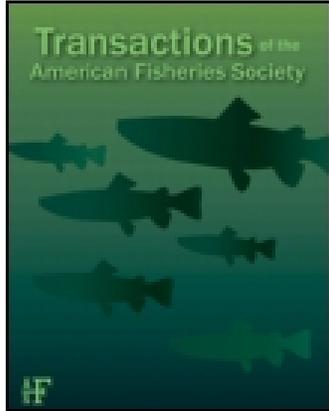


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ARTICLE

Effects of Temperature on Age-0 Atlantic Menhaden Growth in Chesapeake Bay

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Abstract

Atlantic Menhaden *Brevoortia tyrannus* is an economically and ecologically important forage fish in the western Atlantic Ocean. In the Chesapeake Bay, its recruitment has been low since the late 1980s, prompting questions on how environmental factors may affect its productivity. Growth is an important component of production, but causes of spatial and temporal variability in growth of age-0 Atlantic Menhaden are not fully understood. Our objective was to quantify the effect of temperature on spatial and temporal variability in growth of age-0 Atlantic Menhaden in Chesapeake Bay. We analyzed data on mean length and temperature for years 1962–2011 from nine regions of Chesapeake Bay. We developed a linear model that relates mean total length of Atlantic Menhaden to cumulative growing degree-days (GDDs) in Chesapeake Bay and validated the model using data that were withheld from the initial parameter estimation. The temperature threshold that best described variability in growth was 14°C, a temperature substantially higher than the physiological threshold for growth. The GDD model explained almost 80% of the variability in mean length over time (within and among years) and among regions. In a model validation exercise, it accurately predicted mean length in tributary subregions of the bay not included in the original model fitting. The GDD model requires only temperature data to effectively predict growth, making it simpler to apply than models requiring more complex approaches.

The Atlantic Menhaden *Brevoortia tyrannus* is an ecologically and economically important clupeid fish that is widely distributed along the northwestern Atlantic coast and its estuaries (Ahrenholz 1991). Adults spawn offshore along the Atlantic coast over a range of 4–6 months during the fall and winter, and after hatching, peak ingress into the estuaries, such as the Chesapeake Bay, occurs in February and March (Warlen 1994; Lozano et al. 2012). Atlantic Menhaden are abundant, support a large, coastwide fishery, and are a major link between primary production and higher trophic levels. They are consumed by recreationally and commercially important fishes, such as Striped Bass *Morone saxatilis* (Fay et al. 1983; Walter et al. 2003), Bluefish *Pomatomus saltatrix* (Harding

and Mann 2001), Bluefin Tuna *Thunnus thynnus* (Butler et al. 2010), and Sandbar Sharks *Carcharhinus plumbeus* (Medved et al. 1985). Additionally, they are consumed by many marine mammals and birds (Ahrenholz 1991). Atlantic Menhaden support large-scale reduction and bait fisheries, and they are the largest fishery in the Chesapeake Bay by volume, with over 100,000 metric tons removed annually (Smith 1999; Houde 2011).

The Chesapeake Bay and its tidal tributaries experience a wide range of environmental conditions that likely affect spatial variability in Atlantic Menhaden growth and production. The production of Atlantic Menhaden has been relatively low over the last two decades, largely because of low recruitment,

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and while overfishing is occurring, the stock is not considered overfished (ASMFC 2012).

Growth in fish primarily is responsive to food and temperature, and variation of these factors has the potential to affect survival (Paloheimo and Dickie 1966). Throughout the Chesapeake Bay, spatial and temporal variability in the growth of age-0 Atlantic Menhaden and its causes are not well understood. Annis et al. (2011) developed a bioenergetics model for age-0 Atlantic Menhaden growth that included the effects of temperature, primary production (level of chlorophyll *a*), and density dependence, as did a similar model by Luo et al. (2001). However, data were available to apply the model to only a few broad regions of the Chesapeake Bay and for a relatively short time interval.

While other controlling factors such as food availability and genetics are important, temperature, which regulates body temperature in ectotherms and affects processes such as consumption, digestion, metabolism, and gas exchange, often is the major factor controlling growth in many fishes (Atkinson 1994). In general, temperatures at the higher end of the range that a species normally experiences result in higher metabolism and growth. A metric that quantifies the heat available in the environment is the growing degree-day (GDD) (Neuheimer and Taggart 2007). The GDD is a measure of heat accumulation above a threshold temperature. In the absence of extreme environmental factors, time spent above the temperature threshold allows for the physiological processes that regulate growth and development (Neuheimer and Taggart 2007). Growing degree-days accumulate throughout the growing season, and fish grow accordingly with each accumulated GDD. Among the sciences, GDD models are successfully and consistently applied in agronomy (Swan et al. 1987) and entomology (Whitfield 1984; Broatch et al. 2006). Recently in fisheries, GDD models have been used to explain development and growth variation in many fishes (Neuheimer and Taggart 2007; Venturelli et al. 2010). Our objectives were to (1) develop a model to explain the variability in the growth of Atlantic Menhaden in Chesapeake Bay as a function of temperature, (2) validate the model with data from Chesapeake Bay regions that were not included in model development, and (3) describe spatial and temporal variability in the growth of age-0 Atlantic Menhaden. We compiled historical data on lengths of Atlantic Menhaden and corresponding temperature data from a variety of resources and locations to calculate GDDs and model mean length to explain the spatial and temporal variation in Atlantic Menhaden sizes.

METHODS

Study site.—Our study area encompassed nine regions of the Chesapeake Bay, including seven tributaries and two parts of the main stem (Figure 1). These regions were chosen because data were available for temperature and age-0 Atlantic Menhaden length. The regions provided a range of temperature and

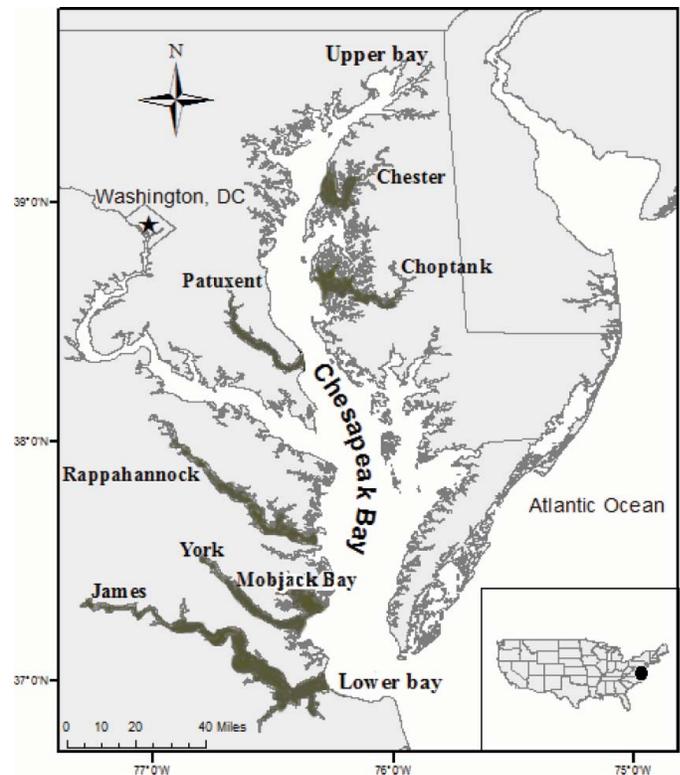


FIGURE 1. Map of the Chesapeake Bay showing the nine regions that provided data for the model. [Figure available online in color.]

salinity conditions. The most up-bay regions experience cooler temperatures and lower salinity on average and are farther from the point of larval ingress at the bay mouth (Lozano and Houde 2013) than more down-bay regions.

Data.—We obtained length data on age-0 Atlantic Menhaden from surveys conducted by the Virginia Institute of Marine Science (VIMS), Maryland Department of Natural Resources (MDNR), and University of Maryland Center for Environmental Science (UMCES). A summary of the data sets is given in Table 1.

Atlantic Menhaden were collected by VIMS every month of the year in their survey of juvenile fish and blue crab *Callinectes sapidus* that samples 60 stations in the Virginia portion of Chesapeake Bay, including the James, York, and Rappahannock rivers; monthly collections between March 2010 and December 2011 were also available from Mobjack Bay. We included VIMS survey data from 1962 to 2011 in our analyses. The type of trawl used changed over the years, with a tickler chain added in 1973, a small mesh liner added in 1979, and net doors added in 1991. The current trawl is a 9.14-m semi-balloon otter trawl with 38.1-mm stretched mesh and a 6.35-mm cod end liner. Atlantic Menhaden were also collected by the VIMS juvenile Striped Bass seine survey in the Rappahannock, York, and James rivers. These samples were collected biweekly from July to mid-September during 1967–1973 and 1980–2011 in nearshore areas. The beach seine was modified

TABLE 1. Data set characteristics from surveys conducted by the Virginia Institute of Marine Science (VIMS), the Maryland Department of Natural Resources (MDNR), and the University of Maryland Center for Environmental Science (UMCES)–Trophic Interactions in Estuarine Systems (TIES) and Chesapeake Bay Fishery-Independent Multispecies Survey (CHESFIMS), and UMCES–Chesapeake Biological Laboratory (CBL).

Survey	Sampling gear	Time period	Sampling site	Period of record
VIMS juvenile finfish and blue crab survey	Otter trawl	Mar–Dec	Virginia portion of Chesapeake Bay	1962–2011
VIMS juvenile Striped Bass survey	Beach seine	Jul–Sep	Rappahannock, York, and James rivers	1967–1973, 1980–2011
MDNR bottom trawl survey	Otter trawl	May–Nov	Chester and Patuxent rivers	1995–2011
UMCES–TIES and CHESFIMS	Midwater trawl	Apr, Jul, Sep, Oct	Main stem of Chesapeake Bay	1995–2006
UMCES–CBL	Midwater trawl/ beach seine	Dec, Feb	Choptank and Patuxent rivers	2010 and 2011

in 1986 from 30.5 m long, 2 m deep, with 6.4-mm mesh to the current 30.5 m long, 1.2 m deep, with 6.4-mm mesh.

In the Maryland waters of Chesapeake Bay, Atlantic Menhaden were collected by the MDNR as part of a bottom trawl survey that began in 1977. However, the measurement of individual lengths of Atlantic Menhaden did not begin until 1995. The MDNR sampled monthly from May to November using a 4.9-m semiballoon otter trawl with 31.8-mm stretched mesh and a 12.7-mm cod end liner. Atlantic Menhaden were collected by UMCES in the main stem of the Chesapeake Bay; these surveys were conducted in April, July, and September during 1995–2000 and included sampling in October during 2001–2006 using an 18-m² midwater trawl with a 3-mm cod end. Additional UMCES surveys were conducted in 2010 and 2011 on the Choptank and Patuxent rivers using the 18-m² midwater trawl with 3-mm cod end and, in nearshore areas, a 30.5-m-long, 1.2-m-deep, 6.4-mm-mesh beach seine with a bag.

We restricted our investigation to age-0 Atlantic Menhaden, which were the dominant age-group in the catches. We established length thresholds to identify age-0 Atlantic Menhaden based on the length–frequency distributions of fish sampled by the VIMS trawl survey during 1962–2003 (Table 2). Atlantic Menhaden less than 55 mm that were sampled from September to December were excluded from analysis because they likely were not from the same cohort as those that ingress to the bay in the winter and spring. Mean total length of age-0 Atlantic Menhaden was calculated for each trawl tow. Because fish in the VIMS surveys were measured to fork length, total length was calculated by multiplying fork length by a

conversion factor of 1.11, based on sampled age-0 Atlantic Menhaden collected by seine in the Patuxent River (M. J. Wilberg, unpublished data). All reported lengths in our analysis are total length.

We used surface water temperatures and mean temperatures above the pycnocline to calculate GDD because Atlantic Menhaden are frequently caught in the surface waters (Friedland et al. 1996) and are thought to spend much of their time feeding in the upper portion of the water column (Gottlieb 1998). Surface temperature data were recorded during each of the VIMS, MDNR, and UMCES surveys. We supplemented these data with temperature data from a depth of 3 m (Chesapeake Bay Program website: www.chesapeakebay.net), a depth approximately half-way between the pycnocline and oxycline in months from spring to fall. We calculated mean temperature in a region for each day across all of the sources and sites that had temperature data. For days with missing temperature observations, daily temperature estimates were obtained by linear interpolation using mean temperature data from that region.

Statistical analysis.—We separated the data for GDD modeling into two sets: one set was used to estimate model parameters (i.e., training) and the other to validate the model. Our principal goal for conducting the validation portion of the analysis was to estimate the skill of the model in predicting growth in regions not included in the initial model (Snee 1977). Data from the James, York, and Rappahannock rivers and the upper bay were used for parameter estimation because of their long sampling history and large numbers of sampled

TABLE 2. Mean TL thresholds by month for age-0 Atlantic Menhaden determined by length–frequency distributions from 1962 to 2003 from the Chesapeake Bay.

Measurement	Jan–Apr	May	Jun	Jul	Aug	Sep	Oct–Dec
Mean TL (mm)	<55	<66	<94	<111	<144	>55 and <166	>55 and <199

age-0 Atlantic Menhaden. We used data from the Patuxent, Choptank, and Chester rivers, Mobjack Bay, and the lower bay to validate the model. We used these systems because they spanned the geographic range of the Chesapeake Bay. The estimation data set had 3,223 Atlantic Menhaden mean length observations, and the validation set included 351 observations.

We calculated the number of GDDs for each day as the mean daily temperature minus the minimum temperature threshold using parameter estimation regions:

$$\text{GDD}_t = T_t - T_0 \text{ if } T_t > T_0,$$

where T_t is the mean daily temperature for day t and T_0 is the minimum temperature threshold (3–20°C). If T_t was less than T_0 , the GDD was assigned a value of 0. We calculated cumulative GDD (CGDD) as the running sum of GDDs in a year up to day t using January 1 as the first day of the year:

$$\sum_{i=1}^t \text{GDD}_i.$$

We considered a range of potential threshold temperatures from 3°C to 20°C in 1°C increments. The lowest temperature of 3°C was chosen because it is the reported minimum viable temperature for Atlantic Menhaden (Lewis 1965). To determine the threshold that best described variability in growth, we fit linear regression models with mean length as a function of CGDDs (1962–2011) and selected the best model using the Akaike information criterion (AIC; Akaike 1973; Burnham and Anderson 2002). The temperature threshold that best described variability in growth was 14°C (AIC weight of 0.56; Figure 2), but 13°C also had substantial support (AIC weight of 0.44). We selected 14°C as the minimum threshold for all subsequent analyses.

Additionally, we used a two-way analysis of variance (ANOVA) to test for the effect of region and year on year-end CGDDs:

$$\hat{Y}_{ij} = \mu + \alpha_i + \beta_j,$$

where \hat{Y}_{ij} is the estimated year-end CGDD, μ is the intercept, α_i is the region effect, and β_j is the year effect. We used data from the James, York, and Rappahannock rivers from 1962 to 2011 as well as data from other regions, such as the Chester, Choptank, and Patuxent rivers, from 1985 to 2011. All factors were treated as fixed effects. We also fitted a model that included a region \times year interaction, but the interaction was not significant, indicating that temperature trends did not differ with region. Therefore, we only present modeling results without the interaction. We evaluated trends in temperature over time (1962–2011) by conducting linear regressions of ANOVA results of year effects on year-end CGDD against

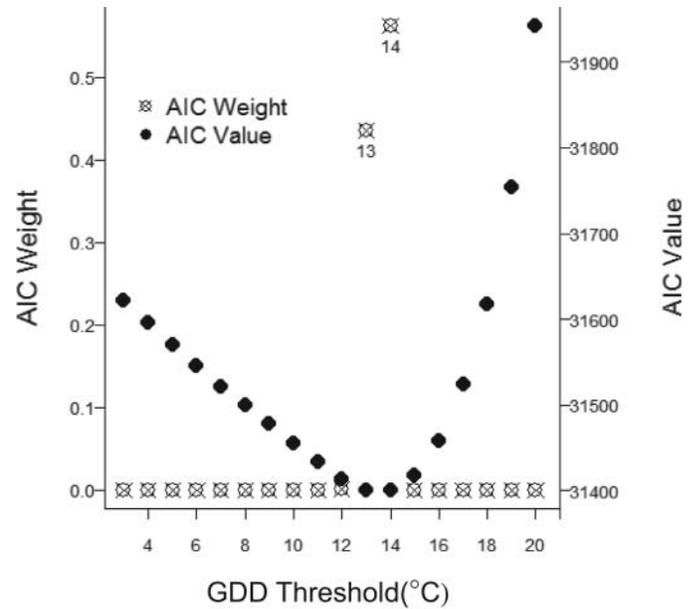


FIGURE 2. Comparison of model fits of growing degree-day (GDD) thresholds (3–20°C) using the Akaike information criterion (AIC). The threshold that best describes variability in growth has the lowest AIC value and highest AIC weight (14°C).

year. Long-term trends in tributary water temperature represent the bay-averaged data well (Najjar et al. 2010).

We used the parameter data set (James, York, and Rappahannock rivers and the upper bay) for the initial model estimation. We fitted a linear regression to relate mean length of Atlantic Menhaden to CGDD:

$$\hat{L} = \alpha + \beta \cdot \text{CGDD},$$

where \hat{L} is total length (mm), α is the intercept (mm), and β is the slope (mm/GDD). We predicted mean length for each collection tow in the validation data set using the initial regression model and calculated the r^2 and root mean square error (RMSE) to evaluate model performance. To evaluate biomass we also calculated annual variation in growth by estimating the mean weight of Atlantic Menhaden at the end of the year by using an allometric relationship between length and weight for age-0 individuals ($W = aL^b$, where W is weight (g), L is length (mm), a is -13.63 , and b is 3.42 ; C. Lozano, Chesapeake Biological Laboratory, unpublished data).

In addition to the Chesapeake Bay-wide characterization of age-0 Atlantic Menhaden growth, we also analyzed regional variation in growth and the effect of collection gear type on the length of fish captured. We applied an analysis of covariance (ANCOVA) to test for the effects of region and gear on the mean length of age-0 Atlantic Menhaden to determine if there were regional differences in growth not attributable to temperature or selectivity of the sampling gears. We could not

fit a model that included both gear and region effects because most regions were sampled with only one gear. In the ANCOVA, length was the dependent variable, CGDD was a covariate, and region and gear were categorical effects:

$$\hat{L}_{i,j} = \beta_0 + \beta_{X_j} X_j + \beta_{\text{CGDD}} \text{CGDD}_i + \beta_{X_j \times \text{CGDD}} (X_j \times \text{CGDD}_i),$$

where β_0 is the intercept, X_j is a categorical region or gear effect, β_{X_j} is the change in mean length per GDD, and $\beta_{X_j \times \text{CGDD}}$ is an interaction term for CGDD and gear or region. All factors and covariates were treated as fixed effects. All analyses were conducted in R version 3.0.3 (R Core Development Team 2011) and all tests were considered to be significant at an α level of 0.05.

RESULTS

The GDDs began accumulating in spring, typically around early May, once water temperatures climbed above the threshold temperature of 14°C, and GDDs eventually leveled out as the water cooled to below 14°C in the autumn, about mid-October (Figure 3). Southern regions of Chesapeake Bay, such as the James, York, and Rappahannock rivers, were warmer on average and therefore accumulated more GDDs than the more northerly regions, such as the upper bay and the Choptank and Chester rivers. Year-end CGDDs differed among years in response to cooler and warmer years, with cooler years accumulating 1,400 CGDDs or less and warmer years accumulating upwards of 2,000 CGDDs. There was significant variation in year-end CGDDs among regions (Figure 4) and years (Figure 5). During 1962–2011, year-end CGDDs increased at a rate of 2.8 GDDs per year in the Chesapeake Bay regions (Figure 5; $t = 2.67$, $df = 47$, $P < 0.01$).

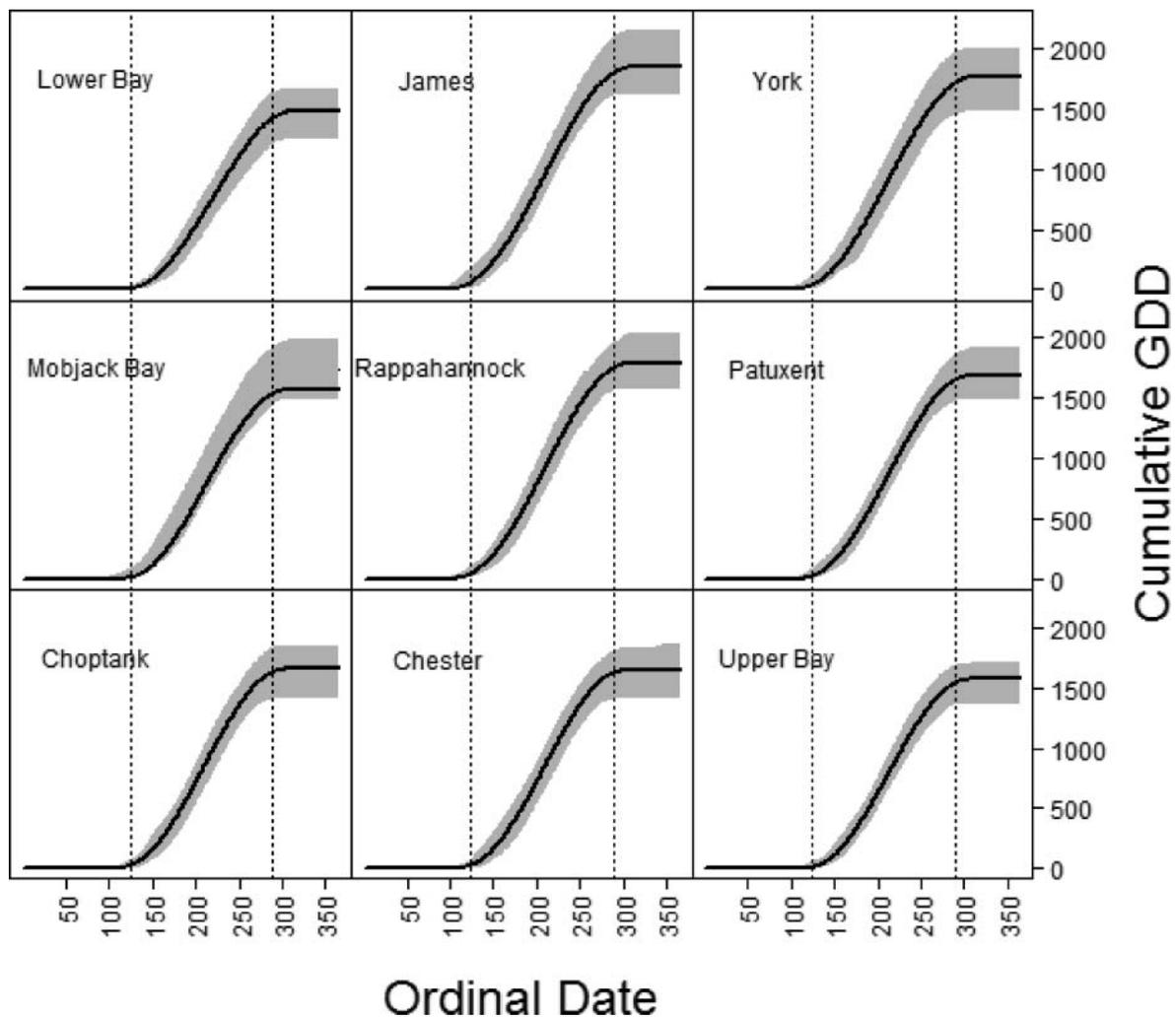


FIGURE 3. Maximum, average, and minimum cumulative growing degree-days (CGDD) by ordinal date (1–365) over all years (1962–2011) for each region (Figure 1) in the study. The shaded area depicts the range of CGDDs at each ordinal date (1–365). The solid line denotes the average CGDD. Vertical dashed lines denote reference points for early May (May 5th) and mid-October (October 17th).

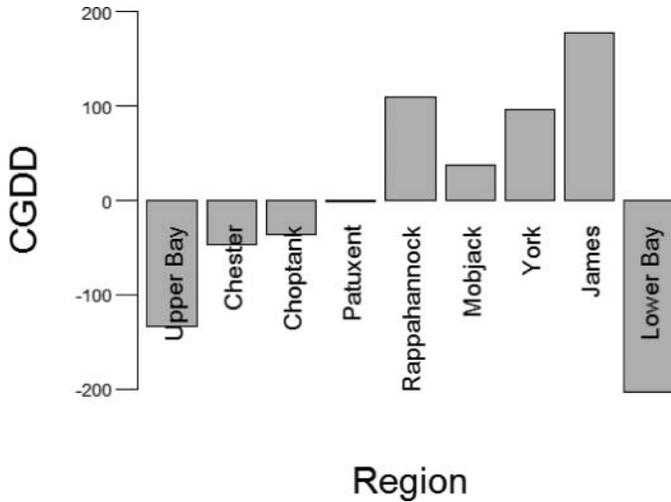


FIGURE 4. Analysis of variance region effect on CGDDs (1962–2011) relative to the CGDD mean.

Year-end CGDDs differed significantly among the regions of Chesapeake Bay ($F_{8, 306} = 28.39, P < 0.001$), with the highest year-end CGDD in the southernmost regions and the lowest in the northern regions, with the exception of the lower bay (Figure 4). The mean CGDD anomalies were highest in the James River (177.8 CGDDs; 95% confidence interval [CI] = 138.8–216.9), followed by the Rappahannock (109.7 CGDDs; 95% CI = 70.3–149.1) and the York (95.5 CGDDs; 95% CI = 56.7–134.4) rivers, indicating that these rivers were, on average, warmer than other regions. Post hoc comparisons using Tukey’s honestly significant difference revealed that the upper

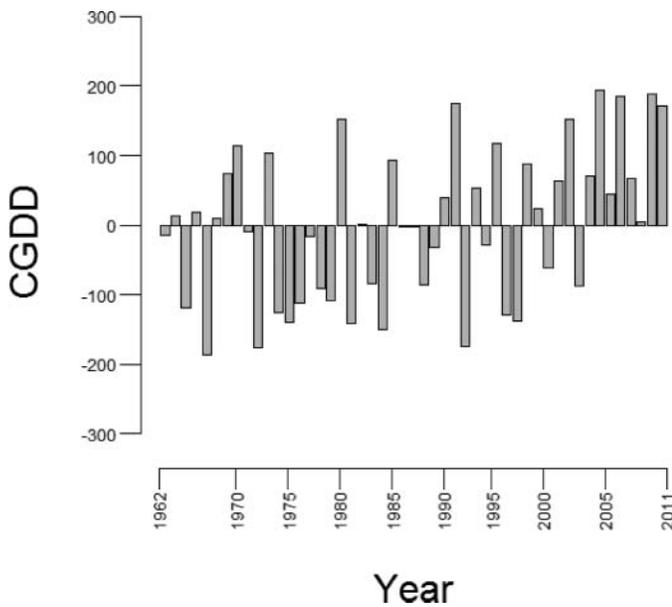


FIGURE 5. Analysis of variance year effect on year-end CGDDs (1962–2011) relative to the CGDD mean. Years with missing temperature data were excluded.

bay and lower bay mean CGDDs were similar ($t = -0.49, df = 324, P = 0.99$) but had significantly lower ($P < 0.001$) mean year-end CGDDs than the bay tributaries and Mobjack Bay. In general, adjacent regions did not differ significantly; for example, the York and Rappahannock rivers ($t = 0.16, df = 324, P > 0.99$) and the Chester and Choptank rivers ($t = -0.24, df = 324, P > 0.99$) were not significantly different from one another. Mean year-end CGDDs also differed significantly among years ($F_{56, 258} = 21.56, P < 0.001$; Figure 5). In the mid-1960s to mid-1980s the year-end CGDDs were usually lower than the overall time series mean (47.24). From 1985 to 2000, year-end CGDDs were variable, and since 2000 most years had CGDDs above the time series mean (Figure 5).

The mean length of age-0 Atlantic Menhaden increased linearly at a rate of 0.053 mm/GDD ($t = 103.83, df = 3,221, P < 0.001; r^2 = 0.77; RMSE = 19.8 \text{ mm}; 95\% \text{ CI} = 0.052\text{--}0.054$; Figure 6). The intercept was 41.4 mm (95% CI = 40.2–42.6), which can be interpreted as the estimated mean length at metamorphosis from the larval to juvenile stage, assuming a constant growth–temperature relationship after metamorphosis. The simple GDD model accurately predicted annual mean lengths of age-0 Atlantic Menhaden in the validation data set and explained 83% of the variability in mean length of these data with an RMSE of 17.3 mm, slightly better than the fit to the estimation data. Juvenile Atlantic Menhaden grew between 0.32 and 0.58 mm/d during summer when water

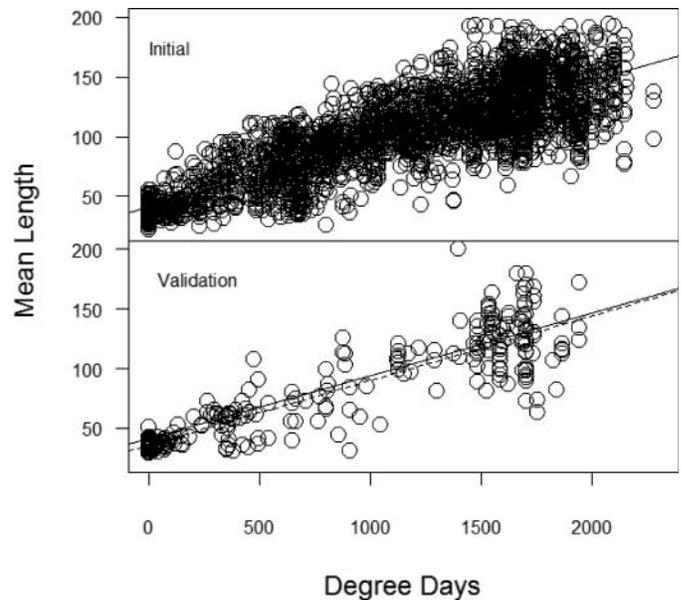


FIGURE 6. Age-0 Atlantic Menhaden mean total length (mm) per sampling event as a function of CGDDs from 1962 to 2011. The upper panel shows the initial model fitting (James, York, and Rappahannock rivers and the upper bay), and the lower panel shows the validation of the remaining regions (Patuxent, Choptank, and Chester rivers, Mobjack Bay, and the lower bay) against initial model fit regression (solid line). The dashed line represents the mean length per tow in the validation regions as a function of CGDDs for comparison.

temperatures were between 20°C and 30°C, respectively. The predicted difference in mean length at the end of a cold year (about 1,400 CGDDs) and a warm year (about 2,200 CGDDs) was approximately 43 mm (115 mm and 158 mm, respectively). The mean weights in cold and warm years were 13.9 g and 40.6 g, respectively, a near three-fold difference.

The simple GDD model also explained among-region variation in age-0 Atlantic Menhaden lengths but fit some regions better than others (Figure 7). For example, the simple GDD model accurately predicted growth in the Patuxent River and lower bay but was less accurate in the upper bay and Chester River. There were significant differences among regions in the relationship between mean length of Atlantic Menhaden and CGDD ($F_{8, 3,564} = 18.71, P < 0.001$). Growth per GDD was highest in the upper bay (0.08 mm/GDD; 95% CI = 0.069–0.094) and lowest in the Chester River (0.02 mm/GDD; 95% CI = 0.002–0.040; Figure 7; Table 3). There was also a

significant effect of gear on CGDDs ($F_{2, 3,570} = 6.219, P = 0.002$; Table 3).

DISCUSSION

Age-0 Atlantic Menhaden growth varied spatially and temporally in Chesapeake Bay from 1962 to 2011, and our simple GDD model successfully explained and predicted spatial and temporal differences in Atlantic Menhaden mean length based on mean water temperatures. Growth rates of age-0 Atlantic Menhaden varied spatially among the regions of Chesapeake Bay but, on the whole, followed a consistent baywide pattern in response to temperature; on average, Atlantic Menhaden growth was slower in many of the northernmost regions than in the southernmost regions of the bay and its tributaries. Temporal patterns in mean size were also largely explained by the rate at which GDDs accumulate each year. Warmer years

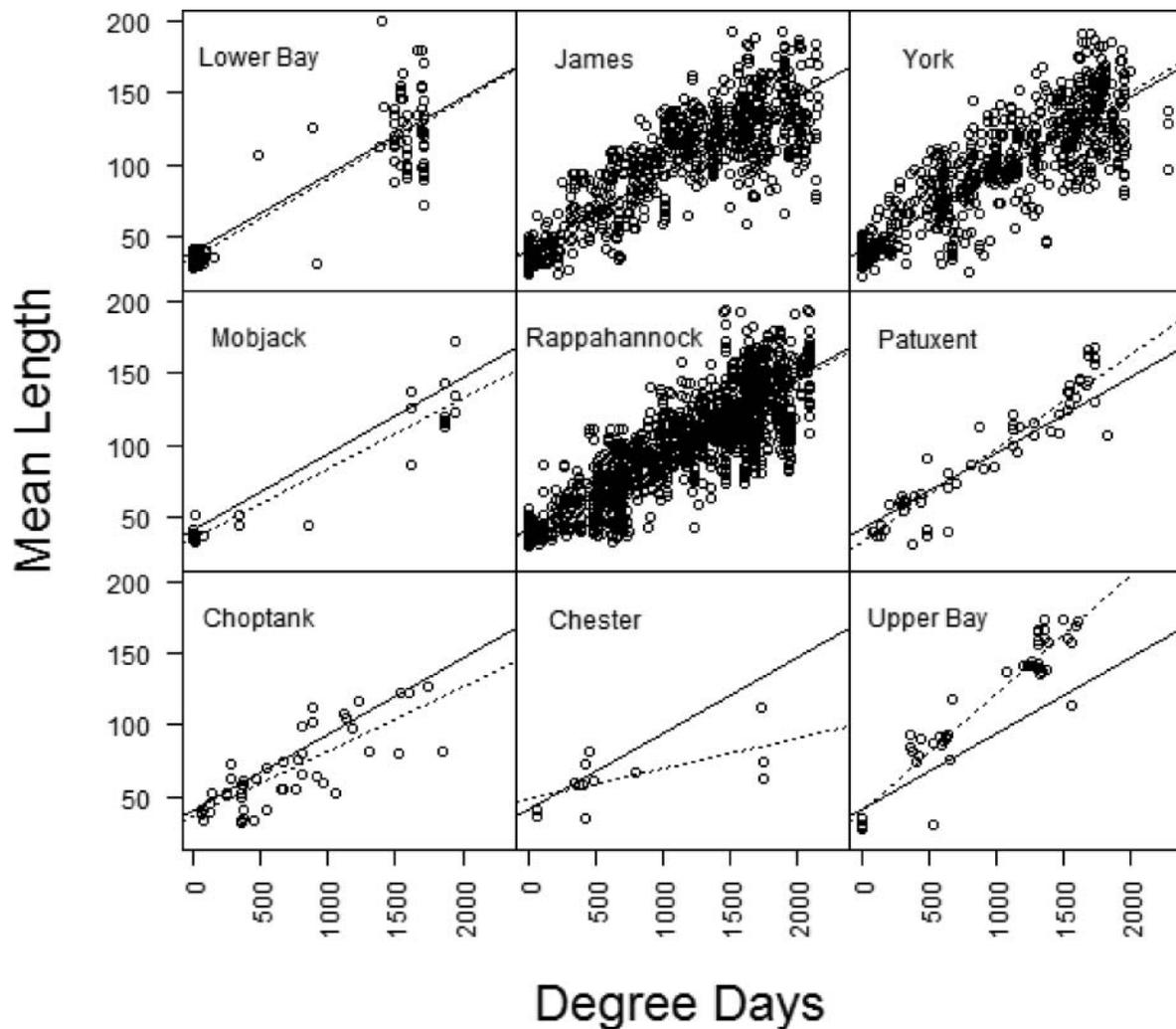


FIGURE 7. Age-0 Atlantic Menhaden mean total length (mm) per sampling event as a function of CGDDs for each region in the model. The solid line represents the initial model-fitting regression. The dashed line represents each region's regression for comparison (in regions where there is little variation from the initial model fitting, the regression lines are visibly stacked).

TABLE 3. Estimates of intercept and slope from ANCOVA tests of age-0 Atlantic Menhaden mean total length (mm) as a function of GDDs in the Chesapeake Bay by region and gear.

Region and gear	Intercept (mm)	SE	Slope (mm/GDD)	SE
Upper bay	40.26	6.94	0.082	0.001
Chester	48.55	9.33	0.021	0.010
Choptank	37.80	5.81	0.044	0.007
Patuxent	33.01	5.98	0.065	0.003
Rappahannock	40.03	2.58	0.052	0.005
Mobjack	36.11	5.11	0.049	0.005
York	41.21	2.61	0.055	0.002
James	42.61	1.11	0.052	0.006
Lower bay	36.36	3.14	0.055	0.002
Midwater trawl	35.56	2.78	0.065	0.003
Seine	44.73	6.25	0.048	0.006
Trawl	40.54	5.62	0.053	0.006

accumulated more GDDs, and thus Atlantic Menhaden in those years tended to be larger.

Although the model explained much of the variation in Atlantic Menhaden growth, we detected significant regional variation. However, we did not observe a latitudinal pattern. Differences among regions could be due to true regional effects (e.g., limited prey in some regions or region-specific, size-selective predation mortality of age-0 fish) or gear effects. We suspect that some of these differences may be caused by differences in selectivity among the gears used in the different regions. However, sampling using midwater and bottom trawls rarely occurred in the same location so it is difficult to determine if the region effects found in growth were due to gear selection or growing conditions. Additionally, the significant effect of gear on mean length could suggest that midwater trawls are more suitable for the capture of large fish than are bottom trawls or seines.

Factors such as density dependence and food availability may contribute to differences in growth rates among regions and over time (Annis et al. 2011). For example, a bioenergetics model has demonstrated the importance of chlorophyll *a*, a measure of phytoplankton standing stock (food of age-0 Atlantic Menhaden), and temperature on the growth of Atlantic Menhaden in Chesapeake Bay (Luo et al. 2001; Annis et al. 2011). Our simpler degree-day model had a predictive ability to explain variability in mean length (RMSE = 17.3 mm) that was similar to the more complicated approach of Annis et al. (2011) (RMSE = 16.5 mm). The bioenergetics model requires more data to predict and describe variability in growth, and data from some variables, such as chlorophyll *a*, are not available for the same temporal or spatial coverage as data for temperature or Atlantic Menhaden size.

The differences in growth rates among the regions show no evidence of counter gradient variation, in which growth rates vary with latitude such that fish in cooler latitudes are able to

keep up with fish in warmer latitudes by an increase in growth rate (Conover 1990). The power of our study to detect such trends is likely low because it included only a relatively small portion of the Atlantic Menhaden's range.

We found an increasing trend in mean year-end CGDDs over time, which could reflect the warming of Chesapeake Bay waters due to climate change. This corresponds with many long-term records that show that water temperature has increased along the Atlantic coast (Kerr et al. 2009) and in the Chesapeake Bay (Najjar et al. 2010). The Chesapeake Bay already has experienced a decrease in the extent of winter ice cover compared with 50 years ago (Boesch 2008). Because our analyses of age-0 Atlantic Menhaden growth were based on a minimum threshold temperature of 14°C for calculating GDDs, our approach does not capture the possible effects of warming during the winter, which have been more significant than those in the summer for the Chesapeake Bay (Wingate and Secor 2008) and coastwide (Frumhoff et al. 2007). In addition to global temperature forcing, local effects of land-use change could also contribute to an increase in water temperature. Urbanization activities in recent decades, including clearing trees and vegetation in riparian zones, increasing water withdrawals and periods of low flows, and releasing heated effluent wastes, can lead to increased water temperatures (Leblanc et al. 1997; Risley 1997).

Based on our model, continued warming may have positive effects on age-0 Atlantic Menhaden growth. While the majority of climate change impacts on the bay and its fishes are negative, some consequences may be positive (Najjar et al. 2010). Tolerance to changes in temperature is lowest in fish inhabiting high and low latitudes and widest in fish inhabiting middle latitudes, for which seasonal temperature extremes are the largest. As such, rising temperatures may favor some fishes in the Chesapeake Bay (Najjar et al. 2010; Pörtner and Peck 2010). Atlantic Menhaden, with wide distributions and temperature tolerance, potentially can benefit from an earlier seasonal initiation of growth (Najjar et al. 2010) and an overall increase in juvenile size in response to a longer growing season and higher GDDs. Our GDD model does not include potential negative effects of high temperature on age-0 Atlantic Menhaden growth. However, within the observed range of temperatures there has not been a negative effect of GDD on mean size.

Our model makes several assumptions about age-0 Atlantic Menhaden and their environment. One assumption is that Atlantic Menhaden remain in a single region during their entire juvenile growth period. Atlantic Menhaden experience a range of variable temperatures as they ingress into the Chesapeake Bay from the coastal ocean and become redistributed among the regions within the bay. However, they likely spend much of their age-0 growth phase during the summer in a single region, based on observed region-specific chemical signatures in their otoliths (Schaffler et al. 2014). If there had been extensive mixing among regions, Atlantic Menhaden would

have experienced homogenization of the effect of degree-days on growth and we would not have been able to detect region effects. An additional model assumption is that temperature records for each of the regions are representative of the entire tributary or region. We believe that the temperature records we used are broadly representative of conditions in each region. Additionally, we assumed the above-pycnocline temperature is the habitat occupied by Atlantic Menhaden, as has been done in other studies (Gottlieb 1998; Annis et al. 2011). Despite these potential concerns, the model explained most of the regional and seasonal interannual variability in mean length of age-0 Atlantic Menhaden.

The model we developed also assumes that Atlantic Menhaden are only positively affected by temperature. The Luo et al. (2001) model was parameterized such that 33°C was the optimal temperature for respiration and 36°C was the maximum temperature for respiration. However, within our data set there were no recorded temperatures above 33°C. Additionally, while the minimum lethal temperature of Atlantic Menhaden is reported to be 3°C (Lewis 1965), larval Atlantic Menhaden have been sampled at 2°C (E. D. Houde, unpublished data). In our data set, temperature was recorded to be below 3°C in 890 instances (4%). Our finding of a linear relationship with temperature is expected because the Chesapeake Bay is in the middle of the range of Atlantic Menhaden (Ahrenholz 1991).

Models, such as ours, that relate mean size to cumulative temperature describe apparent growth, which is the effect of temperature on the growth of survivors. Without tracking a population over time, it is very difficult to separate the effects of size- or age-selective mortality from growth because both processes affect the size distribution of fish. The large difference between the minimum lethal temperature for Atlantic Menhaden and our best estimate of threshold temperature, 14°C, is potentially affected by survival shortly after the ingress of larvae into Chesapeake Bay during the winter months. In this regard, the hatch dates and ingress dates of larval Atlantic Menhaden entering Chesapeake Bay were predominantly in November–December, while the hatch dates of surviving juveniles were predominantly in January–February (Lozano et al. 2012). Larvae hatched in November–December experience a long period of cold temperatures that are unfavorable for growth and survival, while those hatched in January–February would ingress in early spring when temperatures were higher and favorable for growth.

We demonstrated that temperature has a substantial effect on age-0 Atlantic Menhaden growth, with juveniles growing to almost three times the weight in a warm year as in a cold year, and increases in growth could have substantial effects on the ecosystem. The increased growth of Atlantic Menhaden in Chesapeake Bay, assuming that recruitment is constant, would place a higher consumptive demand on their prey in warm years. As age-0 juveniles they are thought to largely feed on phytoplankton (Annis

et al. 2011), and their increased predation could affect primary production dynamics. Additionally, increased growth in warm years could contribute substantially more to Atlantic Menhaden stock biomass than in cooler years and could generate substantially more biomass that would be available to predators, such as Striped Bass. In our analyses, recruitment in Chesapeake Bay was unrelated to CGDDs during 1962–2011 (results not shown). Wood (2000), however, found that warm, dry years were better for Atlantic Menhaden recruitment as there was an earlier spring phytoplankton bloom. If recruitment increases with increasing temperature, then the combined effects of increased growth and recruitment would cause both a higher consumptive demand by Atlantic Menhaden on phytoplankton and result in increased juvenile biomass in the Chesapeake Bay. In coming decades, the expectation for the region is warmer years with greater variability in precipitation (Najjar et al. 2010). Warming may favor Atlantic Menhaden growth in Chesapeake Bay and could generate greater biomass for the stock if recruitment levels continue at the current low levels.

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