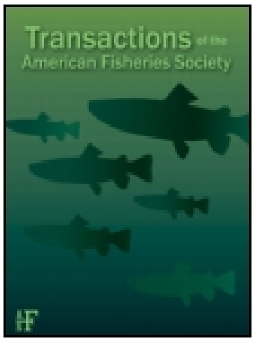

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ARTICLE

Trends in Relative Abundance and Early Life Survival of Atlantic Menhaden during 1977–2013 from Long-Term Ichthyoplankton Programs

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Abstract

The Atlantic Menhaden *Brevoortia tyrannus*, a commercially important clupeid, supports one of the oldest and largest commercial fisheries on the U.S. East Coast. Despite recent increases in adult biomass, juvenile indices have declined coastwide and have remained particularly low in Chesapeake Bay. In order to understand the underlying causes of this decline, knowledge of larval recruitment is essential. We developed an index of larval abundance by using larval data collected from two large-scale ichthyoplankton sampling programs that occurred from Nova Scotia, Canada, to Cape Hatteras, North Carolina, during 1977–1987 and 1999–2013. Larval abundance data were standardized to a day-0 age by applying an age–length key from a study of larval ingress into Chesapeake Bay; a delta-lognormal model was used to account for spatial and temporal changes in sampling. We found that Atlantic Menhaden larval abundance increased from 1977 to 2013 and was highest in the winter; most individuals were detected at nearshore stations. Over our time series, larval abundance corresponded closely to adult spawning stock biomass. Due to the lack of a direct relationship between our larval abundance estimates and a coastwide juvenile index, we examined several environmental factors (temperature, Chesapeake Bay discharge, Atlantic Multidecadal Oscillation [AMO], wind speed, and wind direction) for potential effects on the relative survival of larvae. Larval abundance had a significant negative effect on relative survival. Temperature and to a lesser extent wind speed and AMO appeared to exert the greatest effects on the early life survival of Atlantic Menhaden: cooler temperatures, intermediate wind speeds, and negative-phase AMO were the most favorable for survival. Our findings suggest that the observed reduction in recruitment is not a problem of larval supply but rather is limited by survival between the larval and juvenile stages.

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The Atlantic Menhaden *Brevoortia tyrannus* is an abundant schooling forage fish that plays an important ecological and economic role in coastal and estuarine systems (Vaughan and Smith 1988; Friedland et al. 1989). Atlantic Menhaden serve as prey for a network of predators in the coastal ocean and estuaries and facilitate the upward flux of energy through the food web (Ahrenholz 1991; Annis et al. 2011). Adult Atlantic Menhaden are migratory coastal spawners that move seasonally along the North American coast from Nova Scotia to Florida (Reintjes 1969). The bulk of spawning is traditionally believed to occur in the coastal ocean, peaking during the winter off Cape Hatteras, North Carolina (Ahrenholz et al. 1987). However, some spawning likely takes place throughout the species' range during most of the year (Nelson et al. 1977). Larvae hatch in the coastal ocean and are transported into estuaries, where they continue to grow and metamorphose into juveniles (Ahrenholz 1991). Early studies estimated that the Chesapeake Bay contribution of juveniles to the spawning stock was 68.8% (Ahrenholz et al. 1989; ASMFC 2004). Although Chesapeake Bay is still the primary nursery habitat, contributing proportionally more than other estuaries, recent research suggests that its contribution to the age-1 stock has declined by 16–65% (Anstead and Jones 2014).

The Atlantic Menhaden population has experienced considerable fluctuations in both fishing mortality and biomass (Figure 1; SEDAR 2015). Although the species once supported a coastwide reduction fishery, fishing effort has been concentrated in Chesapeake Bay and offshore of New Jersey for the past decade. Even with such a decline in the spatial range of fishing, Atlantic Menhaden continue to support the largest fishery (by volume) on the U.S. Atlantic coast (SEDAR 2015). Biomass estimates were fairly constant through the 1970s and 1980s, but the stock biomass reached an all-time low in the mid-1990s (Figure 1b; SEDAR 2015). The fishery shrank dramatically during that period, with commercial landings decreasing from 401,200 metric tons in 1990 to 171,200 metric tons in 1999 (SEDAR 2015). Similarly, juvenile abundance in surveys was high in the 1970s and 1980s, but the estimates declined coastwide in the 1990s and have remained relatively stable during the 2000s despite estimated increases in abundance and biomass of the adult stock from 2000 to 2013 (Figure 1c). Because of low age-0 recruitment in the Maryland seine survey since the 1990s, concern has arisen about the state of recruitment to Chesapeake Bay, the most productive nursery area for Atlantic Menhaden (Anstead and Jones 2014). Simultaneously, age-0 surveys north of Chesapeake Bay have shown increasing values (SEDAR 2015).

Potential causes for a change in recruitment can be classified in terms of the impacted life stage (Houde et al. 2011). First, adult population declines that are attributable to overfishing or predation could decrease spawning biomass and resulting recruitment (Houde et al. 2011). Second, Atlantic Menhaden eggs and larvae could be experiencing unfavorable oceanic conditions, leading to increased early life mortality (Houde et al. 2011; Peck et al. 2012) or reductions in the success of larval transport to appropriate nursery habitats (Pineda et al. 2007; Houde et al. 2011). Finally, juvenile Atlantic Menhaden may be exposed to unfavorable conditions in nursery areas, such as increased predation or poor water quality, leading to increased juvenile mortality and decreased recruitment (Houde et al. 2011). In the present study, we focus on trends in Atlantic Menhaden larval abundance and factors that may affect early life mortality.

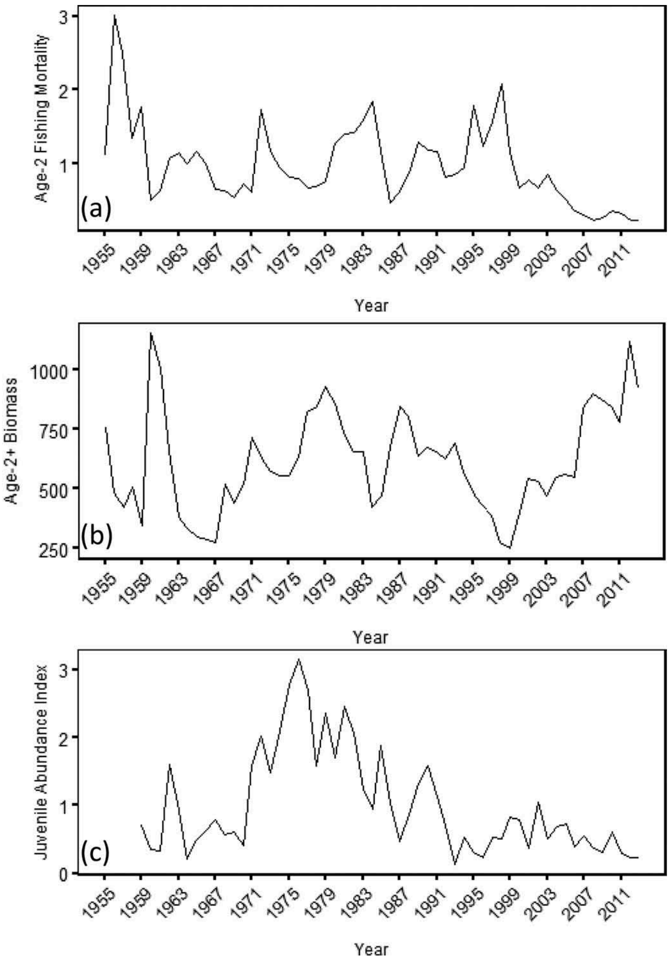

FIGURE 1. Fishing mortality, total biomass, and juvenile abundance of Atlantic Menhaden (from SEDAR 2015): **(a)** fishing mortality at age 2, the most highly selected age; **(b)** predicted biomass (thousands of metric tons) of age-2 and older individuals; and **(c)** scaled juvenile index of abundance, as calculated based on surveys conducted from New England to Georgia.

Larval abundance and early life mortality of Atlantic Menhaden are likely influenced by a combination of factors. Temperature affects the timing of spawning (Stegmann and Yoder 1996; Stegmann et al. 1999). Transport (Epifanio and Garvine 2001), development (Nelson et al. 1977), and temperature may be important factors with effects on early life survival (Lewis 1965; Ferraro 1980). Hydrodynamic conditions can affect early survival because Atlantic Menhaden larvae must be transported into estuarine nursery habitats (Ahrenholz 1991). The ingress of larvae into estuaries is thought to be driven by larval behavior in response to a variety of environmental, tidal, and diurnal cues (Hare et al. 2005; Houde et al., in press). Additionally, increased freshwater flow events from Chesapeake Bay may influence nursery habitat quality (Houde et al., in press) as well as larval transport from the Atlantic coast near Chesapeake Bay and southward (Quinlan et al. 1999); this could affect both the timing and location of larval ingress.

More broadly, large-scale climate variables could be the greatest drivers of recruitment, as they often have effects on several of the previously mentioned environmental variables. Rice et al. (1999) found that variation in patterns of ingress into North Carolina estuaries was driven more by large, climate-scale patterns affecting hydrodynamic conditions rather than by localized variation in spawning. The spatial distribution of larval Atlantic Menhaden showed no significant change in 1999–2008 relative to 1977–1988 (Walsh et al. 2015), suggesting that adult spawning habitats have not changed. The Atlantic Multidecadal Oscillation (AMO) is a measure of large-scale climate variability and is correlated with Chesapeake Bay recruitment of Atlantic Menhaden (Wood and Austin 2009). Differences in circulation patterns on a multidecadal scale could affect the transport of eggs and larvae to estuarine habitats. Additionally, AMO phase is correlated with rainfall in most of North America (Enfield et al. 2001) and could influence Atlantic Menhaden recruitment in a manner similar to the effect of freshwater flow.

The objectives of the present study were to examine trends in Atlantic Menhaden larval abundance over time and to determine factors affecting survival from the larval stage to the juvenile stage. We constructed a larval index of abundance based on data from two long-term ichthyoplankton sampling programs (1977–1987; 1999–2013), and we compared this index with juvenile and adult abundance indices from the most recent stock assessment. Finally, we estimated the relative survival of Atlantic Menhaden between the larval stage and the age-0 juvenile stage and tested for environmental effects on relative survival.

METHODS

Larval data.—Larval data were obtained from two spatially and temporally extensive sampling programs conducted along the U.S. Atlantic coast by the National Oceanic and Atmospheric Administration. Data from the period 1977–1987 were obtained from the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program; 1999–2013 data were obtained from the Ecosystem Monitoring (EcoMon) program. Although EcoMon began in 1992, only ichthyoplankton samples collected since 1999 have been processed. Therefore, our analysis of the EcoMon data set began with data from 2000, which included the entire spawning season beginning in September 1999. The MARMAP and EcoMon surveys sampled the same spatial extent of shelf waters from North Carolina to Nova Scotia on roughly a bimonthly basis. The MARMAP program used a fixed-station design for plankton surveys and a stratified random design for bottom trawl surveys that also collected plankton (Sibunka and Silverman 1984). The EcoMon program used a stratified random design based on the bottom trawl survey strata, which were determined by depth and latitude (Walsh et al. 2015).

Fixed-station surveys are hypothesized to have better precision and a higher power to detect temporal changes in abundance (Warren 1994; Li et al. 2015), whereas surveys of randomly selected stations are less likely to oversample the more-productive and less-productive habitats (McClelland and Sass 2012; Kiraly et al. 2014; Li et al. 2015). Thus, abundance estimates in fishery sampling have shown mixed results when the two methods are compared: fixed-station surveys have been shown to produce equal (King et al. 1981; Bonvechio et al. 2008), lower (Kiraly et al. 2014), or higher (McClelland and Sass 2012; Kiraly et al. 2014) CPUE estimates than random surveys. Even though some surveys used fixed stations during the MARMAP program, the pelagic habitat of those fixed stations was dynamic and variable. Therefore, we thought it would be beneficial and appropriate to examine the two larval time series, particularly since (1) the same spatial area was sampled during both periods; and (2) the strata were used to select stations for incorporation into larval abundance index calculation, thus minimizing the variability due to dynamic pelagic habitats.

Plankton sampling was conducted with a 61-cm bongo net by using double oblique tows, which sampled from the surface to within 5 m of the bottom (to a maximum depth of 200 m in deeper water) and then back to the surface at 2.78 km/h (1.5 knots). The mesh size used for ichthyoplankton sampling was 505 μm during MARMAP and 333 μm during EcoMon. Samples were fixed in a 5% formalin solution at sea, and larvae were transferred to ethanol during processing. Samples were processed at the Morski Instytut Rybacki (Szczecin, Poland) or at the National Marine Fisheries Service's Northeast Fisheries Science Center to determine the counts of all species (identified to the lowest taxon) and to obtain length measurements. Length was measured for up to 50 individuals of each species per tow; if more than 50 individuals were present, a random subsample of 50 individuals was taken to characterize the length composition (notochord length for preflexion larvae; SL for flexion and postflexion larvae).

Some of the sampling methods differed between programs. Environmental data were collected at most of the sampling locations, and sampling techniques and instrumentation varied between MARMAP and EcoMon. During the MARMAP program, water temperatures were collected with a bucket thermometer, a water bottle with a reversing thermometer, a mechanical bathythermograph, or an expendable bathythermograph; salinity was measured by analysis of water samples and a salinometer (Sibunka and Silverman 1984; Holzwarth and Mountain 1990; Mountain et al. 2004). During the EcoMon program, water temperature and salinity were measured by using conductivity–temperature–depth probes (Taylor and Bascuñán 2001; Mountain et al. 2004).

We restricted our analyses to encompass the primary spatial and seasonal occurrence of Atlantic Menhaden larvae on the shelf. Fourteen of the EcoMon program's shallowest strata from southern New England to Cape Hatteras were used because very few Atlantic Menhaden larvae were observed outside of those regions (Figure 2). Similarly, surveys conducted in July and August were excluded because no Atlantic Menhaden larvae were observed during July and only 15 larvae were observed during August over the entire study period, whereas in the other months the number of individuals ranged from 1,468 to 304,931. To capture seasonal spawning dynamics, we treated September as the beginning of the larval year; thus, larvae that hatched during September–December would be added to those that hatched during January–May of the following year. We paired months (September–October, November–December, January–February, March–April, and May–June) to reflect the bimonthly sampling design.

Index of larval abundance.—Prior to constructing our index of larval abundance (I_L), we corrected for differences in mesh size selectivity among programs. The mesh size of the bongo net has a significant effect on selectivity for small larvae (Johnson and Morse 1994). To account for this change in gear, we calculated correction factors for 1-mm size-bins below 10 mm (Table 1) from the MARMAP program data presented by Johnson and Morse (1994) and from the more-updated gear comparison data collected by the EcoMon program during 2010–2014. Using paired t-tests for each size-bin, we found that abundance was significantly different for individuals smaller than 5 mm, and the difference in abundance between mesh sizes decreased with increasing fish size (Table 1). After applying corrections to the raw counts for lengths less than 5 mm, we recalculated the abundance at age and the overall abundance for all Atlantic Menhaden that were collected by the MARMAP program.

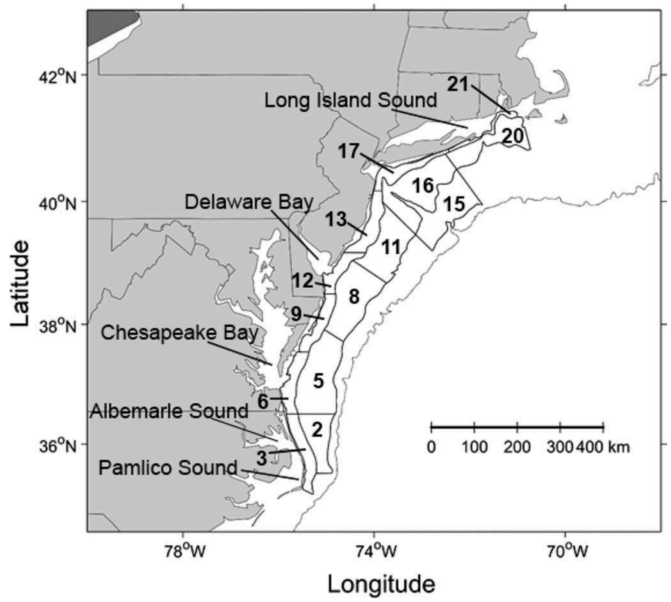

FIGURE 2. Locations of the strata used in ichthyoplankton surveys conducted by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program (1977–1987) and the Ecosystem Monitoring (EcoMon) program (1992 to present) along the Atlantic coast from Nova Scotia, Canada, to North Carolina, USA. Sampling strata are labeled based on their corresponding EcoMon stratum number. Bays are labeled but were not sampled.

We also corrected for variation in the age of larvae caught throughout the sampling season in order to estimate a standardized measure of larval production (see Richardson et al. 2010 for a more in-depth explanation). Mean length at daily age (from Lozano et al. 2012) was used to estimate the ages of all measured larvae, interpolating ages linearly between means. We assumed a constant mortality rate of 0.179 per day (for clupeid species; Houde and Zastrow 1993) and then used this rate to construct an estimate of 0-d-old abundance. The resulting information was then used to further correct larval abundance per tow. We performed a sensitivity analysis using a daily mortality of one-half the literature value at 0.09 per day, and we observed no difference in abundance index trends.

To correct for variation in sampling location and timing, we used a delta-lognormal model to construct the index of larval abundance for Atlantic Menhaden (Chyan-huei Lo et al. 1992; Stefánsson 1999; Maunder and Punt 2004). This type of model separates each observation into two processes: (1) presence–absence and (2) abundance if presence was observed. Presence–absence was modeled using a binomial general linear model with a logistic link function. The positive values were modeled with a lognormal distribution. We adopted a delta-lognormal approach to account for the high number of zeros relative to positive observations (88.7% of observations were zeros). By log-transforming the positive values, we were better able to satisfy the assumption of normality. Positive values were modeled as a linear function of year, month, and stratum,

$$\log_e(A) = \mu + M + Y + S + \varepsilon, \tag{1}$$

where A is the abundance for each tow, adjusted for mortality by larval length; μ is the intercept of the model; M is month; Y is year; S is stratum; and ε is a normally distributed error term. Both portions of the model included the same factors of month, year, and stratum. We used a jackknife routine to obtain estimates of the mean and SE for each of the three model factors. The estimated year effect obtained from the jackknife mean of the delta-lognormal model was then used as our larval index.

TABLE 1. Mean abundance (individuals/m^2; ±SE) of larval (<10-mm) Atlantic Menhaden caught in paired bongo net tows using 333-µm and 505-µm mesh from nine Marine Resources Monitoring, Assessment, and Prediction (MARMAP) cruises (1984 and 1985) and nine Ecosystem Monitoring (EcoMon) cruises (2010–2014). Correction factors used to permit comparison of larvae caught during the MARMAP ichthyoplankton survey (1977–1987; 505-µm mesh) with those caught during the EcoMon survey (2000–2013; 333-µm mesh) were calculated from Johnson and Morse (1994). *N* is the number of paired tows in which at least one individual of the corresponding size-bin was captured and used for comparison. The *P*-values (*P < 0.05) are from paired *t*-tests in which the abundance of paired tows was compared within size-classes.

Fish length (mm)	*N*	Abundance in 333-µm-mesh net	Abundance in 505-µm-mesh net	Correction factor	*P*
<3	640	150.13 ± 19.02	53.92 ± 5.07	2.78	2.28×10^{-9}*
3–4	745	79.11 ± 10.87	49.64 ± 4.03	1.59	2.11×10^{-3}*
4–5	798	68.73 ± 10.58	39.54 ± 3.85	1.74	6.97×10^{-3}*
5–6	793	71.48 ± 16.48	42.89 ± 7.16	1.67	0.113
6–7	790	56.04 ± 11.55	38.99 ± 8.57	1.44	0.238
7–8	735	38.54 ± 5.59	36.27 ± 7.33	1.06	0.796
8–9	685	31.39 ± 5.17	32.05 ± 5.61	0.98	0.913
9–10	602	27.92 ± 4.31	31.15 ± 5.62	0.90	0.441

Juvenile abundance index.—Data from 16 fishery-independent surveys were combined to generate an index of abundance (I_J) for young-of-the-year (age-0) juvenile Atlantic Menhaden (see SEDAR 2015 for survey details). In short, the surveys were conducted via beach seining and trawling and spanned the area from New England to Georgia. The surveys included both fixed-site and stratified random designs. A hierarchical model (Conn 2010) that allows for different abundance trends in different regions was used to estimate the aggregate I_J. These data have been used to describe age-0 abundance for the Atlantic Menhaden stock assessment (SEDAR 2015) and for other studies (Buchheister et al. 2016). Patterns in relative abundance across surveys within a region were similar regardless of the survey design (SEDAR 2015; Buchheister et al. 2016).

Survival index.—To estimate whether survival changed over time and to test whether early life survival was related to a suite of environmental factors, we constructed an index of survival based on our I_L and the I_J from the most recent Atlantic Menhaden stock assessment (SEDAR 2015). The survival index was calculated as

$$I_S = \log_e\left(\frac{I_J}{I_L}\right), \qquad (2)$$

where I_S is the early life survival index, I_J is the age-0 juvenile index, and I_L is the larval abundance index. The survival index follows the traditional form used in many stock–recruitment analyses that incorporate additional explanatory variables (Quinn and Deriso 1999). Because each annual I_L value includes larvae from September of the previous year through June in the year of interest, we are capturing the larval population that would most likely be contributing to the I_J, which follows the traditional January-to-January calendar year.

We obtained climate data (AMO, wind, freshwater flow, and temperature; Table 2) for inclusion as covariates in our survival model. We used information from the September–June period for AMO, freshwater flow, and coastal temperature. However, we only used wind information representing the November–March period—the critical part of the year when late-stage larvae ingress into Chesapeake Bay (Lozano et al. 2012). Similarly, we used Chesapeake Bay temperature information for the November–April period in order to include the entire window of time from (1) survival of ingress to (2) when the bulk of the youngest fish metamorphose into juveniles. Although surface temperature measurements were only from the Patuxent River, temperature in the major tributaries and the main stem of Chesapeake Bay are highly correlated (J. Humphrey, University of Maryland Center for Environmental Science, personal communication).

All environmental variables except for coastal water temperature were summarized into year-class-based indices by calculating the arithmetic mean of values across the appropriate time scale (Table 2; Supplementary Figure S.1 avilable in the online version of this article). The coastal water temperature data were obtained from surface water temperature measurements that were collected during MARMAP and EcoMon cruises. However, not all of the cruises had temperature data available for each sampling event, particularly during the earlier time series. For this reason, annual average temperature was constructed by using a linear model with month, season, and sampling stratum as categorical variables,

$$T_C = \mu + M + Y + S + \varepsilon, \qquad (3)$$

where T_C is coastal temperature; µ is the intercept of the model; *M* is month; *Y* is year; *S* is stratum; and ε is a normally distributed error term. The linear model explained the coastal temperature observations quite well (R^2 = 0.86).

We used a linear model to examine the relationship between I_S and several environmental variables,

$$I_S = \mu + I_L + \text{AMO} + T_B + T_C + F + W_D + W_S + \varepsilon, \qquad (4)$$

TABLE 2. Environmental data included in a model examining the early life survival of Atlantic Menhaden (AMO = Atlantic Multidecadal Oscillation; CBL = Chesapeake Biological Laboratory, University of Maryland; NOAA = National Oceanic and Atmospheric Administration; USGS = U.S. Geological Survey; EcoMon = Ecosystem Monitoring program; MARMAP = Marine Resources Monitoring, Assessment, and Prediction program).

Data	Units	Location of collection	Source	Month range
AMO	NA	NA	NOAA	Sep–Jun
Wind speed	m/s	Norfolk, Virginia	NOAA	Nov–Mar
Wind direction	degrees	Norfolk, Virginia	NOAA	Nov–Mar
Freshwater flow	ft^3/s ($1\ ft^3/s = 0.0283\ m^3/s$)	Chesapeake Bay mouth	USGS	Sep–Jun
Chesapeake Bay temperature	°C	Solomons, Maryland	CBL	Nov–Apr
Coastal temperature	°C	NA	EcoMon/MARMAP surveys	Sep–Jun

where μ is the intercept; AMO is the calculated AMO index; T_B is the Chesapeake Bay temperature index; T_C is the coastal temperature index; F is the mean freshwater flow from Chesapeake Bay during September–June; W_D is the wind direction index measured at Norfolk (Virginia) International Airport; W_S is the wind speed index measured at Norfolk International Airport; and ε is a normally distributed error term. Use of a linearized Ricker model that is modified to include environmental variables is a common technique for evaluating potential environmental effects on spawning success by comparing recruits to survivors (Prager and MacCall 1993; Jacobson and MacCall 1995). We conducted a linear regression of all model subsets in R software and then performed a comparison of Akaike's information criterion with a correction for small sample size (AIC_c) to select the best model of larval survival. We used the AIC_c because the number of observations was low relative to the number of estimated parameters (Burnham and Anderson 2002). We tested for the significance (α = 0.05) of environmental factors' effects on survival based on our best-fitting models.

RESULTS

The I_L for Atlantic Menhaden increased over time (Figure 3). The lowest observed value occurred in 1988, and the peak estimate occurred in 2008. The I_L values remained relatively constant and low during 1977–1988. Beginning in 2000, the trend showed that Atlantic Menhaden larval abundance increased substantially such that the slope of the best-fitting line was 39 units/year, compared with a slope of 13 units/year for the period 1977–1988. Furthermore, the six-highest I_L values corresponded to years of sampling by the most recent program (i.e., EcoMon). The eight remaining years from that same survey (in order of highest to lowest abundance: 2002, 2007, 2000, 2006, 2001, 2003, 2009, and 2005) were comparable to the I_L values from the earlier sampling program (MARMAP).

Larval abundance peaked during November–December and to a lesser extent during January–April (Figure 4). Larval abundance was lowest in the north, with highest observations in shallow strata off the North Carolina coast (Figure 4). Additionally, larval abundance was higher in shallow, nearshore strata than in deepwater strata of similar latitude.

Despite interannual fluctuations between consecutive years, overall relative survival decreased during 1977–2013 (Figure 5). The I_S displayed a slight negative correlation with the I_L (correlation coefficient = –0.004, $P < 0.001$; Table 3; Figure 5). Inclusion of environmental variables resulted in improved AIC_c scores over models that did not include such variables (Table 3). The 10 best models had similar AIC_c scores with values ranging from 20.509 to 23.848, which were all lower than that of the null model ($AIC_c = 25.422$). The Chesapeake Bay temperature index was included in 8 of the 10 best-performing models. In six of those eight models, we detected a significant negative effect of Chesapeake Bay temperature ($P < 0.05$; Table 3; Figure 6b), with coefficients between –0.481 and –0.346. Second to Chesapeake Bay temperature, the coastal temperature index was included in five of the top-10 models; however, the effect was smaller in magnitude, with coefficients from –0.254 to –0.139, and was only significant in the two models that did not include Chesapeake Bay temperature ($P < 0.05$; Table 3; Figure 6c). Although there was an obvious relationship between Chesapeake Bay and coastal temperatures, the two indices had only a moderate positive correlation (Pearson's product-moment correlation coefficient [Pearson's r] = 0.52). Wind speed was not found to have a significant effect on survival but was included as a factor in three of the top models (Table 3). However, the relationship between wind speed and survival may be nonlinear, with optimal survival at speeds averaging between 5 and 6 m/s (Figure 6e). Wind speed and the AMO were negatively correlated (Pearson's $r = –0.78$) and had the strongest correlation of all variables used. Multicollinearity was considered in this analysis, as it can cause major problems when including variables with a bivariate correlation of 0.90 or higher, and inflation of the SEs can occur with bivariate correlations as small as 0.70 (Tabachnick and Fidell 2001). However, only the correlation between wind speed and the AMO was above this threshold (Figures S.1, S.2), and the two variables did not co-occur in any of the top models. Thus, we are confident that variance inflation associated with multicollinearity was not an issue in

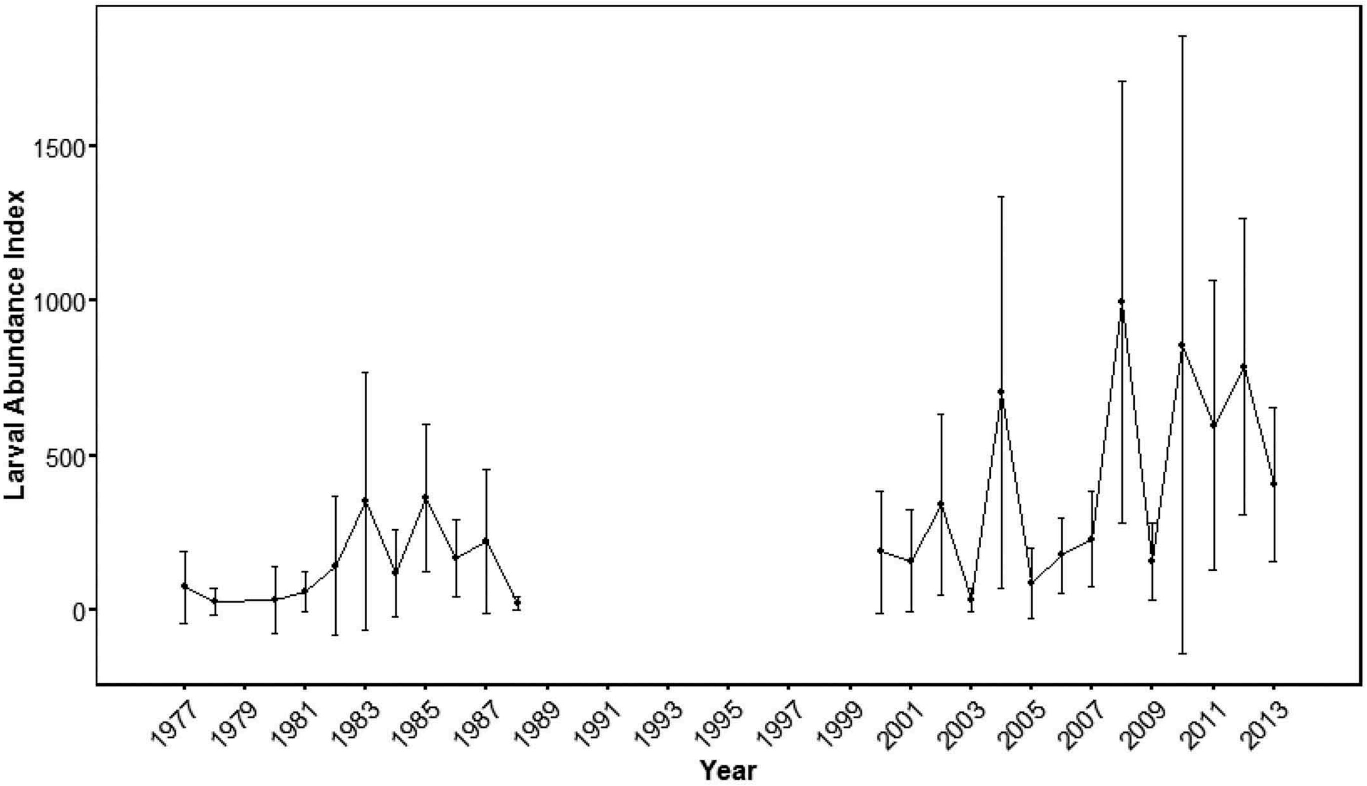

FIGURE 3. Atlantic Menhaden larval abundance index (relative effect sizes from a linear model estimating relative larval abundance) constructed from two ichthyoplankton surveys (Marine Resources Monitoring, Assessment, and Prediction program, 1977–1987; and Ecosystem Monitoring program, 2000–2013) conducted along the Atlantic coast from southern New England to Cape Hatteras, North Carolina (strata are shown in Figure 2). Error bars represent approximate 95% confidence intervals (±2 SE) obtained from a jackknife procedure and a delta-lognormal model.

this analysis. The AMO, freshwater flow, and wind direction did not have significant effects on I_S (Table 3; Figure 6b, d, f).

DISCUSSION

Atlantic Menhaden larval abundance has increased substantially since the late 1970s. The observed increase in I_L was comparable to the recent increase in population fecundity (i.e., estimated egg production) from the 2015 Atlantic Menhaden stock assessment (SEDAR 2015). The stock assessment estimates of population fecundity approximately doubled between 2000–2004 and 2006–2013, similar to our I_L. We did not observe the same pattern of interannual variability in I_L during the 1980s as was present in the stock assessment estimates. However, the fishery-independent data on adults included in the assessment only extended as far back as 1988. Thus, it is not surprising that short-time-scale variability did not match up well in the early period. The high I_L in the most recent period is a positive sign for Atlantic Menhaden populations, and both I_L and population fecundity appear to have been on the rise in the past decade; this corresponds with the sustained low fishing mortality estimates that have been observed since 2000 (Figure 1a; SEDAR 2015).

Comparison of our analysis with the age-2+ (adult) biomass estimated in the most recent stock assessment (SEDAR 2015) revealed a relationship between I_L and the adult spawning stock, particularly for the most recent sampling program (EcoMon; Figure 7), and the pattern was strongest for the period after 1999. We have greater confidence in this later period due to the reduction in mesh size, which in turn increased the probability of detecting the smallest larvae (particularly < 9 mm) and exhibited decreasing effects at larger sizes. Additionally, the adult fishery-independent data used in the stock assessment only cover the period since 1988, so the adult biomass estimates based on data collected before 1988 may be less reliable. Furthermore, although we included a correction for the change in mesh size between the two ichthyoplankton surveys, it is possible that Atlantic Menhaden larval abundance from the MARMAP program was still underestimated due to a reduced ability to detect the smallest (<5-mm) larvae. Nevertheless, these results strongly suggest that the coastwide reduction in juvenile abundance is not a problem of larval supply.

The seasonal and spatial patterns observed in the larval abundance data generally agree with the previously described

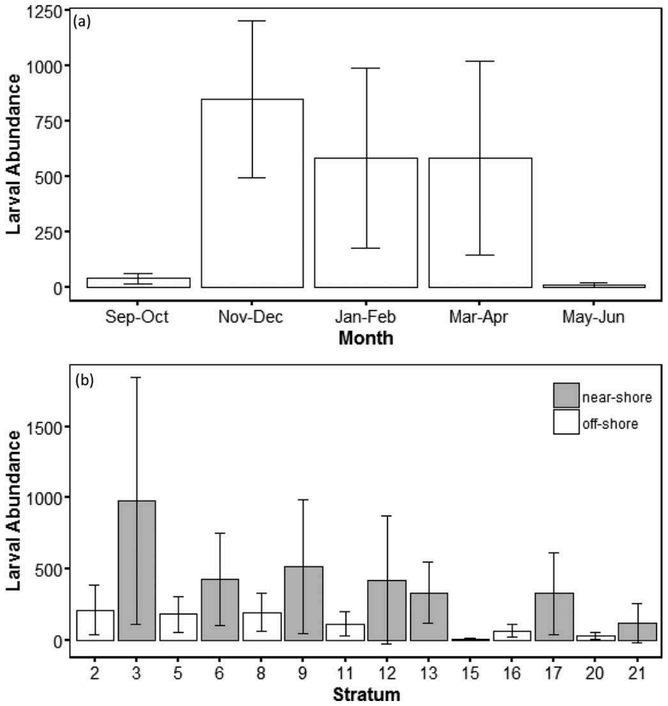

FIGURE 4. Relative effect size (unitless measure showing differences in abundance) on the arithmetic scale for each month **(a)** and stratum (**b**; see Figure 2 for locations) based on a delta-lognormal linear model estimating relative abundance of Atlantic Menhaden larvae from two ichthyoplankton surveys (Marine Resources Monitoring, Assessment, and Prediction program, 1977–1987; and Ecosystem Monitoring program, 2000–2013) conducted along the Atlantic coast from southern New England to Cape Hatteras, North Carolina. Error bars represent approximate 95% confidence intervals obtained from a jackknife procedure and a delta-lognormal model.

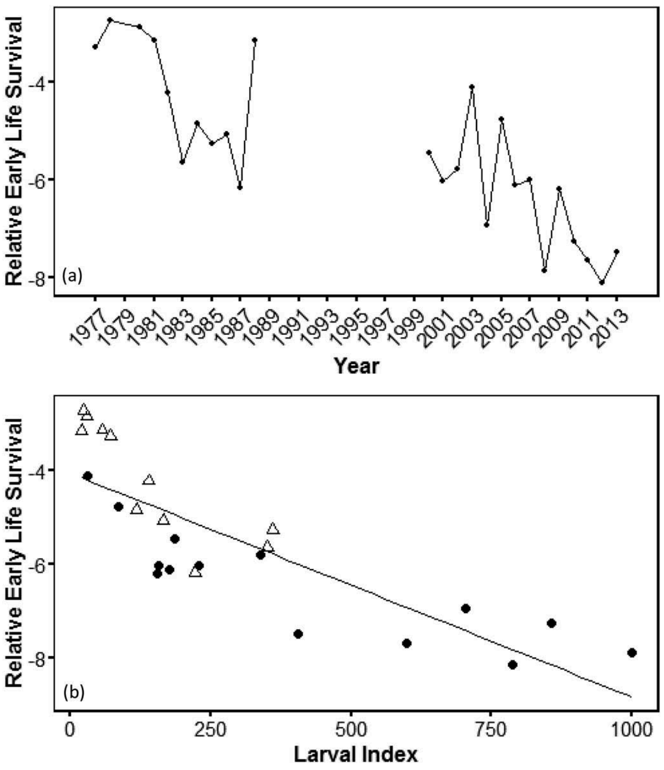

FIGURE 5. Relative early life survival of Atlantic Menhaden **(a)**, calculated as the natural logarithm of the juvenile index (from the 2015 stock assessment) divided by the index of larval abundance for each year; and linear regression **(b)** showing the relationship (fitted line) between relative survival and relative larval abundance from two ichthyoplankton surveys (Marine Resources Monitoring, Assessment, and Prediction program, 1977–1987 [open triangles]; and Ecosystem Monitoring program, 2000–2013 [shaded circles]) conducted along the Atlantic coast from southern New England to Cape Hatteras, North Carolina ($P < 0.001$).

spawning pattern exhibited by Atlantic Menhaden. Peak spawning occurred in winter off the coast of Cape Hatteras (Dryfoos et al. 1973; Nicholson 1978). Larval abundance was higher in November and December than at any other time of the year (Figure 4). Similarly, we observed that the highest larval abundance, on average, was present off the coast of North Carolina. However, shallow strata all along the Atlantic coast had comparable abundance estimates, with average means between 12% and 53% of what was observed near North Carolina. Spawning in these more northerly strata likely takes place during the adults' north-to-south migration, which begins in the late summer (Judy and Lewis 1983; Ahrenholz 1991; Berrien and Sibunka 1999). In addition, our finding of higher abundances in shallow strata corresponds with previous modeling research (Stegmann et al. 1999).

Our study excluded some shallow-water habitat and the southernmost portion of the Atlantic Menhaden's spatial range, but we think that the results should still be fairly robust. Some spawning has been documented as occurring within Narragansett Bay, Rhode Island (Keller et al. 1999). However, based on the general observed trend of southward increases in larval abundance (Figure 4) coupled with the generally accepted theory of a southward increase in migratory spawning behavior (Ahrenholz 1991), we assume that the abundance of larvae in these northern estuaries is negligible in comparison with the scope of the study. The accepted view of Atlantic Menhaden migratory dynamics includes an age-based stratification along the Atlantic coast, with the population south of North Carolina mostly consisting of age-0 and age-1 individuals (Nicholson 1978). Based on this assumption, the majority of the spawning stock biomass would exist within the range of our surveys. However, further research into the age distribution of Atlantic Menhaden, particularly in the southern portion of the range, would be valuable. Additionally, Quinlan et al. (1999) found that due to hydrological conditions, larvae that are spawned south of Cape Hatteras are unlikely to be transported northward to nursery areas such as Chesapeake Bay and Delaware Bay. The majority of the surveys included in the I_J are from North Carolina and northward; larval supply to estuaries north of Cape Hatteras is hypothesized to originate

TABLE 3. Model selection results (AIC_c = Akaike's information criterion with a correction for small sample size) and coefficients from the null model and the top-10 best-performing (based on AIC_c) linear models of Atlantic Menhaden survival (I_L = larval index of abundance; AMO = Atlantic Multidecadal Oscillation; b_temp = mean Chesapeake Bay winter–spring temperature collected from the Patuxent River; c_temp = average coastal temperature derived from measurements taken during two ichthyoplankton surveys [Marine Resources Monitoring, Assessment, and Prediction; and Ecosystem Monitoring]; flow = mean freshwater flow from the mouth of Chesapeake Bay; wind_spd = wind speed collected at Norfolk [Virginia] International Airport; wind_dir = wind direction collected at Norfolk International Airport). Values in bold italics indicate that the parameter is significant ($P < 0.05$).

Model	I_L	AMO	b_temp	c_temp	flow	wind_spd	wind_dir	AIC_c
Null model + b_temp	***–0.004***	–	***–0.447***	–	–	–	–	20.509
Null model + b_temp + wind_spd	***–0.004***	–	***–0.409***	–	–	0.449	–	22.125
Null model + b_temp + c_temp	***–0.004***	–	***–0.346***	–0.139	–	–	–	22.134
Null model + b_temp + wind_dir	***–0.004***	–	***–0.481***	–	–	–	–0.005	22.918
Null model + AMO + b_temp	***–0.004***	–0.973	***–0.400***	–	–	–	–	22.933
Null model + c_temp + wind_spd	***–0.004***	–	–	***–0.254***	–	0.704	–	23.147
Null model + b_temp + c_temp + wind_spd	***–0.004***	–	–0.284	–0.165	–	0.536	–	23.329
Null model + c_temp	***–0.004***	–	–	***–0.244***	–	–	–	23.689
Null model + b_temp + flow	***–0.004***	–	***–0.441***	–	0.016	–	–	23.696
Null model + b_temp + c_temp + wind_dir	***–0.004***	–	–0.284	–0.165	–	–	0.536	23.848
Null model	***–0.005***	–	–	–	–	–	–	25.422

primarily from spawning that occurs north of each estuary, and larvae are transported to the estuary by southwestward, along-shelf currents (Quinlan et al. 1999; Stegmann et al. 1999).

Although the data used in our analysis were collected by two sampling programs that used slightly different techniques, we do not believe that this difference affected the outcome of our work. In analyses not reported here, we ran the same models separately on the MARMAP and EcoMon data sets, and we achieved very similar results in the I_L and I_S patterns. The primary differences between the two programs were minor variations in sampling frequency as well as a change in mesh size from 505 μm to 333 μm. We accounted for sampling changes by including month as a factor in our linear model; the change in mesh size was addressed by applying a selectivity correction to the MARMAP data based on the results of Johnson and Morse (1994), who performed a gear comparison test for the exact survey included in our analyses. Although the data from MARMAP were lower on average than those from EcoMon sampling, larval abundance values from the beginning of the EcoMon period (early 2000s) are similar to those from the MARMAP survey and are in accordance with the changes estimated during the stock assessment. We believe that the value of tracking population-level changes in larval abundance over such a long time period far outweigh the potential problems of combining data from the two programs.

We estimated a substantial decline in survival of Atlantic Menhaden over time (Figure 5). We found higher larval abundance during the EcoMon period than during the MARMAP program (Figure 3). However, the average juvenile abundance (Figure 1c; SEDAR 2015) showed the reverse trend. Our survival index, I_S, was simply the ratio of these two indices. Thus, declining survival is expected. Density dependence has been proposed to have a role in Atlantic Menhaden populations (e.g., Schaaf and Huntsman 1972; Nelson et al. 1977; Reish et al. 1985). Two possible underlying mechanisms include adult predation on eggs and larvae (Nelson et al. 1977) and decreased growth prior to recruitment due to limited resources (Reish et al. 1985). If density-dependent growth does affect Atlantic Menhaden survival, this effect would become greater in years with warmer average temperatures (e.g., the EcoMon period) due to increased metabolic demands and higher rates of starvation (Houde 1989).

We expected to see a relationship between Atlantic Menhaden survival and the AMO based on a previous study of fish populations in Chesapeake Bay. Wood and Austin (2009) found that decadal-scale variability, similar to the AMO, accounted for the majority of variation in fish abundance. The most likely mechanism they proposed for such a relationship was the impact of broad-scale environmental factors on shelf-spawning species (e.g., Atlantic Menhaden) at multiple life stages. Such broad patterns would be difficult to detect using any one environmental factor. Wood and Austin (2009) also detected evidence supporting a significant regime shift in 1992, which negatively affected coastal-spawning species like the Atlantic Menhaden. The AMO phase was negative in the 1980s and 1990s and has moved into a positive phase since the late 1990s (Nye et al. 2013). Our results do not refute the importance of decadal-scale variation: overall, survival was higher when the AMO was negative and vice versa. However, when used as an annual predictor of early life survival, the AMO did not perform as well as other environmental variables (Figure 6a). If this is an important factor driving Atlantic Menhaden survival, then it is possible that some of the observed decline is part of a naturally occurring

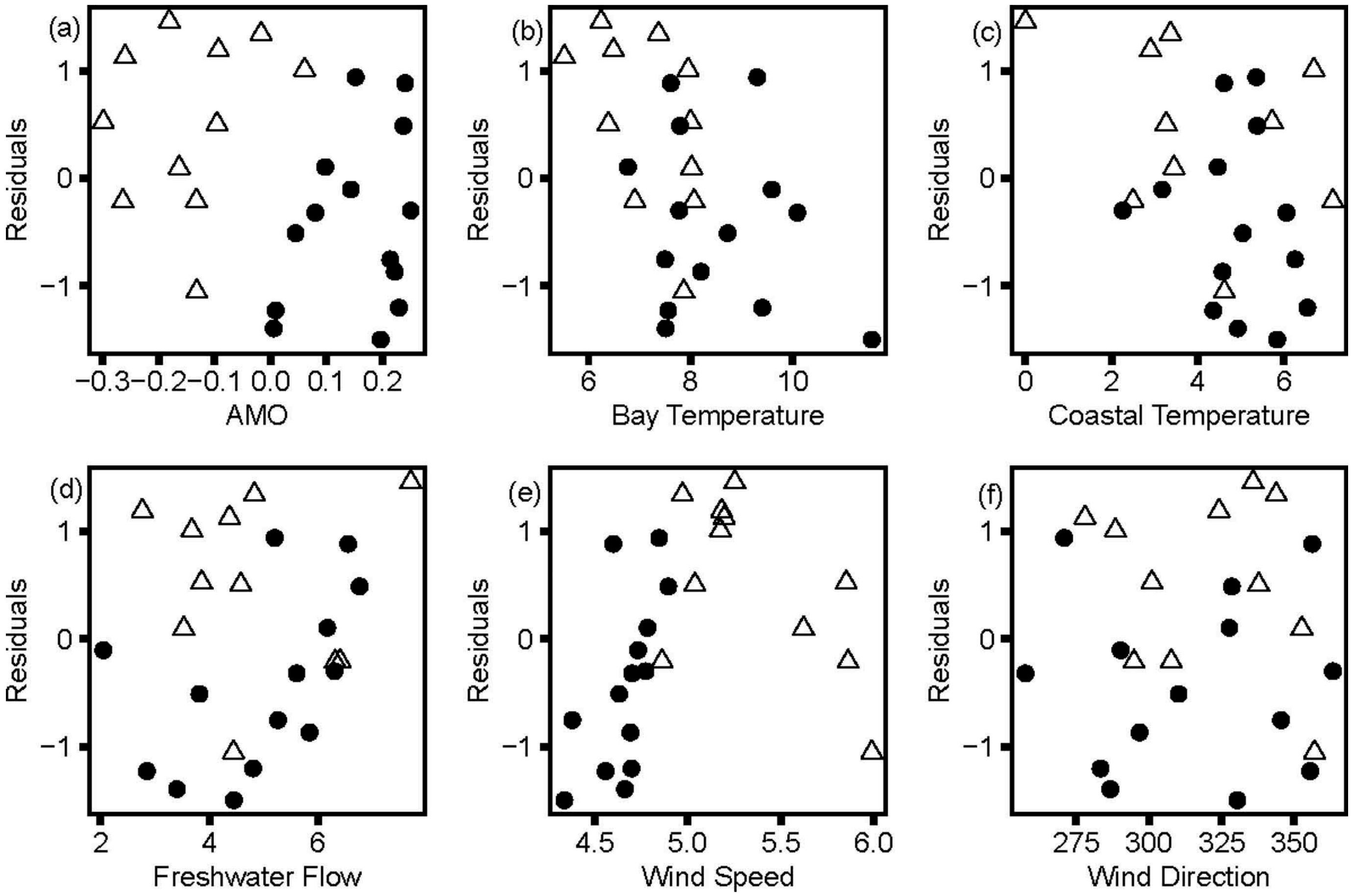

FIGURE 6. Marginal effects from a linear model of Atlantic Menhaden survival plotted against six environmental variables: **(a)** Atlantic Multidecadal Oscillation (AMO) averaged over September–June; **(b)** mean Chesapeake Bay temperature (°C) during November–April, taken from the Patuxent River; **(c)** coastal temperatures (°C) modeled from two ichthyoplankton surveys (Marine Resources Monitoring, Assessment, and Prediction program, 1977–1987 [open triangles]; and Ecosystem Monitoring program, 2000–2013 [shaded circles]) conducted along the Atlantic coast from southern New England to Cape Hatteras, North Carolina; **(d)** mean freshwater flow (10,000 ft^3/s; 1 $ft^3/s = 0.0283\ m^3/s$) discharged from Chesapeake Bay during November–March; **(e)** mean wind speed (m/s) at Norfolk (Virginia) International Airport; and **(f)** wind direction (degrees from north) at Norfolk International Airport.

cycle. Unfortunately, our data do not span an entire AMO cycle.

The AMO might not be affecting Atlantic Menhaden equally over their entire range. Specifically, juvenile survival in Chesapeake Bay was inversely correlated with the AMO, whereas survival in southern New England estuaries was positively correlated with the AMO (Buchheister et al. 2016). Therefore, the large spatial scale of our analysis would not work well in detecting potential effects at a more regional scale.

Temperature effects on the early lives of fishes are complex due to trade-offs between increased growth rates with warmer spring temperatures and lower survival as temperatures increase and food availability declines (Deegan 1990). However, Chesapeake Bay temperature or coastal temperature had a significant negative effect on survival in all 10 of the best-fitting models. We found that Chesapeake Bay temperature was the best environmental predictor of early life survival. Although our temperature index was constructed from data collected in Chesapeake Bay, the mean winter-to-spring water temperatures of the five major estuaries along the northeastern U.S. coast (Chesapeake Bay, Delaware Bay, Long Island Sound, Narragansett Bay, and Buzzards Bay) are fairly well correlated (Bell et al. 2014). Thus, the temperature index was also reflective of other important nursery areas, such as Delaware Bay (Light and Able 2003) and Albemarle Sound (Stegmann et al. 1999). Coastal temperature was the second-best predictor of survival, with a slightly smaller negative effect. Despite the similarity between the two temperature variables, they reflect two different life stages of Atlantic Menhaden. Coastal temperature mainly affects eggs and larvae, whereas Chesapeake Bay temperature mainly affects older larvae and juveniles (Ahrenholz 1991). Thus, our findings may indicate that the influence of declining estuary conditions on early life survival is greater than that of coastal conditions.

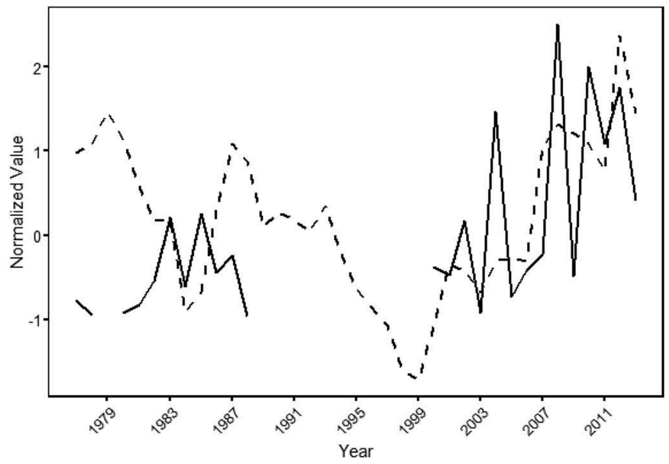

FIGURE 7. Normalized values of estimated biomass for age-2 and older Atlantic Menhaden (dashed line; SEDAR 2015), plotted with normalized larval abundance index values (solid line; as seen in Figure 3).

Wind speed could affect early life survival through multiple mechanisms, such as feeding and transport. Due to the planktonic nature of Atlantic Menhaden larvae, particularly the young larvae, early transport is predominately driven by physical factors, such as wind-driven Ekman transport (Epifanio and Garvine 2001). Of course, the directionality of wind can also be important depending on the depth at which larvae are occurring. For example, up-estuary wind would favor surface-oriented larvae. However, during their ingress into Delaware Bay, Atlantic Menhaden larvae are evenly distributed among depths (Schieler et al. 2014). We expected wind speed at particularly high and low levels to have a negative effect on survival, as some wind mixing could increase larval prey occurrence, whereas too much turbulence could do the opposite (Maillet and Checkley 1991). The present results suggest that there is an optimum range of wind speed for Atlantic Menhaden survival, although more work in this area is needed because we had relatively few observations for high average wind speeds. Our finding is reminiscent of the “optimal environmental window” theory (Cury and Roy 1989), which shows that pelagic fish have their best reproductive success in upwelling environments when the wind speeds are at intermediate levels that maximize larval predation success. Additionally, we only considered linear relationships for environmental variables, so a nonlinear relationship in which intermediate values are more favorable than both high and low values does not match the assumptions of the survival model we used.

We found no evidence that wind direction affects the survival of larval Atlantic Menhaden. Successful ingress of Atlantic Menhaden larvae is a complex process that requires larval transport to estuary mouths, which is thought to be primarily north of estuaries on the northeastern U.S. coast (Quinlan et al. 1999; Stegmann et al. 1999). Up-estuary transport to juvenile habitats occurs via residual bottom-water inflow and wind forcing (Hare et al. 2005). We expected that winds coming from the northeast would be the most ideal for successful ingress of larvae into Chesapeake Bay, thus increasing survival, because northeast winds produce significant residual inflow on the inlet’s northern side, where the potential source of larvae occurs (Valle-Levinson et al. 2001). However, wind direction was fairly consistent across years, coming from the northwest—the direction that is most efficient at flushing water out of the bay (Valle-Levinson et al. 2001). The level of variation we did observe appeared to have no effect on survival. Schieler et al. (2014) also detected no relationship between Atlantic Menhaden ingress into Delaware Bay and along-shelf or along-estuary winds.

Freshwater flow had no significant effect on Atlantic Menhaden survival. We expected that years with higher mean freshwater flow would promote ingress. Higher freshwater flow could mean greater ingress via increased residual bottom-water inflow (Hare et al. 2005). Additionally, greater freshwater flow may increase the abundance of prey, particularly copepods (Houde et al., in press). However, there was no evidence of a relationship between flow and Atlantic Menhaden survival. This may be attributable to the length and coverage of our time series, as any environmental variables with weak to moderate effects would be difficult to detect in this type of analysis due to the many potential sources of variation.

The Atlantic Menhaden is one of the most abundant forage fish species along the Atlantic coast and transfers substantial amounts of energy through the food web. The most recent stock assessment reported a healthy population, with high abundance and no overfishing in recent years. Our analysis of two large-scale ichthyoplankton surveys indicated that the number of Atlantic Menhaden larvae increased substantially in the last decade, which corresponds well with the most recent estimates of spawning stock biomass from the stock assessment. Pre-recruit survival, however, appears to have decreased substantially in recent years. This study highlights the importance of early life conditions—particularly estuarine temperature and, to a lesser extent, coastal temperature and perhaps wind and climatic variables—in ensuring high recruitment to the juvenile population and subsequently to the Atlantic Menhaden fishery.

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REFERENCES

Ahrenholz, D. 1991. Population biology and life history of the North American menhadens, *Brevoortia* spp. Marine Fisheries Review 53:3–19.

Ahrenholz, D. W., J. F. Guthrie, and C. W. Krowse. 1989. Results of abundance surveys juvenile Atlantic and Gulf menhaden, *Brevoortia tyrannus* and *B. patronus*. NOAA Technical Report NMFS-TR-84.

Ahrenholz, D., W. Nelson, and S. Epperly. 1987. Population and fishery characteristics of Atlantic Menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 85:570–600.

Annis, E. R., E. D. Houde, L. W. Harding, M. E. Mallonee, and M. J. Wilberg. 2011. Calibration of a bioenergetics model linking primary production to Atlantic Menhaden *Brevoortia tyrannus* growth in Chesapeake Bay. Marine Ecology Progress Series 437:253–267.

Anstead, K. A., and C. M. Jones. 2014. The impact of multiple nursery areas on the population structure of Atlantic Menhaden, *Brevoortia tyrannus*. Doctoral dissertation. Old Dominion University, Norfolk, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2004. Atlantic Menhaden stock assessment report for peer review. ASMFC, Stock Assessment Report 04-01 (Supplement), Arlington, Virginia.

Bell, R., J. Hare, J. Manderson, and D. Richardson. 2014. Externally driven changes in the abundance of Summer and Winter flounder. ICES Journal of Marine Science 71:2416–2428.

Berrien, P. L., and J. Sibunka. 1999. Distribution patterns of fish eggs in the U. S. Northeast Continental Shelf ecosystem, 1977–1987. NOAA Technical Report NMFS-145.

Bonvechio, K. I., M. S. Allen, T. F. Bonvechio, and T. P. Coughlin. 2008. Comparison of Largemouth Bass assessment metrics between standardized and historical sampling designs at six Florida lakes. North American Journal of Fisheries Management 28:1132–1137.

Buchheister, A., T. J. Miller, E. D. Houde, D. H. Secor, and R. J. Latour. 2016. Spatiotemporal dynamics of Atlantic Menhaden (*Brevoortia tyrannus*) recruitment along the northwest Atlantic Ocean. ICES Journal of Marine Science 73:1147–1159.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Chyan-huei Lo, N., L. D. Jacobson, and J. L. Squire. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. Canadian Journal of Fisheries and Aquatic Sciences 49:2515–2526.

Conn, P. B. 2010. Hierarchical analysis of multiple noisy abundance indices. Canadian Journal of Fisheries and Aquatic Sciences 67:108–120.

Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciences 46:670–680.

Deegan, L. A. 1990. Effects of estuarine environmental conditions on population dynamics of young-of-the-year Gulf Menhaden. Marine Ecology Progress Series 68:195–205.

Dryfoos, R. L., R. P. Cheek, and R. L. Kroger. 1973. Preliminary analysis of Atlantic Menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated from tag returns. U.S. National Marine Fisheries Service Fishery Bulletin 71:719–734.

Enfield, D. B., A. M. Mestas-Nuñez, and P. J. Trimble. 2001. The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U.S. Geophysical Research Letters 28:2077–2080.

Epifanio, C. E., and R. W. Garvine. 2001. Larval transport on the Atlantic Continental Shelf of North America: a review. Estuarine, Coastal, and Shelf Science 52:51–77.

Ferraro, S. P. 1980. Embryonic development of Atlantic Menhaden, *Brevoortia tyrannus*, and a fish embryo age estimation method. U.S. National Marine Fisheries Service Fishery Bulletin 77:943–949.

Friedland, K., D. Ahrenholz, and J. Guthrie. 1989. Influence of plankton on distribution patterns of the filter-feeder *Brevoortia tyrannus* (Pisces: Clupeidae). Marine Ecology Progress Series 54:1–11.

Hare, J. A., S. Thorrold, H. J. Walsh, C. Reiss, A. Valle-Levinson, and C. M. Jones. 2005. Biophysical mechanisms of larval fish ingress into Chesapeake Bay. Marine Ecology Progress Series 303:295–310.

Holzwarth, T. J., and D. G. Mountain. 1990. Surface and bottom temperature distributions from the Northeast Fisheries Center spring and fall bottom trawl survey program, 1963–1987, with addendum for 1988–1990. National Marine Fisheries Service, Northeast Fisheries Science Center, Reference Document 90-03, Woods Hole, Massachusetts.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. U.S. National Marine Fisheries Service Fishery Bulletin 87:471–495.

Houde, E. D., E. R. Annis, L. W. Harding Jr., M. E. Mallonee, and M. J. Wilberg. In press. Factors affecting the abundance of age-0 Atlantic Menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. ICES Journal of Marine Science. DOI: 10.1093/icesjms/fsw063.

Houde, E. D., C. Lozano, E. R. Annis, L. W. Harding Jr., D. H. Secor, M. J. Wilberg, and R. J. Wingate. 2011. Recruitment of Atlantic Menhaden to Chesapeake Bay: ecological processes during the larval–juvenile transition. International Council for the Exploration of the Sea, Annual Meeting Report, Copenhagen.

Houde, E. D., and C. E. Zastrow. 1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. Bulletin of Marine Science 53:290–335.

Jacobson, L. D., and A. D. MacCall. 1995. Stock–recruitment models for Pacific Sardine (*Sardinops sagax*). Canadian Journal of Fisheries and Aquatic Sciences 52:566–577.

Johnson, D. L., and W. W. Morse. 1994. Net extrusion of larval fish: correction factors for 0.333-mm versus 0.505-mm-mesh bongo nets. Northwest Atlantic Fisheries Organization Scientific Council Studies 20:85–95.

Judy, M. H., and R. M. Lewis. 1983. Distribution of eggs and larvae of Atlantic Menhaden, *Brevoortia tyrannus*, along the Atlantic coast of the United States. NOAA Technical Report NMFS-SSRF-774.

Keller, A. A., G. Klein-MacPhee, and J. St. Onge Burns. 1999. Abundance and distribution of ichthyoplankton in Narragansett Bay, Rhode Island, 1989–1990. Estuaries 22:149–163.

King, T. A., J. C. Williams, W. D. Davies, and W. L. Shelton. 1981. Fixed versus random sampling of fishes in a large reservoir. Transactions of the American Fisheries Society 110:563–568.

Kiraly, I. A., S. M. Coghlan Jr., J. Zydlewski, and D. Hayes. 2014. Comparison of two sampling designs for fish assemblage assessment in a large river. Transactions of the American Fisheries Society 143:508–518.

Lewis, R. M. 1965. The effect of minimum temperature on the survival of larval Atlantic Menhaden, *Brevoortia tyrannus*. Transactions of the American Fisheries Society 94:409–412.

Li, B., J. Cao, J. Chang, C. Wilson, and Y. Chen. 2015. Evaluation of effectiveness of fixed-station sampling for monitoring American lobster settlement. North American Journal of Fisheries Management 35:942–957.

Light, P. R., and K. W. Able. 2003. Juvenile Atlantic Menhaden (*Brevoortia tyrannus*) in Delaware Bay, USA, are the result of local and long-distance recruitment. Estuarine, Coastal, and Shelf Science 57:1007–1014.

Lo, N. C., L. D. Jacobson, and J. L. Squire. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. Canadian Journal of Fisheries and Aquatic Sciences 49:2515–2526.

Lozano, C., E. D. Houde, R. L. Wingate, and D. H. Secor. 2012. Age, growth and hatch dates of ingressing larvae and surviving juveniles of Atlantic Menhaden *Brevoortia tyrannus*. Journal of Fish Biology 81:1665–1685.

Maillet, G., and D. M. Checkley Jr. 1991. Storm-related variation in the growth rate of otoliths of larval Atlantic Menhaden *Brevoortia tyrannus*: a time series analysis of biological and physical variables. Marine Ecology Progress Series 79:1–16.

Maunder, M. N., and A. E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research 70:141–159.

McClelland, M. A., and G. G. Sass. 2012. Assessing fish collections from random and fixed site sampling methods on the Illinois River. Journal of Freshwater Ecology 27:325–333.

Mountain, D. G., M. H. Taylor, and C. Bascuñán. 2004. Revised procedures for calculating regional average water properties for Northeast Fisheries Science Center cruises. National Marine Fisheries Service, Northeast Fisheries Science Center, Reference Document 04-08, Woods Hole, Massachusetts.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic Menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 75:23–41.

Nicholson, W. R. 1978. Movements and population structure of Atlantic Menhaden indicated by tag returns. Estuaries 1:141–150.

Nye, J. A., M. R. Baker, R. Bell, A. Kenny, K. H. Kilbourne, K. D. Friedland, E. Martino, M. M. Stachura, K. S. Van Houtan, and R. Wood. 2013. Ecosystem effects of the Atlantic Multidecadal Oscillation. Journal of Marine Systems 133:103–116.

Peck, M. A., K. B. Huebert, and J. K. Llopiz. 2012. Intrinsic and extrinsic factors driving match–mismatch dynamics during the early life history of marine fishes. Advances in Ecological Research 47:177–302.

Pineda, J., J. A. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22–39.

Prager, M. H., and A. D. MacCall. 1993. Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern Anchovy *Engraulis mordax*, Pacific Sardine *Sardinops sagax*, and Chub Mackerel *Scomber japonicus*. U.S. National Marine Fisheries Service Fishery Bulletin 91:10–327.

Quinlan, J., B. Blanton, T. J. Miller, and F. E. Werner. 1999. From spawning grounds to the estuary: using linked individual-based and hydrodynamic models to interpret patterns and processes in the oceanic phase of Atlantic Menhaden *Brevoortia tyrannus* life history. Fisheries Oceanography 2 (Supplement):224–246.

Quinn, J. T., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, Oxford, UK.

Reintjes, J. W. 1969. Synopsis of biological data on the Atlantic Menhaden, *Brevoortia tyrannus*. U.S. Fish Wildlife Service, Circular 320, Washington, D.C.

Reish, R. L., R. B. Deriso, D. Ruppert, and R. J. Carroll. 1985. An investigation of the population dynamics of Atlantic Menhaden (*Brevoortia tyrannus*). Canadian Journal of Fisheries and Aquatic Sciences 42(Supplement 1): S147–S157.

Rice, J. A., J. A. Quinlan, S. W. Nixon, W. F. Hettler Jr., S. M. Warlen, and P. M. Stegmann. 1999. Spawning and transport dynamics of Atlantic Menhaden: inferences from characteristics of immigrating larvae and predictions of a hydrodynamic model. Fisheries Oceanography 8 (Supplement 2):93–110.

Richardson, D., J. A. Hare, W. J. Overholtz, and D. L. Johnson. 2010. Development of long-term larval indices for Atlantic Herring (*Clupea harengus*) on the Northeast U.S. Continental Shelf. ICES Journal of Marine Science 67:617–627.

Schaaf, W. E., and G. R. Huntsman. 1972. Effects of fishing on the Atlantic Menhaden stock: 1955–1969. Transactions of the American Fisheries Society 101:290–297.

Schieler, B. M., E. A. Hale, and T. E. Targett. 2014. Daily variation in ingress of fall-spawned larval fishes into Delaware. Estuarine, Coastal, and Shelf Science 151:141–147.

SEDAR (Southeast Data, Assessment, and Review). 2015. SEDAR 40: Atlantic Menhaden stock assessment report. SEDAR, North Charleston, South Carolina.

Sibunka, J. D., and M. J. Silverman. 1984. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1983). Atlas Number 1, summary of operations. NOAA Technical Memorandum NMFS-F/NEC-33-306.

Stefánsson, G. 1999. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES Journal of Marine Science 53:577–588.

Stegmann, P. M., J. A. Quinlan, F. E. Werner, B. O. Blanton, and P. Berrien. 1999. Atlantic Menhaden recruitment to a southern estuary: defining potential spawning regions. Fisheries Oceanography 8(Supplement 2):111–123.

Stegmann, P. M., and J. A. Yoder. 1996. Variability of sea-surface temperature in the South Atlantic Bight as observed from satellite: implications for offshore-spawning fish. Continental Shelf Research 16:843–861.

Tabachnick, B. G., and L. S. Fidell. 2001. Using multivariate statistics. Allyn and Bacon, Boston.

Taylor, M. H., and C. Bascuñán. 2001. Description of the 2000 oceanographic conditions on the Northeast Continental Shelf. National Marine Fisheries Service, Northeast Fisheries Science Center, Reference Document 01-01, Woods Hole, Massachusetts.

Valle-Levinson, A., K. C. Wong, and K. T. Bosley. 2001. Observations of the wind-induced exchange at the entrance to Chesapeake Bay. Journal of Marine Research 59:391–416.

Vaughan, D. S., and J. W. Smith. 1988. Stock assessment of the Atlantic Menhaden, *Brevoortia tyrannus*, fishery. NOAA Technical Report NMFS-63.

Walsh, H. J., D. E. Richardson, K. E. Marancik, and J. A. Hare. 2015. Long-term changes in the distributions of larval and adult fish in the northeast U. S. shelf ecosystem. PLoS (Public Library of Science) ONE [online serial] 10(9):e0137382.

Warren, W. G. 1994. The potential of sampling with partial replacement for fisheries surveys. ICES Journal of Marine Science 51:315–324.

Wood, R. J., and H. M. Austin. 2009. Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, US. Canadian Journal of Fisheries and Aquatic Sciences 66:496–508.