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Original Article

Factors affecting the abundance of age-0 Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay

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The abundance of prerecruit, age-0 Atlantic menhaden (*Brevoortia tyrannus*), declined to low levels in Chesapeake Bay in the 1990s, after two decades of high abundances in the 1970s–1980s. Environmental factors and trophodynamics were hypothesized to control age-0 menhaden abundance. Data on age-0 menhaden abundance from seine and trawl surveys were analysed with respect to primary productivity, chlorophyll *a* (Chl *a*), and environmental variables. Abundance from 1989 to 2004 was strongly correlated with metrics of primary production and euphotic-layer Chl *a*, especially during spring months when larval menhaden transform into filter-feeding, phytoplanktivorous juveniles. Correlation, principal components, and multiple regression analyses were conducted that identified factors associated with age-0 menhaden abundance. Primary production, Chl *a*, and variables associated with freshwater flow, e.g. Secchi disk depth and zooplankton assemblages, were correlated with age-0 menhaden abundance. Lengths of age-0 menhaden were positively related to mean levels of annual primary production. However, lengths were negatively related to age-0 menhaden abundance, indicating that growth may be density-dependent. The identified relationships suggest that numbers of menhaden larvae ingressing to Chesapeake Bay and environmental factors that subsequently control primary productivity and food for juveniles within the Bay may control recruitment levels of Atlantic menhaden.

Keywords: environmental factors, growth variability, primary production, recruitment variability, spatial variability.

Introduction

The Atlantic menhaden (*Brevoortia tyrannus*) is an abundant clupeid fish and important forage for many piscivores (Rogers and Van den Avyle, 1983; MDSG, 2009). The Atlantic menhaden also supports the largest fishery landings on the east coast of the United States and within Chesapeake Bay (SEDAR, 2015). The Bay serves as a major nursery for juvenile menhaden (MDSG, 2009). Abundance levels of age-0 juveniles in Chesapeake Bay have varied by two orders of magnitude over the past six decades. A series of low-abundance years in the late 1950s and 1960s was followed by high abundances in the 1970s and 1980s, and most recently by 20+ years of consistently low-recruitment success. Historically, the Chesapeake Bay has contributed an estimated 68% of recruits to the coastal population (MDSG, 2009; ASMFC, 2010).

Atlantic menhaden inhabits the coastal ocean, embayments, and estuaries from Florida to Maine. The population consists of a single coast-wide stock (Ahrenholz, 1991). Most spawning occurs on the continental shelf during fall and winter from the mid-Atlantic to the Carolinas (Reintjes and Pacheco, 1966; Rogers and Van den Avyle, 1983; Ahrenholz, 1991; MDSG, 2009). Eggs and larvae mostly occur over the continental shelf and are dispersed coastward where late-stage larvae enter estuaries and grow to the juvenile stage (Warlen, 1994; Rice *et al.*, 1999; SABRE, 1999; Warlen *et al.*, 2002; Lozano and Houde, 2013). Variability in success of larval transport to estuaries is one hypothesized cause of recruitment variability. A 3-year survey at the mouth of Chesapeake Bay indicated that numbers of ingressing larvae varied ninefold among years, but abundances of juveniles in the following months were not concordant with those of ingressing larvae (Lozano *et al.*, 2012; Lozano and Houde, 2013). We propose that factors controlling production of juveniles within Chesapeake Bay may generate interannual variability in the abundance of juvenile, age-0 Atlantic menhaden.

Purse-seine fishing does not target or land substantial amounts of age-0 menhaden (ASMFC, 2012) and consequently is not likely to be a cause of low abundances of age-0 prerecruits or a contributor to "localized depletion" of Atlantic menhaden in Chesapeake Bay (MDSG, 2009). Atlantic menhaden supports Chesapeake Bay's largest fishery, with annual landings often exceeding 100 000 metric tons during recent decades (Smith, 1999; ASMFC, 2010, 2012; Houde, 2011; SEDAR, 2015). The purse-seine reduction fishery in the Bay mostly lands 1- to 3-year-old menhaden. Since 1990, age-0 Atlantic menhaden abundance levels in the Bay have been near historical low levels (MDSG, 2009; ASMFC, 2010, 2012; SEDAR, 2015). Predation on age-0 and older Atlantic menhaden by piscivorous fish, such as striped bass *Morone saxatilis*, and by many avian predators is substantial within the Bay and coast-wide, to the extent that biomass removed by predation could be of the same magnitude as mortality from the fishery (Uphoff, 2003; Walter *et al.*, 2003).

Variability of water quality, climate conditions, predation rates, primary productivity, and associated phytoplankton levels in the Bay are probable causes of interannual variability of survival, growth, and recruitment levels in Atlantic menhaden. Its larvae are zooplanktivores (June and Carlson, 1971; Lozano, 2011), but after transforming to juveniles at 35–40 mm length, age-0 Atlantic menhaden becomes filter-feeders, retaining small phytoplankton, zooplankton, and detritus on their gillrakers and branchial apparatus (Friedland *et al.*, 1984, 1989, 2006). As they grow, individuals become less efficient at filtering small phytoplankton and more dependent on zooplankton as prey by their second year of life (Friedland *et al.*, 2006; Lynch *et al.*, 2010). Results of bioenergetics modelling support the hypothesis that age-0 Atlantic menhaden production is related to the level of phytoplankton biomass in Chesapeake Bay (Luo *et al.*, 2001; Brandt and Mason, 2003; Annis *et al.*, 2011), and a degree-days model indicates a strong effect of temperature on growth (Humphrey *et al.*, 2014).

Here, we evaluated factors that may contribute to interannual variability of age-0 Atlantic menhaden production and abundance in Chesapeake Bay. A retrospective analysis of abundance and growth was conducted based on the analysis of data for age-0 Atlantic menhaden from trawl and seine surveys. We hypothesized that variability in abundance is, at least in part, controlled in the age-0 juvenile stage during estuarine residency and depends on seasonal and interannual variability in phytoplankton biomass, levels of primary production, and other environmental factors.

Methods

We analysed survey data on indices of abundances and lengths of age-0 Atlantic menhaden to detect if variability was related to water quality, phytoplankton biomass, and primary production in Chesapeake Bay and its tributaries (Figure 1). Correlation and regression analyses and multivariate statistical analysis (principal component analysis) were used to identify and evaluate factors related to age-0 Atlantic menhaden abundance. Multiple regression models were run to evaluate statistical relationships between age-0 abundance and environmental/hydrographic variables. Historical growth rates of age-0 Atlantic menhaden and their interannual and decadal patterns were estimated from mean lengths in the length frequency distributions of age-0 menhaden collected in trawl surveys conducted by the Virginia Institute of Marine Science (http://www.vims.edu/research/departments/fisheries/programs/juvenile_surveys/index.php) and the University of Maryland Center for Environmental Science (http://hjort.cbl.umces.edu/chesfims.html).

Menhaden abundance and distribution

The index of abundance was derived from catch-per-unit effort (number per haul) data for age-0 Atlantic menhaden in a multi-decadal seine survey. We analysed data for years 1959–2005 that were obtained in the mid- and upper Chesapeake Bay and tributaries (corresponding to mesohaline and oligohaline salinity zones, respectively) in the Maryland Department of Natural Resources (MD DNR) striped bass juvenile index survey (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx). The MD DNR annual abundance indices for age-0 Atlantic

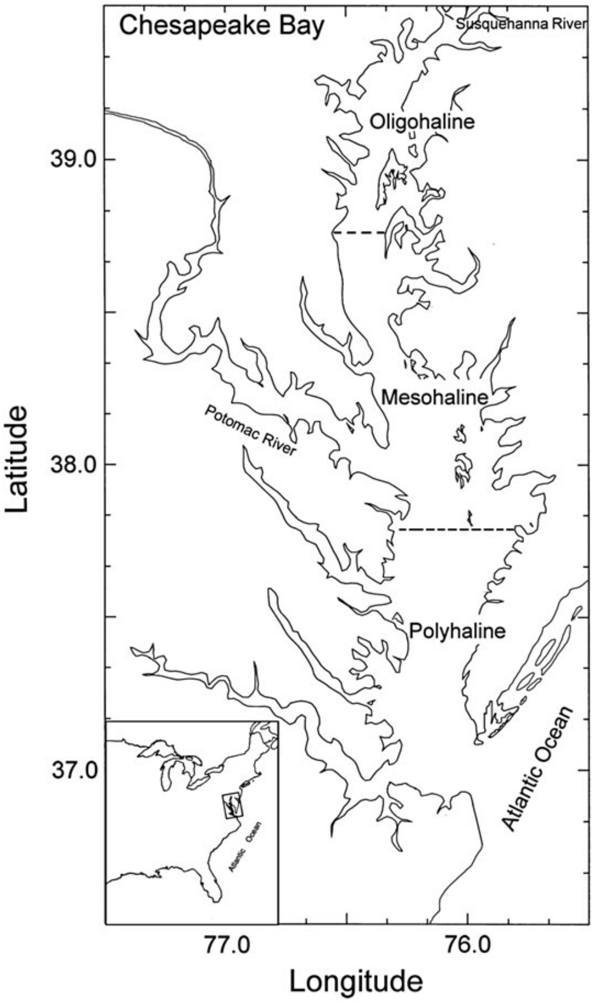


Figure 1. Chesapeake Bay and tributaries where age-0 Atlantic menhaden were surveyed. Oligohaline, mesohaline, and polyhaline salinity zones correspond to upper, mid-, and lower Bay, respectively, in the text and Table 2.

menhaden are the geometric mean catches per seine haul. In our analyses, we weighted the MD DNR abundance indices by the respective surface areas (Cronin, 1971) of each tributary or region in the seine survey. Our indices are the geometric means of seine catches made in July, August, and September from sites sampled in the upper Bay, and the Choptank, Nanticoke, and Potomac rivers (Figure 1). Abundance indices were not standardized relative to spawning biomass of adult Atlantic menhaden (i.e. recruit per spawner) because no stock–recruitment relationship has been observed over the past six decades (SEDAR, 2015), and the fraction of the coast-wide adult stock that contributes to age-0 abundance in Chesapeake Bay is unknown.

Additionally, relative regional abundances of age-0 Atlantic menhaden were calculated for three Bay regions (lower, mid-, and upper) from survey catches in an 18-m^2 midwater trawl with 4-mm codend meshes (Jung, 2002; Jung and Houde, 2003). For this analysis, age-0 individuals collected in spring (April–May), summer (June–July), and fall (October) research cruises (http://hjort.cbl.umces.edu/chesfims.html) conducted by the University of Maryland Center for Environmental Science (UMCES) over a 6-year period (1995–2000) were analysed. Mean catches per 20-min trawl were weighted by the relative volumes of the three designated regions (lower Bay = 1.0; mid-Bay = 0.63; upper Bay = 0.33 to estimate regional relative abundances). Data from the UMCES trawl surveys in 1995–2000, supplemented with additional data from 2001 to 2004, on age-0 Atlantic menhaden lengths for years 1995–2004 were available (http://hjort.cbl.umces.edu/chesfims.html) to evaluate the relationship between size in September and annual euphotic-layer Chl *a* and integrated primary production.

Growth

Interannual variability of growth was analysed by correlating lengths of age-0 Atlantic menhaden from TIES–CHESFIMS (http://hjort.cbl.umces.edu/chesfims.html) midwater-trawl collections with euphotic-layer Chl *a* and annually integrated primary production (Miller, 2006) for years 1995–2004. Additionally, interannual variability in growth was analysed with respect to estimated relative abundance to evaluate possible density-dependence. For that analysis, we utilized monthly length data from the VIMS trawl survey in the Virginia portion of Chesapeake Bay during 1962–2003 (http://www.vims.edu/research/departments/fisheries/programs/juvenile_surveys/index.php) to calculate a growth rate anomaly for each year. To obtain growth rate anomalies, we calculated the difference between the modelled estimate of asymptotic length over all years and subtracted that estimate from the estimated asymptotic length for each year. Annual growth anomalies were compared with age-0 Atlantic menhaden relative abundances. A flexible approach to model growth was adopted that described mean length during the year as a logistic function of time:

$$L_{y,t,i} = L_0 + \frac{G_{\max,y}}{1 + e^{-k(t-t_m)}} + \varepsilon_i,$$

where $L_{y,t}$ was mean length in year y and month t for sample i, L_0 was mean starting length, $G_{\max}$ was the difference in mean length at the beginning and end of the year, k and t_m were parameters that described how growth rate changed during the year, and ε was a normally distributed random error. An annual growth rate anomaly was estimated by allowing $G_{\max}$ to be a normally distributed random effect. The model was fitted using AD Model Builder (Fournier *et al.*, 2012). Possible density-dependence was tested by relating the random effect for growth rate anomaly during a year to the age-0 Atlantic menhaden abundance index using simple linear regression.

Water quality, nutrient loading, and freshwater flow

Monitoring data were obtained from the data hub of the Chesapeake Bay Program (CBP) (http://www.chesapeakebay.net/data). We analysed data on water temperature (upper 8 m of the water column), salinity, density (Sigma-*t*), dissolved oxygen, Chl *a*, phaeopigments, total nitrogen (N) and phosphorus (P), total dissolved N and P, silica, and Secchi disk depth for mainstem monitoring stations in the Bay from 1985 to 2005 (Table 1). Mean values of these variables were parsed seasonally: spring (March–May), summer (June–August), fall (September–November), and annually (January–December). These data were used to generate baywide means and were also separately analysed for two salinity zones (Figure 1) defined by latitude: mesohaline (37.81–38.80°N), and oligohaline (38.81–39.66°N). We did not analyse water quality and environmental data from the lower Bay's polyhaline salinity zone (36.95–37.80°N) because survey index data we used to estimate abundance of age-0 menhaden were restricted to Maryland waters (oligohaline and mesohaline salinity zones).

Data on freshwater flow and nutrient loading to Chesapeake Bay were obtained from the US Geological Survey website (http://waterdata.usgs.gov/nwis) and analysed by season. Flow data were for the Susquehanna River that enters at the head of Chesapeake Bay and accounts for $>50\%$ of the Bay's freshwater input. Abundance and growth of age-0 Atlantic menhaden were analysed with respect to levels and variability of hydrographic and environmental data.

Before statistical analyses, abundance data for age-0 Atlantic menhaden were $\log_{10}$-transformed to meet the assumption of normal distribution. Environmental data were tested for normality (Lilliefors or Shapiro–Wilk test) and non-normal data were logarithmically ($\log_{10}$) transformed before analysis. The data receiving $\log_{10}$ transformation are indicated in Table 1.

Primary production

Fine-scale information on spatial and temporal variability of Chl *a* were from sensors on light aircraft obtained from the Chesapeake Bay Remote Sensing Program (CBRSP). CBRSP conducted flights at weekly or more frequent intervals along prescribed flight tracks. A catalogue of remotely sensed Chl *a* observations, improved by regional processing approaches and algorithms (Magnuson *et al.*, 2004; Harding *et al.*, 2005), was available (http://www.cbrsp.org) from ~180 flights in 1989–2004. The remotely sensed Chl *a* data were aggregated by season and salinity zones in the Bay. Aircraft overflights were coordinated with shipboard surveys to obtain *in situ* data on Chl *a* for calibration and validation (Harding *et al.*, 1994; Harding and Perry, 1997) and to support depth-integrated models (DIMs) of primary production (Scardi and Harding, 1999; Harding *et al.*, 2002).

The combination of remotely sensed data and DIM spatially explicit estimates of daily primary production (g C m^{-2} d^{-1}) were integrated over time to give seasonal and annual primary production (Harding *et al.*, 2002; Adolf *et al.*, 2006; Miller, 2006). Months covered by aircraft measurements (generally March to October) encompassed spring maximum of euphotic-layer Chl *a* and the summer maximum of primary production (Malone, 1992; Harding *et al.*, 2002, 2005). These measures of phytoplankton biomass and primary production were analysed with respect to

Table 1. Environmental (water quality and plankton) variables included in simple correlations with age-0 Atlantic menhaden abundance.

Independent variables	Sample size	Correlation coefficient	Probability
Annual[a]			
Primary productivity	16	**0.54**	**0.030***
Surface Chl *a*	16	0.18	0.509
Euphotic Chl *a*	16	**0.63**	**0.009****
Pheopigments	21	−0.36	0.107
Temperature	21	0.02	0.921
Salinity	21	0.40	0.076
Density (σ_t)	21	0.41	0.065
Dissolved oxygen	21	−0.06	0.794
Secchi depth	21	**0.60**	**0.004****
Total dissolved nitrogen	21	0.12	0.594
Total dissolved phosphorus	21	−0.00	0.992
Silica	21	−0.39	0.079
Susquehanna River discharge	21	**−0.44**	**0.047***
Susquehanna nitrogen load	21	−0.20	0.378
Susquehanna phosphorus load	21	−0.39	0.081
Total zooplankton abundance[a]	18	**−0.63**	**0.005****
Acartia sp.	18	0.26	0.305
Eurytemora affinis[a]	18	**−0.51**	**0.031***
B. longirostris[a]	18	**−0.56**	**0.016***
Cyclopoda[a]	18	**−0.47**	**0.050***
Harpacticoda[a]	18	**−0.51**	**0.030***
All copepods[a]	18	**−0.47**	**0.050***
Rotifers	18	−0.22	0.377
Water quality PCA factor 1	18	0.43	0.055
Water quality PCA factor 2	18	0.04	0.857
Zooplankton PCA factor 1	18	**−0.57**	**0.014***
Zooplankton PCA factor 2	18	0.18	0.468
Spring[a]			
Primary productivity	17	**0.54**	**0.024***
Surface Chl *a*	17	0.06	0.811
Euphotic Chl *a*	17	0.45	0.071
Pheopigments	21	**−0.50**	**0.021***
Temperature	21	−0.13	0.574
Salinity	21	0.34	0.135
Density (σ_t)	21	0.35	0.126
Dissolved oxygen	21	0.11	0.620
Secchi depth	21	**0.60**	**0.004****
Total dissolved nitrogen	21	−0.02	0.941
Total dissolved phosphorus[a]	21	0.26	0.264
Silica[a]	21	**−0.46**	**0.036***
Susquehanna River discharge	21	−0.35	0.118
Susquehanna nitrogen load[a]	21	−0.10	0.653
Susquehanna phosphorus load	21	−0.17	0.469
Total zooplankton abundance[a]	18	**−0.53**	**0.025***
Acartia sp.	18	0.41	0.091
Eurytemora affinis[a]	18	−0.37	0.132
B. longirostris[a]	18	**−0.51**	**0.032***
Cyclopoda[a]	18	−0.41	0.088
Harpacticoda[a]	18	**−0.65**	**0.004***
All copepods[a]	18	−0.33	0.178
Rotifers	18	−0.31	0.213
Water quality PCA factor 1	18	0.38	0.094
Water quality PCA factor 2	18	−0.29	0.200
Zooplankton PCA factor 1	18	**0.58**	**0.012***
Zooplankton PCA factor 2	18	0.09	0.727

Menhaden data are the area-weighted abundances from the Maryland DNR seine survey indices (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx). Water quality data (years 1985–2005) were downloaded from the CPB web pages (http://www.chesapeakebay.net/data). Primary production and Chl *a* data (years 1989–2004) were from the Chesapeake Bay Remote Sensing Program (http://www.cbrsp.org). Spring months include March through May.

[a] Log-transformed.

Significant correlations are in bold. *$p < 0.05$, **$p < 0.01$.

Table 2. Mean relative abundances (number per 20-min tow) of age-0 Atlantic menhaden from the baywide TIES trawl survey program (1995–2000) (Jung, 2002; Jung and Houde, 2003; http://hjort.cbl.umces.edu/chesfims.html).

Annual						
Whole Bay (July and October)	1995	1996	1997	1998	1999	2000
	0.11	0.89	5.58	0.18	1.40	0.11
Annual						
Upper Bay only (July and October)	1995	1996	1997	1998	1999	2000
	0.35	5.30	31.80	0.90	8.20	0.50
Regional						
(July and October)	Lower	Mid	Upper			
	0.06	0.05	2.57			
Seasonal						
(all regions)	Apr–May		Jun–Jul	Sept–Oct		
	0.05		0.76	0.16		

Survey cruises were conducted in April–May, July, and October. Mean abundances were volume-weighted for the three bay regions (lower, mid-, and upper) to better represent annual, seasonal, and regional relative abundances in Chesapeake Bay. Weighting factors: Lower Bay = 1.0; Mid-Bay = 0.63; Upper Bay = 0.33.

abundances of age-0 Atlantic menhaden for 1989–2004. These data were $\log_{10}$-transformed before generating mean values and subsequently back-transformed (Harding *et al.*, 2002) and expressed as geometric means. These means did not require further transformation before correlation analyses.

Zooplankton

Data on zooplankton abundance were available for stations in the Maryland portion of the mainstem Bay. These data, collected bimonthly by the CBP for years 1985–2002, were analysed with respect to age-0 Atlantic menhaden abundance. Only data for CBP sites in the mid and upper regions of Maryland's portion of the Bay (up-Bay of the Potomac River, Figure 1) were reliable and included in our analyses. CBP zooplankton monitoring was terminated after 2002, limiting the time-series data for this analysis. Zooplankton data were tested for normality (Lilliefors or Shapiro–Wilk test) and non-normal data were logarithmically ($\log_{10}$) transformed before analysis (as indicated in Table 1).

Linking recruitment to primary production and environmental variables

Pearson correlation coefficients were calculated to determine whether age-0 Atlantic menhaden abundance was correlated with euphotic-layer Chl *a* and annually integrated primary production for 1989–2004, the period encompassed by the aircraft remote-sensing data. Additionally, we conducted a retrospective analysis on a longer time-series of data to estimate euphotic-layer Chl *a* from 1966 to 2006 using historical and monitoring data from the CBP (http://www.chesapeakebay.net/data). This analysis allowed us to correlate the abundance of age-0 Atlantic menhaden with euphotic-layer Chl *a* for a four-decade period, including years of low and high Atlantic menhaden abundance.

Pearson correlation analysis was used to identify other environmental variables with potential influence on age-0 Atlantic menhaden abundance in the Bay. Measurements of these environmental variables were available for a 21-year period (1985–2005) from CBP monitoring data (Table 1). The correlation analysis relating survey indices of annual age-0 Atlantic menhaden abundance and environmental variables was conducted on baywide, annually averaged data and on data aggregated by season and salinity zone. Following the correlation analysis, principal component analysis (PCA) was conducted on environmental variables to detect gradients (factor scores) of water quality and zooplankton variables, and to consolidate the number of variables considered for subsequent multiple regression analysis. Multiple linear regressions were fit in a forward, stepwise approach in which area-weighted Maryland index estimate of age-0 Atlantic menhaden abundance was the dependent variable. Environmental variables and PCA factor scores comprised the independent variables that were considered and tested. Correlation matrices from which multiple regressions were generated included all available data, but only years with complete data for all variables (1989–2002) were included in the multiple regressions to avoid bias from missing data (non-randomly distributed in the dataset) in the correlation matrix.

The accepted multiple regression model was developed from seasonally and regionally aggregated data. Independent variables initially included in the model were based on significant ($p < 0.05$) correlations. Variables related to individual zooplankton taxa were not considered for inclusion in the multiple regression modelling, but the zooplankton PCA factor 1 score was considered for inclusion. The independent variables for potential inclusion in the model were: primary production, euphotic Chl *a*, silica, Susquehanna River discharge, Secchi disk depth, and zooplankton PCA factor 1 score. Statistical analyses were conducted with Statistica 12 (StatSoft Inc., 2014).

Results

Variability of age-0 Atlantic menhaden abundance

Interannual variability of relative abundance of age-0 Atlantic menhaden from the Maryland DNR seine survey spanned a >100-fold range from 1959 to 2010 (Figure 2). Four features in the abundance time-series were recognized. The first, a period of low abundance in the 1960s (mean seine survey index value = 0.59), was followed by a period of peak abundance in the 1970s (mean = 12.04), a period of moderately high, but declining abundance, from 1981 to 1992 (mean = 5.26), and low abundance from 1993 to 2010 (mean = 0.71). The highest relative abundance, recorded in 1977 (Figure 2), was more than twice the level in any other year. The current period of low abundance since 1993 resembles the period from 1959 to 1972, but has been of longer duration.

Despite its relatively small area and volume, the oligohaline salinity zone of Chesapeake Bay supports most age-0 Atlantic menhaden (Table 2). Volume-weighted, relative abundance estimates from the baywide midwater-trawl surveys in 1995–2000 (TIES Program), years when overall abundances of age-0 Atlantic menhaden were low, varied ∼50-fold. Lowest abundances occurred in 1995 and 2000; highest abundance occurred in 1997. Age-0

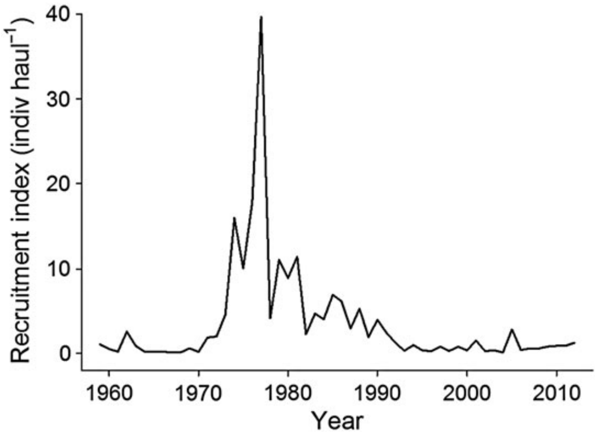


Figure 2. Maryland age-0 Atlantic menhaden recruitment index (geometric mean of number per seine haul), based on data from the Maryland DNR seine survey (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx). This metric is area-weighted for river systems included in the survey.

menhaden were uncommon in spring, but were common during summer and fall when they were more than 40 times more abundant in the upper Bay's oligohaline salinity zone than in mesohaline or polyhaline salinity zones (Table 2).

The longer term MD DNR seine survey used to evaluate relationships between environmental factors and age-0 Atlantic menhaden abundance was conducted in the mesohaline and oligohaline salinity zones (mid and upper Bay) and tributaries. For 6 years with coincident sampling (1995–2000), $\log_{10}$ mean abundances from the TIES upper Bay midwater-trawl and MD DNR seine estimates were highly correlated ($r = 0.80$, $p = 0.051$).

Primary production and age-0 Atlantic menhaden abundance

The abundance index of age-0 Atlantic menhaden derived from MD DNR seine surveys was positively related to remotely sensed phytoplankton biomass (euphotic-layer Chl *a*) and primary production in the 1989–2004 period (Figure 3). In monthly and seasonal analyses, we detected significant, positive correlations between the area-weighted MD DNR, age-0 Atlantic menhaden abundance estimates, and either primary production or euphotic-layer Chl *a* in spring and early summer (Table 1 and Figure 4) but not in other months.

In a retrospective analysis encompassing four decades (1966–2006), no significant relationship was detected between the MD DNR index of age-0 Atlantic menhaden abundance and surface Chl *a*. This long time-series included periods of both low and high abundances of age-0 Atlantic menhaden (Figure 5). The strong positive correlation between abundance and euphotic-layer Chl *a* that was observed for recent years (1989–2004; Figure 3) was not apparent in the four-decade time-series that only included data on surface Chl *a*. Highest abundances of age-0 menhaden for the four-decade period were associated with moderate surface Chl *a* levels of 5–10 mg m^{-3} (Figure 5) in the meso- (middle) and polyhaline (lower) Bay and 5–15 mg m^{-3} in the upper (oligohaline) Bay.

Age-0 Atlantic menhaden abundance and environmental factors

Correlation analyses on relative abundance of age-0 Atlantic menhaden and environmental variables indicated significant correlations

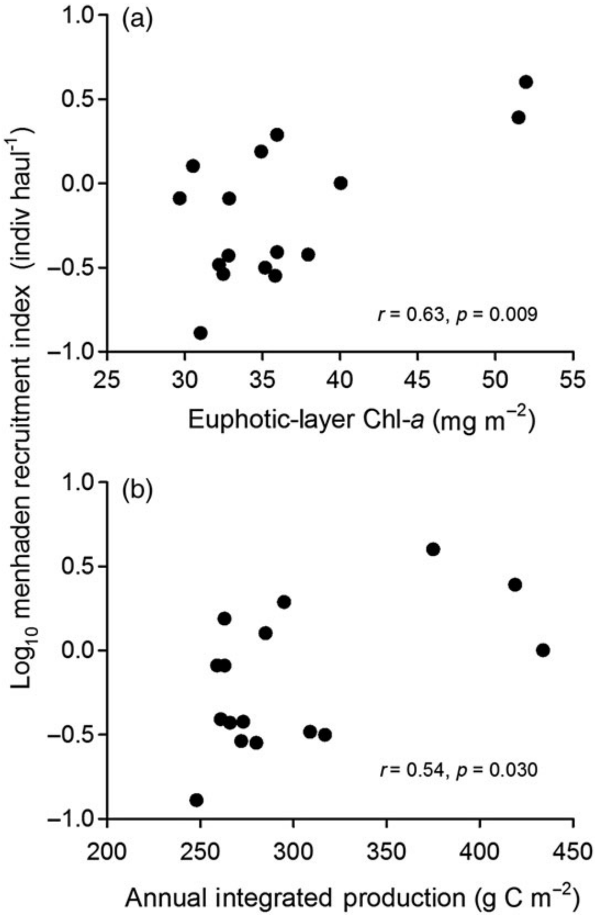


Figure 3. Baywide abundance of age-0 Atlantic menhaden (recruitment index) in relation to baywide euphotic-layer Chl *a* (a) and annual integrated primary production (b) for the period 1989–2004. The $\log_{10}$ baywide menhaden abundance (=recruitment) index (geometric mean of numbers per seine haul) was calculated from area-weighted, aggregated data derived from MD DNR striped bass seine surveys conducted in July, August, and September of each year (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx).

for data aggregated seasonally or annually (Table 1). Correlations were strongest for annual data, and those for spring months were generally stronger than for summer or fall. Correlations based on baywide environmental variables were generally stronger than for environmental variables aggregated by salinity zones. Therefore, our results and subsequent discussion emphasize analyses of baywide spring and annual data (Table 1).

Years of low freshwater flow and low turbidity from 1985 to 2005 supported higher abundances of age-0 Atlantic menhaden. Susquehanna River discharge was negatively correlated with $\log_{10}$ abundance of age-0 Atlantic menhaden for that period (Table 1). Abundance indices were positively correlated with mean baywide Secchi disk depth, indicating higher Atlantic menhaden abundance in years of low turbidity. Abundance was negatively correlated with total zooplankton abundance, and with abundances of the estuarine copepod *Eurytemora affinis*, the cladoceran *Bosmina longirostris*, and with cyclopoid and harpacticoid copepods (Table 1). In spring months, there were significant negative correlations between the abundance of age-0 Atlantic menhaden and both pheopigments

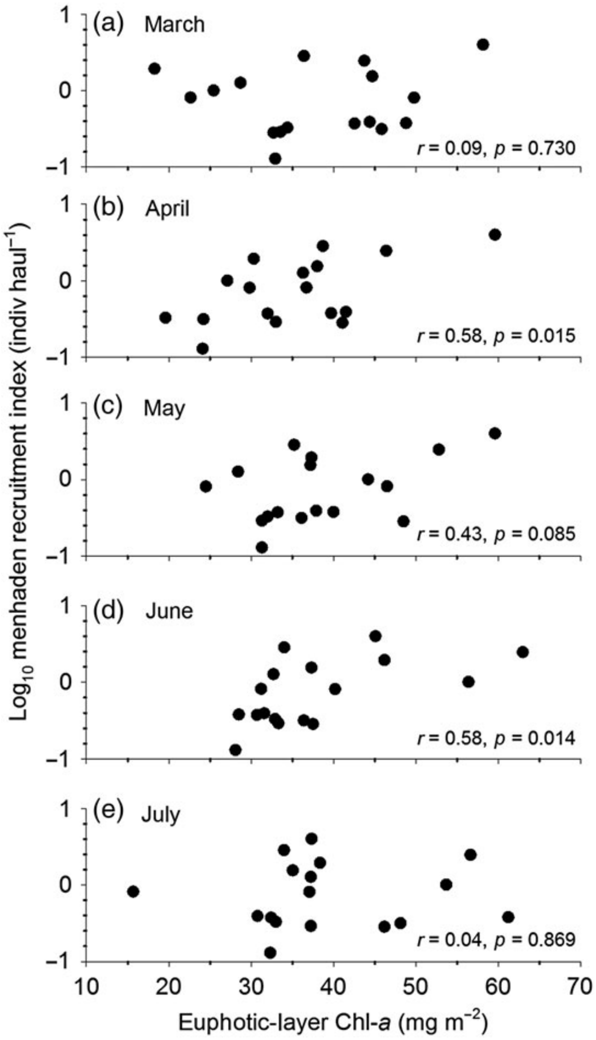


Figure 4. Baywide abundance of age-0 Atlantic menhaden (recruitment index) and mean euphotic-layer Chl *a* for months of March to July 1989–2004 (panels a–e). Correlations were significant for April and June and near-significant for May. The area-weighted $\log_{10}$ abundances are derived from geometric means of numbers per seine haul from the MD DNR surveys conducted in July, August, and September of each year (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx).

and silica. Other simple correlations relating relative abundance of age-0 Atlantic menhaden to water quality variables, including nitrogen, phosphorus, and dissolved oxygen, were not significant (Table 1).

Factor scores for the PCA on water quality variables delineated gradients representing variability of abiotic and biotic factors contributing to Atlantic menhaden recruitment success. PC 1 groupings represent a gradient of freshwater flow (Figure 6). Secchi disk depth and salinity grouped at one end of PC 1, while nutrients grouped at the other end. PC 2 likely represents a temperature gradient, with water temperature and dissolved oxygen scoring at opposite ends. PC 1 and PC 2 scores for water quality (Figure 6) were not significantly correlated with the age-0 Atlantic menhaden abundance index (Table 1) and therefore, were not included in multiple regression models.

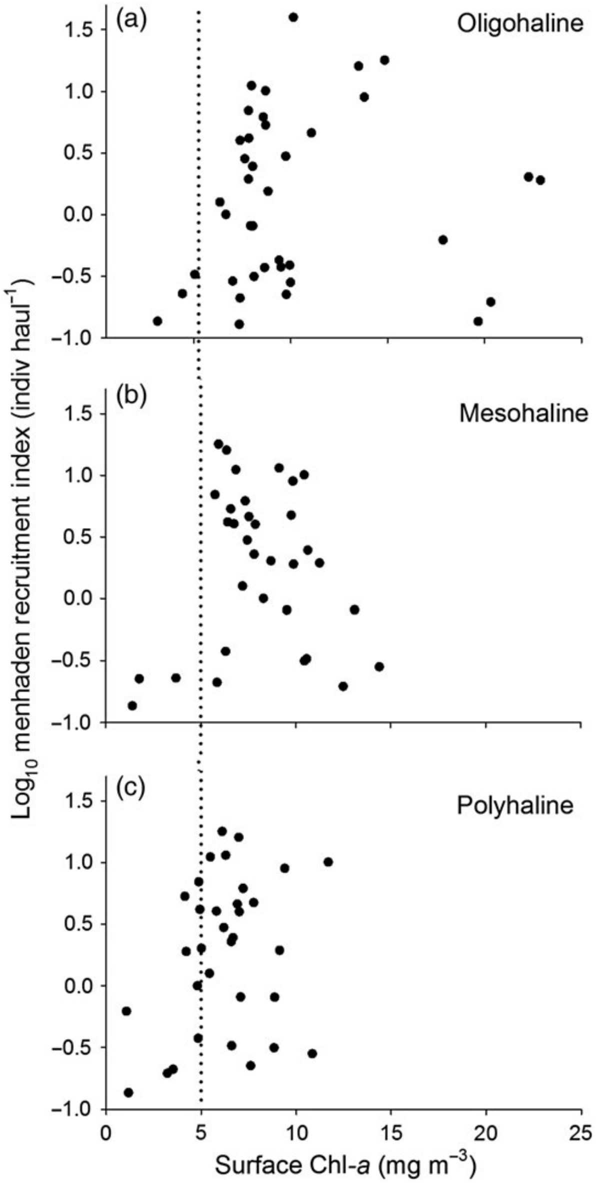
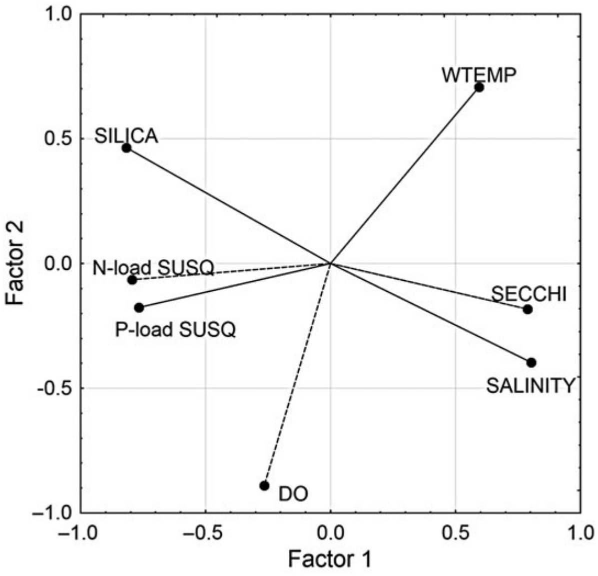


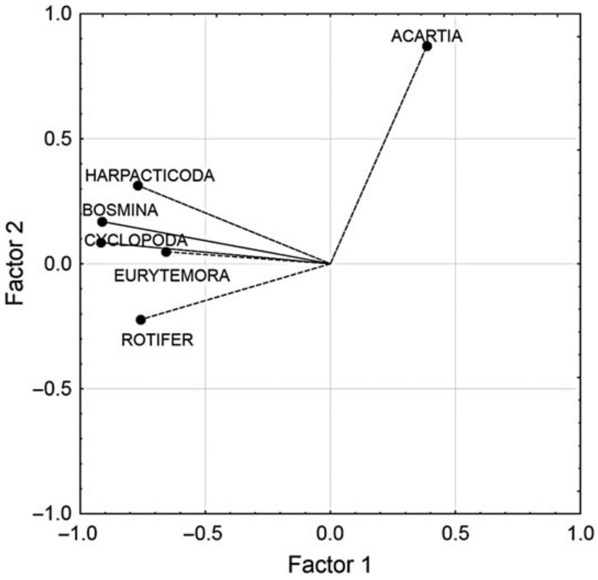
Figure 5. $\log_{10}$ abundance (recruitment index) of age-0 Atlantic menhaden (number haul^{-1}) vs. annual mean surface Chl *a* (mg m^{-3}) in the oligohaline = upper (a), mesohaline = mid- (b), and polyhaline = lower (c) bay for the period 1966–2006. The baywide menhaden abundance index was calculated using area-weighted, aggregated data from the MD DNR and VIMS juvenile striped bass seine surveys. Vertical dotted line represents a probable threshold Chl *a* ~5 mg m^{-3} below which age-0 menhaden abundances (i.e. recruitments) tend to be low.

The PCA on zooplankton data resulted in PC 1 scores that separated taxa along a gradient of freshwater discharge, with the marine-estuarine copepod *Acartia tonsa* at one end and oligohaline, freshwater-tolerant taxa such as *E. affinis* and *B. longirostris* at the opposite end (Figure 7). PC 1 scores from the zooplankton PCA were significantly correlated with the age-0 Atlantic menhaden abundance index (Table 1). The PC 1 score for zooplankton was the only PCA factor considered for inclusion in multiple regression analyses.



Variable	PC 1	PC 2
DO	−0.21	−0.92
Salinity	0.82	−0.32
Silica	−0.84	0.40
WTemp	0.38	0.83
Secchi	0.80	−0.10
N-load	−0.79	−0.06
P-load	−0.76	−0.16

Figure 6. PCA and factor (PC) scores for water quality variables in spring months. Water quality variables are plotted with respect to their factor 1 and factor 2 scores. Variables include: dissolved oxygen (DO), salinity (SALINITY), Secchi disk depth (SECCHI), water temperature (WTEMP), Susquehanna River phosphorus load (P-load SUSQ), Susquehanna River nitrogen load (N-load SUSQ), and Susquehanna River silica load (SILICA) in the mainstem Bay. Data are mean values for spring months (1985–2005) from monitoring cruises of the CBP.



Variable	PC 1	PC 2
Acartia	0.39	0.87
Eurytemora	−0.66	0.05
Bosmina	−0.91	0.17
Cyclopoda	−0.92	0.08
Harpacticoda	−0.77	0.31
Rotifera	−0.76	−0.22

Figure 7. PCA and factor (PC) scores for zooplankton in spring months. Zooplankton abundance variables are plotted with respect to their factor 1 and factor 2 scores. Variables include the abundance of copepods *A. tonsa* and *E. affinis*, broader groupings of harpacticoid and cyclopoid copepods, cladoceran *B. longirostris*, and rotifers. All data are means for spring months (1985–2002) from the CBP. Zooplankton data used in the PCA are from the Maryland portion of Chesapeake Bay (http://www.chesapeakebay.net/data).

Table 3. Multiple regression models describing the abundance of age-0 Atlantic menhaden (R) in relation to independent variables: primary production (PP) and Secchi disk depth (Secchi).

Season	Model	R^2	Probability
Annual	$R = -2.793 + 1.231[\text{Secchi}] + 0.003[\text{PP}]$	**0.53**	**0.007****
Spring	$R = -1.804 + 0.001[\text{PP}] + 0.701[\text{Secchi}]$	**0.49**	**0.009****
Summer	$R = -1.944 + 0.0004[\text{PP}] + 0.862[\text{Secchi}]$	0.27	0.110
Fall	No variables in equation	–	–

Significant regressions are in bold. **$p < 0.01$.

Forward, stepwise multiple regressions were run with $\log_{10}$ abundance of age-0 Atlantic menhaden as the dependent variable. The models explaining the largest proportion of variability in the abundance of age-0 Atlantic menhaden included data on independent variables primary production and Secchi disk depth on both an annual basis and for spring months (Table 3). Primary production and Secchi disk depth were not significantly correlated in the annual ($r = 0.37, p = 0.17$) or spring ($r = 0.02, p = 0.95$) analyses, making it unlikely that collinearity affected the model. No significant multiple regression models were obtained for summer and fall data.

Growth variability

For 1995–2004, mean total lengths of age-0 Atlantic menhaden sampled in September during TIES and CHESFIMS trawling surveys (http://hjort.cbl.umces.edu/chesfims.html) were highly variable, ranging from ∼130 to ∼180 mm (Figure 8). In these years, there was a positive correlation between the length attained in fall months and annually integrated primary production. Annual growth anomalies in November (derived from the VIMS trawl survey Atlantic menhaden lengths) indicated an approximate 50-mm difference in mean length between years when menhaden grew fastest and slowest, 1967 and 1979, respectively (Figure 9). Growth anomalies were significantly related to age-0 Atlantic menhaden abundance ($p < 0.001$), indicating possible density-dependent growth (Figure 9).

Discussion

The abundance of age-0 Atlantic menhaden in Chesapeake Bay has been consistently low from the early 1990s to 2014, following a period of high abundance that lasted more than 15 years in the 1970s–1980s. The present period of low abundance is similar to that observed in the 1960s (Figure 2), a period when the adult menhaden stock was more heavily exploited by the coast-wide fishery than it is today (McHugh, 1969; MDSG, 2009; SEDAR, 2015). Chesapeake Bay historically supplied >68% of the recruits to the Atlantic

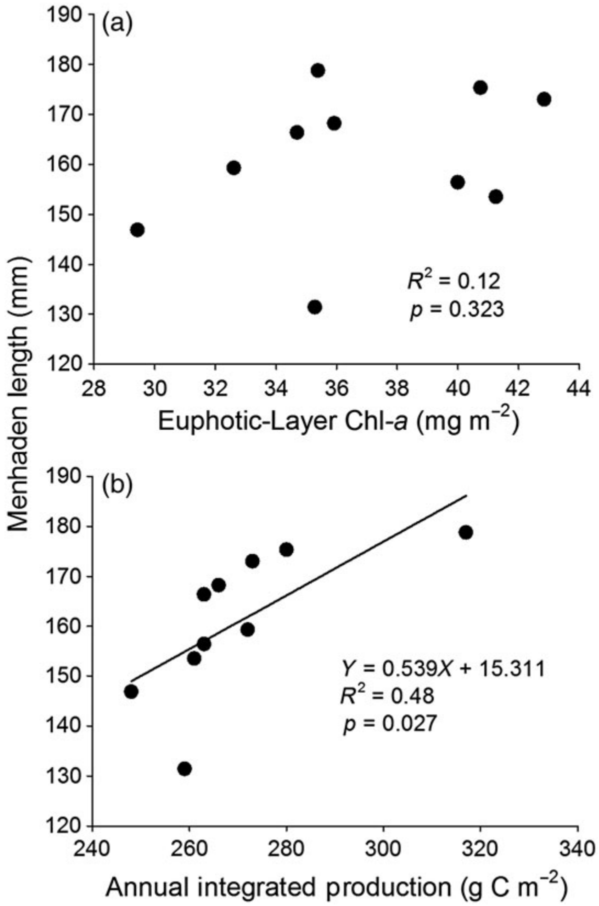


Figure 8. Mean total lengths of age-0 Atlantic menhaden in September from TIES – CHESFIMS midwater-trawl surveys relative to baywide euphotic-layer Chl *a* (a) and annually integrated primary production (1995 – 2004) (b).

menhaden fishery (MDSG, 2009). Although the most recent stock assessment indicates that the Atlantic menhaden fishery is neither overfished nor experiencing overfishing (SEDAR 2015), the consistently low recruitments for the past 20+ years concern fishery managers who strive to ensure a sustainable menhaden fishery while conserving the ecosystem services of this forage species as prey for fish, avian, and marine mammal predators (Pikitch *et al.*, 2012).

Age-0 Atlantic menhaden, while common throughout the Bay, were more than 40 times more abundant in the oligohaline, upper region of the main stem Chesapeake Bay than in the mid or lower Bay regions. The MD DNR index abundances, derived from menhaden seined in the mid and upper Bay mainstem and tributaries, were strongly correlated with the TIES upper Bay midwater-trawl abundances, indicating that the long-term DNR data are appropriate to use in evaluating factors related to the abundance of age-0 Atlantic menhaden in the Bay. Recent investigations, utilizing otolith microchemistry (Schaffler *et al.*, 2014), indicated that spatial distributions of age-0 Atlantic menhaden are stable regionally within Chesapeake Bay during the spring-to-fall period of residency. It is probable that the observed spatial and regional distributions of age-0 Atlantic menhaden represent associations with phytoplankton concentrations, which are highest in the oligohaline upper Bay, a circumstance like that reported by Friedland *et al.* (1996) for North Carolina estuaries.

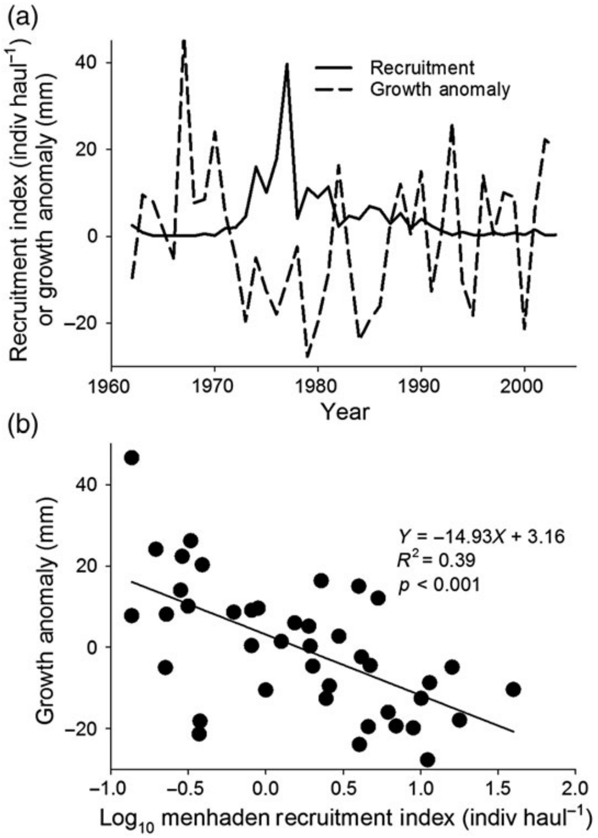


Figure 9. Annual growth anomalies (mm year^{-1}) from the VIMS trawl survey and recruitment index (geometric mean catch-per-seine haul) from the Maryland DNR seine survey of age-0 Atlantic menhaden in Chesapeake Bay from 1962 to 2003. The upper panel (a) depicts growth anomalies (referenced to November in each year) and relative abundances over time. The lower panel (b) provides the linear regression relationship between growth anomaly and the MD DNR, age-0 menhaden abundance index (http://dnr2.maryland.gov/fisheries/pages/striped-bass/juvenile-index.aspx).

The variability in the abundance of age-0 Atlantic menhaden could be generated by climate-mediated effects operating either in the coastal ocean or within Chesapeake Bay itself. Much, and possibly most, of the interannual variability may be generated offshore in the coastal ocean before larval Atlantic menhaden enter the Chesapeake Bay. Several factors could generate interannual variability in larval ingress, including variable abundance of adult spawners, shifts in spawning areas and times, variable larval survival (Reintjes and Pacheco, 1966; Ahrenholz, 1991; Warlen *et al.*, 2002; MDSG, 2009), and variable ocean dispersal (e.g. Ekman transport) to estuaries (Nelson *et al.*, 1977; Hare *et al.*, 1999; Quinlan *et al.*, 1999; Rice *et al.*, 1999; MDSG, 2009). Ingress of larvae to Chesapeake Bay in three recent years (2006, 2007, and 2008) varied ninefold, but Lozano and Houde (2013) found no concordance between observed larval ingress and subsequent abundance of age-0 juveniles, indexed by the MD DNR seine survey, in those years. This observation lends support to the hypothesis that abundance of age-0 juveniles, at least in some years, is determined after the larval stage, in the period when larvae are transitioning to the juvenile stage, or during the juvenile stage itself within the Chesapeake Bay. Except for the estimates of variability in larval ingress in three recent years (Lozano and Houde, 2013), there are no historical estimates to evaluate the relationship between numbers of ingressing larvae and subsequent abundance of age-0 juveniles.

We documented consistent positive relationships between measures of primary productivity and abundance of age-0 Atlantic menhaden in Chesapeake Bay from 1989 to 2004, years when remotely sensed Chl *a* data were available. For individual months, it must be emphasized to note that the correlation between abundance of age-0 Atlantic menhaden and either primary production or euphotic Chl *a* was significant only for spring and early summer, suggesting that the spring bloom, which is responsive to winter freshwater flow (Miller and Harding, 2007), exercises control over juvenile menhaden production, at least under climate conditions that prevailed in the 1989–2004 period. However, in our retrospective analysis that encompassed four decades, 1966–2006, there was no obvious relationship between the abundance of age-0 Atlantic menhaden and surface Chl *a*. In that 40-year period, it is notable that abundance was consistently low in years when annual mean surface Chl *a* was at lowest or highest observed levels (Figure 5), suggesting a threshold mean level of surface Chl *a* of ~5 mg m^{-3}, below which abundances of age-0 Atlantic menhaden are low, a possible indication of poor feeding conditions for the phytoplanktivorous juvenile Atlantic menhaden. In contrast, low abundances in years of exceptionally high Chl *a* could represent a response to diminished water quality in those years, including widespread hypoxia (Kemp *et al.*, 2005). The ambiguous multi-decadal relationship between the abundance of age-0 Atlantic menhaden and Chl *a* points to the probable importance of other environmental and climatic factors, and also to the lack of knowledge of interannual variability in supply (ingress) of larval menhaden to Chesapeake Bay.

Primary production and euphotic-layer Chl *a* in the spring months were strong predictors of age-0 Atlantic menhaden abundance in the 1989–2004 period. These months coincide with the peak larval-to-juvenile transition period when menhaden initiate filter-feeding on phytoplankton (June and Carlson, 1971), suggesting that food availability during this critical transition from zooplankton-feeding to phytoplanktivory was a key factor controlling production of young menhaden in recent years. The mechanism by which phytoplankton availability mediates recruitment level is not certain, but feeding conditions are implicated. Here, we show that age-0 Atlantic menhaden grew faster and were larger in years of high primary production. Recent bioenergetics modelling indicated faster growth in years of high phytoplankton stock (Annis *et al.*, 2011). Additionally, size- or growth rate-selective predation when feeding conditions are poor could expose smaller individuals to higher predation pressure, leading to high cumulative mortality (Houde, 2016) that could generate or contribute to the observed variability in the abundance of age-0 Atlantic menhaden under an annually variable phytoplankton food source.

In spring months, diatoms constitute the dominant fraction of Chesapeake Bay phytoplankton (Adolf *et al.*, 2006; Marshall *et al.*, 2006) and contribute most to phytoplankton biomass and primary production. Diet studies on age-0 Atlantic menhaden indicate that diatoms are a common component (Peck, 1893; June and Carlson, 1971) and common diatoms in Chesapeake Bay, such as *Skeletonema costatum*, are retained efficiently on gillrakers of age-0 Atlantic menhaden (Friedland *et al.*, 1984, 2006). While other phytoplankton taxa likely contribute to the diet, diatoms may be most important from April to June when Atlantic menhaden initiate filter-feeding.

Our correlation results were consistent with the hypothesis that freshwater input into Chesapeake Bay, at least historically, played an important role in the recruitment process of age-0 Atlantic menhaden. Freshwater flow from December through April is a key factor controlling interannual variability of primary production in Chesapeake Bay, including the level, spatial disposition, and quality of phytoplankton production (Adolf *et al.*, 2006; Miller *et al.*, 2006; Harding *et al.*, 2015), zooplankton community structure (Kimmel *et al.*, 2006, 2009), and fish recruitment levels (Wood and Austin, 2009). While abundance of age-0 Atlantic menhaden tended to be lower in years of high Susquehanna River discharge, the simple correlation between abundance and annual flow (Table 1) was only marginally statistically significant and it was not significant in spring months. Some factors that covaried with freshwater input, however, were correlated with menhaden abundance. For example, Secchi disk depth, a measure of light penetration, was inversely correlated with Susquehanna River discharge. In turn, the abundance of age-0 Atlantic menhaden was positively correlated with Secchi disk depth, both annually and during spring months, indicating higher abundance in years of low Susquehanna River discharge.

Several correlations between the abundance of age-0 Atlantic menhaden and zooplankton taxa were observed that were related to interannual variability in Susquehanna River discharge. The abundance of age-0 Atlantic menhaden was negatively correlated with that of the oligohaline, estuarine copepod *E. affinis* and other freshwater/estuarine zooplankton taxa such as the cladoceran *B. longirostris* that are more abundant in low-salinity, wet years (Kimmel *et al.*, 2006, 2009). In contrast, the relationship between the abundance of age-0 Atlantic menhaden and that of the marine-estuarine copepod *A. tonsa*, which is most abundant in years of low freshwater input to the Bay (Kimmel *et al.*, 2009), was weakly positive.

In the Gulf of Mexico, Govoni (1997) reported an inverse relationship between Mississippi River flow in winter and annual recruitment of age-0 Gulf menhaden *Brevoortia patronus*. He attributed the inverse relationship with a possible negative influence of high flow on retention of menhaden larvae in the Mississippi River's plume. However, Govoni (1997) also provided evidence of enhanced recruitment during a 15-year period of relatively high Mississippi flows that apparently raised the overall level of productivity in the northern Gulf of Mexico. In Louisiana estuaries, Deegan (1990) reported a negative effect of combined high Mississippi River discharge and low temperature on growth and survival of age-0 Gulf menhaden, attributing effects to lowered estuarine productivity and food availability under those conditions. A recent, comprehensive analysis of recruitment of Gulf menhaden (Sanchez-Rubio and Perry, 2015) indicated complex spatial and temporal relationships between recruitment potential and climate regimes, particularly the Atlantic Multidecadal Oscillation (AMO) and ENSO events, with highest recruitments in the northern Gulf of Mexico occurring during climate regimes favouring high freshwater discharge from the Mississippi River.

Weather conditions favourable for the recruitment of Atlantic menhaden in Chesapeake Bay historically were broadly associated with relatively warm and dry conditions in the Mid-Atlantic region during late winter and early spring (Wood, 2000; Wood *et al.*, 2004; Kimmel *et al.*, 2009). Decadal variability in conditions that favour recruitment of offshore-spawning fish such as Atlantic menhaden are believed to be associated with two regime shifts since the 1960s (Austin, 2002; Wood and Austin, 2009). Weather and regional climate patterns, including wetter weather patterns in the Mid-Atlantic region in late winter and early spring, favour recruitment success of anadromous fish but not offshore spawners such as Atlantic menhaden. A recent analysis of coast-wide recruitment variability in Atlantic menhaden and factors controlling it lends strong support to decadal-scale climate variability, e.g. AMO, as a contributing factor (Buchheister *et al.*, 2016).

Many of the environmental variables included in our correlation analyses did not show consistent or significant relationships with age-0 Atlantic menhaden abundance. There is evidence that temperature experienced by age-0 Atlantic menhaden in Chesapeake Bay during the spring to fall months strongly affects seasonal and interannual variability in growth (Annis *et al.*, 2011; Humphrey *et al.*, 2014). For the years in our analysis, we found no significant relationship between mean temperatures and abundance levels of age-0 menhaden, similar to results of Pincin *et al.* (2014) for Maryland's Coastal Bays. Nutrient loadings (nitrogen and phosphorus) were not significantly correlated with abundance of age-0 Atlantic menhaden although silica level had a weak negative correlation with abundance in spring months. In a multivariate PCA approach, Love *et al.* (2006) reported that, in some Chesapeake tributaries, particularly the Patuxent River, the MD DNR index of abundance of age-0 Atlantic menhaden increased with increasing total dissolved phosphorus and decreasing total dissolved nitrogen. However, Love *et al.* (2006) noted that abundance of age-0 Atlantic menhaden in most Chesapeake tributaries could not be explained by water quality gradients, a result consistent with our analyses conducted on a baywide spatial scale.

Predation probably is an important but variable source of mortality affecting age-0 Atlantic menhaden abundance that we were unable to examine. Predation by striped bass has been proposed as a cause of interannual variability in menhaden recruitment (Uphoff, 2003). A modified Ricker stock–recruitment model for Atlantic menhaden that incorporated a measure of striped bass abundance provided some support for the striped bass predation hypothesis, at least in recent years (mid-1980s to present) when abundance of age-0 Atlantic menhaden has been low (Zhang *et al.*, 2011). Other predators, e.g. many piscivorous fish and birds, may be important in controlling age-0 menhaden abundance, but their impacts are unevaluated.

Analysis of length frequency distributions of age-0 Atlantic menhaden from trawl surveys conducted since the 1960s in the Virginia portion of Chesapeake Bay (http://www.vims.edu/research/departments/fisheries/programs/juvenile_surveys/index.php) revealed considerable interannual variability in mean lengths by November, near the end of the growing season. Mean lengths differed >50 mm among years, but were in the range reported for age-0 Atlantic menhaden, both coastally (Ahrenholz, 1991) and in Chesapeake Bay (McHugh *et al.*, 1959). Moreover, the observed differences in lengths among years suggested that growth may be density-dependent. Growth was notably slower in the 1970s during high-abundance years, but was faster in the 1960s and during the most recent two decades when abundances were low (MDSG, 2009). Resource competition might explain the density-dependence, as found for age-0 striped bass in Chesapeake Bay where growth is strongly density-dependent (Martino and Houde, 2012). Temperature and Chl *a* also are important factors affecting growth of age-0 Atlantic menhaden (Annis *et al.*, 2011; Humphrey *et al.*, 2014), which could dampen density-dependent variability in growth. Our observations in Chesapeake Bay support the proposal by Ahrenholz (1991) who noted probable density-dependent growth in his examination of coast-wide length distributions of age-0 Atlantic menhaden.

Based on bioenergetics modelling, Luo *et al.* (2001) proposed that production and the carrying capacity of age-0 Atlantic menhaden in Chesapeake Bay were determined by available phytoplankton food. Our results provide indirect support for that proposal. Model-derived estimates of consumption have indicated that Atlantic menhaden, especially age-0 individuals that depend primarily on phytoplankton as food, potentially are important consumers and controllers of phytoplankton in Chesapeake Bay (Gottlieb, 1998; Dalyander and Cerco, 2010). Recent evidence indicates that consumption of phytoplankton by age-1 and older Atlantic menhaden that also are abundant in Chesapeake Bay is inefficient and unlikely to exercise significant control over phytoplankton and water quality (Lynch *et al.*, 2010; Friedland *et al.*, 2011).

Although we could not specify causes of the decline in the abundance of age-0 Atlantic menhaden over the past two decades in Chesapeake Bay, we did identify a strong linkage to levels of primary production and phytoplankton biomass since the late 1980s. Although frequently hypothesized, relationships between primary production and recruitment levels in marine fish are only infrequently confirmed (Platt *et al.*, 2003; Eliasen *et al.*, 2011; Leaf and Friedland, 2014). In Chesapeake Bay since the late 1980s, age-0 Atlantic menhaden tended to be more abundant in years of high primary production and phytoplankton biomass, particularly during the April to June period when juvenile menhaden acquire the ability to filter-feed and consume small algal cells as food. Climate-related variables, for example freshwater flow and turbidity levels, and zooplankton indicators helped to recognize factors associated with variability in recruitment over the past two decades under the existing environmental conditions. But, it is not certain that the same factors operated in the 1970s when abundances of age-0 Atlantic menhaden were higher by more than an order of magnitude, or in the 1960s when abundances were as low as at present. Furthermore, offshore processes, acting on spawning by adults or on egg and larval survival before entry to Chesapeake Bay and other Atlantic coast estuaries (SABRE, 1999; Lozano and Houde, 2013; Buchheister *et al.*, 2016), could be the strongest controllers of age-0 Atlantic menhaden abundance. While our analysis indicates that abundance was positively correlated with phytoplankton production and biomass during the 1989–2004 period, this correlation was not apparent in earlier decades when production of age-0 Atlantic menhaden was higher in Chesapeake Bay.

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