifanio 1994; Reiss and McConaugha 1999). In my surveys, larval menhaden were more abundant above the pycnocline in 2005-06 but there were no differences in concentrations of larvae above or below the pycnolcine in the other two

years. In surveys on the continental shelf, Govoni and Pietrafesa (1994) and Joyeux (1998) also did not find defined patterns in vertical distributions of Atlantic menhaden, spot, and Atlantic croaker larvae. In the offshore collections, the center of mass of Atlantic menhaden larvae distributions was at mid-depth to surface (Govoni and Pietrafesa 1994). These authors argued that, based on physical processes, larvae at those depths could be advected shoreward. Joyeux (2001) suggested a disconnect between larval retention in estuaries and tide patterns, contending that since Atlantic menhaden do not exhibit vertical migrations, tide reversal cannot be a mechanism for retention in an estuary. Wind patterns, especially north components of wind, have been correlated with larval ingress (Hettler and Hare 1998; Hare *et al*. 2005).

At the mouth of Chesapeake Bay, Hare *et al*. (2005) reported, based on a two-day intensive study, that wind forcing could contribute to up-Bay movement of larval Atlantic menhaden. The lack of consistent vertical distributions and tide-stage patterns of larval menhaden occurrences and concentrations across the Chesapeake Bay mouth in my study suggests that larvae arriving at the Bay mouth migrate up-bay by processes other than selective vertical migrations cued to tides. However, reaching conclusions requires further research on offshore and nearshore wind patterns and frequencies of winds with respect to menhaden larvae abundance. Another potentially important consideration to explain up-bay movement of larval menhaden is larval size and ontogenetic stage. The mean lengths of menhaden larvae ingressing into Chesapeake Bay were > 25 mm TL. These late-stage larvae are better equipped for horizontal, directed swimming than smaller larvae (Shanks 1995). Swimming speeds of 15-mm menhaden larvae were

reported to be 1 to 2 body lengths per second (De Vries *et al*. 1995). It is conceivable that up-bay movement is in large part a result of horizontal up-bay swimming.

A shift in spawning areas or times may contribute to seasonal variability in abundance of ingressing menhaden larvae observed at the mouth of Chesapeake Bay. Seasonal ingress to the Bay mouth varied among years, peaking earliest in 2007-08, the year of highest ingress. Based on evidence from past research, variability in timing and geographic distribution of the spawning migration by Atlantic menhaden adults, along with transport variability, are realistic circumstances that could generate different ingress patterns. Information on inter-annual variability in spawning migration patterns is limited but the Marine Resource Monitoring Assessment and Prediction (MARMAP) program provided a ten-year comparison of Atlantic menhaden egg distributions along the Atlantic coast (Berrien and Sibunka 1999). From those surveys, Berrien and Sibunka (1999) showed that patterns of egg distributions from 1977-87 varied considerably inter-annually. Such year-to-year variability in spawning patterns and thus areas where eggs and larvae originate may be a cause of inter-annual variability in dispersal and monthly patterns of larval abundance at the Chesapeake Bay mouth.

Hydrographic and wind conditions along with spawning location and timing are likely to be important factors controlling the transport of larval menhaden from offshore to the vicinity of Chesapeake Bay. Based on simulated trajectories of larvae, Quinlan *et al*. (1999) hypothesized that larval ingress to mid-Atlantic estuaries is supplied by spawning events on the mid-Atlantic shelf during fall months. They also hypothesized that spawning south of Cape Hatteras during the winter may not be a significant source of menhaden larvae to mid-Atlantic estuaries. During fall when spawning occurs in the

mid-Atlantic region winds directed to the south and southwest directions may cause larvae to drift in a southward, along-shore direction (Werner *et al*. 1999). This process was hypothesized to deliver larvae to both mid-Atlantic and south Atlantic estuaries (Hare *et al*. 1999; Werner *et al*. 1999). In the December through March period winds shift and are usually directed to the southeast or east in the mid-Atlantic and thus the model predicts that South Atlantic sources of menhaden larvae are no longer possible. However, by late winter, spawning is concentrated in the South Atlantic Bight and it must be considered as a potential source of larvae.

There is observational evidence of mid-Atlantic ingress originating from southern sources. In my research, larval ingress during March and April probably originated from southern sources where major spawning occurs in the winter months. Spawning during late winter is mostly absent in the mid-Atlantic (Higham and Nicholson 1964; Berrien and Sibunka 1999) because temperatures are < 13^{o}C, a threshold below which menhaden are not believed to spawn. Larvae collected in March and April had hatch dates in the winter (Chapter 3) and therefore must have originated from the South Atlantic Bight where temperatures were favorable for spawning. One possible mechanism for ingress from spawning in the South Atlantic Bight is entrainment and northward transport by the Gulf Stream. Two studies that included observations on age of menhaden have suggested that larvae ingressing into mid-Atlantic estuaries (New Jersey and Delaware) during the early spring originated from spawning sources south of Cape Hatteras (Warlen *et al*. 2002; Light and Able 2003). Warlen *et al*. (2002) based their conclusion on evidence that hatch-date distributions overlapped for larvae ingressing into New Jersey estuaries and North Carolina estuaries. The period of overlap for these hatch dates occurred during

the winter when spawning activity is concentrated south of Cape Hatteras. Light and Able (2003) agreed with this explanation and contended that spawning in the mid-Atlantic was not likely during late winter because temperatures were too cold. Warlen *et al*. (2002) and Light and Able (2003) suggested that northward transport of larvae to mid-Atlantic estuaries was via transport in the Gulf Stream. The mechanisms for this mode of transport have not been fully explored but Hare and Cowen (1991, 1993) have suggested possible scenarios on how fish larvae may become entrained into the Gulf Stream, transported to the north, and subsequently advected shoreward. They suggested that warm core rings may be a mechanism to transport bluefish *Pomatomus saltatrix* larvae shoreward from the Gulf Stream. Although the mechanisms that deliver menhaden larvae to the Mid-Atlantic from the South Atlantic Bight have not been fully explained, an alternative mechanism, briefly mentioned in Quinlan *et al*. (1999), suggests that a northward-flowing, nearshore current could potentially deliver southern-spawned larvae into mid-Atlantic estuaries based on modeled wind fields.

My results cannot be interpreted to provide support for or against northward transport of larval menhaden from the South Atlantic Bight to the Chesapeake Bay. The mean age at ingress, an indicator of the transport period, for larval menhaden entering the Chesapeake Bay during the three-year study was less than two months post-hatch during each year of the study (Chapter 3). The mean age at ingress of menhaden larvae in March and April was not older than the mean age at ingress for other months. Since late winter spawning is known to be mostly concentrated in the South Atlantic Bight, it is very likely that larvae ingressing into Chesapeake Bay during March and April originated from the South Atlantic Bight. If larvae ingressing into the Chesapeake Bay during

March and April were transported via the Gulf Stream and then subsequently advected across the shelf to the Bay, transport period for those larvae would seemingly have been longer and thus larvae collected at ingress would have been older. Although Atlantic menhaden in the South Atlantic Bight have been reported to spawn in close proximity to the Gulf Stream (Checkley *et al*. 1988, Checkley *et al*. 1999), the process of advection back onto the continental shelf could be complex. Govoni and Pietrafesa (1994) suggested that some menhaden larvae originating from spawning near the Gulf Stream could become entrained in it. Although Gulf Stream transport of larvae is a possible mechanism for larval transport to mid-Atlantic estuaries, further research is needed to evaluate this mechanism. Transport of larvae via a nearshore northward current, as proposed by Quinlan *et al*. (1999), also requires further investigation.

In another modeling study, Rice *et al*. (1999) reported inter-annual differences in transport trajectories of menhaden larvae using a three-dimensional wind and tide-driven hydrodynamic model. During strong southward winds, menhaden larvae were advected from the mid-Atlantic to estuaries in the South Atlantic Bight. When those winds were weak, modeled advection to the South Atlantic Bight was not possible and modeled larvae originating in the Mid-Atlantic were not observed in South Atlantic estuaries. If the model and interpretation by Rice et al (1999) are correct, the processes and variability in winds and tides they infer possibly could explain some of the variability in observed inter-annual and monthly differences in patterns of ingress to Chesapeake Bay.

The occurrences and concentrations of ingressing menhaden larvae at the Chesapeake Bay mouth are patchy in space and time. The frequency of zero catches of larval menhaden was high at the Bay mouth. For all years combined, 54% of the samples

contained zero Atlantic menhaden larvae. The number of samples with zero Atlantic menhaden larvae was lowest in 2007-08 (42%) and highest in 2006-07 (66%). The standard deviation of daily mean larval concentrations increased with increasing mean larval concentration suggesting that larval catches at the Chesapeake Bay mouth are patchy and that ingress through the Bay mouth likely occurs in pulses. Warlen's (1994) study on ingress of Atlantic menhaden to a North Carolina estuary produced a similar result as did research on ingress of other fish (Hettler *et al*. 1997).

Warlen (1992) and Boehlert and Mundy (1988) provide another hypothesis that might help explain pulsed ingress of larvae into estuaries. Warlen (1992) reported that transport of menhaden larvae to North Carolina estuaries is biphasic and that larval pooling apparently occurs in the nearshore environment just prior to estuarine ingress. The mechanism for this process is likely a consequence of behavioral responses to the physical environment, especially to tides. Net flow from an estuary is offshore; thus, a larva must respond behaviorally to the physical environment to move into an estuary (Boehlert and Mundy 1988). Weinstein *et al*. (1980) found that flounder *Paralichthys spp*. larvae near a North Carolina inlet used selective tidal stream behavior and were mostly near surface at night during flood tides when movement of water is into an estuary. Conversely, during ebb tides, the flounder larvae migrated to near bottom to avoid advection. Menhaden larvae at the Bay mouth during my study were not more abundant during flood tides at night. Schaffler *et al*. (2009), in research on Atlantic croaker larvae, did not find evidence for behavioral responses in ingress to Chesapeake Bay. Larval pooling of Atlantic menhaden prior to ingress has not been fully explored but it might explain why transport rates of North Carolina menhaden from offshore to

nearshore progressively decline as the larvae approach the shore (Warlen 1992). The mean age at ingress of Atlantic menhaden at the Chesapeake Bay mouth (Chapter 3) and ages of larvae reported in Warlen (1992) from North Carolina were similar, suggesting that similar transport times are occurring in both systems. However, since transport distances are not the same, it is possible that larval pooling at the estuary mouth in one or both systems may play a role.

Some bio-physical mechanisms that are important in the nearshore transport of menhaden larvae also may be important for up-estuary transport when the larvae reach the entrance of an estuary. Once larvae have reached the mouth of Chesapeake Bay, up-bay transport may be fairly rapid. Ages at ingress suggest that new cohorts of larvae were sampled at the Bay mouth in each monthly cruise (Chapter 3). Moreover, the extrapolated abundance of larvae at the Bay mouth experienced large day- to-day differences, further evidence that larvae may ingress rapidly and continue up-estuary movement. Also, mean ages of menhaden larvae collected in the upper Chesapeake Bay, nearly 300 km from the mouth, were found to be approximately 30 days older than larvae collected at the Bay mouth (Houde *et al*. 2009) providing evidence that recruitment to the upper estuary can occur within 30 days after ingress. In their two-day study, Hare *et al*. (2005) suggested that residual bottom inflow and wind-induced flux are important up-bay transport mechanisms for larval menhaden. They found that menhaden larvae were more likely to be near the surface during flooding tides, resulting in potential up-bay movement. During ebbing tides, Hare et al. reported that larvae had positioned themselves near bottom where they potentially could continue up-bay movement using residual bottom inflow. In my more extensive research, larval distributions in the water

column or at tide stages did not show clear patterns suggesting that other factors such as horizontal swimming or wind-induced flux may be more important for up-bay movement.

Overall, catches of menhaden larvae were higher at night than during the day but in 2005-06 larval catches were higher during the day. It should be noted that very few samples were taken during the day during 2005-06 (i.e., small number of samples). There were strong differences in larval concentrations between day and night in the other two years when concentrations were much higher at night. This finding may have important implications concerning ingress and up-bay recruitment of larvae into Chesapeake Bay. Weinstein *et al*. (1980) suggested that larvae of other species (spot and flounder) migrate to the surface at night and use flood tides for ingress into estuaries. A factor to consider in day-night comparisons is catchability. Gear avoidance may be reduced under low light conditions. The mean length of larvae entering Chesapeake Bay was significantly longer at night compared to the mean length of larvae captured during the day, suggesting that avoidance of the Tucker trawl by larger larvae might have been reduced under low light conditions. Further research and analysis are required to specifically test for differences in larval concentrations between day and night in relation to tide stages and vertical positioning in the water column.

During this study, ingress of Atlantic menhaden larvae was found to be quite variable. Inter-annual ingress varied nine-fold. Monthly ingress patterns varied inter-annually. The year of highest ingress 2007-08 experienced higher early-season ingress. Late-season ingress was low in all years except in March 2008. In Chapter 3 larval menhaden ages, hatch dates, and growth rates were shown to vary inter-annually and monthly. The mean age at ingress of larvae entering Chesapeake Bay was significantly

older in 2006-07 than in the other two years (Chapter 3). The lowest ingress occurred in 2006-07, suggesting that longer transport periods are associated with lower magnitudes of ingress. Also, as previously noted, there was a lack of concordance between larval ingress and YOY recruitment indices despite the observed nine-fold variability in larval ingress. Young-of-the-year menhaden recruitment has been low but quite stable in recent years (Figure 1.1). Similar recruitment levels occurred in the 1960s. Recruitment indices in the 1970s were much higher but they also were more variable. It is unfortunate that there were no measures of ingress levels during the 1970s. Ingress levels in that period may have been considerably higher than those I observed.

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Table 2.1. Research cruise dates, mean surface temperatures (°C), number of stations sampled per cruise, number of ichthyoplankton samples per cruise, total number of Atlantic menhaden larvae collected, and mean total length (mm), and length ranges from the ingress surveys at the Chesapeake Bay mouth. All except two of the cruises were conducted on RV *Aquarius*. Samples were collected at sites indicated in Figure 2.1.

Cruise Dates	Temp	No. Stations	No. Samples	No. Larvae	Length-range
7-8 Dec '05	9.1	8	20	109	22.5, 10.5-33.5
9-11 Jan '06	6.7	15	34	531	27.6, 6.6-38.0
13-15 Feb '06	5.8	15	36	528	26.5, 12.0-36.0
27-19 Mar '06	8.9	19	38	6	27.0, 24.0-30.5
12-13 Apr '06	12.4	12	28	7	28.1, 27.0-30.0
6-8 Nov '06	14.0	25	58	30	22.9, 18.0-27.0
5-6 Dec '06	14.0	18	38	40	31.0, 25.0-35.0
11-12 Jan '07	11.0	26	56	10	33.6, 27.0-40.0
19-21 Feb '07	7.3	32	72	808	27.9, 9.0-37.0
20-22 Mar '07	9.8	29	66	24	26.6, 21.0-31.8
23-25 Apr '07	10.5	21	46	28	29.0, 23.0-33.5
12-14 Nov '07[1]	13.9	24	90	128	24.0, 20.0-29.0
27-30 Nov '07	12.2	16	44	1079	29.1, 11.0-32.0
10-13 Dec '07	9.9	31	69	5650	28.4, 16.0-34.0
14-16 Jan '08	7.4	12	32	172	29.4, 20.0-37.0
25-26 Feb '08[1]	7.2	28	55	258	27.3, 16.0-36.5
17-18 Mar '08	9.7	9	22	367	26.7, 17.0-31.0
10 Apr '08	11.4	10	24	65	28.8, 24.0-35.0

[1]Cruises conducted on RV *Hugh Sharp* as part of the regional larval ingress program supported by Maryland, Delaware, and Virginia Sea Grant.

Table 2.2. Mean water-column temperatures (°C) and salinities. Monthly and annual means at the Chesapeake Bay mouth, averaged from CTD or YSI sonde depth profiles taken at each station during the three-year study.

	2005-06		2006-07		2007-08	
	Temp	**Sal**	**Temp**	**Sal**	**Temp**	**Sal**
Nov	no data	no data	no data	no data	13.85*	28.94*
Nov	no data	no data	14.29	26.86	12.42	29.47
Dec	9.20	23.83	11.39	27.64	10.35	28.94
Jan	7.01	25.47	10.33	25.74	7.05	26.23
Feb	6.04	22.98	4.53	27.08	7.18*	27.47*
Mar	8.50	28.58	7.44	24.90	9.64	25.10
Apr	11.68	26.35	12.38	26.39	11.31	23.21
Annual	8.25	25.60	9.65	26.35	10.31	27.68

* This row indicates data from cruises onboard the RV Hugh R. Sharp.

Table 2.3. Mean temperatures and salinities at the Chesapeake Bay mouth at above (Top) and below (Bot) pycnocline in the water column for each cruise and year during the three year study.

	Temperature		Salinity	
	Top	Bot	Top	Bot
Dec '05	9.16 (0.07)	9.25 (0.11)	23.63 (0.37)	24.03 (0.44)
Jan '06	6.87 (0.07)	7.15 (0.09)	23.97 (0.60)	26.89 (0.63)
Feb '06	5.96 (0.07)	6.11 (0.09)	22.48 (0.45)	23.48 (0.58)
Mar '06	8.63 (0.07)	8.38 (0.05)	27.55 (0.60)	29.60 (0.35)
Apr '06	12.06 (0.12)	11.30 (0.20)	25.06 (0.73)	27.65 (0.60)
Year	8.30 (0.24)	8.20 (0.20)	24.64 (0.33)	26.54 (0.35)
Nov '06	14.25 (0.09)	14.33 (0.08)	26.46 (0.46)	27.25 (0.47)
Dec '06	11.34 (0.10)	11.45 (0.11)	27.17 (0.53)	28.11 (0.46)
Jan '07	10.08 (0.09)	11.58 (0.13)	24.21 (0.41)	27.28 (0.46)
Feb '07	4.49 (0.13)	4.57 (0.14)	26.68 (0.32)	27.47 (0.29)
Mar '07	7.57 (0.08)	7.31 (0.05)	23.65 (0.51)	26.15 (0.61)
Apr '07	13.31 (0.21)	11.45 (0.20)	23.49 (0.86)	29.05 (0.64)
Year	9.75 (0.28)	9.56 (0.26)	25.37 (0.23)	27.33 (0.21)
Nov '07*	13.84 (0.11)	13.86 (0.10)	28.55 (0.37)	29.33 (0.33)
Nov '07	12.35 (0.09)	12. 50 (0.11)	29.09 (0.48)	29.85 (0.48)
Dec '07	10.31 (0.06)	10.39 (0.08)	28.62 (0.18)	29.25 (0.15)
Jan '08	6.85 (0.14)	7.24 (0.20)	25.59 (0.43)	26.87 (0.53)
Feb '08	7.14 (0.03)	7.23 (0.03)	26.80(0.39)	28.15 (0.35)
Mar '08	9.64 (0.07)	9.64 (0.06)	24.07 (0.39)	26.13 (0.63)
Apr '08	11.59 (0.08)	11.04 (0.19)	21.51 (0.67)	24.91 (1.11)
Year	10.28 (0.20)	10.34 (0.21)	27.07 (0.23)	28.28 (0.20)

Table 2.4. Mean total lengths (mm) of measured Atlantic menhaden larvae collected at the Chesapeake Bay mouth during the three-year program. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean lengths in any two cruise months sharing a letter do not differ significantly.

Year	Mean Length	Tukey	se	n
2005-06	26.88	A	0.12	1172
2006-07	27.94	B	0.1	939
2007-08	28.13	B	0.05	3342

Table 2.5. Mean total lengths (mm) of Atlantic menhaden larvae collected at the Chesapeake Bay mouth during each cruise in the three-year program. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean lengths in any two cruise months within each year sharing a letter do not differ significantly.

Month	Mean Length	se	n	Tukey
Dec '05	22.66	0.54	106	AC
Jan '06	27.59	0.18	531	B
Feb '06	27.00	0.14	522	B
Mar '06	27.00	1.17	6	BC
Apr '06	28.07	0.41	7	B
Nov '06	22.90	0.35	29	A
Dec '06	30.97	0.44	39	B
Jan '07	33.60	1.19	10	BC
Feb '07	27.91	0.10	810	D
Mar '07	26.49	0.53	23	D
Apr '07	28.97	0.44	28	CD
Nov '07*	24.07	0.19	122	A
Nov '07	28.17	0.13	430	B
Dec '07	28.58	0.05	1990	B
Jan '08	29.36	0.26	163	CDF
Feb '08*	27.30	0.17	282	CE
Mar '08	26.66	0.11	290	DE
Apr '08	28.78	0.29	65	BF

* Indicates larvae collected from the RV *Hugh Sharp*.

Table 2.6. Mean total lengths (mm) of larval Atlantic menhaden at the five stations sampled across the Chesapeake Bay mouth. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests.

Station	Mean Length	se	n	Tukey
LH	28.5	0.16	489	A
TC	27.1	0.17	371	B
CC	27.5	0.11	1012	B
MG	27.5	0.08	890	B
NC	25.5	0.09	964	B

Table 2.7. Mean total lengths (mm) of larval Atlantic menhaden that were collected among 4 tide stages. SE is slack before ebb tide, E is ebbing tide, SF is slack before flood tide, and F is flooding tide. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests.

Tide	Mean Length	se	n	Tukey
SE	29.5	0.17	172	A
E	27.9	0.08	996	A
SF	27.6	0.4	129	A
F	27.3	0.07	2430	A

Table 2.8. Analysis of variance table for the nested ANOVA used to evaluate larval concentrations of Atlantic menhaden at the Chesapeake Bay mouth. The table includes degrees of freedom, sum of squares, mean squares, Fisher's *F*-value, and *p*-values for each of the terms in the analysis.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Year	2	203.79	101.89	57.67	< 2.2E-16
Month within Year	15	716.48	47.77	27.03	< 2.2E-16
Tide within Year	9	139.30	15.47	8.76	1.86E-12
Top vs. bot within Year	3	27.07	9.02	5.11	0.002
Day vs. night within Year	3	231.45	77.15	43.66	< 2.2E-16
Station within Year	12	33.49	2.79	1.58	0.093
Tide within Month-within Year	29	88.37	3.05	1.72	0.011
Top vs. bot within Month-within Year	15	43.55	2.90	1.64	0.058
Day vs. night within Month-within Year	13	191.26	14.71	8.33	1.23E-15
Station within Month-within Year	58	122.39	2.11	1.19	0.161
Total	160	1797.15	276.86	156.42	< 2.2E-16
Residuals	623	1100.81	1.77		

Tide = tide stage; Top vs Bottom = above vs below pycnocline; Month = cruise; Station is the sampling site at the Bay mouth; Day vs Night is the comparison of day vs night larval concentrations.

Table 2.9. Calculations; *F*-ratio tests of nested terms. Significance of higher level terms is tested for amount of variability explained compared to lower level terms. A significant *F*-test indicates that the variability accounted in the numerator is greater than the variability accounted by the denominator in the model.

$F_{model} = MS_{model}/MS_{error} = 276.86/1.77 = 156.42$; with 160/623 df; $p < 0.001$

$F_{year} = MS_{year}/MS_{month:year} = 101.89/47.77 = 2.13$; with 2/15 df; $p = 0.153$

$F_{tide:year} = MS_{tide:year}/MS_{tide:month:year} = 15.47/3.05 = 5.07$; with 9/29 df; $p < 0.001$

$F_{dn:year} = MS_{dn:year}/MS_{dn:month:year} = 77.15/14.71 = 5.24$; with 3/13 df; $p = 0.014$

Table 2.10. Geometric means and standard errors (arithmetic means and standard errors are in parentheses) for larval Atlantic menhaden concentrations (number per 100 m^3) in each larval ingress cruise at the Chesapeake Bay mouth. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean concentrations in any two cruise months within each year sharing a letter do not differ significantly.

Cruise	Mean	se	n	Tukey
Dec '05	0.22 (1.82)	0.40 (1.15)	20	A
Jan '06	1.14 (4.40)	0.30 (1.20)	37	B
Feb '06	1.63 (4.62)	0.29 (1.01)	36	B
Mar '06	0.02 (0.04)	0.10 (0.02)	38	A
Apr '06	0.02 (0.07)	0.13 (0.04)	28	A
Nov '06	0.04 (0.17)	0.13 (0.06)	58	A
Dec '06	0.11 (0.34)	0.20 (0.10)	38	A
Jan '07	0.01 (0.04)	0.07 (0.03)	56	A
Feb '07	1.04 (3.71)	0.21 (0.73)	70	B
Mar '07	0.03 (0.11)	0.10 (0.04)	66	A
Apr '07	0.05 (0.18)	0.15 (0.06)	48	A
Nov '07*	0.15 (0.77)	0.21 (0.21)	54	A
Nov '07	0.61 (14.97)	0.41 (8.17)	36	BC
Dec '07	1.36 (23.07)	0.32 (7.33)	70	B
Jan '08	0.30 (2.27)	0.35 (0.90)	32	AC
Feb '08*	0.34 (1.48)	0.23 (0.40)	56	AC
Mar '08	1.16 (5.07)	0.38 (2.45)	22	BC
Apr '08	0.29 (0.84)	0.29 (0.27)	24	AC

Table 2.11. Geometric mean concentrations (number per 100 m^3) of Atlantic menhaden larvae at above (Top) and below (Bottom) pycnocline levels in the water column by year. Arithmetic means are in parentheses. Superscripted letters are Tukey Honestly Significant Difference ranking comparisons between top and bottom for each year.

	Top			Bottom		
Year	**Mean**	**se**	**n**	**Mean**	**se**	**n**
2005-06	0.48 (3.59)^{A}	0.23 (0.78)	79	0.17 (1.07)^{B}	0.19 (0.26)	80
2006-07	0.13 (0.67)^{A}	0.11 (0.15)	168	0.10 (1.11)^{A}	0.12 (0.31)	168
2007-08	0.48 (5.25)^{A}	0.16 (1.87)	147	0.50 (11.63)^{A}	0.20 (3.71)	147

Table 2.12. Geometric mean larval concentrations (number per 100 m^3) (arithmetic means and standard errors are in parentheses) at tide stages. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean lengths in any two tide stages sharing a letter do not differ significantly. SE is slack before ebb tide, E is ebbing tide, SF is slack before flood tide, and F is flooding tide.

Tide	Mean	se	n	Tukey
		2005-06		
SE	0.06 (0.22)	0.65 (0.22)	4	A
E	0.18 (1.72)	0.21 (0.54)	75	A
SF	3.54 (4.33)	0.38 (1.49)	4	A
F	0.44 (2.91)	0.23 (0.69)	76	A
		2006-07		
SE	0.05 (0.38)	0.26 (0.29)	22	A
E	0.08 (0.51)	0.12 (0.12)	128	A
SF	0.07 (0.20)	0.24 (0.08)	20	A
F	0.16 (1.34)	0.13 (0.33)	166	A
		2007-08		
SE	2.30 (6.71)	0.56 (2.41)	12	A
E	0.23 (4.01)	0.14 (2.92)	144	BC
SF	0.55 (2.51)	0.41 (1.23)	20	AC
F	0.95 (15.03)	0.23 (3.68)	118	A

Table 2.13. Geometric mean concentrations (numbers per 100 m^3) of larval Atlantic menhaden collected during the day and night. Arithmetic means are in parentheses. Superscripted letters are Tukey Honestly Significant Difference comparisons between day and night. There is no comparison in April 2006 because no samples were taken at night during that cruise.

	Day			Night		
Cruise	**Mean**	**se**	**n**	**Mean**	**se**	**n**
Dec '05	0.30 (2.26)^{A}	0.47 (1.43)	16	0.04 (0.08)^{A}	0.42 (0.08)	4
Jan '06	2.22 (6.08)^{A}	0.32 (1.73)	24	0.30 (1.31)^{A}	0.49 (0.69)	13
Feb '06	1.86 (5.29)^{A}	0.36 (1.40)	24	1.24 (3.27)^{A}	0.51 (1.11)	12
Mar '06	0.01 (0.03)^{A}	0.09 (0.02)	28	0.03 (0.08)^{A}	0.25 (0.06)	10
Apr '06	0.02 (0.07)	0.13 (0.04)	28	0.00 (0.00)	0.00 (0.00)	0
Year	0.32 (2.60)^{A}	0.19 (0.53)	120	0.28 (1.47)^{B}	0.29 (0.45)	39
Nov '06	0.06 (0.24)^{A}	0.20 (0.11)	30	0.04 (0.09)^{A}	0.15 (0.04)	28
Dec '06	0.04 (0.10)^{A}	0.25 (0.06)	12	0.16 (0.45)^{A}	0.26 (0.14)	26
Jan '07	0.00 (0.01)^{A}	0.05 (0.01)	36	0.03 (0.09)^{A}	0.18 (0.07)	20
Feb '07	0.43 (1.36)^{A}	0.26 (0.34)	36	2.52 (6.19)^{B}	0.28 (1.34)	34
Mar '07	0.01 (0.02)^{A}	0.07 (0.02)	40	0.09 (0.24)^{A}	0.21 (0.09)	26
Apr '07	0.05 (0.18)^{A}	0.20 (0.09)	28	0.05 (0.17)^{A}	0.22 (0.09)	20
Year	0.06 (0.35)^{A}	0.09 (0.08)	182	0.19 (1.53)^{B}	0.14 (0.36)	154
Nov '07*	0.11 (0.55)^{A}	0.34 (0.30)	18	0.18 (0.89)^{A}	0.27 (0.28)	36
Nov '07	0.18 (1.04)^{A}	0.46 (0.55)	14	1.21 (23.84)^{B}	0.56 (13.12)	22
Dec '07	0.08 (3.62)^{A}	0.28 (3.36)	32	9.30 (39.45)^{B}	0.31 (12.68)	38
Jan '08	0.15 (1.11)^{A}	0.37 (0.63)	20	0.79 (4.20)^{A}	0.63 (2.10)	12
Feb '08*	0.52 (1.46)^{A}	0.31 (0.43)	26	0.23 (1.49)^{A}	0.32 (0.64)	30
Mar '08	0.45 (0.70)^{A}	0.36 (0.16)	10	2.44 (8.71)^{A}	0.55 (4.29)	12
Apr '08	0.09 (0.17)^{A}	0.24 (0.05)	14	1.00 (1.79)^{A}	0.41 (0.51)	10
Year	0.18 (1.57)^{A}	0.14 (0.81)	134	1.02 (14.20)^{B}	0.19 (3.71)	160

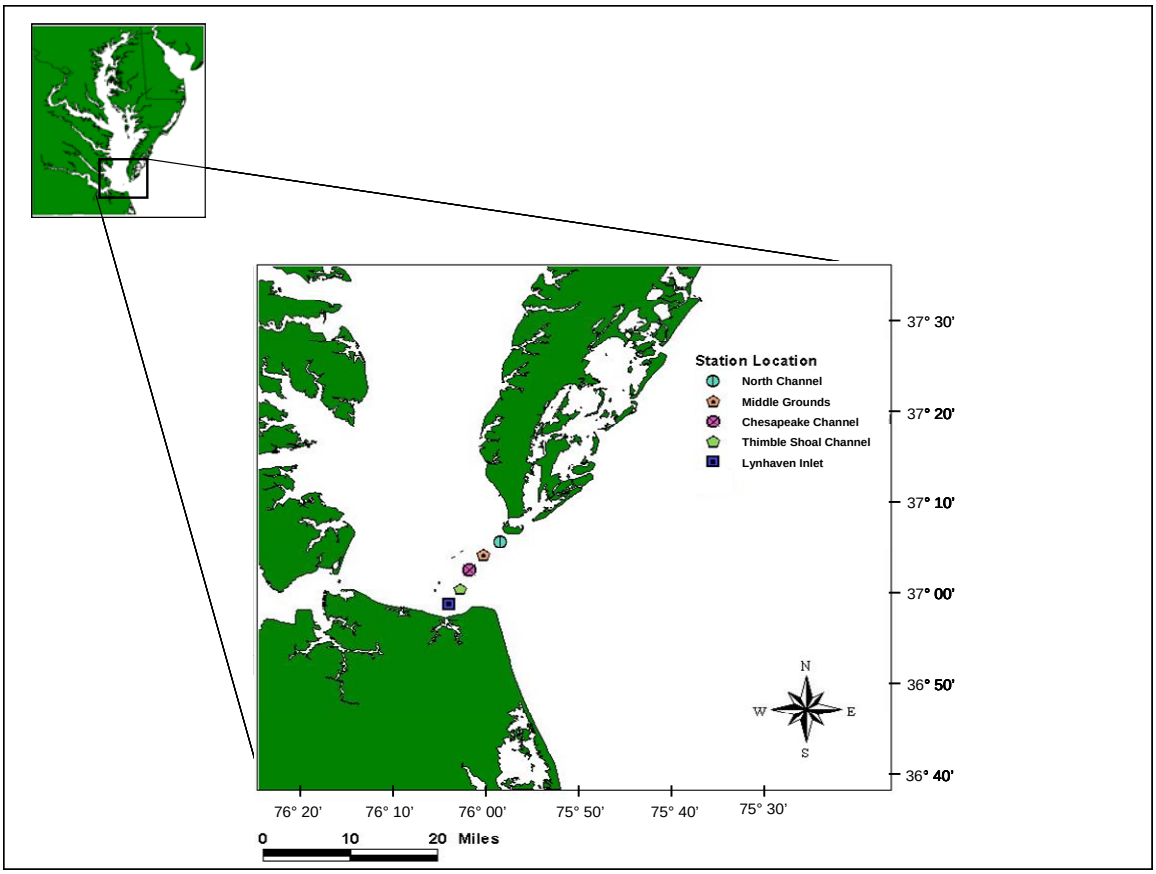

Figure 2.1. Map of study location and sampling sites across the mouth of the Chesapeake Bay.

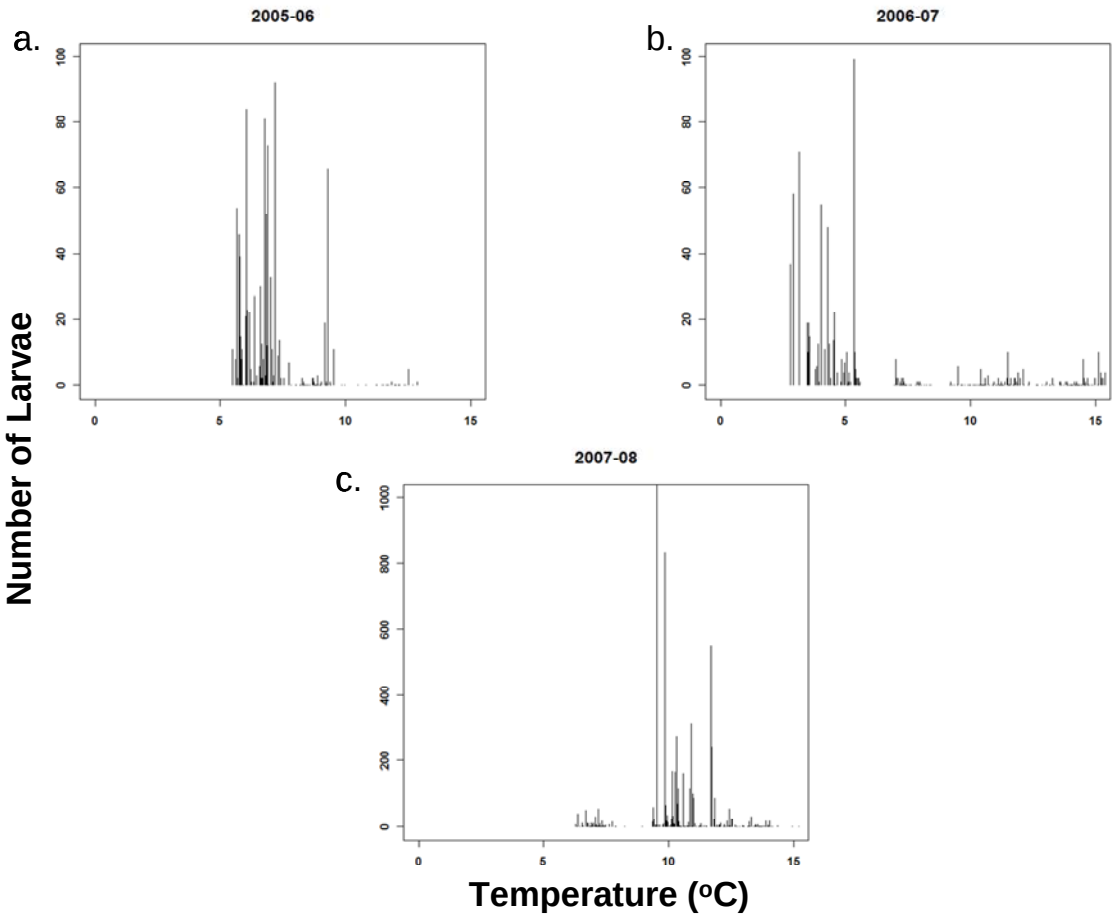

Figure 2.2. Frequencies of Atlantic menhaden larvae catches in relation to mean water-column temperature at the Chesapeake Bay mouth during a) 2005-06, b) 2006-07, and c) 2007-08. Note differences in y-axis scales.

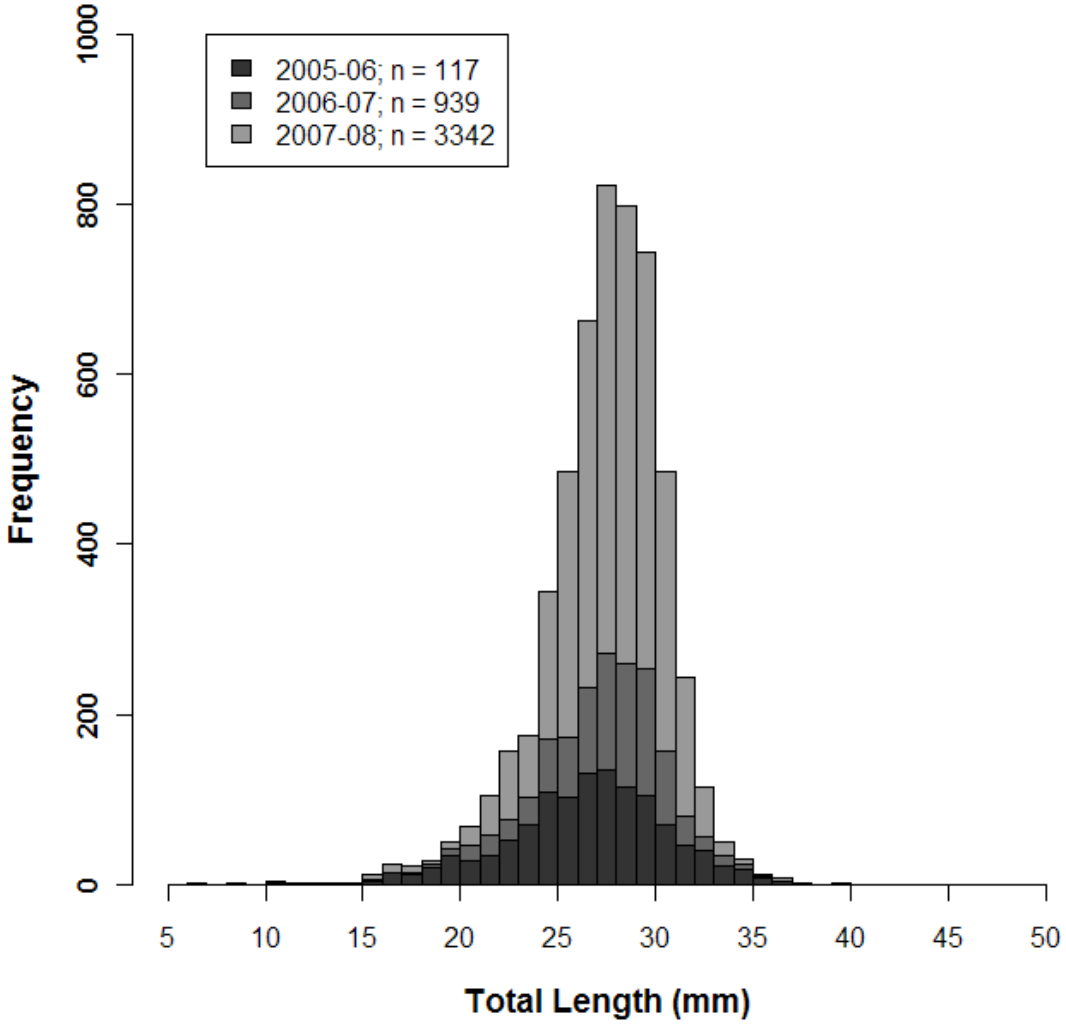

Figure 2.3. Length-frequency distributions of Atlantic menhaden larvae collected at the Chesapeake Bay mouth during the three-year project.

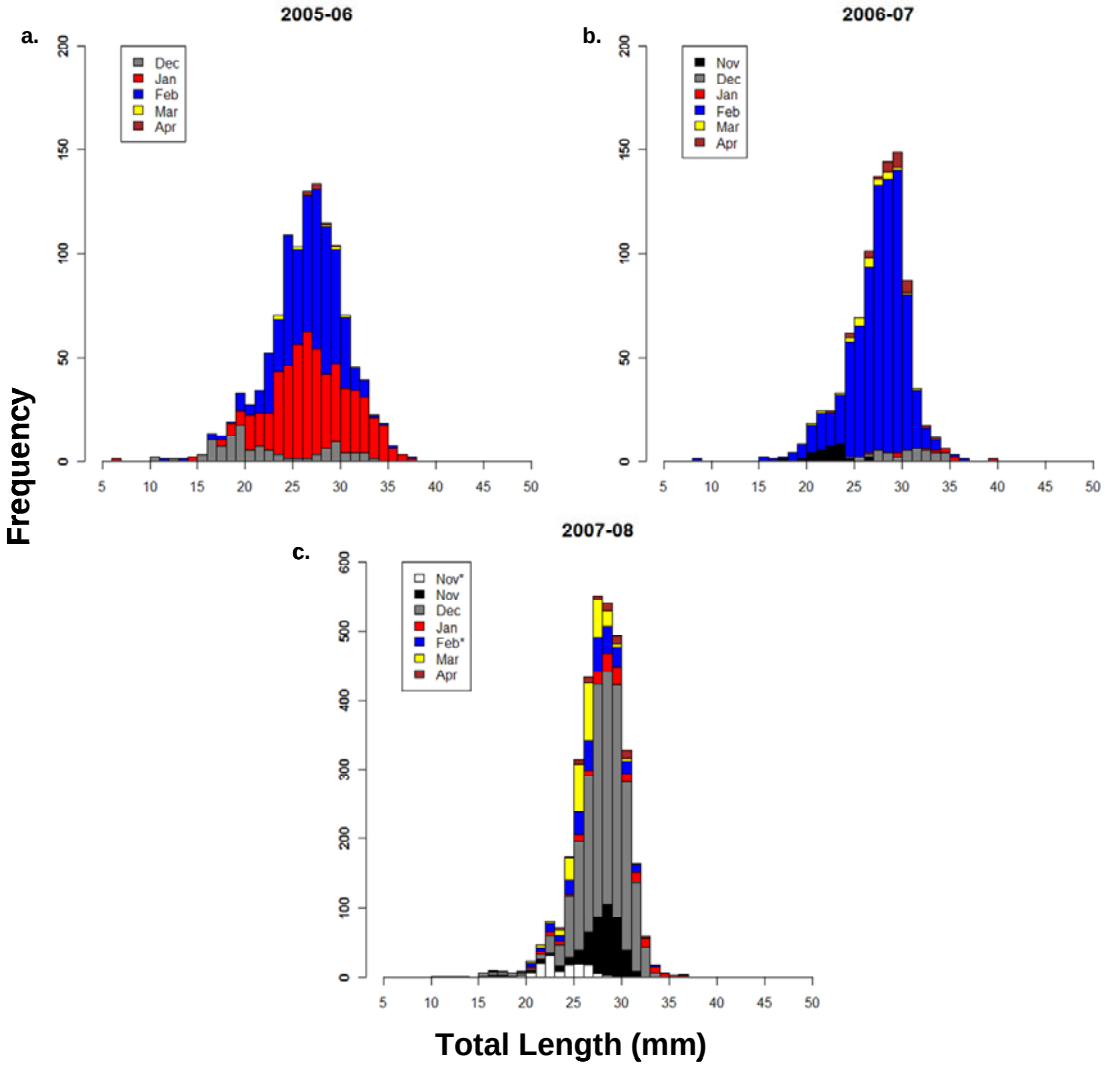

Figure 2.4. Length-frequency distributions of Atlantic menhaden larvae collected at the Chesapeake Bay mouth from a) 2005-06, b) 2006-07, and c) 2007-08. Each distribution is stacked by cruise month. Note differences in y-axis scales. * Indicates larvae from Hugh R. Sharp cruises.

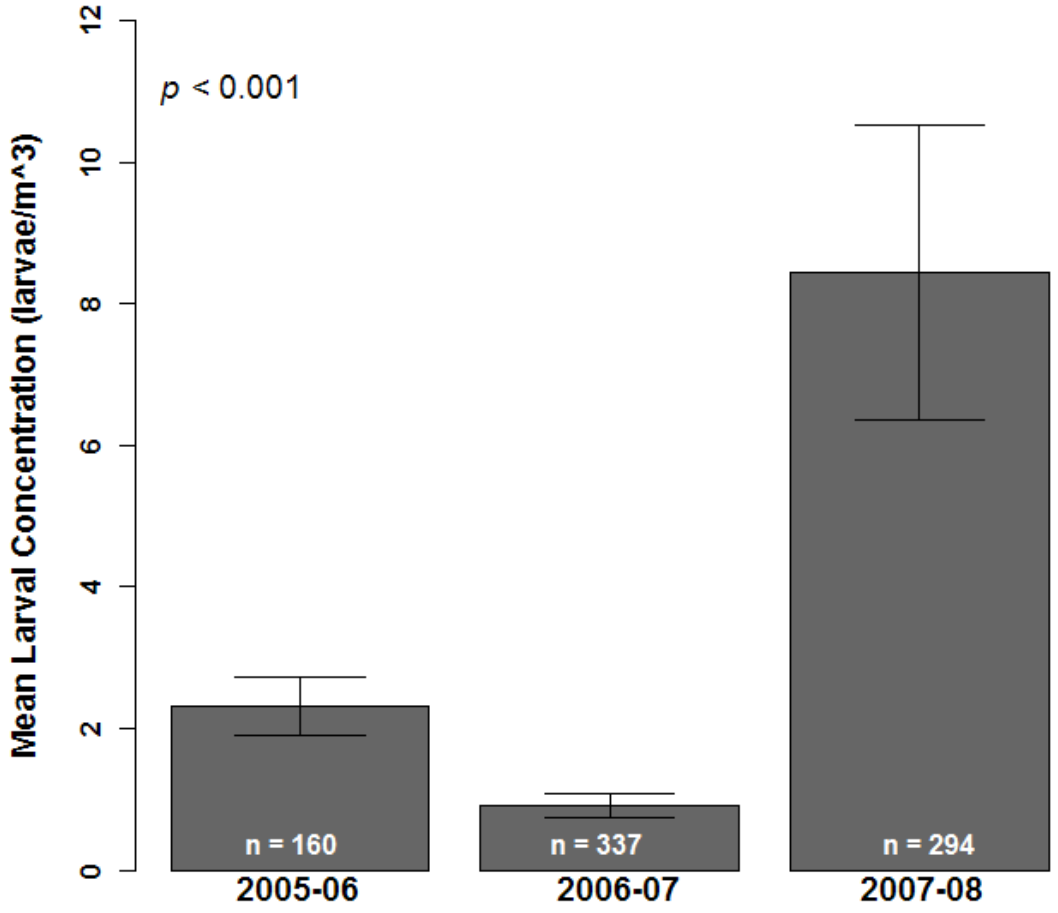

Figure 2.5. Annual mean larval concentrations (number per 100 m^3) ± standard error for Atlantic menhaden larvae collected at the Chesapeake Bay mouth. Larval concentrations were log-transformed for statistical analysis.

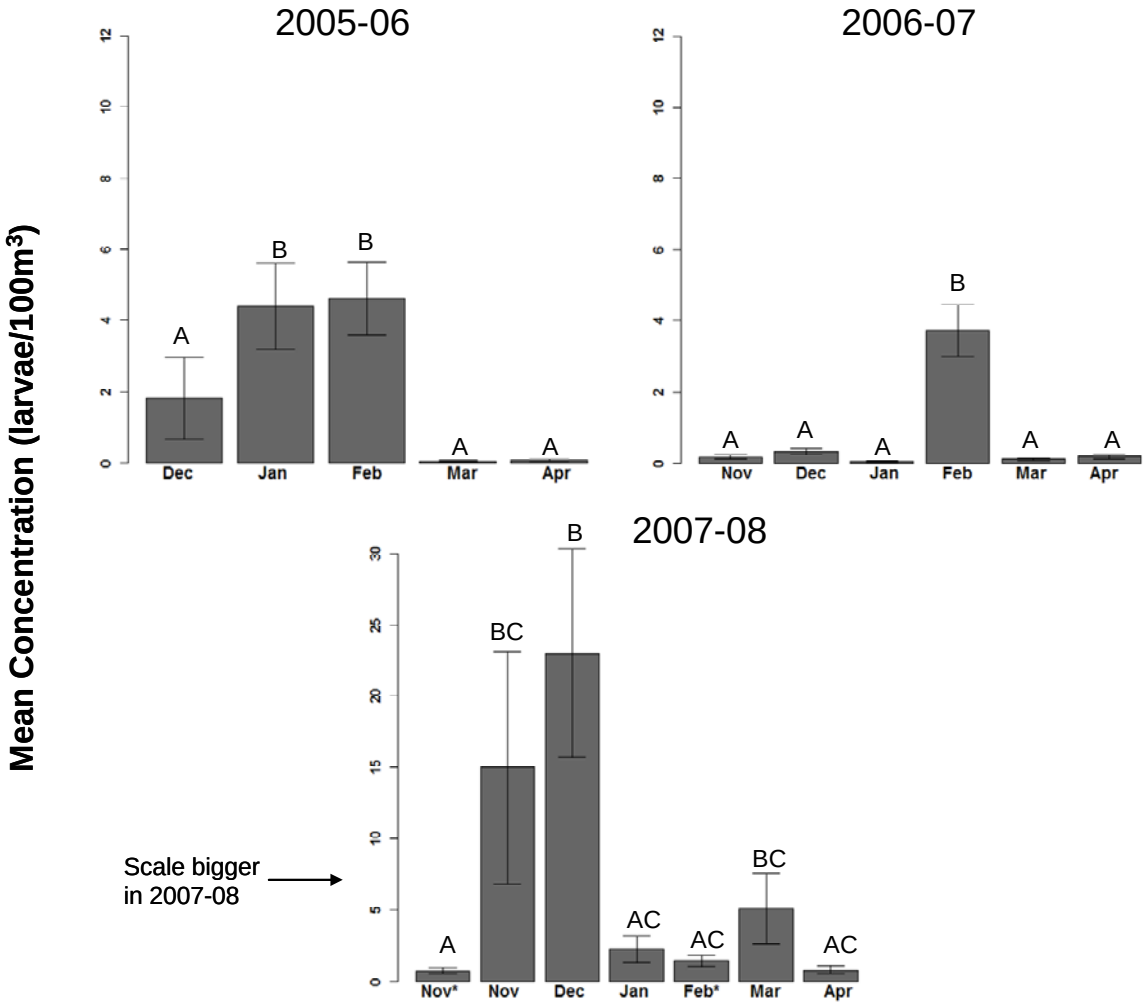

Figure 2.6. Monthly mean Atlantic menhaden larval concentrations (number per 100 m^3) ± standard error at the Chesapeake Bay mouth for a. 2005-06, b. 2006-07, c. 2007-08. Mean concentrations were log-transformed for statistical analysis. Note differences in y-axis scales. Letters above bars are Tukey rankings indicating significance. Bars that share a letter are not significantly different.

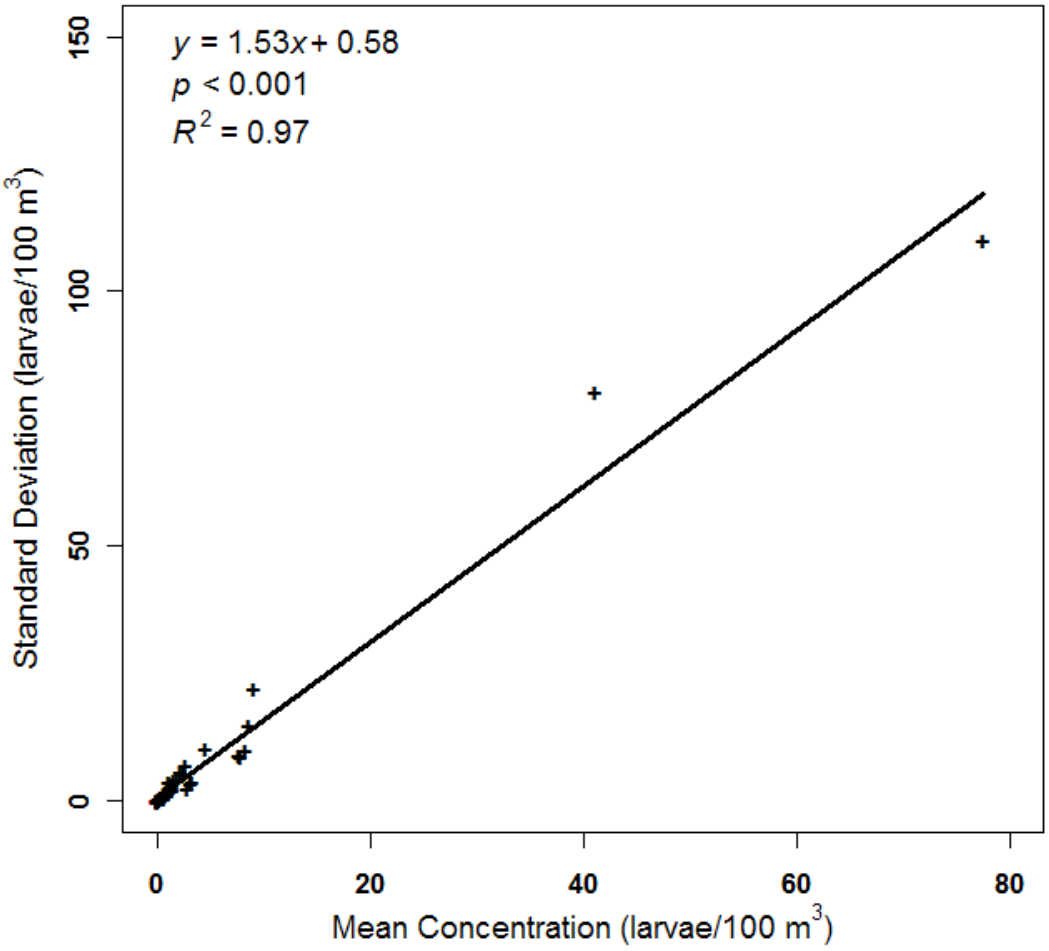

Figure 2.7. Relationship between the standard deviation and the mean concentrations of Atlantic menhaden larvae for each day of sampling during the 18 research cruises at the mouth of the Chesapeake Bay.

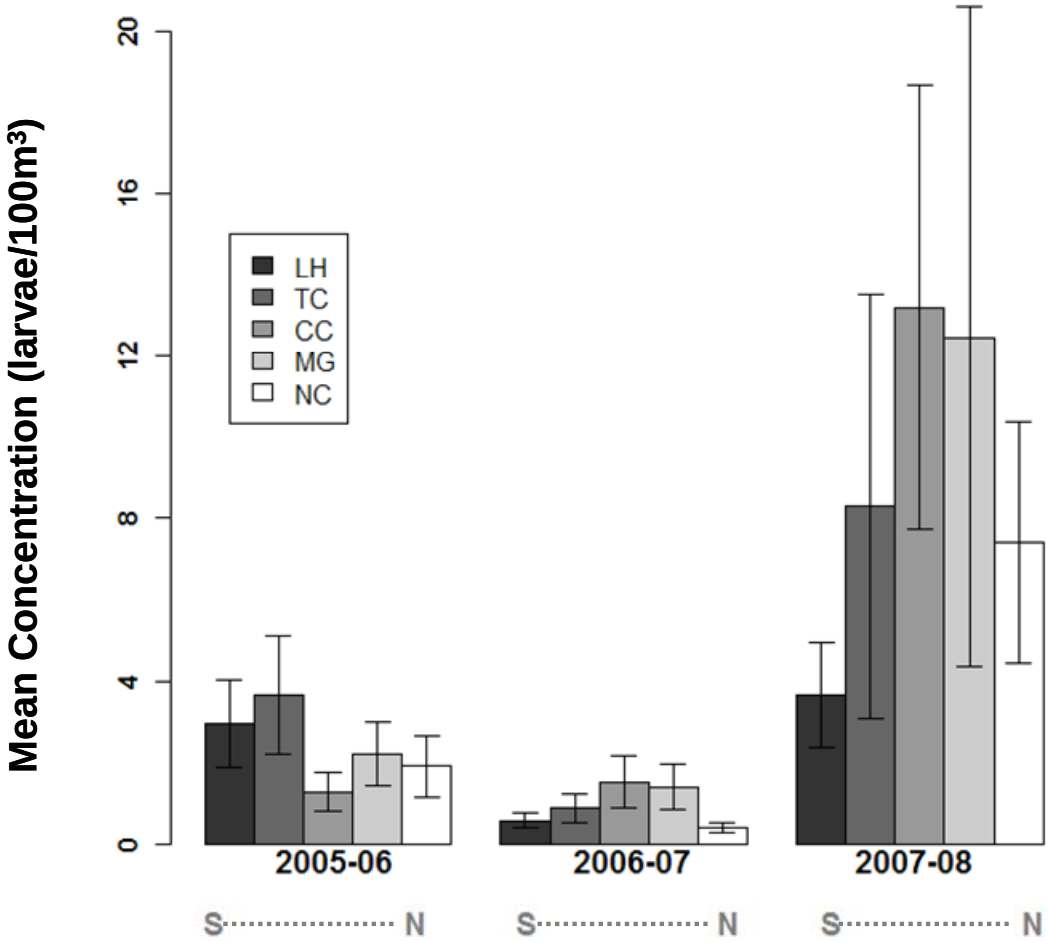

Figure 2.8. Annual mean larval Atlantic menhaden concentrations (number per 100 m^3) ± standard error among stations at the Chesapeake Bay mouth (see Figure 2.1). Mean concentrations were log-transformed for statistical analysis. S indicates south side of Bay mouth; N indicates north side.

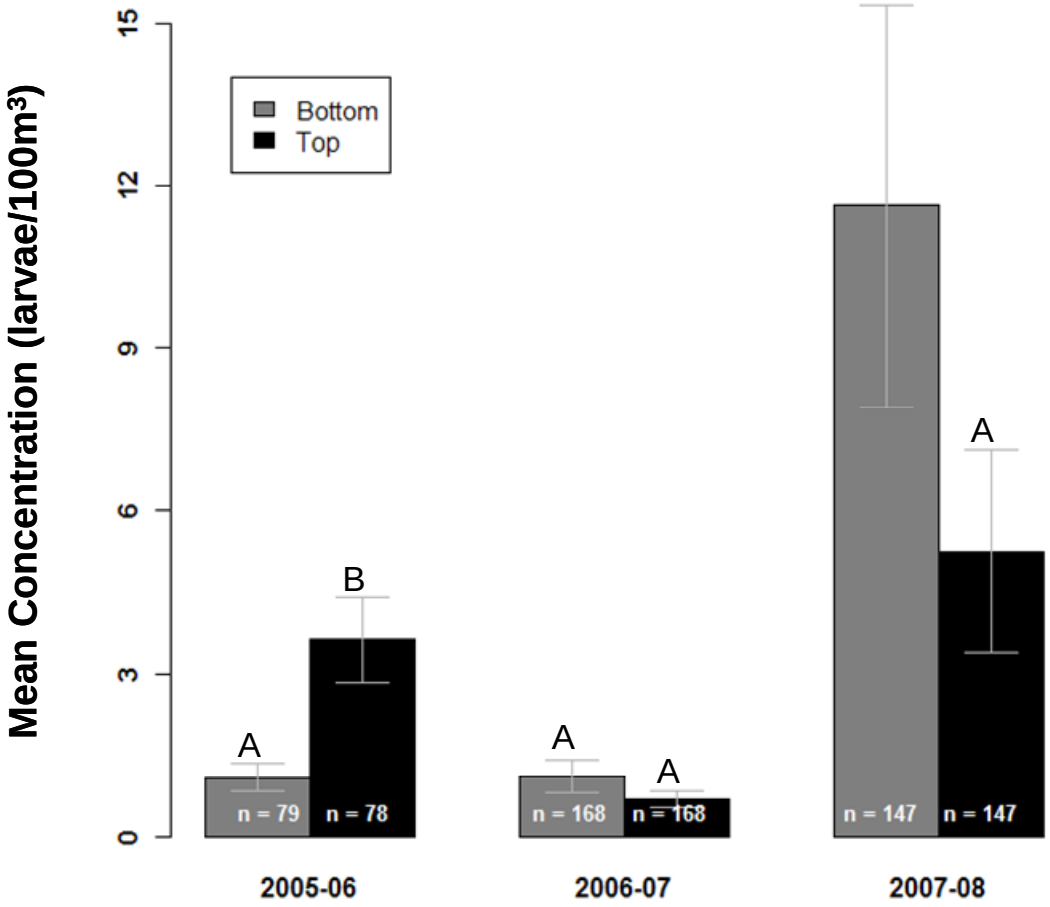

Figure 2.9. Annual comparisons of mean larval concentrations (number per 100 m^3) ± standard error of Atlantic menhaden larvae between above (top) and below (bottom) the pycnocline in the water column at the Chesapeake Bay mouth. Mean concentrations were log transformed for statistical analysis. Letters above bars are Tukey rankings indicating significance. Bars that share a letter are not significantly different.

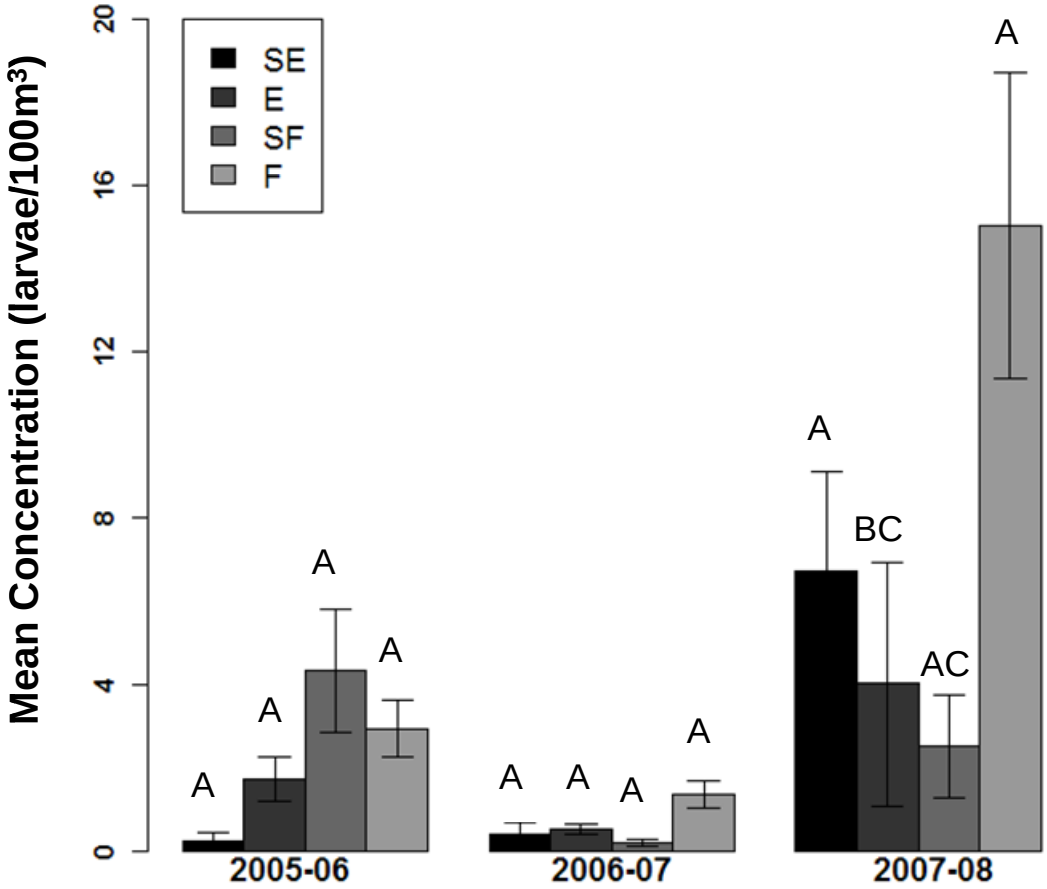

Figure 2.10. Annual mean larval concentrations (number per 100 m^3) ± standard error at each of the four tide stages. Mean concentrations were log-transformed for statistical analysis. SE is slack before ebb tide, E is ebbing tide, SF is slack before flood tide, and F is flooding tide. Letters above bars are Tukey rankings indicating significance. Bars that share a letter are not significantly different.

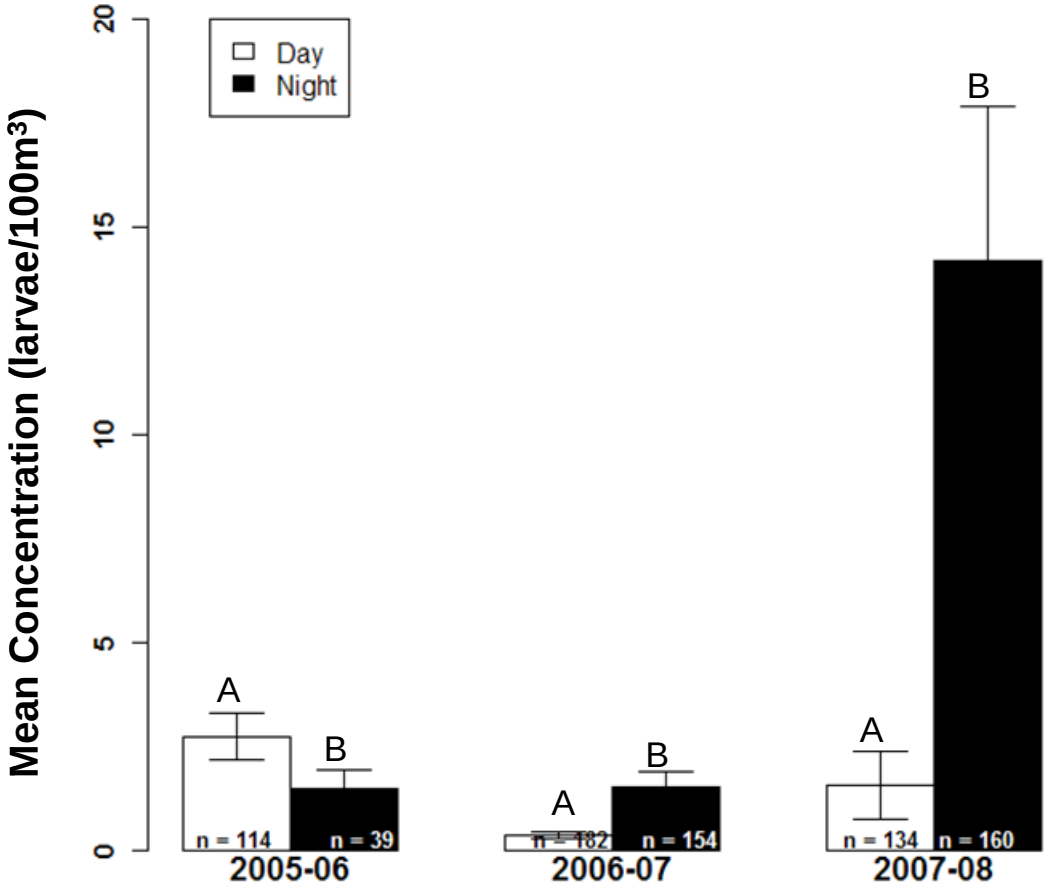

Figure 2.11. Annual mean larval Atlantic menhaden concentrations (number per 100 m^3) ± standard errors for day and night collections. Mean concentrations were log-transformed for statistical analysis. Letters above bars are Tukey rankings indicating significance. Bars that share a letter are not significantly different.

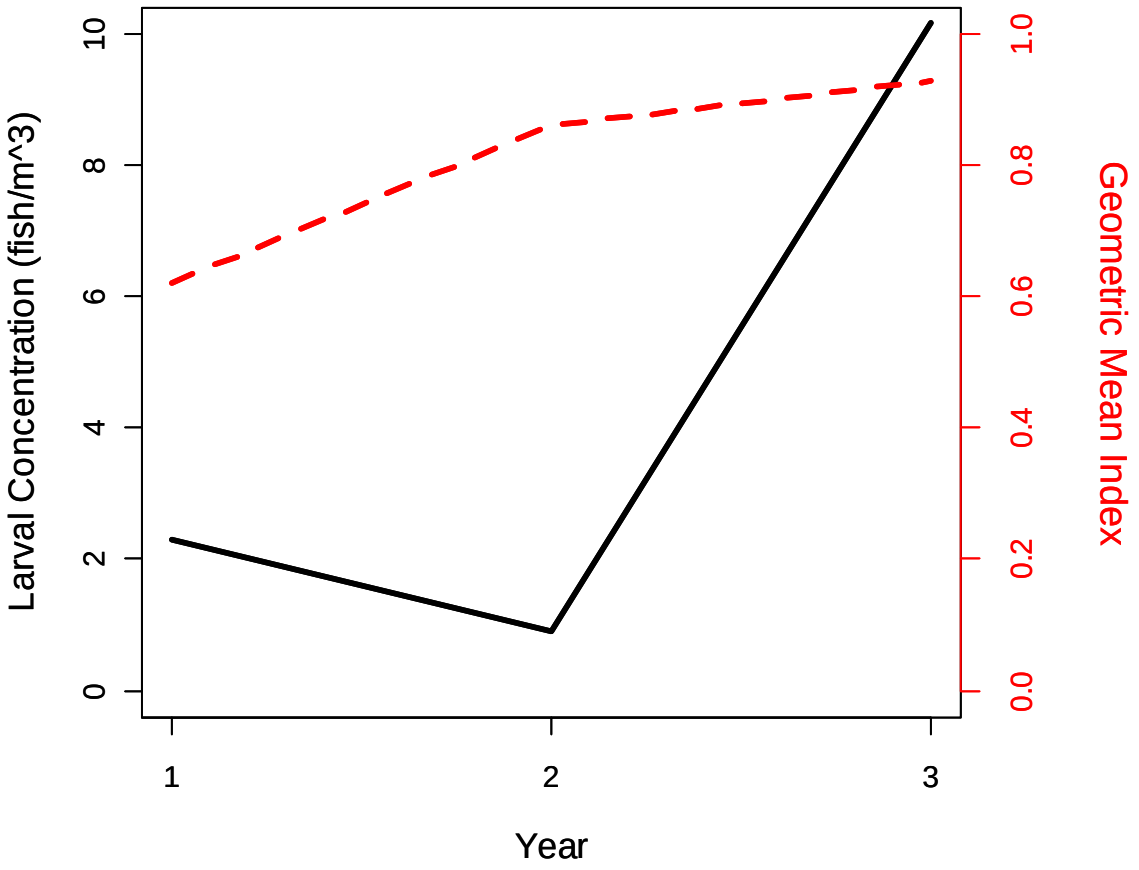

Figure 2.12. Three-year comparison of larval concentrations (solid line) at the Chesapeake Bay mouth with Bay-wide geometric mean index of young-of-the-year abundance of juvenile menhaden (broken line) for the years 1) 2005-06, 2) 2006-07, and 3) 2007-08. YOY geometric mean values were taken from MD DNR juvenile index seine survey data (*http://dnr.maryland.gov/fisheries/juvindex/index.asp*) based on mean catches from three summer surveys.

Chapter 3: Inter-annual variability in growth, hatch-dates, and feeding dynamics of late-stage Atlantic menhaden larvae

Abstract

A three-year sampling survey was conducted at the mouth of the Chesapeake Bay to evaluate ingress of Atlantic menhaden larvae and to document their ages, hatch dates and growth rates. Otolith microstructure analysis was conducted on ingressing larvae to provide estimates of ages (and transport time), hatch-date distributions, and larval-stage growth rates. Ingressing larvae were hatched from September to March and > 90% of larvae were hatched prior to 15 December during each of the three years. The clear progression of modal hatch dates by cruise month indicated that a new pool of larvae ingressing from offshore was being sampled during each cruise. The overall mean age-at-ingress was 47 days post-hatch and ranged from 9-96 days during the three years. The mean age-at-ingress was significantly older in 2006-07 (50 days post-hatch) compared to 2005-06 (44 days post-hatch) and 2007-08 (46 days post-hatch). Mean growth rate was fastest in 2006-07 (0.57 mm/day) compared to 2005-06 and 2007-08 (0.52 mm/day in these years). A Laird-Gompertz growth model indicated that larvae grew fastest from 21-30 days post-hatch in each year. Based on a shift in allometric growth, larvae were judged to begin metamorphosis at a mean length of 27.69 mm. Copepods were the dominant prey consumed by ingressing larvae but other taxa, including barnacle nauplii and cladocerans, were important. Feeding incidence and success were higher in 2006-07 than in 2005-06 and 2007-08.

Introduction

The Atlantic menhaden *Brevoortia tyrannus* is distributed from the Canadian maritimes to Florida. It is among the most abundant fishes in coastal embayments, estuaries, and neritic coastal habitat and supports a major fishery in the mid-Atlantic region (MDSG 2009). Spawning by Atlantic menhaden has been recorded in every month of the year at some locations along the Atlantic coast (Higham and Nicholson 1964). On the mid-Atlantic coast, eggs have been collected from May through November and in January (Berrien and Sibunka 1999). Adult menhaden migrate northward in the spring and southward in the fall (Dryfoos *et al*. 1973; Nicholson 1978). They spawn in the mid-Atlantic primarily from August through January with a peak in the September through November period (Berrien and Sibunka 1999). From January through early March, intensive spawning is mostly concentrated off the Carolinas, south of Cape Hatteras (Higham and Nicholson 1964; Judy and Lewis 1983).

Most menhaden larvae hatch in the coastal ocean and are subsequently transported shoreward to embayments and estuaries. Little is known about the process of dispersal and transport. Larvae have been collected up to 40-miles offshore, providing evidence that a considerable fraction of spawning occurs at offshore locations (Massmann *et al*. 1962). Massmann *et al*. also noted a progressive decrease in size of larvae with distance from shore. Atlantic menhaden collected upon entry to estuaries usually are late-larval stages. Transport from the offshore environment may be quite rapid (Warlen 1992, 1994; Warlen *et al*. 2002; Light and Able 2003). Warlen (1992)

suggested, based on estimated ages of larvae collected at incremental distances offshore from North Carolina, that dispersal of larvae is biphasic, estimating that shoreward transport is initially rapid at approximately 80 km in 30 days (2.7 km/day), but then slower at about 20 km in the next 20 days (1.0 km/day). Warlen postulated that larvae accumulate near estuaries and embayments just prior to entry.

The paucity of age and growth research on early life stages of Atlantic menhaden is an impediment to relating hatch dates and locations to transport times to Chesapeake Bay. Analysis of otolith-increment microstructure has been used to estimate age and growth rates of Atlantic menhaden larvae (Maillet and Checkley 1990; Warlen 1992, 1994; Warlen *et al*. 2002; Light and Able 2003). Increments in otoliths are deposited at a rate of one per day (Maillet and Checkley 1990; Warlen 1992). Based on otolith-estimated ages, spawning and hatch dates have been back-calculated (Warlen 1994) to determine the relative contributions of temporal spawning events to ingress of larvae to a North Carolina estuary. Several surveys have collected larval Atlantic menhaden near the mouth or within the Chesapeake Bay (Hildebrand and Schroeder 1928; Pearson 1941; Massmann *et al*. 1954, 1962; Olney and Boehlert 1988; Hare et al. 2005; my Chapter 2) but research on age and growth of larvae is lacking. Most research on age and growth of larval Atlantic menhaden has been conducted on larvae from waters off North Carolina and Delaware. Warlen (1992) found that ages of larvae at ingress to estuaries are not only indicators of hatch dates, but potentially of transport rates and distance of spawning from shore.

Growth and growth patterns of early life stages of Atlantic menhaden have been described (Lewis *et al*. 1972; Powell and Phonlor 1986; Maillet and Checkley 1990,

1991; Warlen 1992). Based on otolith-aged larvae and a fitted growth model Warlen (1992) estimated that Atlantic menhaden larvae collected at ingress to a North Carolina estuary grew at average rates of 0.47 mm/day for ages 1 to 20 days, 0.36 mm/day for ages 21 to 40 days, and 0.18 mm/day for ages 41 to 60 days old. Maillet and Checkley (1990, 1991) reported a mean growth rate of 0.48 mm/day for laboratory-reared Atlantic menhaden larvae from 0 to 50 days old in one study and 0.37 mm/day for 13 to 20 day-old larvae in a second study.

Lewis *et al*. (1972) described ontogeny and growth of early life stages of Atlantic menhaden, and recognized three growth stanzas. The first stanza was characterized as larval growth and encompassed the period from hatch (3.6 mm total length) to the attainment of 30 mm total length (TL). The second stanza characterized growth during the pre-juvenile, metamorphosing stage from 30 mm to attainment of full juvenile characteristics (38 mm TL). Ontogenetic development from newly-hatched larva to the juvenile stage has been estimated to be 38 to 40 days post-hatch based on alimentary tract length and morphology (June and Carlson 1971; Lewis *et al*. 1972).

There are few reports of feeding by Atlantic menhaden larvae in the sea and no evaluation of feeding with respect to sizes or growth rates. Laboratory research has indicated that larval menhaden begin feeding at four days post-hatch (Powell and Phonlor 1986; Lippson 1991). Larval-stage menhaden are active predators on zooplankton (June and Carlson 1971). June and Carlson (1971) reported gut contents of larval Atlantic menhaden from 19 to 34 mm fork length (FL) collected at the entrance to Delaware Bay. Fifty-nine percent of the larvae had empty alimentary tracts. Copepods comprised 99% of the diets of those larvae and, of the identifiable copepods, 19% by number were

Centropages spp. Laboratory-reared, late-stage larvae and pre-juvenile menhaden had fed mostly on *Acartia spp*. copepods (June and Carlson 1971). The dominant prey of Atlantic menhaden larvae collected from the Newport River estuary, North Carolina, was copepods, which were reported to comprise 99% by number of their diets (Kjelson *et al*. 1975). Of those copepods, 40% were *Centropages spp*., 30% were *Acartia spp*., and 22% were harpacticoid copepods.

In this Chapter I report on the ages and hatch dates of larval Atlantic menhaden collected at the mouth of Chesapeake Bay, their growth rates during the oceanic phase of the larval stage, and feeding of larvae collected at the Bay mouth. Ages of Atlantic menhaden larvae at ingress were determined by analyzing otolith increment microstructure. Variability in ages of larvae at ingress was compared for collections made during three spawning years (2005-06, 2006-07 and 2007-08). Otolith-derived age estimates were used to back-calculate hatch- and spawn-date distributions. Growth rates were estimated and compared among years and months. Foods of menhaden larvae at the Chesapeake Bay mouth were identified and variability in feeding by larval menhaden was described, characterized, and compared among months and years.

I hypothesized that age at ingress would vary monthly and inter-annually, possibly in response to different environmental conditions experienced by menhaden larvae in the coastal ocean or with respect to variability in spawning times and locations. I predicted that mean daily growth rates would vary monthly and inter-annually, primarily in relation to variable temperatures in the late fall to winter period when most larvae ingress to the Bay (see Chapter 2). Based on published reports on menhaden feeding, I predicted that copepods would be the most common prey of menhaden larvae

at the Chesapeake Bay mouth and that feeding success would vary among years and months.

Methods

Study area and Surveys

Ingressing Atlantic menhaden larvae were collected at the mouth of the Chesapeake Bay. The mouth is 18-km wide and extends south to north from Cape Henry to Fisherman's Island, Virginia. There are three shipping channels of different depths at the Bay mouth (Chapter 2, Figure 2.1). The Chesapeake Channel is near the center of the Bay entrance and is 17.7-m deep. The northernmost channel, the North Channel, is 14-m deep. Between those two channels is a shallow flat, the Middle Grounds, with depths 11.3 to 14.1 m (Valle-Levinson *et al*. 2001). At the southern side of the Bay mouth is the Thimble Shoal Channel, with depths from 8.0 to 11.8 m (Valle-Levinson and Lwiza 1998).

A sampling transect was designated across the Chesapeake Bay mouth, located approximately 1.5 km seaward of the Chesapeake Bay Bridge/Tunnel (Chapter 2, Figure 2.1). Four stations were sampled on the designated transect in December 2005. Five fixed stations were designated and sampled on the 17 remaining survey cruises during the three-year study.

A total of 18 survey cruises was conducted in the December 2005 to April 2008 period (Chapter 2, Table 2.1). Cruises were conducted from November to April, the season when peak larval ingress was expected to occur. All except two of the cruises

were on the University of Maryland Center for Environmental Science's (UMCES) 20.0-m research vessel, R/V *Aquarius*. The remaining two cruises were on the University of Delaware's 44.5-m research vessel, RV *Hugh Sharp*.

Ichthyoplankton and zooplankton samples were collected at each station on the RV *Aquarius* cruises with a 1-m^2 mouth-opening Tucker trawl equipped with 280-µm mesh nets. A Tucker trawl, equipped with 1-mm mesh nets, was used for the two cruises onboard the R/V *Hugh Sharp*. The Tucker trawl had two nets. Flowmeters were mounted in the mouths of each net to allow calculation of volume filtered. The 280-µm mesh nets collected fish larvae as well as mesozooplankton in the size range eaten by larval menhaden. The Tucker trawl with 1-mm meshes captured ingressing menhaden larvae, which are usually > 20-mm total length, but did not sample small ichthyoplankton or mesozooplankton.

In each deployment of the Tucker trawl, one net was fished obliquely from near-bottom to the pycnocline and the second was fished from the pycnocline to surface. On most deployments, tow durations for each net were four minutes (mean volume filtered = 216.31 m^3 ± 60.39 se). At several stations during the February 2007 cruise, tows were extended to six minutes to increase numbers of larval menhaden in catches (mean volume filtered = 463.96 m^3 ± 14.32 se). On each cruise, a station was sampled at least twice and up to four times a day to encompass two photic periods (night and day) and a range of tide stages. Samples were preserved in 100% ethanol.

Hydrography

Depth profiles of hydrographic conditions were obtained at each station using a CTD (conductivity, temperature, and depth). The CTD recorded temperature, salinity, chlorophyll and dissolved oxygen profiles at each station on each cruise. On occasions when the CTD was not available- - (Days 2 and 3 in the March 2007cruise, all stations in the April 2007 cruise, and one station in the November 2007 cruise) a YSI sonde was used to record temperature and salinity at 1-m depth intervals. Tide stages and predicted water current directions and velocities were obtained from tide charts using the Capn Voyager software (Star Technologies) Tides 32. The tide stage at the time each station was sampled was recorded.

Mean values of temperature and salinity over the entire water column were calculated for each station occupation. A nested Analysis of Variance (ANOVA) was used to test for inter-annual and among-months differences in mean temperature and salinity at the Bay mouth. Tukey's Honestly Significant Difference (HSD) multiple comparisons test was used to discriminate significant differences among mean temperatures and salinities.

Laboratory Procedures

Ichthyoplankton and zooplankton samples were processed in the laboratory. Menhaden larvae were removed from the plankton samples. A total of 9,840 menhaden larvae were collected in the three-year survey (Chapter 2, Table 2.1). Subsamples of larvae were analyzed. For samples with high numbers of larvae, a random sample of 100 larvae was measured to represent the length distribution sampled on a cruise. For aging

and feeding analyses, up to five larvae from the above-pycnocline sample and five from the bottom-pycnocline sample were selected if sufficient larvae were available. All larvae for feeding and aging analyses were measured to the nearest 0.1 mm prior to dissection. For the aging and feeding analyses, totals of 251, 240, and 243 larvae were analyzed from 2005-06, 2006-07, and 2007-08 collections, respectively.

Foods and Feeding

Gut contents of larvae were examined. Under 20X magnification and using a fine-tipped wire probe, the entire gut was removed from the body of a larva. The buccal cavity and anterior portion of the digestive tract also were examined for possible prey. All prey items were enumerated and identified, and then preserved in 100% ethanol.

Categories of prey that were analyzed included: copepods, copepod nauplii, cladocerans, barnacle nauplii, bivalve larvae, ostracods, decapods, polychaetes, tunicate larvae, metatrochophores, and digested material. The copepod category was further subdivided into the genera: *Centropages*, *Acartia*, *Temora*, *Caligus*, and *Labidocera*. Those copepods were not identified to the species level but likely species were: *Centropages typicus* (Van Engle and Tan 1965), *Acartia tonsa* and *A. clausi* (Heinle 1972), *Temora longicornis and T. turbinata* (Van Engle and Tan 1965), *Caligus* unidentified (Chesapeake Bay Program 2007), and *Labidocera aestiva* (Van Engle and Tan 1965).

Otolith Preparation

The sagittal otoliths were removed from the auditory capsules of menhaden larvae using a modification of methods described by Secor *et al*. (1992) and Maillet and Checkley (1990). Both left and right saggitae were removed and mounted on microscope slides. They were fixed onto the slides using clear nail polish, one otolith with cusp side up and the other with cusp side down. Otoliths were examined under a compound microscope at 600x magnification. Images of otoliths were taken and saved for each otolith pair. The best of each pair was used to count daily increments. Early in the analysis, a second reader examined and counted increments on a small subsample of 10 randomly selected otoliths; agreement in counts was 100 percent, indicating that a single reader's counts could be accepted.

Zooplankton Analyses

Aliquots of zooplankton from Tucker-trawl samples were identified and concentrations were estimated. Samples from the RV *Hugh Sharp* cruises in early November 2007 and February 2008 were not included in the analyses because they were collected using 1-mm mesh nets that did not retain zooplankton of sizes consumed by menhaden larvae. Each Tucker-trawl sample was brought to a standard volume of 1 liter. Three 1-ml aliquots were examined to identify and quantify zooplankton numbers. The mean count for the three aliquots was accepted to estimate zooplankton concentrations. For aliquots that qualitatively were judged to have very high concentrations, i.e., >> 100 zooplankton per 1 ml, the standard 1-liter sample was split and the half sample then

diluted to 1-liter volume before 1-ml aliquots were drawn and examined. Zooplankton in each 1-ml aliquot were identified and enumerated.

Zooplankton concentrations were estimated from the 1-ml aliquots. The mean number of zooplankton in a 1-ml aliquot was multiplied by the standardized sample volume to obtain the total number of zooplankton in the sample. The total number of zooplankton in the sample was divided by the volume of water filtered by the Tucker-trawl tow for that sample to obtain the zooplankton concentration (number per cubic meter). Concentrations of individual zooplankton taxa also were estimated. Mean zooplankton concentrations were compared among cruises (in effect months) to detect seasonal trends and among years using nested ANOVA followed by Tukey HSD multiple comparisons test.

Ages, hatch-dates, and growth

Ages and Lengths

Age in days from hatch was estimated from the daily increment counts of each otolith. Maillet and Checkley (1990) had determined that the time from hatch to formation of the first increment is 3 to 4 days. Accordingly,

$$\textit{Age from Hatch} = \textit{Total increments} + 3 \textit{ days}$$

Mean ages of otolith-aged larvae were compared to determine if they differed from cruise-to-cruise (i.e., seasonal differences) and among the three years in a nested ANOVA. Tukey HSD was used to discriminate significant differences in mean ages among cruises and years.

The protocol for measuring menhaden larvae was to measure total lengths (TL) of all larvae in samples containing < 100 larvae and a random subsample of 100 in samples with > 100 larvae. Lengths of unmeasured larvae in samples that had > 100 menhaden larvae were estimated from the length-frequency distributions of measured larvae and proportional assignment of lengths to unmeasured larvae. The proportion of larvae in each 1-mm length bin was determined for each sample. Mean lengths from only the measured larvae were tested and compared among monthly cruises and among the three years in a nested ANOVA followed by Tukey HSD.

Larvae that were not aged from otolith increments were assigned ages from an age-length key that was developed using a protocol described by Isermann and Knight (2005). The software developed by Isermann and Knight (2005) is in the *SAS*-language that was translated by Ogle, Derek H (http://www.rforge.net/FSA) to the *R*-language. The age-length key allowed assignment of an estimated age to all larvae in the collections.

Hatch-Dates

Hatch dates were back-calculated directly for otolith-aged larvae and estimated for larvae that were not aged from the age-length key. Back-calculations of hatch dates were obtained by subtracting the age of larvae in days from the date of capture and adding 3 days:

$$\textit{Hatch date} = \textit{Date of capture} - (\textit{Age in days} + 3\ \textit{days})$$

A hatch-date frequency distribution was derived for larvae collected in each cruise. These unadjusted distributions were adjusted to provide an estimate of hatch-date distributions for each year.

The age-frequency distributions of larvae were adjusted by accounting for effects of natural mortality on the observed age distribution of larvae in collections and by accounting for differential sampling effort among cruises. A conservative estimate of natural mortality rate of menhaden larvae, $M = 0.15\text{-d}^{-1}$, was assigned based on reported larval natural mortality rates of clupeoid larvae at temperatures in the range experienced by menhaden larvae (Houde and Zastrow 1993). This mortality rate was applied to the unadjusted hatch-date frequencies of larvae in all cruises to reconstruct the probable abundances at hatch in each of the three years. Hatch-date frequencies were adjusted further by accounting for differences in sampling effort among cruises. This was done by dividing the total number of larvae in each hatch date bin within a cruise by the number of samples taken during a cruise to standardize the distributions. Finally, an adjustment was made on the hatch-date frequencies to account for differences in number of days included in cruises and days represented by each cruise. This was accomplished by multiplying hatch-date frequencies for each individual cruise by the extrapolated number of days that each cruise represents. The adjusted hatch-date frequency distributions were then used to determine relative cumulative frequencies of larval hatch dates in each year. This procedure allowed determination of the cumulative monthly percent contributions of ingressing larvae at the Chesapeake Bay mouth.

Growth

Growth of menhaden larvae was modeled by fitting length-at-age data of otolith-aged larvae to a Laird-Gompertz model (Maillet and Checkley 1991; Warlen 1992; Piscart *et al*. 2003). Laird-Gompertz models were fit to the length-on-age relationships

for larvae in each year. The models were forced through the intercept length = 3.6 mm TL, the length of menhaden at hatch (= age zero) to insure that it was accurately represented in the models. The model is:

$$L_t = L_0 e^{k(1-e^{-at})}$$

where L_t is length at age t days, L_0 is length-at-hatch- -set to 3.6 mm in all model fits, k is the rate of decay of the initial instantaneous growth rate, and a is a dimensionless parameter. Mean growth rates were derived for larvae at 10-day age intervals from the fitted models in each year.

The Laird-Gompertz model allowed hindcasting of estimated growth-rates to ages when menhaden larvae were offshore and not sampled, before they had arrived at the Chesapeake Bay mouth. Warlen (1994) used a similar method to determine larval growth patterns and rates. Coefficients (k) were compared among years using pairwise t-tests, based on the parameter estimates and variances for each year (Bolz and Lough 1983; Quinn and Deriso 1999).

Weight-length

The weight-length relationship of menhaden larvae from the mouth of Chesapeake Bay was determined. For all larvae that were aged, lengths and weights were obtained for this analysis. Weights were obtained using a microbalance. Based on a weight-length relationship, Lewis *et al*. (1972) characterized the allometric changes during ontogeny of early-life stages of Atlantic menhaden and identified three stages that they referred to as stanzas. Larvae from my research fall into their larval and pre-juvenile stanzas. Because there was a noted shift in the relationship between weight and length

during ontogeny, I fit a piecewise linear regression to the log-log weight-on-length relationship of menhaden larvae to evaluate the shift. I used a technique for breakpoint estimation in piece-wise linear regression using iteration (Ryan and Porth 2007) based on the power model formulated from the log-log weight-on-length relationship. Regression relationships were obtained for data from the three years combined and also for data from each individual year.

Foods and Feeding

Prey incidence, the percent of menhaden larvae that contained at least one prey item in their guts, was calculated by cruise (i.e., month) and year. An r x 2 test of independence was used to test for differences in the proportion of larvae that contained at least one prey item in their gut among the three years and among months in each year.

In an additional analysis of prey incidence, a logistic regression was used to test the probability of a prey item occurring in a larval gut at larval total lengths, in a procedure similar to that used by Wheeler and Allen (2003). This approach tests for differences in the rate at which the probability of occurrence of a prey item in the gut changes during growth of larvae among years. The binary response variable, presence or absence of prey, was tested against total length of menhaden larvae, years, and the interaction of total length with years as predictors. The model used in the analysis was:

$$\text{Logit}(p) = B_0 + B_1\text{L} + B_2\text{year} + B_3\text{year*L},$$

where logit(p) is the logistic probability of prey occurring in a larval gut, B_0 is the intercept, L is total length in mm, year is year of the three-year study, and year*L is the interaction between length and year. The significance of individual model terms was

tested with a Wald test using robust standard errors for validation of inclusion of each model term (Croux *et al*. 2003). A type III Chi-square Wald test was used to test the performance of the full model, with all model terms included, in comparison to the null model which includes only estimates of the intercept and not the explanatory terms (Hausman 1978).

The success of feeding was analyzed by evaluating total number of prey items occurring in larval menhaden digestive tracts. This analysis was conducted using a quasi-Poisson regression analysis with independent variables larval total length and year. This method was selected because the distribution of total number of prey per larval gut had a Poisson-like distribution that was overdispersed. A high proportion of larvae had zero prey in their guts. The quasi-Poisson model was selected rather than a negative binomial model based on the argument that it generally handles overdispersed data more efficiently (Hoef and Boveng 2007). Based on a preliminary run of the quasi-Poisson regression analysis, the interaction of larva length and years on the number of prey items in guts was found to be not significant and therefore was not included in the final analyses. The resulting model tests for differences in total number of prey per larval gut among years and larval length. The model used in the final analysis is:

$$\log(P) = B_0 + B_1\mathrm{L} + B_2\mathrm{Y},$$

where $\log(P)$ is the logarithm response of the total number of prey per gut in relationship to a linear combination of the predictors, B_0 the intercept, L total length (mm) of larvae, and Y the year designated as a dummy variable with the levels -1, 0, and 1. This model describes number of prey per gut. The significance of the model terms was tested using a Wald test on the robust standard errors for validation of inclusion of the model terms in

the model (Croux *et al*. 2003). A type III Chi-square Wald test was then used to test the performance of the full model, with all model terms included, compared to the null model which includes only an estimate of the intercept, excluding other model terms (Hausman 1978).

Prey Selection

The proportions of types of prey in larval menhaden diets were calculated. The four most common prey in diets were analyzed to determine if menhaden larvae had shown preference for them as prey. The four most common prey groups were copepods, barnacle nauplii, cladocerans, and bivalve larvae. Proportions of these four prey groups were evaluated and compared among cruises to determine if there was a seasonal trend and among years to determine if there were inter-annual differences in prey selection.

A prey preference index was used to determine if menhaden larvae selected prey types. The proportions of zooplankton concentrations were calculated for zooplankton prey groups that were important larval prey. For copepods, all taxa of copepods were pooled in this analysis. The Strauss (1979) index of prey selectivity was used to compare relative proportions of zooplankton by group in larval menhaden diets to the relative proportions of those same zooplankton available at the Chesapeake Bay mouth:

$$S = r_i - p_i,$$

where r_i is the proportion of prey i in the larval guts and p_i is the proportion of prey type i available in the environment. The calculated index, S, can range from -1.0 to +1.0. Positive index values from this analysis indicate selection for zooplankton type i; zero values indicate no selection for or against a prey type; and negative values indicate

avoidance. Variance estimates were calculated using the method described by Strauss (1982), followed by t-tests to determine if index values, *S*, differed significantly from zero.

The possible relationship between zooplankton concentrations and menhaden larvae concentrations in samples was tested by calculating Pearson correlation coefficients. This relationship was tested in each of the three years

Results

Hydrography at the Chesapeake Bay Mouth

Mean water-column temperatures at the Bay mouth during cruises ranged from 4.53°C to 14.29°C over the three-year study (Chapter 2, Table 2.2). The mean temperatures differed significantly among years (nested ANOVA, $p < 0.001$). The mean water temperature was lowest in 2005-06 ($\bar{x}$ = 8.25 °C ± 0.16 se), intermediate in 2006-07 ($\bar{x}$ = 9.65 °C ± 0.19 se), and highest in 2007-08 ($\bar{x}$ = 10.31 °C ± 0.15 se) (Chapter 2, Table 2.2). In each of the years, the within-year monthly (i.e., among cruises) mean water temperatures also differed significantly (nested ANOVA, $p < 0.001$). Only in January and February 2008 were temperatures not significantly different.

Mean water-column salinity at the Bay mouth ranged from 22.98 to 29.47 among cruises (Table 2.2). The mean salinity was lowest in 2005-06 ($\bar{x}$ = 25.60 ± 0.25 se), intermediate in 2006-07 ($\bar{x}$ = 26.35 ± 0.16 se), and highest in 2007-08 ($\bar{x}$ = 27.68 ± 0.12 se). Mean salinity differed significantly among the three years (nested ANOVA, $p < 0.001$) and among months within each year ($p < 0.001$). The mean salinity in 2005-06

was significantly lower than in 2006-07 ($p = 0.004$) and 2007-08 ($p < 0.001$). Mean salinity in 2006-07 was significantly lower than the mean salinity in 2007-08 ($p < 0.001$).

Catches of Larvae

A total of 9,840 larvae was collected at the Chesapeake Bay mouth (Chapter 2, Table 2.1). Catches and concentrations of larvae were highest in 2007-08 and lowest in 2006-07 (Chapter 2, Figure 2.2). The highest catches occurred at different temperatures during the three years. In 2005-06, the highest catches occurred at temperatures between 5 and 10 ^{o}C (Figure 2.2a). In 2006-07, highest catches were at temperatures < 6 ^{o}C (Figure 2.2b) while in 2007-08 highest catches were made at > 9 ^{o}C (Figure 2.2c).

Ages, Lengths, and Hatch Dates

Lengths

The length-frequency distributions of menhaden larvae were similar among years (Chapter 2, Figure 2.3). In each year the modal length was 27.00 mm TL. The mean lengths of larval menhaden differed significantly among the three years ($p < 0.001$). The mean length in 2005-06 ($\bar{x} = 26.88$ mm ± 0.12 se) was significantly smaller than in the other years; mean lengths did not differ between 2006-07 ($\bar{x} = 27.94$ mm ± 0.10 se) and 2007-08 ($\bar{x} = 28.13$ mm ± 0.05 se) (ANOVA and Tukey's HSD, $p = 0.178$) (Chapter 2, Table 2.3).

Mean lengths of menhaden larvae differed significantly among cruises within each year ($p < 0.001$) (Table 2.4). In each year, mean lengths were significantly smaller

in the first cruise (November or December) than in other months. No other seasonal patterns in mean lengths were recorded.

Length-frequency distributions of ingressing larval menhaden were very similar among cruises (Chapter 2, Figure 2.4). Virtually all larvae were in the 15 to 35-mm TL range and the overall range was from 6 to 40 mm TL. There was a clear bimodality in the length-frequency distribution of larvae collected during the December 2005 cruise, but the distributions appeared to be uni-modal in remaining cruises. The length distributions in November 2006 and November 2007 tended to be skewed toward smaller lengths.

Ages

The mean age-at-ingress, based on otolith-aged larvae, was 47 days post-hatch. Mean age differed significantly among years (nested ANOVA, $p < 0.001$). The oldest mean age-at-ingress was observed in 2006-07 ($\bar{x}$ = 49.85 d ± 0.86 se). It was significantly older than mean age in 2005-06 ($\bar{x}$ = 44.20 d ± 0.66 se) ($p < 0.001$) and in 2007-08 ($\bar{x}$ = 46.03 d ± 0.56 se) ($p < 0.001$). Mean ages in 2005-06 and 2007-08 did not differ ($p = 0.092$) (Table 3.1).

The mean age of menhaden larvae differed significantly among cruises (i.e., months) within each year (Table 3.2; Figure 3.1). In 2005-06, mean age was significantly lower in December ($\bar{x}$ = 41.10 d ± 1.68 se) than in all other cruises except March ($\bar{x}$ = 40.75 d ± 3.01 se) when only four larvae were available to be aged (Table 3.2). In 2006-07, the mean age of larvae in November ($\bar{x}$ = 30.93-d ± 0.73 se) was > 10 d younger than the mean age in any other cruise. The oldest mean age in 2006-07 was observed in

January ($\bar{x}$ = 63.00 d ± 4.01 se) when only 10 larvae were available for aging. That value was the oldest monthly mean age at ingress observed in the three-year program. Unlike 2005-06 and 2006-07, lowest mean ages in 2007-08 were not observed in November or December, but in February ($\bar{x}$ = 36.17 d ± 1.46 se) and March ($\bar{x}$ = 42.95 d ± 1.16 se) (Table 3.2; Figure 3.1).

Hatch dates

The earliest back-calculated hatch date of menhaden larvae in 2005-06 was on 7 October 2005 and the latest was on 9 March 2006. In 2006-07, hatch dates ranged from, earliest on 23 September 2006 to latest on 17 March 2007. In 2007-08, the earliest hatch date was 24 September 2007 and the latest 03 March 2008 (Figure 3.2). In 2005-06, the highest frequency of hatch dates occurred in November 2005. These larvae were collected during the January 2006 cruise. The highest frequency of hatch dates in 2006-07 occurred over the period from mid-November through mid-December 2006. Larvae hatched in that period were mostly collected during the February 2007 cruise. In 2007-08, the most frequent hatch dates occurred earlier than in other years, with highest frequencies observed from October through mid-November. Larvae hatched in that period were collected during the November and December 2007 cruises. The near absence of larvae hatched in December 2007 is notable (Figure 3.2).

Most ingressing larvae in the three-year program had hatch dates that occurred before January. The percentage of larvae hatched by December 15 was 97% in 2005-06, 98% in 2006-07, and 91% in 2007-08. The proportion of larvae hatched by December 15

in 2007-08 was somewhat lower because of a relatively large contribution of larvae hatched in January-February 2008.

Also common among the three years was a clear progression of the modal hatch dates of larvae by cruise month, indicating that a new pool of ingressing larvae from offshore was being sampled during each cruise (Figure 3.2). There was little to no overlap in the hatch-date distributions of larvae collected on different cruises.

Growth Rates

Growth Rates

The Laird-Gompertz model provided excellent fits to the length-on-age relationships of larval menhaden in each of the three years (Figure 3.3). Growth rates of menhaden larvae were highest in the 21-30-day age interval in each year (Table 3.3). Growth rates in the 21 - 30 day interval were 0.56 mm/day in 2005-06, 0.61 mm/day in 2006-07, and 0.56 mm/day in 2007-08. After age 40 days, growth rates declined and slowest growth rates were observed in the 70 - 80-day age interval. Growth rates in that 10-day age interval were 0.37 mm/day in 2005-06, 0.36 mm/day in 2006-07, and 0.39 mm day in 2007-08. The decay rate coefficient (k parameter in the Laird-Gompertz models) was significantly higher in 2006-07 ($k = 2.28$) than in 2007-08 ($k = 2.16$) (t-test, $p < 0.001$). The k parameter in 2005-06 ($k = 2.21$) was not significantly different from k in the other two years.

Weight-Length Relationship

For all three years combined, the piece-wise power model explained 95 percent of the variability in the weight-on-length relationship compared to only 88 percent explained by a simple power model (Figure 3.4 a-b). The piece-wise model estimated a breakpoint, c, at 27.69 mm TL. The allometric power coefficient at lengths < c is b_1 = 5.06 and at lengths > c it is b_2 = 5.46. These coefficients were comparatively higher than the allometric coefficient in the simple power regression model (b = 4.64) (Figure 3.4a).

The break points, c, in the weight-length relationships for each year were 29.00 mm TL in 2005-06, 27.56 mm TL in 2006-07, and 34.23 mm TL in 2007-08. In 2005-06 the allometric coefficient is b_1 = 4.89 for lengths < c and b_2 = 5.94 for lengths > c. In 2006-07 b_1 = 4.83 for lengths < c and b_2 = 5.63 for lengths > c. In 2007-08, b_1 = 4.68 for lengths < c and b_2 = 4.71 for lengths > c.

Larval Menhaden Feeding

Prey Types

Ten prey types were identified in guts of Atlantic menhaden larvae collected at the Chesapeake Bay mouth (Table 3.4). The most common prey types were copepods, cladocerans, barnacle nauplii, and bivalve larvae. The genera of copepods in the larval diet were similar among years, with *Acartia spp*. and *Centropages spp*. dominating. In 2005-06, 59.8 percent of the copepods were *Acartia*, 39.1 percent were *Centropages*, and 1.1 percent was the parasitic genus *Caligus*. *Caligus* parasites were found only in the guts of and not attached to the body of menhaden larvae. In 2006-07, 41.3 percent of the copepods were *Acartia*, 56.4 percent were *Centropages*, 1.1 percent were *Temora*, and

1.1 percent were *Caligus*. In 2007-08, 54.9 percent of the copepods were *Acartia*, 44.4 percent were *Centropages*, and 0.7 percent were *Temora*. Cladocerans in the diets were mostly of the species *Podon polyphemoides* and *Evadne tergestina*. Barnacle nauplii in diets were *Balanus spp.*, most likely *Balanus vestnusus*.

In each of the three years only two prey types contributed ≥ 70 percent by number to the larval menhaden diets (Figure 3.5 a-c). In all years, the dominant four prey were copepods, cladocerans, barnacle nauplii, and bivalve larvae. Copepods were the principal prey in each year (Figure 3.6 a-c). The mean number of copepods per larval gut was 0.38 (± 0.05 se) in 2005-06, 0.97 (± 0.13 se) in 2006-07, and 0.71 ± (0.11 se) in 2007-08. The mean number of copepods per gut differed among years ($p < 0.001$). An ANOVA followed by Tukey's test indicated that the mean number of copepods per gut in 2005-06 was significantly lower than the mean number in 2006-07 ($p < 0.001$) and marginally lower than in 2007-08 ($p = 0.047$). Mean number of copepods per gut did not differ in 2006-07 and 2007-08 ($p = 0.185$).

In 2005-06, 46.3 percent of the larval menhaden diet was copepods, 32.5 percent was barnacle nauplii, 13.8 percent was cladocerans, and 1.1 percent was bivalve larvae (Table 3.5). In 2006-07, copepods increased to 67.7 percent of the diet. In that year, bivalve larvae also were more common in the larval diets (13.9%) and barnacle nauplii were less common (10.7%). In 2007-08, 70.1 percent of the larval diet was copepods and 14.2 percent was barnacle nauplii, while cladocerans and bivalve larvae were less important. Monthly patterns observed in larval menhaden diets were consistent, with copepods dominating the diet during each month (Table 3.6; Figure 3.7 a-c).

Larval Feeding: Prey Incidence

Prey incidence in guts of menhaden larvae 1) averaged 55% over all cruises in the three-year program, 2) ranged from 7% to 100% among cruises, and 3) was highest on average (77%) in 2006-07 (Table 3.7). There was monthly variability in prey incidence. For example, in April 2006, 67 percent of the larvae had at least one prey in their guts compared to only 25 percent in March 2006. Prey incidence during 2006-07 was consistently high among months, except for March 2007 when only 48 percent of the larvae had at least one prey in their guts. The low average prey incidence in 2007-08 was attributable to the particularly low incidences in December (11%) and February (7%). The average incidence for the remaining months in 2007-08 was 56%

The percentage of larvae with at least one prey occurrence relative to the number with empty guts differed significantly among years (Chi-square = 74.15: $p < 0.001$) (Table 3.8). In 2005-06, no differences were detected in prey incidence among months (Chi-square = 3.57: $p > 0.05$) (Table 3.9a). In 2006-07, there were significant among-month differences (Chi-square = 35.66: $p < 0.001$) (Table 3.9b). Prey incidences were highest in November 2006, December 2006, and January 2007 when nearly all larvae had prey in their guts (Table 3.9). In 2007-08, the among-month differences in prey incidence also were significant (Chi-square = 46.56: $p < 0.001$) when incidences were lowest in December 2007 and in February (Table 3.9c).

The probability of prey occurrence in the gut of a menhaden larva, derived from logistic regression (Table 3.10; Figure 3.8), increased with larval length ($p < 0.001$). The rate of increase in probability of prey occurrence in larval guts with respect to total length

was significantly faster in 2005-06 compared to 2006-07 ($p = 0.001$) and 2007-08 ($p = 0.007$).

Feeding Success: Number of prey per gut

Feeding success, defined as the number of prey per gut, increased with larval length and differed significantly among the three years as interpreted from the quasi-Poisson regression ($p < 0.001$). Mean numbers of prey per gut ranged from 1.12 in 2007-08 to 2.25 in 2006-07. Feeding success was significantly higher in 2006-07 than in 2005-06 ($p < 0.001$) or 2007-08 ($p < 0.001$) (Figure 3.9) but judged to be similar in 2005-06 and 2007-08 ($p = 0.154$). Feeding success increased in relation to larval length for all years combined ($p < 0.001$), especially for > 30-mm larvae (Figure 3.10). The number of prey per gut as a function of menhaden length was not tested for individual years because the interaction between length and years was not significant and therefore excluded from the model.

Zooplankton Availability

Concentrations of mesozooplankton, the primary prey for menhaden larvae at the Bay mouth, differed significantly among years ($p < 0.001$) (Figure 3.11). Mean total zooplankton concentrations at the Bay mouth did not differ significantly among years (ANOVA, $p = 0.079$) (Table 3.11). In 2007-08, there were no data available in February to include in the estimate of mean concentration for that year.

Mean total zooplankton concentrations differed among cruise months ($p < 0.001$) (Table 3.12). In 2005-06 and 2007-08, highest mean concentrations were in April, but in

2006-07 highest concentrations occurred in November. There was no clear pattern of seasonal variability in zooplankton concentrations (Table 3.12).

The most abundant zooplankton taxa at the mouth of the Chesapeake Bay were the copepods *Acartia tonsa* and *Centropages typicus*, the cladocerans *Podon polyphemoides* and *Evadne tergestina*, and barnacle nauplii that probably were *Balanus vestnusus*. The mean concentrations for these taxa were similar among years (Figure 3.12). Copepods made up ≥ 70 percent of the zooplankton composition at the Chesapeake Bay mouth (Table 3.13). Copepods constituted the dominant zooplankton taxa during each cruise month of the study (Table 3.14).

Prey Selectivity

Larvae of Atlantic menhaden were not particularly selective with respect to feeding on any of the four most common prey types in their diet. Strauss's index values ranged from -0.24 to +0.12 during the three years (Table 3.15). These index values did not differ significantly from zero ($p \geq 0.05$). Analyzing by cruise, the monthly Strauss's index values ranged from -0.36 to +0.47. Only two instances of significant selectivity were found (Table 3.16). Cladocerans were positively selected in March 2006 ($S = + 0.47$; $p = 0.019$) and copepods were positively selected in November 2006 ($S = + 0.23$; $p = 0.049$). There was no correlation between zooplankton concentrations and menhaden larvae concentrations at the Bay mouth ($r = -0.013$).

Discussion

Atlantic menhaden larvae hatch offshore and disperse to bays and estuaries on the North American east coast during the late-larval stage, approximately 6-8 weeks after being spawned. In my collections at the Chesapeake Bay mouth, larvae ranged from 6.6 to 40.0 mm TL, averaging 27.8 mm TL, and 46.7 days in age. Variability in ocean conditions on the continental shelf was hypothesized to be a probable source of inter-annual differences in sizes and growth rates of ingressing larvae. The time that larvae are resident in the vicinity of the Bay mouth is not known, but the relatively uniform length range and the progression of hatch dates of larvae collected in the surveys indicate that larvae dispersing from offshore to the Bay mouth do not spend a lengthy period at the Bay mouth. Larvae at ingress have spent most of their lives in the offshore environment and thus were mostly subject to offshore conditions, which presumably were warmer temperatures and higher salinities, prior to ingress.

The mean age at ingress into Chesapeake Bay for Atlantic menhaden larvae ranged from 31 to 63 days post-hatch in all months. These ages at ingress are similar to age at ingress in North Carolilna and Delaware (Warlen 1992; Warlen *et al*. 2002) and also age at ingress of larval gulf menhaden *Brevoortia patronus* (Warlen 1988). The mean age of ingressing larvae at the Chesapeake Bay mouth did not differ greatly among cruises or inter-annually. The observed mean age was 14 days younger than mean age at estuarine recruitment into North Carolina estuaries (61 days) (Warlen 1992, 1994). Warlen *et al*. (2002) reported that age at ingress of menhaden larvae into Delaware Bay, another mid-Atlantic estuary, was on average 10 days younger than larvae ingressing into

North Carolina estuaries and thus it is similar to my estimated mean age at ingress, 46.7 days, into Chesapeake Bay. The difference in mean age at ingress between North Carolina and the Delaware-Chesapeake regions may be a consequence of differences in transport mechanisms and distances from spawning areas. The Chesapeake Bay is located in the southern portion of the mid-Atlantic region and offshore spawning by menhaden in that region is thought to make substantial contributions to larvae that recruit into North Carolina estuaries, based primarily on interpretations from circulation models (Quinlan et al. 1999; Rice *et al*. 1999; Stegmann *et al*. 1999; Werner *et al*. 1999). If true, menhaden larvae hatched in the mid-Atlantic Bight must disperse over greater distances to reach North Carolina estuaries than to Chesapeake Bay and this could partly account for the greater age at ingress observed in North Carolina.

Although mean age of menhaden larvae at the Chesapeake Bay mouth differed among the three years of my research, the ages were remarkably similar, differing by only 6 days. Larvae entering the Chesapeake Bay in 2006-07 were older than larvae entering during the other years. Variability in transport times of larvae to Chesapeake Bay potentially can result from numerous causes, including variability in offshore circulation and variability in adult menhaden spawning migrations and locations. Warlen *et al*. (2002) noted inter-annual differences in the mean age at ingress of Atlantic menhaden entering Beaufort Inlet, North Carolina, and Little Egg Inlet, New Jersey. The mean age at ingress to Beaufort Inlet was 60.7 days in 1989-90, 58.6 days in 1990-91, and 69.3 days post-hatch in 1992-93. Differences in mean age at ingress to the New Jersey inlet during the same years were less variable. The mean ages in New Jersey were

54.3, 52.7, and 50.9 days post-hatch. No attempt was made to explain causes of the observed variability (Warlen et al. 2002).

There was no seasonal pattern or trends in ages of ingressing menhaden larvae sampled at the Chesapeake Bay mouth. Ages of larval Atlantic menhaden ingressing into North Carolina estuaries increased seasonally (from December to March) from 41 to 79 days post-hatch (Warlen 1992), suggesting a shift in transport conditions during the season. Mean ages of menhaden larvae at the Chesapeake Bay mouth, however, ranged from 40 to50 days post-hatch in all months except for November 2006 (mean age = 31 d) and January 2007 (mean age = 63 d). The seasonal pattern observed in North Carolina by Warlen (1992) may be unique to that region because of hydrographic patterns or possibly a seasonal shift in the source region of larvae that are dispersed to the Carolina coast if spawning shifts from the Mid-Atlantic to South Atlantic. Alternatively, Warlen suggested that an increase in offshore flow in the late season could prolong transport time.

The hatch-date frequencies in my analysis have been adjusted to account for cumulative mortality of larvae in the population before sampling. A conservative estimate of mortality rate (0.15 d^{-1}) was applied to all ages in the unadjusted frequency distributions of larvae. Houde and Zastrow (1993) estimated the mean mortality rate of clupeiform larvae to be 0.179 d^{-1}. If the daily mortality of menhaden larvae were higher or lower than 0.15d^{-1}, the frequency distributions of hatch dates will be biased, especially for derived dates of the oldest larvae in my samples. Estimates of mortality of Atlantic menhaden larvae in the offshore environment are not available. Although potentially biased, my hatch-date frequency distributions are better than frequencies calculated

without considering the cumulative effects of mortality. Estimating mortality of larvae in the offshore environment is an important future research need. Measures of offshore mortality, if undertaken, also should be age-specific to account for probable declines in the rate with age and size (Houde 1997).

Hatch dates of Atlantic menhaden larvae at the Chesapeake Bay mouth ranged from late September to early March, indicating a protracted season of spawning that supplies recruits to the Bay. Spawning by Atlantic menhaden in the mid-Atlantic occurs during the fall and moves southward, and is mostly south of Cape Hatteras, North Carolina, by December (Higham and Nicholson 1964; Judy and Lewis 1983; Berrien and Sibunka 1999). Based on collections from the Marine Monitoring and Assessment and Prediction Program (MARMAP) (Berrien and Sibunka 1999), Stegmann *et al*. (1999) concluded that eggs of Atlantic menhaden are absent in the Mid-Atlantic region at temperatures < 12^{o}C. More than 90 percent of the menhaden larvae ingressing into Chesapeake Bay were hatched before mid-December in each of the three years. Because menhaden larvae hatch ≤ 2 days after eggs are spawned (Kuntze and Radclife 1917), temperatures experienced by newly-hatched larvae must be similar to those at spawning. In each of the three years, surface water temperatures approximately 27 km offshore of Chesapeake Bay dropped below 12^{o}C before mid December (Figure 3.13), suggesting that conditions had become unsuitable for spawning in this region. Menhaden larvae in my collections with hatch dates after December were uncommon in 2005-06 and 2006-07. In 2007-08, larvae with hatch dates in December were absent but hatch dates were observed between January and late February 2008.

The observed hatch-date distribution in 2007-08 indicated potential bimodality in either spawning activity or a shift in the region of origin of the larvae. Spawning by Atlantic menhaden in the Mid-Atlantic has been reported to be bimodal, with spawning occurring during a southward migration in the fall and again during a spring northward migration (Nicholson 1971; Judy and Lewis 1983). The high number of menhaden larvae that ingressed into Chesapeake Bay during March 2008 had hatch dates from late January to late February 2008. Based on larval and adult distributions, spawning is thought to concentrate in the South Atlantic Bight (SAB) during that period (Higham and Nicholson 1964; Judy and Lewis 1983; Berrien and Sibunka 1999). Temperatures in the SAB remain favorable for spawning in January and February and the SAB is a probable source of larvae recruiting into Chesapeake Bay. Although the mechanisms that deliver menhaden larvae to the Mid-Atlantic from the SAB have not been fully explained, model simulations on time-independent, constant-wind fields during the spring (Quinlan *et al*. 1999) suggested that a northward-flowing, nearshore current can potentially deliver southern-spawned larvae into mid-Atlantic estuaries.

Peak hatch dates of larval menhaden in the Chesapeake Bay in 2005-2008 differed from peak hatch dates of surviving juveniles in summers of 2006-2008, based on otolith-aging analysis of juveniles from Virginia and Maryland sub-estuaries in the Bay (Secor and Wingate unpublished data; Houde et al. 2009). Hatch dates of larval menhaden peaked in the October to December period but the hatch dates of juvenile survivors peaked in the January - February period. This suggests that, although there were strong contributions to ingress of menhaden larvae to Chesapeake Bay from hatching in October - December, survival of these early-hatched individuals was low in

the years of my research. Menhaden hatched in the October - December period entered the Bay as late-stage larvae from November - February. Temperatures experienced by larvae upon entrance to Chesapeake Bay in the December – February period were the coldest observed in each of the three years. It is possible that under such conditions survival of ingressing menhaden larvae hatched in October-December was lower than survival of ingressing larvae hatched in late winter but ingressing to the Bay in the late February to April period.

Light and Able (2003) and Warlen *et al*. (2002) also reported recruitment of menhaden into mid-Atlantic estuaries with spawn dates in the winter period when spawning is thought to occur in the SAB. They speculated that northward transport was possible by entry of the larvae into the Gulf Stream. Checkley *et al*. (1988) reported catches of small menhaden larvae off North Carolina near the western edge of the Gulf Stream. This mechanism is possible, although the processes that allow larvae to leave the Gulf Stream and disperse toward estuaries were not described.

The mean, age-specific growth rates of menhaden larvae, estimated from the Laird-Gompertz models fit to data in each year, exceeded 0.50 mm/d in the first 50 days posthatch. This mean growth rate was similar to the mean growth rate (0.48 mm/day) directly measured from otolith aging of small menhaden larvae off North Carolina by Maillet and Checkley (1991). In each of the three years of my research, fastest growth occurred in the 21-30 day-old period. Growth rates of larvae older than 50 days clearly declined. My growth rates and patterns differed to a degree from those reported and summarized by Warlen (1992). His Laird-Gompertz model and derived growth rates indicated fastest growth in the 1-20 day age interval, with declines thereafter. In my

study, mean growth rates increased in each 10-day age interval until 30 days post-hatch (Table 3.3). The difference in estimated growth rates of younger larvae between the Warlen (1992) study and mine could be in part an artifact. Relatively few young larvae were available in my research, which required forcing the Laird-Gompertz model through the y-intercept at 3.6 mm, the known size-at-hatch of menhaden larvae, to obtain a fit and estimates of growth rates for larvae < 20 days old, which were hardly represented in my samples (Figure 3.3).

The Laird-Gompertz parameter, *k*, was significantly higher in 2006-07 compared to 2007-08, indicating a faster rate of decay from the initial instantaneous growth rate, although not necessarily faster growth, which was faster in 2006-07 than in other years (see Table 3.3). The inter-annual variability in the parameter *k* indicates differences in growth rates. Inter-annual differences in growth rates of gulf menhaden larvae have been reported (Warlen 1988). The mean growth rates of gulf menhaden larvae from the Gulf of Mexico in the first 60 days after hatch was 0.39 mm/day (Warlen 1988), rates slower, on average, than those I estimated for Atlantic menhaden at the Chesapeake Bay mouth. Warlen (1988) attributed inter-annual differences in growth rates of gulf menhaden larvae to inter-annual variability in offshore conditions, especially temperature.

Estimates of growth of larval menhaden collected at the Chesapeake Bay mouth represent primarily growth that had occurred during the oceanic phase under warmer temperature conditions than those near the Chesapeake Bay mouth. I had no measure of inter-annual variability in offshore environmental conditions or direct estimates of growth in early-stage larvae from offshore that likely had a strong influence on overall growth

dynamics and patterns apparent in larvae collected at the Bay mouth. Obtaining such information is an important need in future research.

The weight-on-length relationship in late-stage menhaden larvae undergoes an ontogenetic shift that already was apparent in some of the larger larvae collected at the mouth of Chesapeake Bay. The allometric coefficient in the power model describing the weight-length relationship increased at a break-point length of 27.69 mm TL. Lewis *et al*. (1972) reported that morphometrics in young Atlantic menhaden collected from North Carolina, had two inflection points. The first point, at 30 mm TL, was described as denoting the onset of metamorphosis to the juvenile stage. This pre-juvenile stage encompassed the 30 - 38 mm TL range. Balon (1984) designated this period of growth, in Atlantic menhaden and other fishes, as saltatory, indicative of a period in ontogeny when rapid changes in form and function are observed. In the pre-juvenile stage of Atlantic menhaden, rate of increase in body depth is rapid (Lewis *et al*. 1972). Other, quite drastic, ontogenetic changes occur during metamorphosis in the gill structures and alimentary tract in preparation for a diet shift from predation on zooplankton to filter-feeding on phytoplankton (June and Carlson 1971). Changes in the alimentary tract began at about 31 mm FL (= 33 mm TL) for larval Atlantic menhaden collected at the Indian River Inlet, Delaware (June and Carlson 1971). The estimated size of change in allometric body growth of 27.69 mm TL for larvae pooled over the three years of my study occurred at a smaller size than reported by Lewis *et al*. (1972) (30 mm TL). The estimated break points in the weight-length relationships in each year of my study indicated variability in estimates of the length at inflection among years. The break points were 29.00 mm TL in 2005-06, 27.56 mm TL in 2006-07, and 34.23 mm TL in

2007-08. The break point reported by Lewis *et al*. (1972) at 30 mm TL was derived from a single year of data whereas the mean inflection point (at 27.69 mm TL) from my study was from three years of data. The average break point taken from my three individual years is 30.26 mm TL, a value similar to that of Lewis *et al*.

Ten different prey types were identified in the diets of larval Atlantic menhaden. In each year, 2 or fewer prey types dominated, composing > 70% of larval menhaden diets. Copepods were the most common prey, accounting for > 60% of the prey, by number, in the larval diets for each year. Copepods were reported to compose 99% of the diet in larval menhaden from the Newport River estuary, North Carolina (Kjelson *et al*. 1975) and from Indian River Inlet, Delaware (June and Carlson (1971). Copepods are usually reported as the most common prey of coastal and estuarine larval fishes. For example, the most common prey of larvae of 12 species in Biscayne Bay, Florida, was copepods and copepod nauplii (71%) (Houde and Lovdal 1984). Copepods often are reported to be preferred prey for larvae of clupeoid fishes such as herring *Clupea harengus* (Hardy 1924; Bowers and Williamson 1951). The diet of small (< 9 mm notochord length NL) gulf menhaden larvae was a combination of zooplankton and phytoplankton (Stoecker and Govoni 1984). In the Gulf of Mexico, gulf menhaden < 6 mm TL were shown to mostly feed on copepods and phytoplankters (Govoni *et al*. 1983). In the same region, spot and Atlantic croaker had fed almost exclusively on zooplankters (Govoni *et al*. 1983). Govoni *et al*. (1983) noted that the diets of small gulf menhaden larvae shifted to feeding exclusively on zooplankton as they grew.

Although diet studies on larval menhaden are uncommon, results from the present study apparently are unique in that prey types other than copepods were at least

moderately important in larval menhaden diets at the Chesapeake Bay mouth. Barnacle nauplii, cladocerans, and bivalve larvae were substantial components of the diet. In each year, barnacle nauplii were second in percent composition, by number. Cladocerans ranked third in percent composition in 2005-06 and 2007-08 but bivalve larvae were third in number in 2006-07. None of these zooplankters were reported in diet studies on menhaden larvae of the same size by June and Carlson (1971) for larvae from the Delaware Bay or by Kjelson *et al*. (1975) for larvae in North Carolina estuaries.

The diets of larval Atlantic menhaden at the mouth of the Chesapeake Bay largely were representative of the proportional representation of prey available to them near the Bay mouth. The larvae did not appear to be highly selective in their feeding. Three of the top four prey types in larval guts (copepods, barnacle nauplii, and cladocerans) also occurred at the highest mean concentrations in zooplankton samples at the Chesapeake Bay mouth. The concentration of bivalve larvae at the Bay mouth was relatively low but was highest in 2006-07 and in 2007-08, the years when they were most common in larval guts. The numerical abundance of mesozooplankton at the Bay mouth was dominated by copepods during the three-year study. The annual prey selectivity index (Strauss 1979) values I derived did not surpass a value of ± 0.24 for any of the prey in any year and did not differ significantly from zero. Monthly Strauss index values for each of the top four prey types did not surpass a value of ± 0.47 and only two monthly values were significantly different from zero.

Inter-annual variability in feeding success did not follow a pattern similar to observed differences in zooplankton concentrations. Zooplankton concentrations also were not correlated with larval concentrations at the Bay mouth. Total zooplankton

concentrations were lowest in 2007-08. However, the number of prey in guts of larval menhaden was significantly higher in 2006-07 than in the other two years. Caution is needed when interpreting feeding success of larval Atlantic menhaden. June and Carlson (1971) found that menhaden larvae may instantaneously defecate their gut contents during capture. This is a common occurrence among fish larvae with straight, tube-like guts that characterize all clupeoid fish larvae (Blaxter 1965; Hay 1981; Fernandez and Gonzalez-Quiros 2006). Furthermore, June and Carlson (1971) reported that most larval gut contents were expelled in violent spasms when living menhaden larvae were placed into Formalin solution. Gut fullness of clupeoid fish larvae has been reported to be lower in general than in other taxa (Pepin and Penney 2000). The high percentage of menhaden larvae with empty guts (Table 3.7) that I observed probably resulted from stress during collection.

Feeding success of larval menhaden that I analyzed was length-dependent as has been demonstrated for most fish larvae (Miller *et al*. 1988). Number of prey per gut increased exponentially as larval length increased, indicating a rapid increase in feeding success as larvae grew. The probability of larvae having at least one prey item in their guts was also length-dependent. This relationship differed inter-annually. The probability of successful feeding by larvae increased at a faster rate in 2005-06, with respect to total length, than in the other two years.

In this research I have shown that the mean time from hatch to estuarine ingress to Chesapeake Bay was 47 days and that most ingressing larvae had hatched in the November – December period. Back-calculated peak hatch-dates of larval menhaden ingressing to Chesapeake Bay were poorly represented in YOY juvenile menhaden

sampled during summer months suggesting selective survival that favored late-hatched larvae in the 2005-2008 period. Mean growth during the oceanic phase of larval Atlantic menhaden, estimated from growth models, varied inter-annually but ranged from 0.52 to 0.57 mm/day. Atlantic menhaden experience a saltatory change in allometry of body growth between 27 and 35 mm TL that, combined with the low temperatures encountered near the Bay mouth, may be the principal causes of declining growth rates. As menhaden larvae grow larger their feeding success increases. In the Chesapeake Bay, larval menhaden fed predominantly on copepods, but other prey types not previously reported in diet studies on larval menhaden were commonly eaten. It would be valuable to establish a consistent sampling program for larval menhaden at the Chesapeake Bay mouth to monitor ingress of menhaden larvae, its inter-annual variability, the condition, growth and ages of ingressing larvae, and the relationship to late-summer abundance of YOY juveniles in the Bay. Additionally, a program to determine the offshore dynamics of spawning, egg and larvae ecology, and transport pathways would greatly expand our knowledge of recruitment processes in Atlantic menhaden.

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Table 3.1. Mean ages (days) of Atlantic menhaden larvae from otolith-aged larvae collected at the Chesapeake Bay mouth during the three-year program. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean age sharing a letter do not differ significantly.

Year	Mean Age	Tukey	se	n
2005-06	44.20	A	0.66	251
2006-07	49.85	B	0.86	240
2007-08	46.03	A	0.56	243

Table 3.2. Mean ages of Atlantic menhaden larvae from otolith-aged larvae collected at the Chesapeake Bay mouth during the three-year program. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean ages for cruise months sharing a letter do not differ significantly.

Month	Mean Age	se	n	Tukey
Dec '05	41.10	1.68	31	A
Jan '06	44.64	1.03	96	B
Feb '06	44.50	1.03	114	B
Mar '06	40.75	3.01	4	AB
Apr '06	50.00	3.79	6	B
Nov '06	30.93	0.73	29	A
Dec '06	57.14	1.09	36	BC
Jan '07	63.00	4.01	10	B
Feb '07	51.83	1.29	114	D
Mar '07	46.13	1.58	23	D
Apr '07	50.39	1.35	28	CD
Nov '07	46.77	0.83	82	A
Dec '07	49.25	1.18	36	AB
Jan '08	50.83	1.56	30	B
Feb '08*	36.17	1.46	30	C
Mar '08	42.95	1.16	39	C
Apr '08	49.73	1.44	26	AB

Table 3.3. Mean growth rates (ĝ = mm/d) at 10-day age intervals for Atlantic menhaden larvae. Growth rates were calculated from Laird-Gompertz growth-model fits in each year (Figure 3.3).

2005-06		2006-07		2007-08	
Age Interval	***ĝ***	**Age Interval**	***ĝ***	**Age Interval**	***ĝ***
1-10	0.46	1-10	0.53	1-10	0.45
11-20	0.53	11-20	0.60	11-20	0.53
21-30	0.56	21-30	0.61	21-30	0.56
31-40	0.54	31-40	0.57	31-40	0.55
41-50	0.50	41-50	0.51	41-50	0.51
51-60	0.45	51-60	0.45	51-60	0.47
61-70	0.41	61-70	0.40	61-70	0.43
71-80	0.37	71-80	0.36	71-80	0.39

Table 3.4. Prey types and frequency of occurrence in the guts of Atlantic menhaden larvae collected at the Chesapeake Bay mouth in the three-year program.

Prey	2005-06	2006-07	2007-08
Metatrochophore	3	1	0
Bivalve veligers	5	35	22
Copepod	109	242	176
Copepod nauplii	7	0	1
Ostracod	4	0	0
Cladoceran	46	49	7
Barnacle nauplii	71	45	35
Polychaete	2	0	2
Decapod	0	3	0
Tunicate	0	0	9
Total Larvae	**251**	**540**	**243**

Table 3.5. Percentages (by number) of total prey by prey type in the guts of Atlantic menhaden larvae collected at the Chesapeake Bay mouth in the three-year program.

Prey	2005-06	2006-07	2007-08
Copepods	46.3	67.7	70.1
Barnacle nauplii	32.5	10.7	14.2
Cladocerans	13.8	5.4	3.9
Bivalve larvae	1.0	13.9	7.0
Other	6.4	2.3	4.8

Table 3.6. Monthly percent of total prey by prey type in the guts of Atlantic menhaden larvae collected at the Chesapeake Bay mouth in the three-year program.

Cruise	Copepod	Cladoceran	Barnacle nauplii	Bivalve larvae	Other
Dec '05	80	13	2	0	5
Jan '06	61	6	31	0	2
Feb '06	32	16	40	2	10
Mar '06	50	50	0	0	0
Apr '06	40	40	20	0	0
Nov '06	100	0	0	0	0
Dec '06	45	4	12	39	0
Jan '07	47	36	11	0	6
Feb '07	77	5	5	11	2
Mar '07	100	0	0	0	0
Apr '07	65	3	27	0	5
Nov '07	80	4	2	10	4
Dec '07	87	0	0	13	0
Jan '08	68	0	8	13	11
Mar '08	59	0	35	2	4
Apr'08	66	14	16	0	4

Table 3.7. The percentage of Atlantic menhaden larvae with at least one prey item in their guts, i.e., 'prey incidence' for each month that was sampled at the Chesapeake Bay mouth.

Month	2005-06	2006-07	2007-08
Nov	no data	97%	37%
Dec	45%	97%	11%
Jan	47%	100%	60%
Feb	55%	68%	7%
Mar	25%	48%	64%
Apr	67%	86%	62%
Annual	51%	77%	39%

Table 3.8. Test of independence for the proportion of Atlantic menhaden larvae that had at least one prey (prey column) in their gut relative to the number with empty guts (empty) in the three-year program. The column 'tot' is the total number of fish in each year, $\hat{p}$ is the proportion of larvae with prey in their gut and $\hat{p}$ (prey) is that proportion multiplied by the number of larvae with prey in their gut.

	prey	**empty**	**tot**	$\hat{p}$	$\hat{p}$ ***(prey)***
2005-06	145	140	285	0.51	73.77
2006-07	185	55	240	0.77	142.60
2007-08	95	148	243	0.39	37.14
					253.52
tot	425	343	768	0.55	235.19
		Chi-square =	74.15		$p < 0.001$
		df = 2			

Table 3.9. Test of independence for the proportion of larval Atlantic menhaden that had at least one prey in their gut (prey) relative to the number with empty guts (empty) among cruise months in a) 2005-06, b) 2006-07, and c) 2007-08. The column 'tot' is the total number of fish in each month, $\hat{p}$ is the proportion of larvae with prey in their gut and $\hat{p}$ (prey) is that proportion multiplied by the number of larvae with prey in their gut.

		2005-06			
	prey	**empty**	**tot**	$\hat{p}$	$\hat{p}$***(prey)***
Dec	15	18	33	0.45	6.82
Jan	45	51	96	0.47	21.09
Feb	80	66	146	0.55	43.84
Mar	1	3	4	0.25	0.25
Apr	4	2	6	0.67	2.67
					74.66
tot	145	140	285	0.51	73.77
		Chi-square =	3.57		$p > 0.05$
		df = 4			
		2006-07			
	prey	**empty**	**tot**	$\hat{p}$	$\hat{p}$ ***(prey)***
Nov	28	1	29	*0.97*	*27.03*
Dec	35	1	36	0.97	34.03
Jan	10	0	10	1.00	10.00
Feb	77	37	114	0.68	52.01
Mar	11	12	23	0.48	5.26
Apr	24	4	28	0.86	20.57
					148.90
tot	185	55	240	0.77	142.60
		Chi-square =	35.66		$p < 0.001$
		df = 5			
		2007-08			
	prey	**empty**	**tot**	$\hat{p}$	$\hat{p}$ ***(prey)***
Nov	30	52	82	*0.37*	*10.98*
Dec	4	32	36	0.11	0.44
Jan	18	12	30	0.60	10.80
Feb	2	28	30	0.07	0.13
Mar	25	14	39	0.64	16.03
Apr	16	10	26	0.62	9.85
					48.23
tot	95	148	243	0.39	37.14
		Chi-square =	46.56		$p < 0.001$
		df = 5			

Table 3.10. Logistic regression summary table for the probability of an Atlantic menhaden larva having at least one prey item in its gut as a function of larva length, year, and the interaction of larva length and year. The Estimate column provides estimates of the model coefficients, SE is standard error, z is z-score, and Pr(> |z|) is the *p*-value.

	Estimate	SE	z	Pr (> |z|)
Intercept	-8.92	1.26	-7.06	< 0.001
Total Length	0.35	0.05	7.18	< 0.001
Year	7.6	4.95	4.43	< 0.001
Total Length*Year	-0.35	0.18	-5.43	< 0.001

Table 3.11. Mean total zooplankton concentrations (number per m^3) at the mouth of the Chesapeake Bay in the three-year program. The column labeled months represents the total number of cruise months included in the analysis. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean concentrations differed significantly among years (Tukey column; different letters indicate significant differences).

Year	Mean Concentration	Tukey	se	n	Months
2005-06	1664.56	A	130.81	83	5
2006-07	1618.26	A	226.81	101	6
2007-08	1164.51	A	116.79	83	5

Table 3.12. Mean total zooplankton concentrations (number per m^3) by month at the mouth of the Chesapeake Bay during the three-year program. The 'n' column represents the number of samples used to calculate the mean. The column 'Tukey' is the outcome of the Tukey Honestly Significant Difference multiple comparisons tests. Mean concentrations for cruise months sharing a letter do not differ significantly.

Month	Mean Concentration	Tukey	se	n
Dec '05	844.02	A	172.04	14
Jan '06	1420.21	A	174.89	17
Feb '06	1798.83	A	168.13	22
Mar '06	1227.63	A	112.83	10
Apr '06	2517.41	A	401.5	20
Nov '06	2582.18	A	1003.44	19
Dec '06	574.84	B	60.08	14
Jan '07	1452.05	AB	214.36	10
Feb '07	898.22	AB	215.61	20
Mar '07	1798.87	AB	319.24	22
Apr '07	2142.23	AB	487.37	16
Nov '07	946.31	A	306.51	19
Dec '07	559.01	A	80.79	20
Jan '08	985.37	A	551.33	9
Mar '08	1493.37	A	165.16	16
Apr '08	1827.99	A	180.71	19

Table 3.13. Zooplankton taxa composition (percent by number) at the Chesapeake Bay mouth during 2005-08.

Zooplankton	2005-06	2006-07	2008-09
Copepods	70.5	74.1	80.0
Cladocerans	6.7	5.5	1.2
Barnacale nauplii	20.9	11.3	13.0
Bivalve larvae	0.1	1.6	1.6
Other	1.8	7.5	4.2

Table 3.14. Monthly zooplankton taxa composition (percent by number) at the Chesapeake Bay mouth during the three-year program.

Cruise	Copepods	Cladocerans	Barnacle nauplii	Bivalve larvae	Other
Dec '05	92.37	3.40	2.22	0.15	1.86
Jan '06	64.11	2.36	29.58	0.33	3.62
Feb '06	50.70	14.51	33.65	0.01	1.13
Mar '06	81.75	3.38	12.89	0.02	1.96
Apr '06	76.63	5.60	16.74	0.02	1.01
Nov '06	77.36	0.82	3.53	0.07	18.22
Dec '06	74.19	1.83	9.02	7.24	7.72
Jan '07	53.58	37.33	7.13	0.13	1.83
Feb '07	76.68	1.03	9.46	2.34	10.49
Mar '07	90.73	1.65	5.09	0.54	1.99
Apr '07	56.77	5.55	36.25	0	1.43
Nov '07	86.06	0.34	2.57	1.75	9.28
Dec '07	87.75	0.48	2.40	4.02	5.35
Jan '08	80.19	0.09	16.98	1.12	1.62
Feb '08	33.96	0.50	0.36	0	65.18
Mar '08	79.47	0.59	18.39	0.15	1.40
Apr '08	66.18	3.94	28.03	0.48	1.37

Table 3.15. Strauss selectivity index values for the four most common prey found in the guts of Atlantic menhaden larvae during the three-year program.

Year	Copepods	Cladocerans	Barnacle nauplii	Bivalves larvae
2005-06	-0.24	+0.07	+0.12	+0.01
2006-07	-0.06	0	-0.01	+0.12
2007-08	-0.1	+0.03	+0.01	+0.05

Table 3.16. Strauss selectivity index values for the four most common prey found in the guts of Atlantic menhaden larvae for monthly cruises during the three-year program. Index values significantly different from zero (*t*-test) are in boldface.

Cruise	Copepods	Cladocerans	Barnacle nauplii	Bivalve larvae
Dec '05	-0.12	+0.1	0	0
Jan '06	-0.03	+0.04	+0.02	0
Feb '06	-0.18	+0.01	+0.06	+0.02
Mar '06	-0.32	**+0.47**	-0.13	0
Apr '06	-0.36	+0.34	+0.03	0
Nov '06	**+0.23**	-0.01	-0.04	0
Dec '06	-0.29	+0.02	+0.03	+0.32
Jan '07	-0.07	-0.01	+0.04	0
Feb '07	0	+0.04	-0.04	+0.08
Mar '07	+0.09	-0.02	-0.05	-0.01
Apr '07	+0.08	-0.03	-0.09	0
Nov '07	-0.06	+0.03	-0.01	+0.09
Dec '07	0	0	-0.02	+0.08
Jan '08	-0.12	0	-0.09	+0.12
Mar '08	-0.21	-0.01	+0.16	+0.02
Apr '08	0	+0.11	-0.12	0

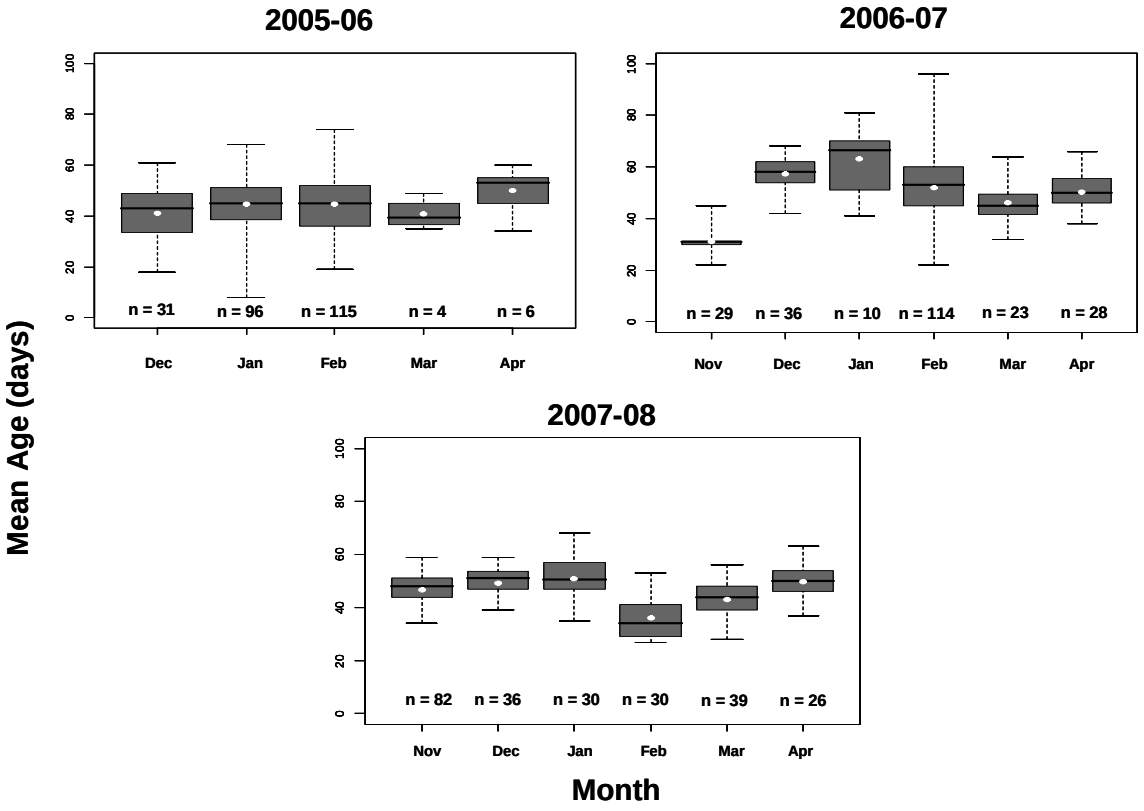

Figure 3.1. Box-whisker plots of mean ages of otolith-aged Atlantic menhaden larvae collected at the Chesapeake Bay mouth during the three-year program. The boxes represent the two inter-quartiles and the whiskers extend to the extreme ages. The horizontal line subdividing each box represents the median and the white circle the mean.

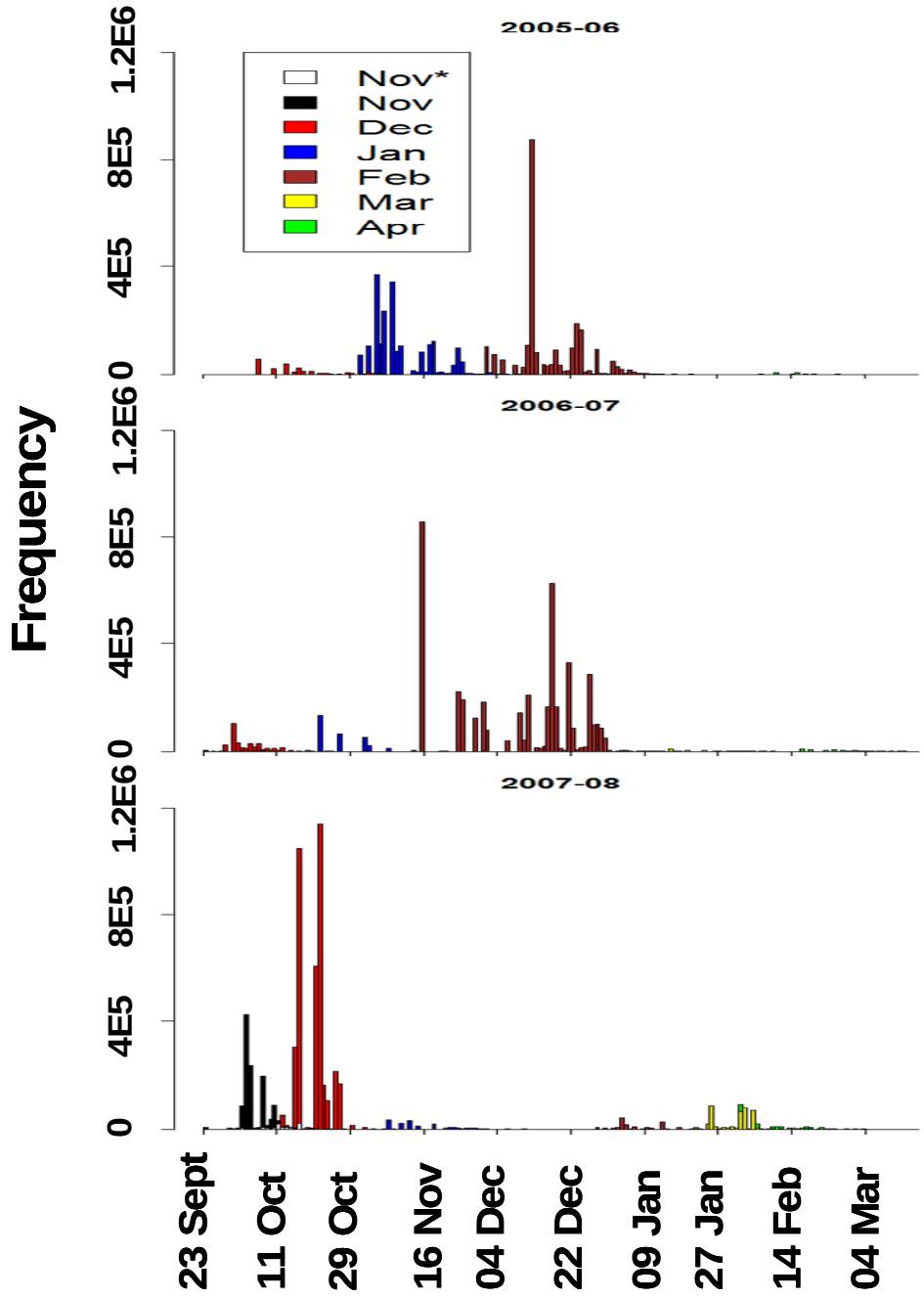

Figure 3.2. Back-calculated hatch-date frequency distributions for Atlantic menhaden larvae collected at the Chesapeake Bay mouth during the three-year program. The frequencies are mortality- and effort-adjusted numbers of larvae in 1-day hatch-date bins.

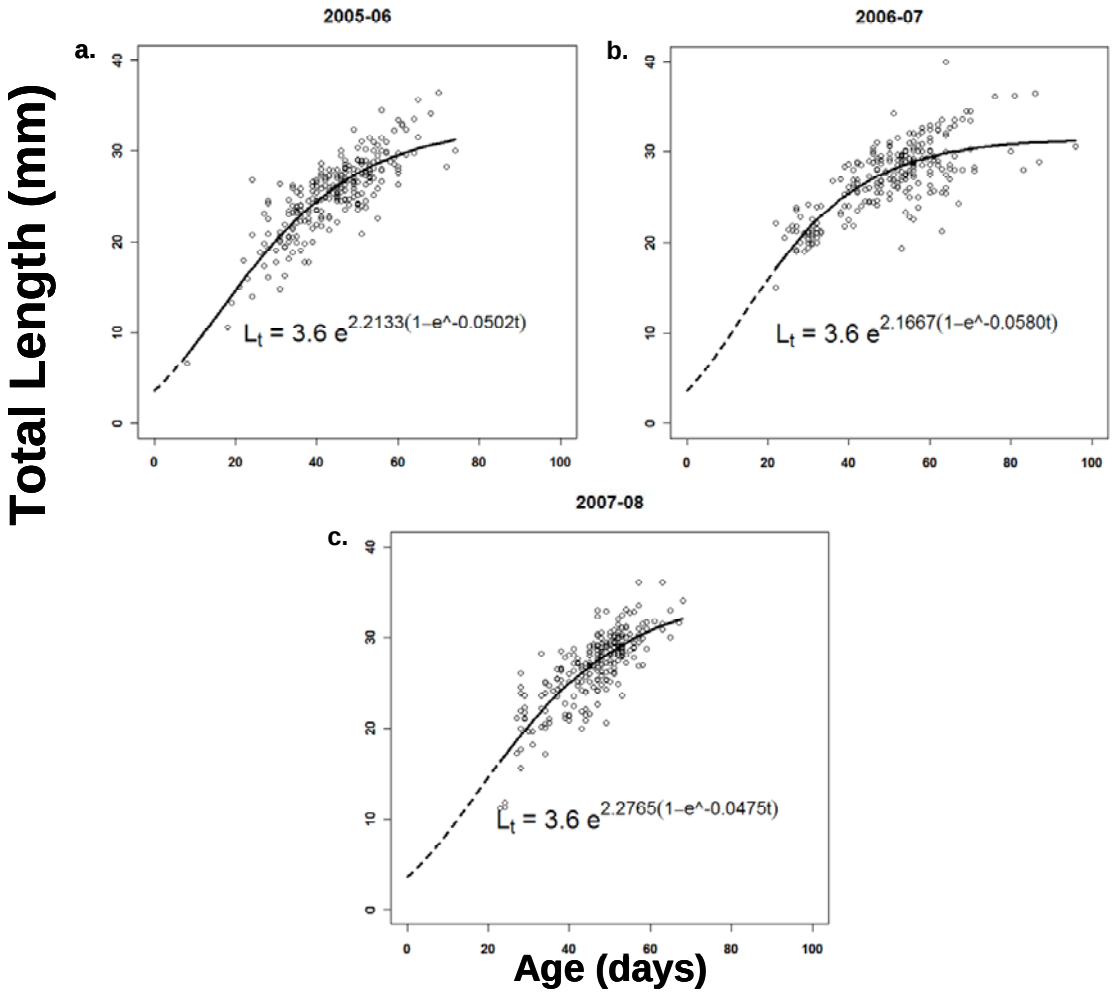

Figure 3.3. Laird-Gompertz model fits to length-on-age relationships for otolith-aged Atlantic menhaden larvae collected at the Chesapeake Bay mouth in a) 2005-06, b) 2006-07, and c) 2007-08.

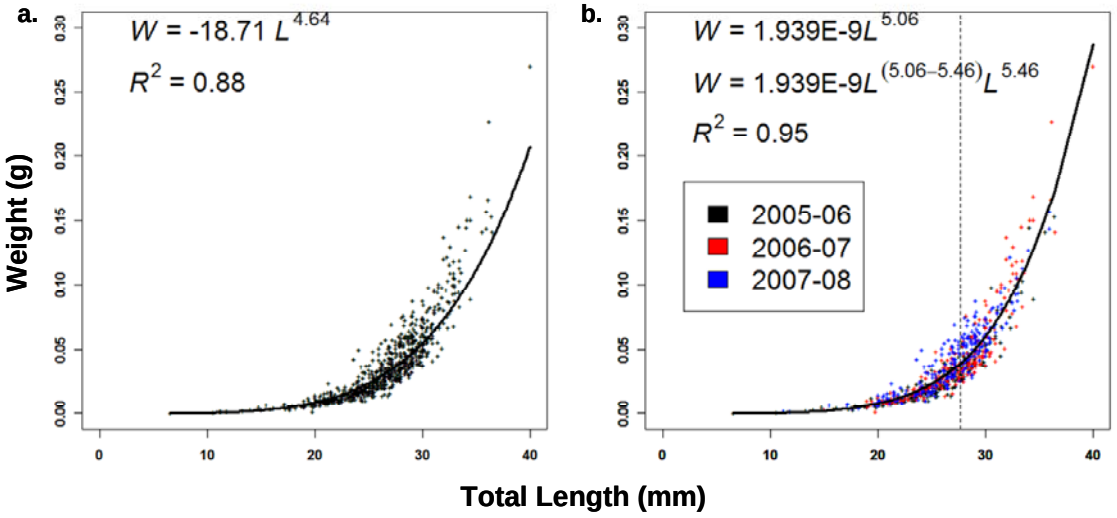

Figure 3.4. Weight-length relationships of Atlantic menhaden larvae collected over three years at the Chesapeake Bay mouth using a) a power regression model, and b) a piece-wise regression model. The vertical dotted line indicates the predicted breakpoint c = 27.69 mm. In figure b) the top equation is the fitted model for lengths < c and the second equation is for lengths ≥ c. The data is color coded by year in figure b).

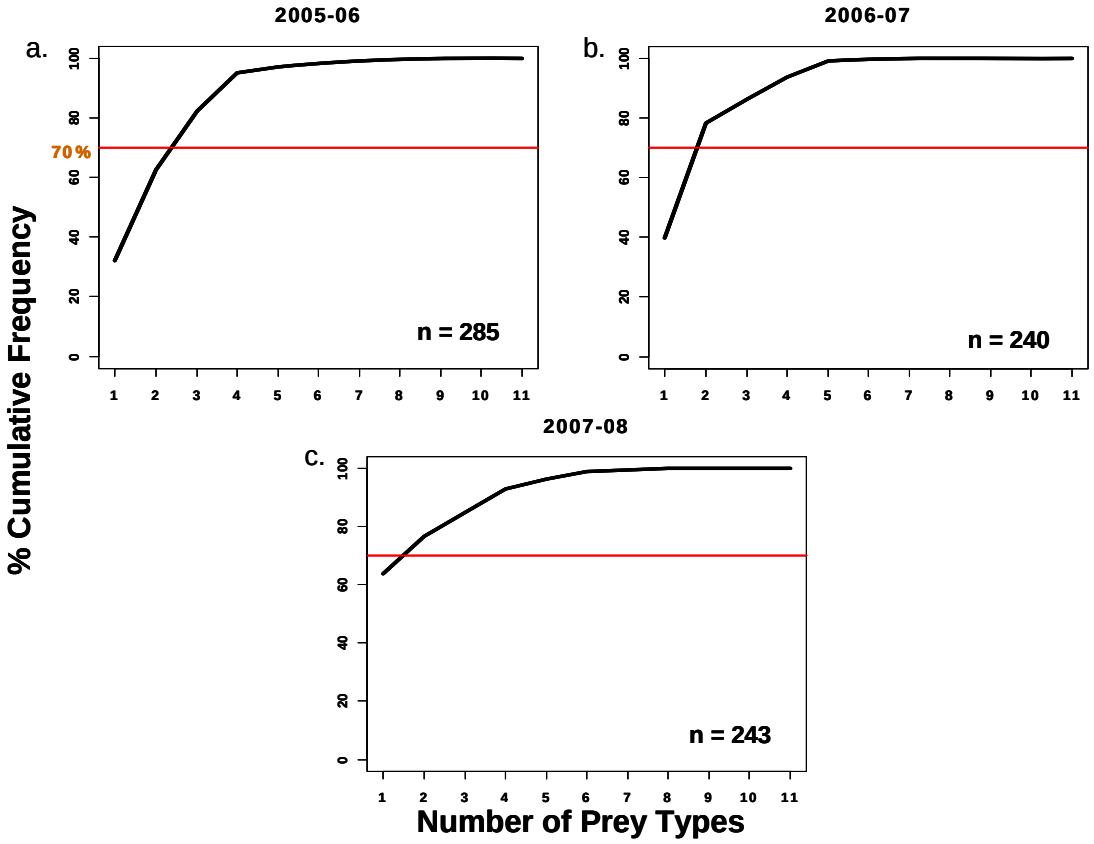

Figure 3.5. Percent cumulative frequency by number of prey types found in the guts of Atlantic menhaden larvae collected at the Chesapeake Bay mouth in the three-year program. The horizontal red lines represent 70 percent of the larval Atlantic menhaden diet.

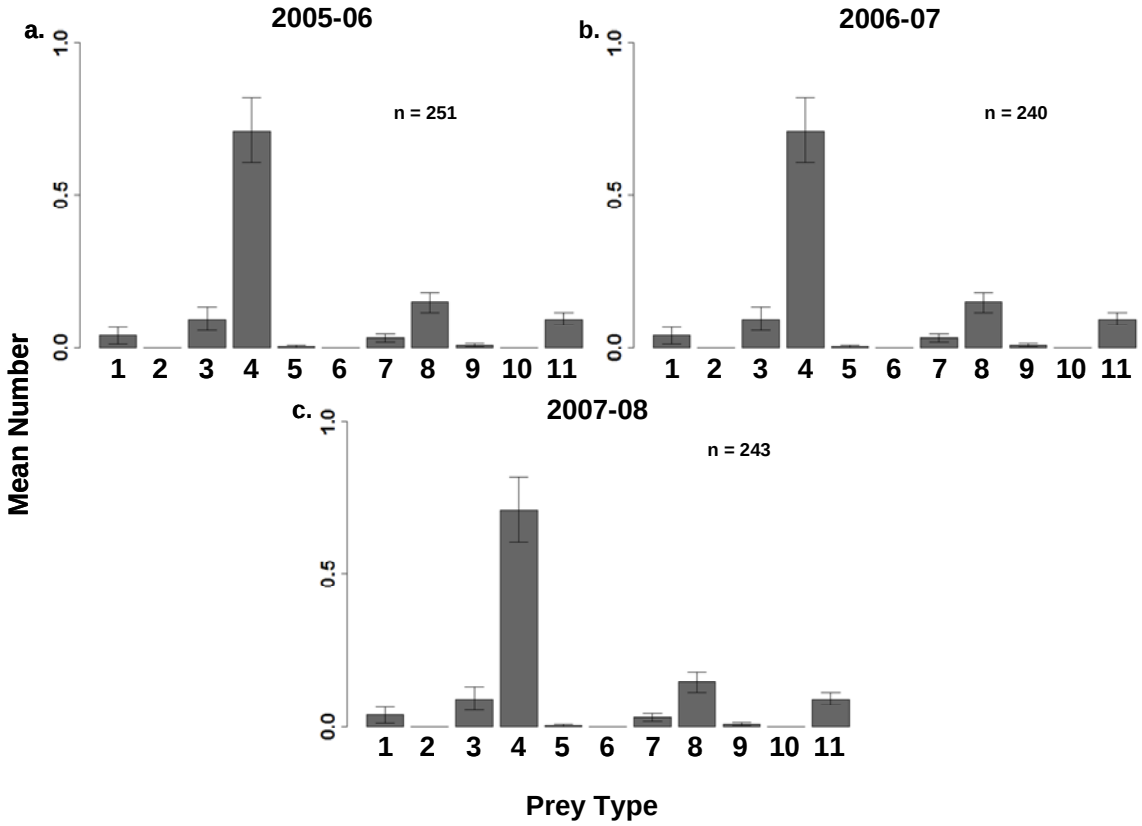

Figure 3.6. Mean number of each prey type per larval gut for Atlantic menhaden larvae collected at the mouth of the Chesapeake Bay in the three-year program. 1= tunicate larvae, 2 = metatrochophore, 3 = bivalve larvae, 4 = copeod, 5 = copepod nauplii, 6 = ostracod, 7 = cladoceran, 8 = barnacle nauplii, 9 = polychaete larvae, 10 = decapod, 11 = digested material.

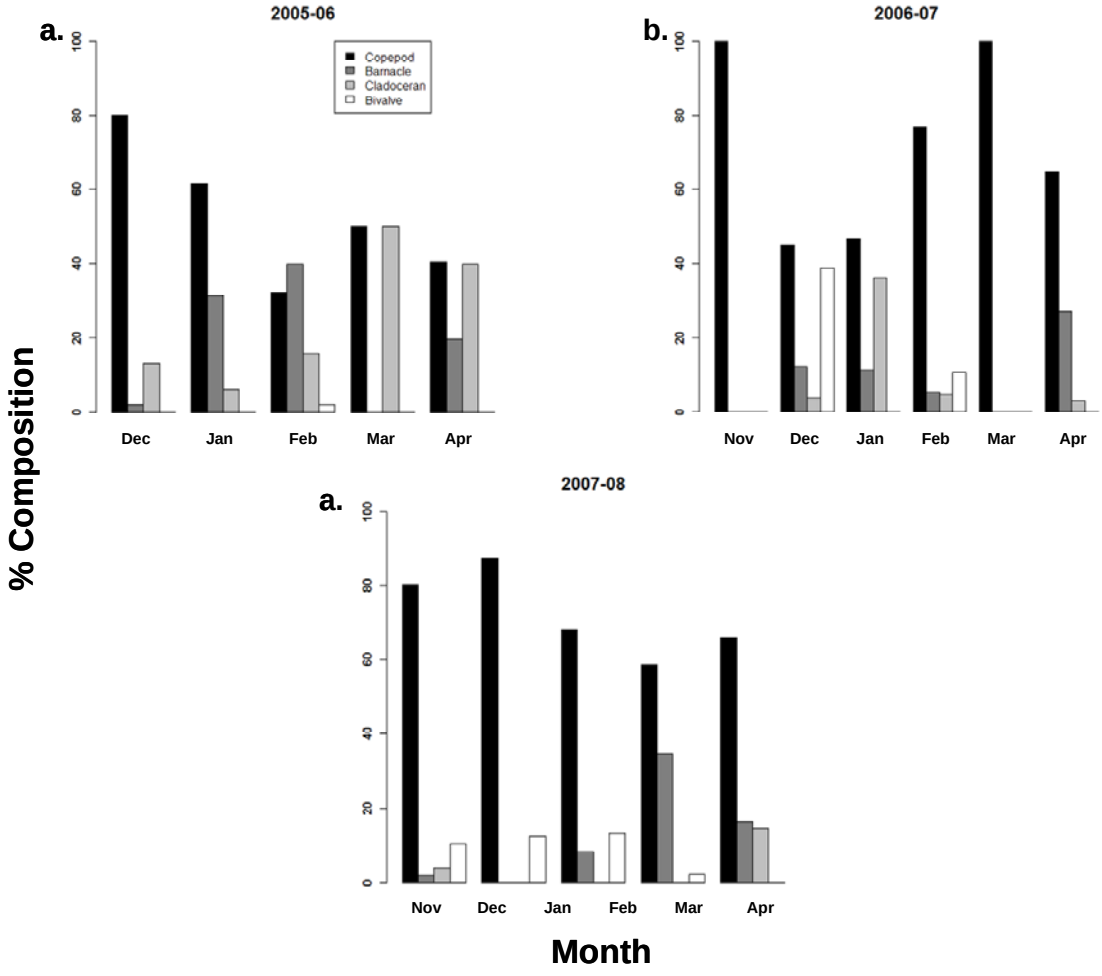

Figure 3.7. Monthly percentage prey composition in the diets of Atlantic menhaden larvae collected at the Chesapeake Bay mouth during a) 2005-06, b) 2006-07, and c) 2007-08.

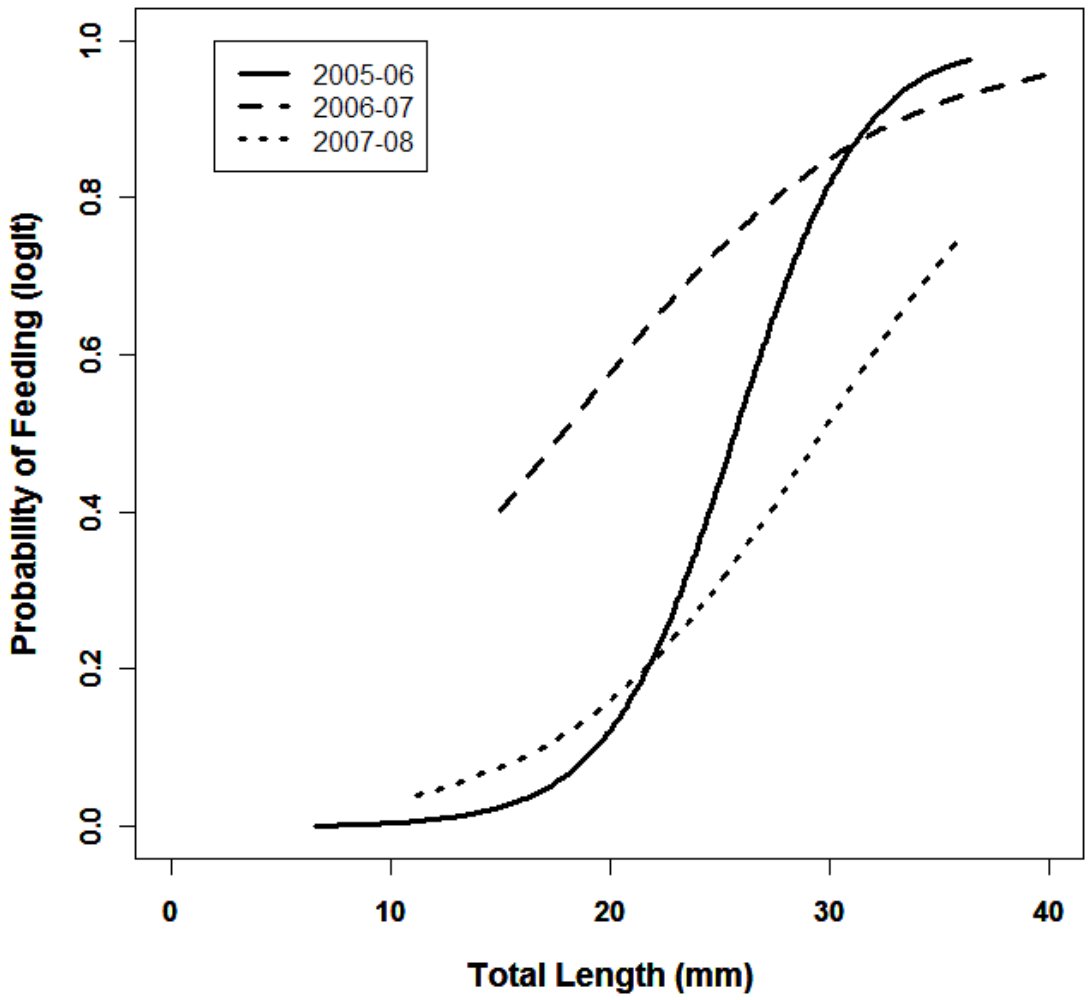

Figure 3.8. Logistic regressions relating probability of at least one prey in the gut of an Atlantic menhaden larva and larva length. The logit probability regressions are given for each year.

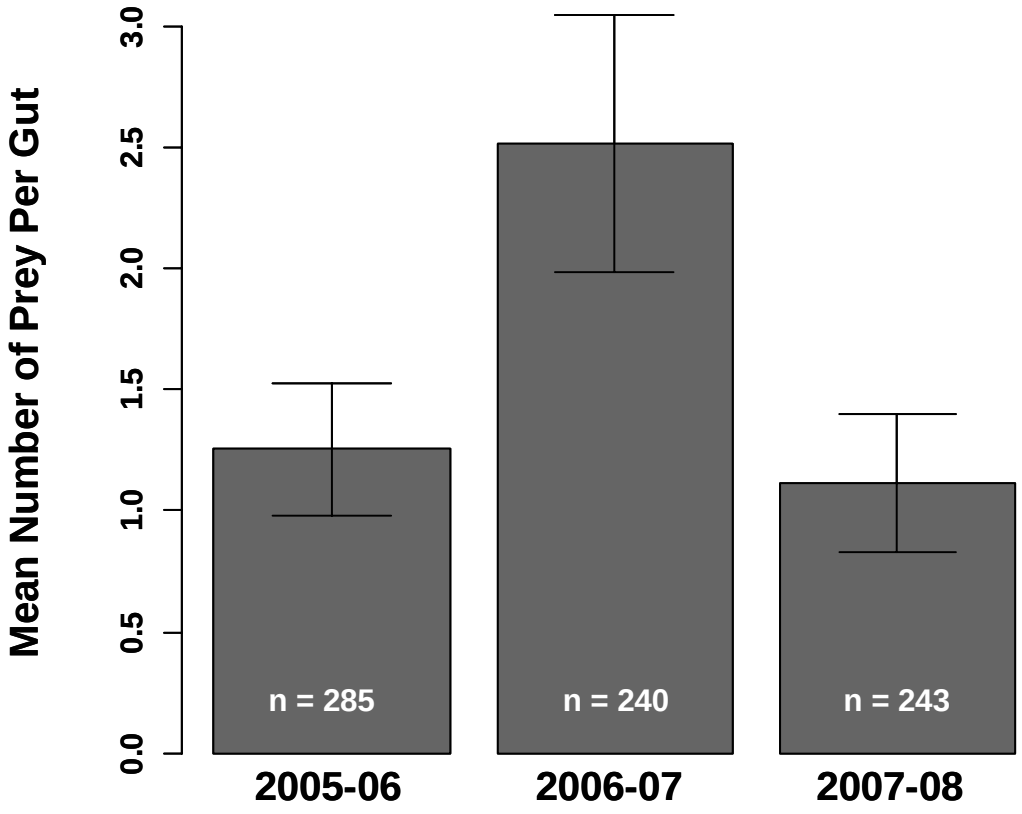

Figure 3.9. Feeding success, defined as mean number of prey per gut, for Atlantic menhaden larvae collected at the Chesapeake Bay mouth in the three-year program.

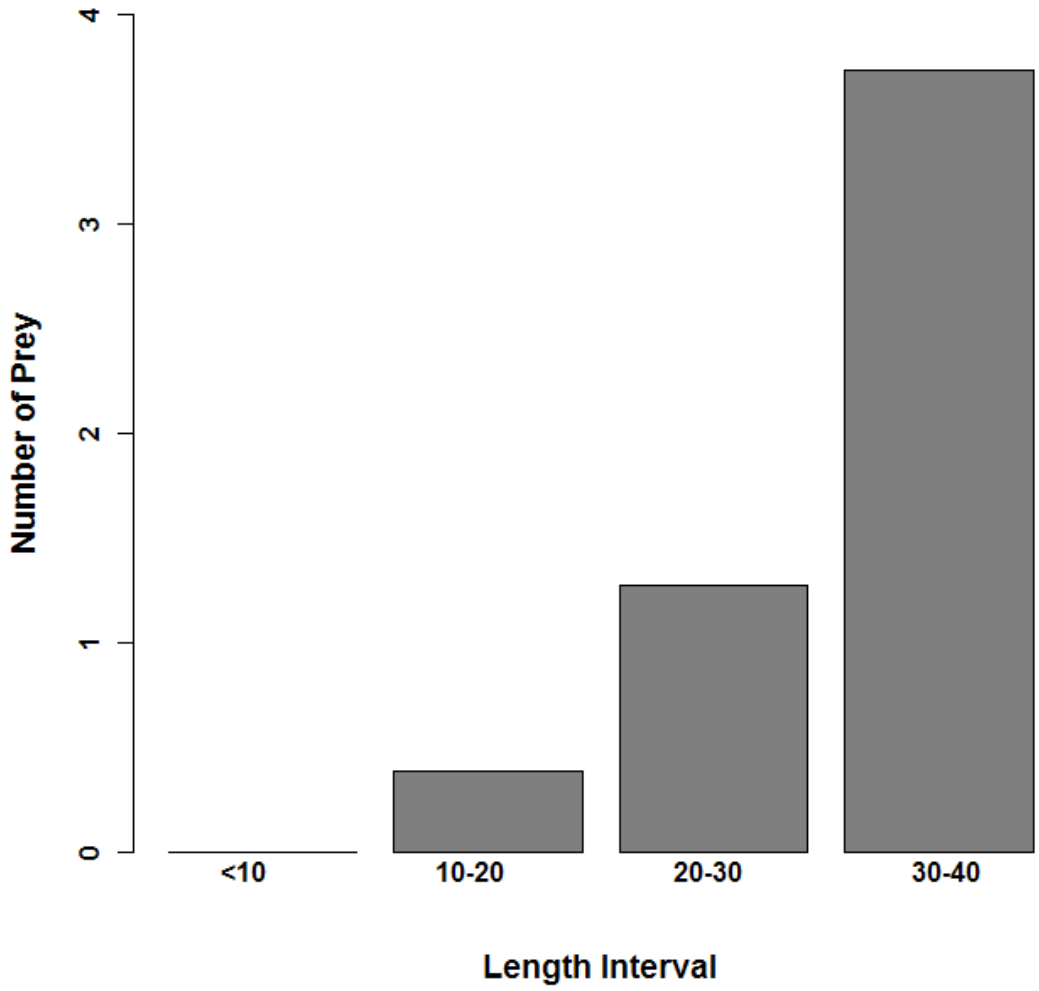

Figure 3.10. Mean total number of prey per larva by length intervals for larval Atlantic menhaden in relation to total length (mm). The < 10 mm length bin is represented by a single fish.

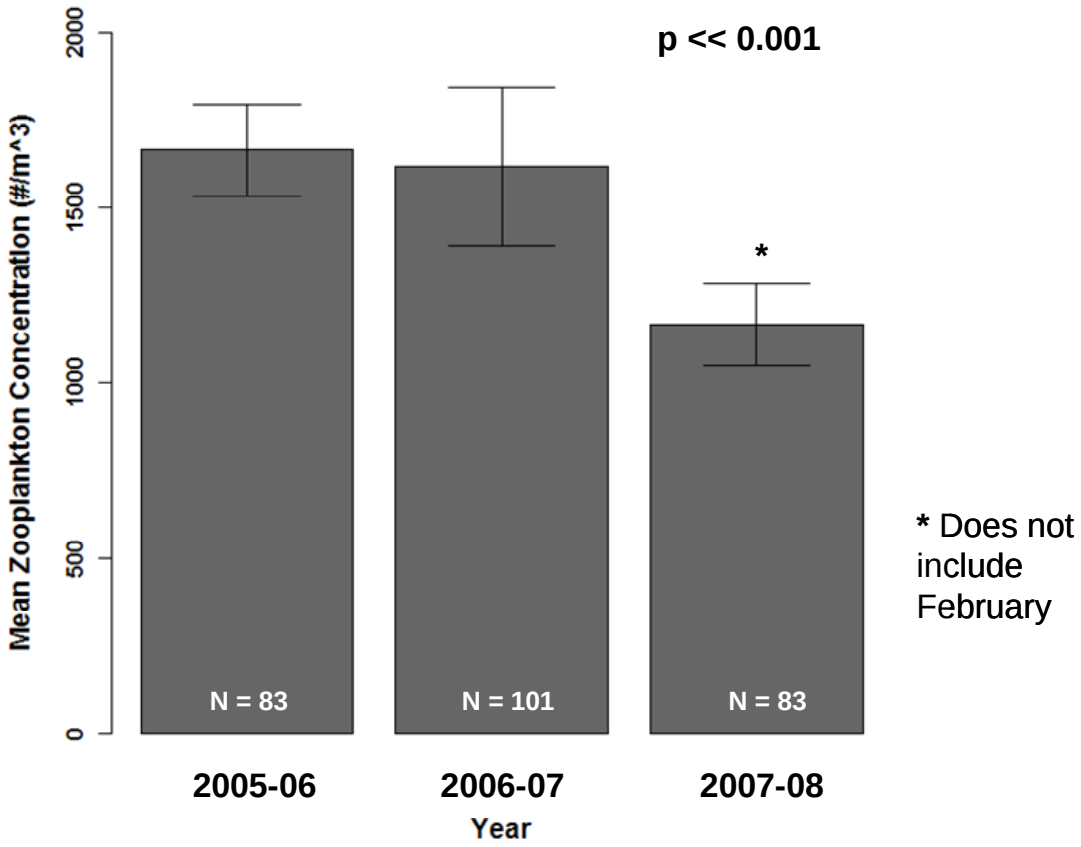

Figure 3.11. Arithmetic mean total zooplankton concentrations at the mouth of the Chesapeake Bay during the three-year program. (December to April 2005-06; November to April 2006-07 and 2007-08)

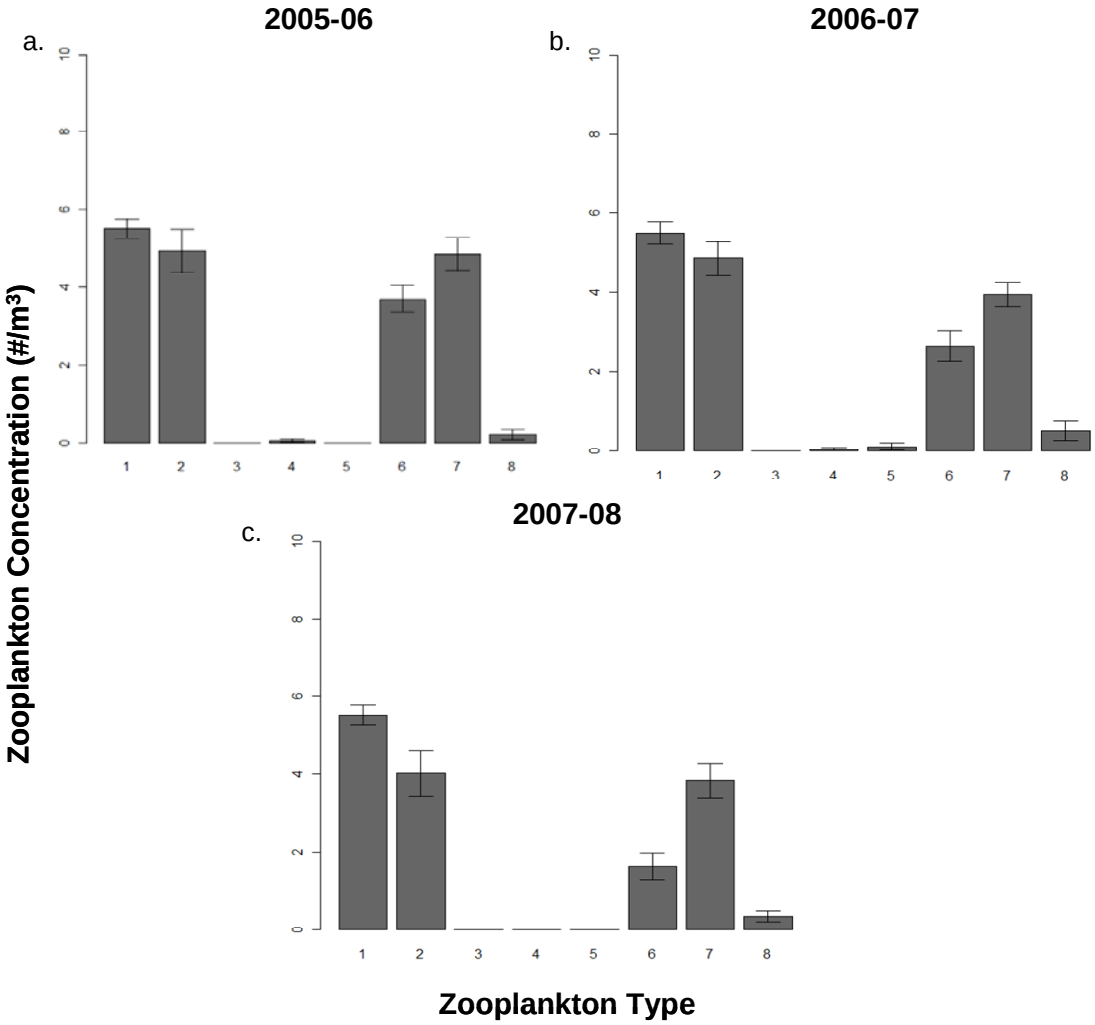

Figure 3.12. Mean zooplankton concentrations by zooplankton taxon for a) 2005-06, b) 2006-07, and c) 2007-08. The taxa are 1) *Acartia*, 2) *Centropages*, 3) *Calanus*, 4) *Oithona*, 5) *Evadne* 6) *Podon*, 7) *Balanus*, and 8) Gastropod veligers.

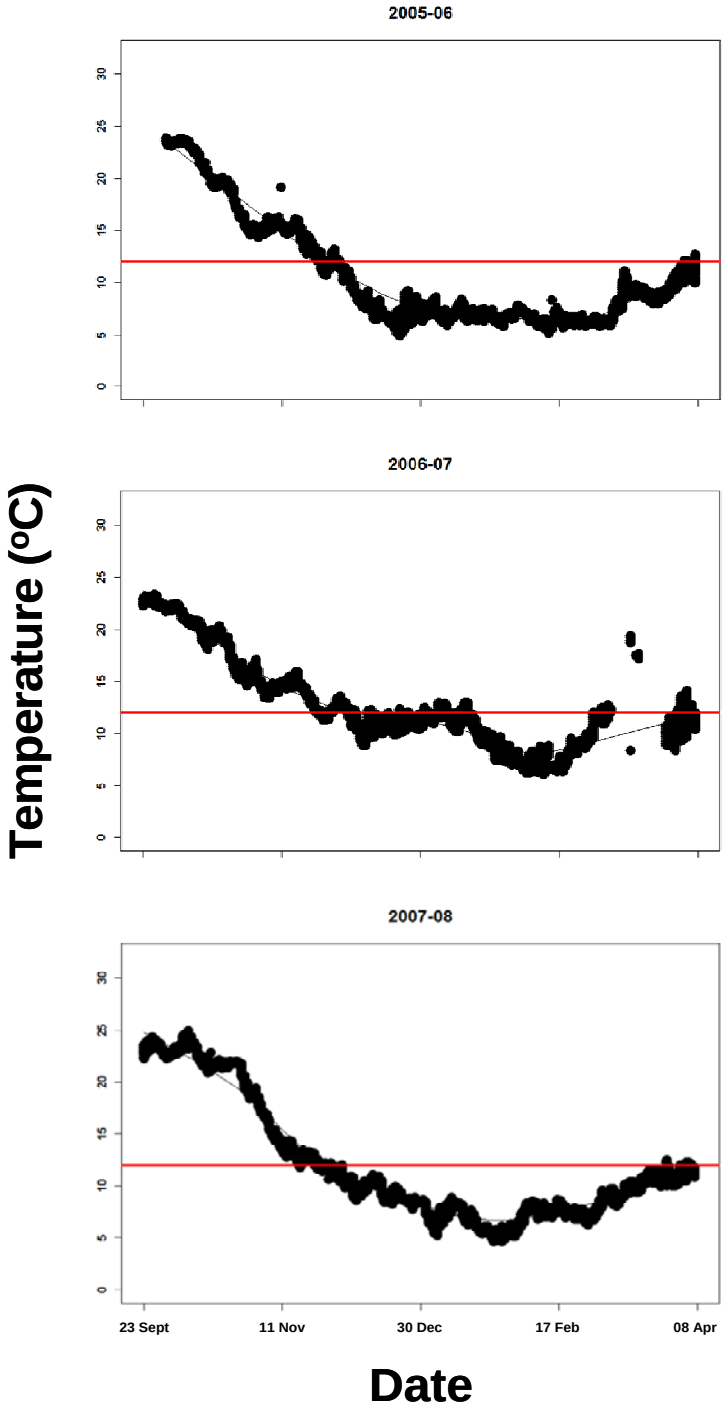

Figure 3.13. Surface water temperatures offshore of Chesapeake Bay from early September through early April in 2005-06, 2006-07, and 2007-08. The horizontal red line is 12 °C. The data represents real time water temperature measurements taken from Virginia Light Buoy (36°54'35" N 75°42'35" W), NOAA National Data Buoy Center.

Chapter 4: Conclusions, Summary, and Synthesis

Conclusions

Recruitment of young-of-the-year (YOY) Atlantic menhaden in Chesapeake Bay and other estuaries relies, in part, on the supply of larvae from the coastal ocean. It was hypothesized that supply would vary inter-annually at the Chesapeake Bay mouth. Recruitment levels of YOY menhaden in Chesapeake Bay have been low since a decline occurred in the late 1980s. In my three-year study annual and monthly ingress levels were variable, as hypothesized, with mean concentrations differing nine-fold among years. Overall variability in inter-annual ingress levels was in large part attributed to highly variable monthly ingress patterns. The two years of moderate or high ingress levels (2005-06 and 2007-08, respectively) experienced relatively high monthly ingress in the November-February period unlike 2006-07 when ingress was high only in February. Ingress was low during April in each of the three years. For levels of ingress observed in the three years of this program, inter-annual patterns were not concordant with YOY recruitment levels in the Bay that differed only two-fold.

No clear spatial patterns in either vertical distribution or horizontal distribution across the mouth of Chesapeake Bay were observed. Larvae were more abundant, on average, above the pycnocline in 2005-06 but did not differ in mean concentration above or below the pycnocline in the other two years. There were no differences in mean larval concentrations among the five stations along a sampling transect across the mouth of Chesapeake Bay, although there were day-to-day differences. Patterns of larval occurrence with respect to tide stages were not clearly predictable, although there was a

tendency for estimated larval concentrations to be higher on flooding tides compared to ebbing tide stages. Menhaden larvae were more abundant in night catches, a pattern often described in ichthyoplankton surveys, possibly because sampling is more efficient and escapement by larvae is lower at night.

Mean age-at-ingress, an indicator of the period of transport from offshore to Chesapeake Bay, differed significantly inter-annually although differences were relatively small. Monthly frequency distributions of larval ages-at-ingress were consistent (mostly 30 to 60 days post-hatch) and did not exhibit a seasonal pattern as reported for ingress of Atlantic menhaden larvae in North Carolina estuaries (Warlen 1992). Ingress of menhaden into Chesapeake Bay was mostly the result of spawning on the continental shelf before mid-December. Larvae hatched in the December-February period probably originated south of Cape Hatteras where spawning activity is reported to occur during this period (Higham and Nicholson 1964; Judy and Lewis 1983).

Growth rates of Atlantic menhaden larvae that were ingressing into Chesapeake Bay were similar to reported rates of Atlantic menhaden ingressing into other estuaries (Maillet and Checkley 1991; Warlen 1992). The growth coefficient in Laird-Gompertz models fit to the length-at-age data differed significantly, but not greatly, among years and was highest in 2006-07, the year of lowest ingress. In all years, age-specific growth rates were highest for larvae in the 21-30 days post-hatch age interval. Age-specific growth rates steadily declined after 30 days post-hatch. A shift in the allometric power coefficient describing the weight-length relationship of larvae was evident at a mean total length of 27.7 mm, which is near the size described as the length at onset of metamorphosis in previous studies (Lewis *et al*. 1972; Balon 1984).

The dominant prey type of menhaden larvae at the Chesapeake Bay mouth was copepods in each year. Only two prey types accounted for more than 70% by number of the larval menhaden diet in each of the three years. The four most common prey types in larval diets were also the four most common types of zooplankton available at the Bay mouth. The probability of feeding and feeding success increased with larval size.

Chapter 2 Summary: Larval Ingress

Ingress was lowest in 2006-07, highest in 2007-08 and intermediate in 2005-06. The arithmetic mean ingress concentration of menhaden larvae was nine times higher in 2007-08 than in 2006-07. In the 2005-06 and 2006-07 ingress years, monthly ingress levels were highest in February 2006 and 2007. But, in the 2007-08 year, ingress was highest in December 2007. Ingress in 2006-07 was consistently low, except for February 2007. Ingress levels were low in April of each year. Mean concentrations were 2.32 larvae/100 m^3 in 2005-06, 0.90 larvae/100 m^3 in 2006-07 and 8.44 larvae/100 m^3in 2007-08. Mean larval concentrations were higher above the pycnocline in 2005-06, but were evenly distributed in the water column in the other two years. Mean larval concentrations did not differ among sampling stations across the mouth of the Chesapeake Bay. Larvae were significantly less abundant during ebbing tides in 2007-08 but no differences in mean concentrations were observed among tide stages in the other two years. Larvae were significantly more abundant at night; the mean concentration over the three-year study was 7.35 larvae/ m^3 at night but 1.35 larvae/ m^3 during the day, suggesting that the larvae were more vulnerable and/or available to the Tucker trawl at night.

Chapter 3 Summary

Mean age at ingress was significantly older in 2006-07 (50 days) compared to 2005-06 (44 days) and 2007-08 (46 days). Monthly mean ages at ingress tended to be younger in November and December than later in the season. Monthly mean ages at ingress ranged from 31 to 63 days. Hatch dates ranged from late September to mid-March in all years. More than 90% of larvae ingressing into Chesapeake Bay had hatch dates prior to 15 December in each of the three years. Mean growth rates of larvae through the first 50 days of life, derived from Laird-Gompertz models, were > 0.50 mm/day in each year. Fastest growth rates occurred in the 21-30 days post-hatch period, with substantial declines in growth rates of larvae older than 30 days. The Laird-Gompertz growth coefficient, *k*, was significantly higher in 2006-07 compared to 2007-08. Weight-length relationships shifted during growth and ontogeny, experiencing a breakpoint in allometry at 27.7 mm total length, indicating onset of metamorphosis.

The most common prey of larval menhaden at the Bay mouth is copepods. Barnacle nauplii, cladocerans, and bivalve veligers were also common in larval menhaden diets. Larval menhaden diets largely reflected what was available to them in the zooplankton at the mouth of Chesapeake Bay. Variability in feeding success did not follow a pattern similar to fluctuations in zooplankton concentrations at the Bay mouth. Highest feeding incidence and feeding success were observed in 2006-07 when mean zooplankton concentrations were lowest. Feeding success and the probability of successful feeding increased with respect to larval length in each year.

Synthesis

In this study, ingress, age at ingress, feeding incidence and success, and growth all experienced some degree of inter-annual variability. Unexpectedly, the year of lowest ingress, 2006-07, was the year when age at ingress was oldest, feeding success was highest, and growth rate was fastest. Age-at-ingress and growth rates both were highest in 2006-07 indicating that size was larger and ontogenetic stage of larvae was more advanced at the Bay mouth in this year. Feeding was size-dependent in each year but the most successful feeding, observed in 2006-07, did not correspond with 2007-08, the year when larvae were most abundant and had greatest mean larval length.

Level of larval ingress of menhaden did not correspond to subsequent YOY recruitment levels of juveniles in Chesapeake Bay, as indexed by the Maryland Department of Natural Resources juvenile index surveys (*http://dnr.maryland.gov/fisheries/juvindex/index.asp*). The 9-fold variability in larval ingress levels did not correspond to similar variability in YOY recruitment levels, which were low in each of the three years. At the ingress levels and variability observed, other factors such as mortality during the juvenile stage after ingress may be more important controllers of recruitment than abundance at ingress. In the 1970s, YOY recruitment levels in the Chesapeake Bay were both higher and more variable than in the most recent 20 years. It is possible that levels of larval abundance presently observed at the Bay mouth are substantially lower than levels decades ago when menhaden recruitments were higher, but there are no surveys or data to corroborate that possibility. Measures of ingress, if monitored annually, could be important to understand the relationship between

larval supply and recruitment under variable and changing climate regimes that likely are occurring.

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