



2020

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Vaskar Nepal
Virginia Institute of Marine Science

Mary C. Fabrizio
Virginia Institute of Marine Science

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Recommended Citation

Nepal, Vaskar and Fabrizio, Mary C., Density-Dependence Mediates the Effects of Temperature on Growth of Juvenile Blue Catfish in Nonnative Habitats (2020). *Transactions of the American Fisheries Society*, 149(1), 108-120.
10.1002/tafs.10217

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ARTICLE

Density-Dependence Mediates the Effects of Temperature on Growth of Juvenile Blue Catfish in Nonnative Habitats

Vaskar Nepal*  and Mary C. Fabrizio 

Virginia Institute of Marine Science, William & Mary, Post Office Box 1346, Gloucester Point, Virginia 23062, USA

Abstract

The combined effects of conspecific density and climate warming on the vital rates of invasive fish species have not been well studied, but may be important in predicting how successful they will be in the future. We evaluated the effects of temperature and population density on monthly time series of sizes of age-0 Blue Catfish *Ictalurus furcatus* in the James, York, and Rappahannock River subestuaries (defined here as tidally influenced bodies of water that feed into the Chesapeake Bay) from 1996 to 2017, using growing degree-days (GDDs, °C day) as a measure of thermal time. Our predictive linear mixed-effects model explained 86% of the variation in the length of age-0 Blue Catfish. In addition, it indicated a strong positive effect of temperature on the growth rate of age-0 Blue Catfish, with individual fish biomass during warm years up to 63% higher than during cool years. Growth rate was influenced negatively by the abundance of age-0 and older fish, resulting in at least fourfold differences in the predicted biomass of Blue Catfish by the end of the first year of life depending on conspecific density. We also observed regional differences in the growth rates of Blue Catfish in the three subestuaries we examined; although growth occurred in all subestuaries, growth was highest for the Rappahannock River population even though this river accumulated the fewest GDDs. Rising water temperatures due to global climate change will likely increase the growth rate of age-0 Blue Catfish in the Chesapeake Bay region, potentially intensifying the negative impacts of this invasive species on the ecology of Chesapeake Bay. However, individual populations respond differently to warming temperatures, and thus, potential increases in the growth rate of age-0 Blue Catfish may be partially offset by local conditions that may serve to limit growth.

The Blue Catfish *Ictalurus furcatus* is an invasive species of significant management concern in the Chesapeake Bay region. Originally introduced to the James River (southernmost), York and Rappahannock (northernmost) rivers, this species has undergone considerable population increases as well as range expansions into many subestuaries in the Chesapeake Bay region (Schloesser et al. 2011; Fabrizio et al. 2018), though the populations in the James, York, and Rappahannock rivers remain largely distinct stocks with little mixing among the subestuaries (Higgins 2006). Through competition and predation, Blue Catfish may negatively affect the abundance of local fauna like American Shad *Alosa sapidissima*, river herring *Alosa* spp., Atlantic Menhaden *Brevoortia tyrannus*, and blue crab *Callinectes sapidus*, many of which are of economic

or conservation concern (MacAvoy et al. 2009; Schloesser et al. 2011; Schmitt et al. 2019). Therefore, there is considerable interest in limiting range expansion and minimizing the negative impacts of Blue Catfish on native resources, particularly those that are the targets of restoration efforts (ICTF 2014).

The management of invasive Blue Catfish can be informed by characterization of its population dynamics in the Chesapeake Bay region. The growth of individuals is an essential component of the dynamics of fish populations, and contributes to the variation in mature biomass and production of fish stocks (Kwak and Waters 1997; Stawitz and Essington 2019). Growth during the first few months after hatching is particularly critical in determining the recruitment potential of fishes (Oele et al. 2019),

*Corresponding author: vaskarnepal@gmail.com
Received August 21, 2019; accepted November 12, 2019

and determines the ability of a fish to avoid predation, undergo ontogenetic shifts in diet (Brett 1979), and survive the first winter (Biro et al. 2004). Notwithstanding the effects of genetic makeup, fish growth is largely a function of temperature and food availability (Brett and Groves 1979). Water temperature regulates body temperature in most fishes and affects various physiological processes such as consumption, digestion, metabolism, and ultimately survival (Brett 1979). Similarly, conspecific density can affect the growth of fishes by influencing food and habitat availability (Walters and Post 1993; Walters 2000), though the effects are particularly important during the late-larval to juvenile stage (Cowan et al. 2000). Moreover, if adults and juveniles feed at different rates, on different prey, or in different habitats (i.e., ontogenetic niche shift), the magnitude of the negative effects of adults on the growth of age-0 fish can be different from that of juveniles (Walters and Post 1993). In such cases, accurate characterization of the effects of conspecific density requires partitioning of fish abundance into adult and juvenile components.

In Chesapeake Bay, the effects of conspecific density and temperature on growth of age-0 Blue Catfish have not yet been quantified. While Blue Catfish exhibit relatively high densities in the James, York, and Rappahannock rivers, interannual and spatial variations in abundance exist (Schloesser et al. 2011; Tuckey and Fabrizio 2018). In addition, mean water temperatures in these subestuaries have been increasing for several decades and are expected to continue to increase (Najjar et al. 2009; Humphrey et al. 2014). Although growth tends to decrease with conspecific density and increase with temperature (up to an optimum temperature), the relative influence and overall effects of these factors on Blue Catfish growth are unknown. Will these effects cancel each other out or will the growth rate of age-0 Blue Catfish increase with rising temperatures? Cumulative effects of temperature and density on individual growth will affect future density, biomass, distribution, and ultimately, the impact of this invasive species on local resources.

We quantified the effects of temperature and population density on the growth of Blue Catfish during the first year of life, a period chosen because of its direct link to the success of Blue Catfish in the Chesapeake Bay region. To quantify the effects of temperature, we used growing degree days (GDD, °C day) as a measure of thermal energy transferred from the environment to an ectotherm over any given time period (Charnov and Gillooly 2003; Neuheimer and Taggart 2007). The GDD approach is based on the idea that temperatures above a minimum threshold are conducive to physiological processes including growth; therefore, the growth of an ectothermic organism during a fixed period is proportional to the amount of thermal energy accumulated by the organism during that

period (Neuheimer and Taggart 2007). Due to its simplicity, high performance, and sound physiological underpinning, the GDD approach has been widely used in models to explain variations in development and growth of many freshwater and marine fishes (e.g., Neuheimer and Taggart 2007; Humphrey et al. 2014; Rypel 2014; Ward et al. 2017; Oele et al. 2019). To quantify the effects of conspecific density, we used annual relative abundance indices of Blue Catfish from a fishery-independent survey. Overall, our objectives were (1) to build a predictive model to assess spatial and temporal variability in the growth of age-0 Blue Catfish in three subestuaries of the Chesapeake Bay during a 22-year period, and (2) to predict the length and weight of Blue Catfish under multiple temperature and density scenarios.

METHODS

Sampling of Blue Catfish.—The study area encompassed three subestuaries of the Chesapeake Bay, each with its own stock of Blue Catfish (Figure 1; Tuckey and Fabrizio 2013). The length of age-0 Blue Catfish was obtained from the Juvenile Fish and Blue Crab Trawl Survey (hereafter, “trawl survey”) conducted by the Virginia Institute of Marine Science. Since 1989, the trawl survey has collected monthly samples from 111 stratified random sampling sites (86 random sites; 25 fixed sites) throughout the Virginia portion of the Chesapeake Bay and the tidal portions of its major tributaries (James, York, and Rappahannock River subestuaries). Stratification of sampling sites within the subestuaries is based on depth and longitudinal regions, the latter to account for salinity differences along the longitudinal axis of each river. Collections occurred between the mouth of each subestuary and river kilometer 64.4 measured from the mouth of the subestuary, though Blue Catfish were captured only in oligohaline and mesohaline regions (Figure 1). Note that the range of Blue Catfish in these subestuaries extends into freshwater nontidal habitats beyond the sampling domain of the trawl survey (Schloesser et al. 2011; Tuckey and Fabrizio 2013). Each site was sampled using a 9.1-m semi-balloon otter trawl towed for 5 min along the bottom during daylight hours. All captured individuals were enumerated and their fork lengths (FL) were measured to the nearest mm. Larger catches were subsampled for length measurements according to Tuckey and Fabrizio (2013). Collections were conducted under approved Institutional Animal Care and Use Committee protocols following all applicable U.S. guidelines.

The relative abundance indices for age-0 and older (age 1+, i.e., age 1 and older) groups were estimated from trawl survey catches. Blue Catfish were partitioned into age-0 and older groups based on monthly size thresholds, which had been previously identified from the progression of length-frequency distributions for each month (Tuckey

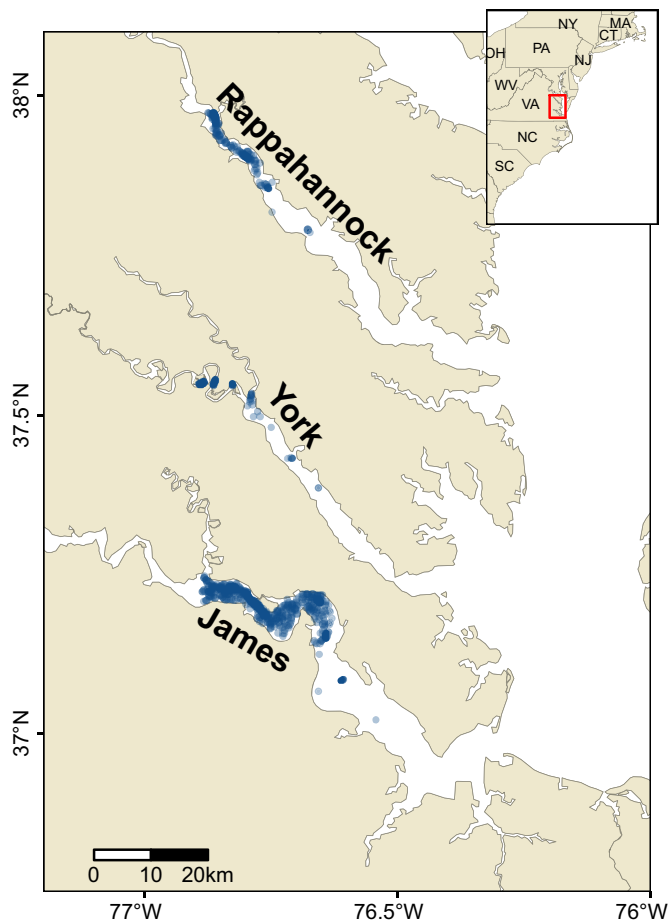


FIGURE 1. Sampling locations for age-0 Blue Catfish during 1996–2017 in three subestuaries of Chesapeake Bay, Virginia. The darker points signify overlap of sampling stations with positive Blue Catfish catch. [Color figure can be viewed at afsjournals.org.]

and Fabrizio 2018). Annual abundance indices for age-0 and older Blue Catfish were calculated separately, and involved a delta lognormal approach following Tuckey and Fabrizio (2013). Briefly, for each subestuary, we estimated the proportion of positive tows and the mean of the \log_e transformed positive catches; the abundance index was then calculated as the product of the proportion of positive catches and the back-transformed, bias-adjusted subestuary means (Tuckey and Fabrizio 2013). Abundance indices for age-0 and older (1+) Blue Catfish are referred to as age-0 and adult indices in this paper, even though Blue Catfish likely do not mature until the age of 4–6 years (Graham 1999).

Water temperature.—Water temperature for each subestuary was obtained from several sources. Bottom water temperature was recorded at all the sampling stations during each sampling cruise of the trawl survey. We supplemented these data with temperature observations from the Virginia Estuarine and Coastal Observing System (available at <http://web2.vims.edu/vecos/>), a standardized

water quality observing system in Chesapeake Bay. Within the sampling domain of this study, the Virginia Estuarine and Coastal Observing System collects continuous measurements of temperature from four fixed stations, and monthly or bimonthly measurements from seven fixed stations. We calculated the mean temperature in each subestuary for each day across all sources and stations. If temperature was not available for any given day, we imputed the temperature estimate by linear interpolation between adjacent dates within the subestuary (i.e., temporal interpolation).

Statistical analysis.—The size distribution across all Blue Catfish sampled between January 1996 and December 2017 was used to calculate the abundance indices as described above, but growth modeling was restricted to age-0 Blue Catfish, which were identified based on finite mixture models of fork length distributions (Scrucca et al. 2016). Specifically, we fit a mixture of normal distributions to month- and subestuary-specific length-frequency distributions using an expectation-maximization algorithm, and length measured to the nearest mm. Individuals associated with the left-most normal distribution represented age-0 fish.

To characterize the effect of temperature on the change in size of Blue Catfish, we calculated the number of GDDs for each day during the year based on observed water temperatures. The cumulative number of GDDs accumulated by fish i was calculated using the following formula:

$$\text{GDD}_i = \sum_{t=1}^N \bar{T}_{ti} - T_b, \quad \bar{T}_{ti} > T_b, \quad (1)$$

where N is the number of days between the first day of interest ($t = 1$; see below) and the day of capture for a fish, is the mean temperature experienced by fish i on day t , and T_b is the base temperature (i.e., the temperature below which growth ceases: Neuheimer and Taggart 2007). Even though the hatch date should be the first day for the calculation of cumulative GDD, hatch dates of individual Blue Catfish were not known. In their native range, Blue Catfish spawn from April to August (Graham 1999; Seibert et al. 2017), and peak spawning occurs during May and June in the Chesapeake Bay region (V. Nepal, unpublished). Age-0 fish may not fully recruit to our sampling gear until September. If we assume a fixed hatch date for the entire year class, we would underestimate the accumulated GDD for fish that actually hatched before the assumed hatch date, and overestimate the accumulated GDD for fish that hatched after the assumed hatch date. To minimize this bias, we followed annual cohorts beginning on September 1, which is when all fish in a given cohort were assumed to have hatched; we followed these fish until August 31 of the following year. Thus, for September–April, we used fish from the first (left-most) normal distribution, and for May–August when

the next cohort was not fully recruited to our gear, we used fish from the second normal distribution identified by the finite mixture models (Figure 2). All fitted mixture models were visually inspected to ensure that individual fish were assigned to a single cohort and that normal distributions were adequate in distinguishing annual cohorts based on FL distributions. Overall, 17,499 individuals were identified as age-0 Blue Catfish.

To validate the age assignment of Blue Catfish used in this study, we compared the length-frequency distribution of age-0 Blue Catfish in this study with that of fish aged using lapillus otoliths by Connelly (2001) and Latour et al. (2013). We further supplemented the database with Blue Catfish that we aged using the same structures. Together, these observations include length and age of 2,758 Blue Catfish captured between 1998 and 2019 that were aged using otoliths. The otolith-aged age-0 fish ranged between 79 and 299 mm, 95% of which had a FL of less than 201 mm. The fish that were assigned ages using finite mixture models in this study ranged between 22 and 219 mm, 99.6% of which had a FL of less than 201 mm. Finally, Rutherford et al. (1995) also found that age-0 and age-1

Blue Catfish could be clearly distinguished from older individuals based on peaks of the length-frequency histograms, validating the ages with readings from spines. Therefore, we contend that assignment of Blue Catfish as age-0 based on FL as done in this study did not bias the overall results.

Because the base temperature (T_b) required for Blue Catfish growth has not been established in an experimental setting, we considered a range of potential T_b values from 0°C to 20°C in 1°C increments. In analyzing the effects of the length of the growing season on mean annual growth of age-0 and age-1 Blue Catfish in the Mississippi River, Rutherford et al. (1995) used a T_b of 15°C, though no justification was provided; mean annual Blue Catfish growth was positively associated with the length of the growing season (Rutherford et al. 1995). In contrast, bioenergetics simulations conducted by Honsey (2018) could not reveal a preferred T_b for Blue Catfish. Here, we calculated the cumulative GDD for each potential T_b between 0°C and 20°C using equation (1), and fit separate linear regression models to relate size of Blue Catfish with the estimated cumulative GDD:

$$FL_i = \mu + \beta GDD_i + \varepsilon_i, \quad (2)$$

where FL_i is the FL of fish i , μ and β are the potential T_b -specific intercept (mm) and slope (mm/GDD) for fish i , and ε_i is the random unexplained error. The observations of the response (FL of individual fish) were the same for all regression models we considered, and the best model was chosen based on the log likelihood of the models. The model with a T_b of 9°C had the highest support (i.e., highest log likelihood), and thus, we chose a T_b of 9°C for subsequent analysis. Comparisons based on an alternative metric, r^2 , also resulted in the preferred T_b of 9°C (results not shown). A T_b of 9°C for Blue Catfish corresponds well with the observation by Weber and Bosworth (2005) that the congeneric species, Channel Catfish *Ictalurus punctatus*, can grow at temperatures as low as 10°C.

Additionally, we characterized spatial and temporal variations in accumulated GDDs. Starting with a data set where each row represents a year-subestuary combination (i.e., 22 years \times 3 subestuaries = 66 rows), we applied a linear model to examine effect of subestuary and year on year-end GDDs:

$$GDD_l = \mu + subestuary_l + \beta year + \varepsilon_l, \quad (3)$$

where GDD_l is the estimated year-end cumulative GDD for subestuary l (James, York, or Rappahannock) during 1995–2016, μ is the mean year-end cumulative GDD, $subestuary_l$ is the additive effect of subestuary l , and β is the common slope for all subestuaries (GDD/year). The fit

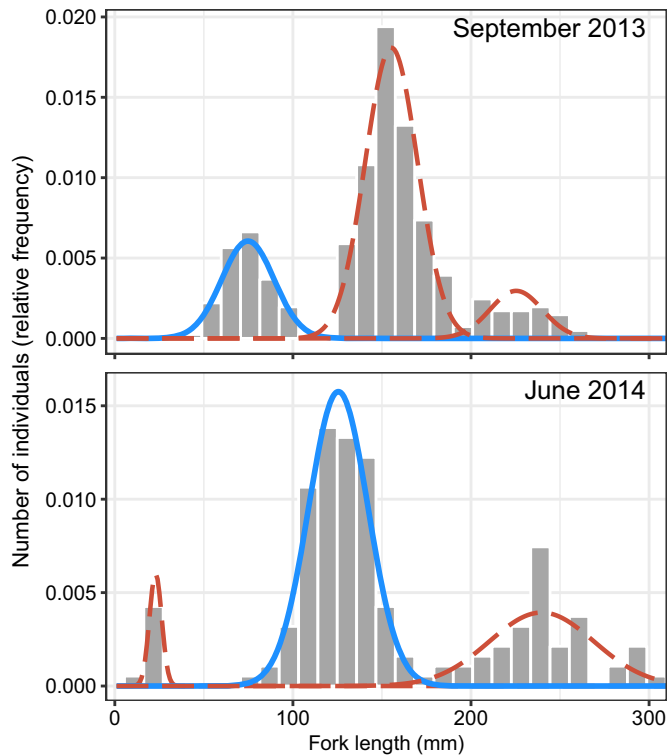


FIGURE 2. An example of the application of finite mixture models on the FL distribution of a Blue Catfish cohort during 2 months. The normal distribution fitted for age-0 individuals used in the analysis is given by the solid blue curve; the dashed red curve represents the normal distribution for older cohorts that were not used in this analysis. Refer to the text for details on the choice of first or second normal distribution curves. [Color figure can be viewed at ajfsjournals.org.]

of an alternative full model including an interaction term was compared with the additive model using Akaike information criterion (AIC) and AIC weight (Burnham and Anderson 2002). In this framework, the model with the lowest AIC value or highest AIC weight represents the most parsimonious fit to the data. In our case, support was substantially higher for the additive model (AIC weight_{interaction} = 0.15; AIC weight_{additive} = 0.85); thus, we only show results for the more parsimonious additive model. Note that the years in equation (3) correspond to cohort years and not calendar years. Even though we modeled the growth of fish collected between January 1996 and December 2017, fish collected between January and August 1996 belonged to the 1995 cohort and were assigned GDDs accordingly. Hence, the first full cohort year in equation (3) was 1996. On the other hand, fish collected during September to December 2017 belonged to the 2017 cohort, but the GDD accumulation for this cohort year was incomplete because the temperature and GDD data did not extend to August 2018. Hence, the last full cohort year considered in equation (3) was 2016.

To assess the effects of conspecific density and thermal history on the growth of Blue Catfish, we used a linear mixed-effects model:

$$\begin{aligned}
 FL_{ijkl} = & \mu + subestuary_l + \beta_1 GDD + \beta_2 age-0 \\
 & + subestuary_l + \beta_3 adult + cohort_j \\
 & + tow(cohort)_{jk} + \varepsilon_{ijkl},
 \end{aligned} \tag{4}$$

where FL_{ijkl} is the FL of i th Blue Catfish collected from tow k in cohort year j in subestuary l , μ is the overall mean FL, $subestuary_l$ the additive effect of subestuary l , β_1 is the partial regression coefficient for cumulative GDD, β_2 is the partial regression coefficient age-0 abundance index, β_3 is the partial regression coefficient for adult abundance index, $cohort_j$ is the random effect of cohort year j , and $tow(cohort)_{jk}$ is the random effect of tow k nested within the cohort year j .

The random effect of cohort was included in the model to account for potential interannual differences in size of Blue Catfish at the start of the year (i.e., the intercept or the FL on September 1); this allowed us to rule out potential confounding effects of warmer or cooler years on fish size at the start of the growth period of interest. We also fit several simpler (i.e., excluding some of the predictive variables) and more complex (i.e., including two-way interactions) models. Models with three-way interactions yielded unrealistic predictions, and were not considered further. To account for potential temporal autocorrelations among GDD measurements through time, we used a first-order continuous autoregressive correlation structure. All competing models were fit using maximum likelihood

and compared using AIC as described above; parameter estimates from the best model were used for further predictions. To ease model interpretation, we centered and scaled the independent continuous variables (GDD, age-0 index, and adult index) and suppressed the intercept (Schielzeth 2010). Model assumptions of normality of the response and residuals as well as homogeneity of variance were checked using histograms and residual plots.

Theoretical and empirical studies have shown that the growth rate of fishes declines nonlinearly with increasing population density (Walters and Post 1993; Post et al. 1999; Ward et al. 2017) as opposed to the linear decline assumed in our linear mixed-effects model. To this end, we also fit nonlinear mixed-effects models that allowed growth rate to decline exponentially with age-0 and adult density. The parameterization of the model followed Ward et al. (2017) and had the following general structure:

$$FL_{il} = \mu + subestuary_l + \beta_1 GDD * e^{-\beta_2 age-0 - \beta_3 Adult} + \varepsilon_{il}, \tag{5}$$

where the terms are as described above. Several nonlinear models, including models with interactions between GDD, subestuary, and age-0 and adult abundance indices, were fit and compared with the linear mixed-effects models using AIC as described above. Because the nonlinear models resulted in suboptimal fits compared with the linear models (based on AIC, results not shown), we present results from only the best linear mixed-effects model (i.e., the model with the lowest AIC and highest AIC weight).

We used cross-validation to evaluate the predictive ability of the best linear mixed-effects model of juvenile Blue Catfish growth in Chesapeake Bay subestuaries. To do this, we randomly partitioned the data into a training subset, which contained approximately 75% of the observations ($n = 13,370$), and a validation subset, which contained the remaining observations ($n = 4,129$). The partition was stratified by subestuary (James, York, and Rappahannock) to ensure that each subestuary contributed approximately 75% of its observations to the training subset. Using the training subset, we fit a linear mixed model with FL as the response as described above in equation (4). The fitted model was then used to predict the length of age-0 Blue Catfish in the validation subset. Performance of the fitted model was evaluated using two metrics. First, as an absolute measure of model fit, we calculated RMSE:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (\widehat{FL}_i - FL_i)^2}{n}}, \tag{6}$$

where RMSE is the average distance between the observed FL (FL_i) and the model predicted FL (\widehat{FL}_i) for fish i .

Therefore, models with higher precision and good predictive performance have low RMSE values when applied to the validation subset. Second, as a relative measure of model fit, we calculated r^2 using the approach described by Nakagawa and Schielzeth (2013). Specifically, we calculated marginal r^2 (the proportion of variation in FL explained by fixed effects only), and conditional r^2 (the proportion explained by both fixed and random effects). For the validation subset, marginal r^2 was calculated as the square of the correlation coefficient between the predicted and observed FL.

To ensure that the data partitioning did not affect our results, we repeated the entire cross-validation exercise 15 times, each time partitioning the data randomly. The same final linear mixed-effects model was selected based on AIC, and the qualitative results based on the selected model did not differ among the data partitioning iterations. Therefore, we show the mean RMSE and r^2 values from the 15 cross-validation outcomes; predictions are based on a randomly chosen cross-validation model.

Following model validation, we used the final selected model to predict the FL of age-0 Blue Catfish at the end of the first year during all years assuming maximum, median, or minimum observed age-0 or adult abundance indices. The FLs, predicted based on the year-end GDDs, were then converted to fish weight by using a length-weight regression specific to age-0 Blue Catfish from the Chesapeake Bay region. The length-weight regression followed an allometric relation given by

$$W = 7.88 \times 10^{-6} \times \text{FL}^{3.092},$$

where W is weight (g). The length-weight regression used a multiplicative error structure to meet the assumption of homogeneity of variance and was based on 316 Blue Catfish (FL < 300 mm) collected from the James and York River subestuaries in 2015–2017. Statistical analysis was performed in R (R Core Team, Vienna) using packages `mclust` (version 5.1), `caret` (version 6.0-84), and `nlme` (version 3.1-139).

RESULTS

In each subestuary, GDDs accumulated rapidly during the first few months (September–October), slowed between late fall and early spring (November–April), and increased again as water temperatures began to rise in April (Figure 3). We found considerable variation in year-end GDDs among years and subestuaries (Figure 4). On average, the Rappahannock River was the coolest of the three subestuaries and accumulated the fewest GDDs (mean = 2,987.5; 95% confidence limit [CL] = 2,926.0 and 3,049.0); James River accumulated the most GDDs (mean = 3,218.0; 95% CL = 3,156.4 and 3,279.3), and York River accumulated

intermediate number of GDDs (mean = 3,142.2; 95% CL = 3,080.8 and 3,203.7; Figure 4). However, all subestuaries showed an increasing trend in the year-end GDD during the sampling period, indicative of warming water temperatures between 1995 and 2016 (Figure 4). The rate of increase in the year-end GDD through time was similar for the three subestuaries, as indicated by a lower AIC value (and higher AIC weight) for the common-slope model (Figure 4); on average, the year-end GDD increased by 17.4 GDD per year during 1995–2016.

The most parsimonious linear mixed model describing the growth dynamics of age-0 Blue Catfish (FL: 22–219 mm) in Chesapeake Bay subestuaries included two-way interactions of GDD with subestuary and adult and age-0 abundance indices (Table 1), suggesting density-dependent and population-specific effects of temperature on the growth rate of juvenile Blue Catfish. The fixed effects in the final model (equation 4: subestuary, GDD, and abundance indices) explained 64% of the variation in FL (marginal $r^2 = 0.64$), and the random effects (year and tow) explained an additional 22% of the total variation in FL (conditional $r^2 = 0.86$). The model was also relatively precise, with the predicted FL of age-0 Blue Catfish differing from the observed by 12.3 mm on average (RMSE = 12.3 mm; 10% of the mean observed FL, which was 123.1 mm). The model performed well on the validation subset with a marginal r^2 of 0.72 and RMSE of 17.2 mm. The growth rate of juvenile Blue Catfish in response to GDD accumulation was highest for the Rappahannock River (effect size 4.8; 95% CL = 2.0 and 7.6) and lowest for the York River (effect size -4.0; 95% CL = -6.9 and -1.1; Table 2). Graphical analysis of conditional modes of the random effect of cohort showed no systematic deviations in size of age-0 Blue Catfish at the start of the season among warm or cool years, implying that our results were not affected by differences in starting size or time of spawning among years. At the end of their first year of growth, Blue Catfish attain the largest size in the Rappahannock River, and the smallest size in the York River (Figure 5). Assuming average adult and age-0 abundance indices, Blue Catfish can be 12.7–17.0% larger in length and 44.9–62.6% greater in weight by the end of their first year during the warmest observed year compared with the coolest observed year (Figure 5). However, both adult and age-0 abundance indices had negative effects on the growth rate of juvenile Blue Catfish (effect size for adult index = -2.0 and 95% CL = -3.2 and -0.9; effect size for age-0 index = -1.4 and 95% CL = -2.5 and -0.3; Table 2 and Figure 6). Therefore, depending on the water temperature and the abundance of age-0 and adults, the overall predicted mean length of juvenile Blue Catfish within a subestuary can change by more than 1.5-fold by the end of the first year; weight can change by more than 4-fold (Figures 6 and 7).

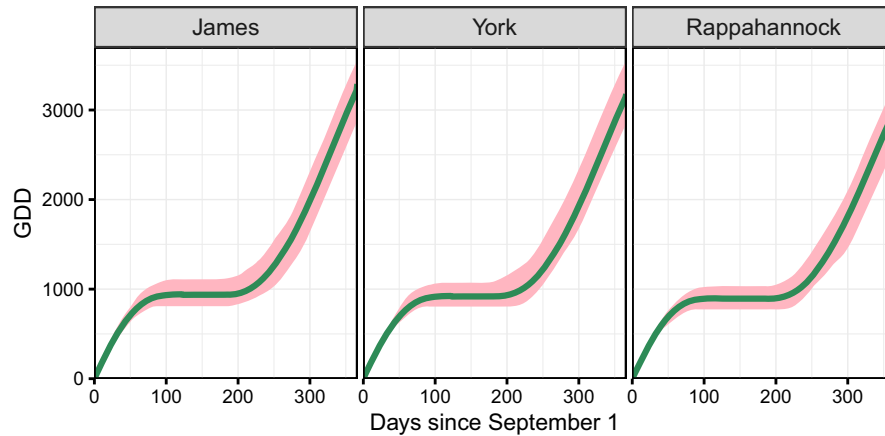


FIGURE 3. The accumulation of GDDs in the James, York, and Rappahannock River subestuaries during 1995–2016. The thick solid line represents the mean cumulative GDDs and the shaded area represents the range of GDDs for each day across the 22 years of the time series. [Color figure can be viewed at afsjournals.org.]

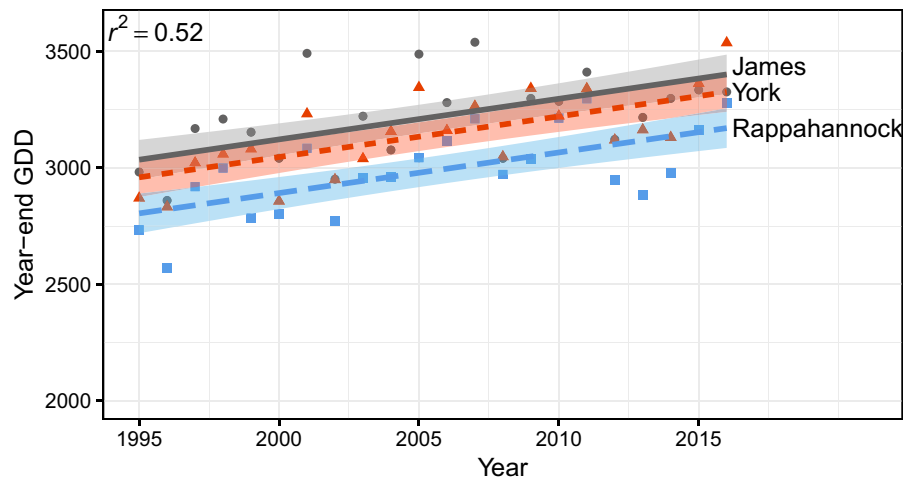


FIGURE 4. The total GDDs accumulated by the James, York, and Rappahannock River subestuaries during each year for the 1995–2016 period. Lines and 95% confidence bands correspond to the best fit linear regression model. [Color figure can be viewed at afsjournals.org.]

DISCUSSION

Our model successfully explained and predicted spatial and temporal variability in mean length of invasive Blue Catfish during the first year of their life in three Chesapeake Bay subestuaries. We demonstrated that temperature has a substantial positive effect and conspecific density has a negative effect on the growth of age-0 Blue Catfish. The continued warming of Chesapeake Bay subestuaries will potentially increase growth rates and juvenile biomass of Blue Catfish, presumably intensifying their impact on native species. However, local conditions unrelated to temperature, such as population density, may curtail growth to some degree in some subestuaries.

We found a linear increase in year-end GDD accumulations in Chesapeake Bay tributaries since 1995. This agrees with other long-term records that show that water

temperature has increased in the Chesapeake Bay (Najjar et al. 2009; Humphrey et al. 2014; Ding and Elmore 2015) and along the entire Atlantic coast (Saba et al. 2016). Such observations reflect the warming of these water bodies due to global climate change, though local effects of change in land-use patterns likely also contribute to the increase in water temperature. Coastal urbanization, runoff from impervious surfaces, and discharges from industrial processes have increased during the past few decades in the Chesapeake Bay watershed, and may contribute to increases in water temperatures throughout the bay (Ding and Elmore 2015).

Water temperature is an important driver of growth rates of juvenile Blue Catfish, with the weight of individuals increasing by up to 62.6% in the warmest observed year compared with the coolest observed year and

TABLE 1. The number of parameters (K), Δ Akaike information criterion (AIC), and AIC weight for alternative models describing the size of age-0 Blue Catfish in Chesapeake Bay subestuaries. Interactions between two independent variables are denoted with a colon between the variables. All competing models have the same random effects structure. The best model, chosen based on highest AIC weight, is highlighted in bold. “Age-0” and “adult” refer to the abundance indices for those age groups.

Independent variables (fixed effects)	K	Δ AIC	AIC weight
GDD	5	305.1	0.00
GDD + subestuary + GDD:subestuary	10	22.5	0.00
GDD + subestuary + adult + GDD:subestuary	11	17.3	0.00
GDD + subestuary + age-0 + GDD:subestuary	11	23.2	0.00
GDD + subestuary + adult + age-0 + GDD:subestuary	12	17.6	0.00
GDD + subestuary + adult + GDD:subestuary + GDD:adult	12	5.9	0.05
GDD + subestuary + age-0 + GDD:subestuary + GDD:age-0	12	21.1	0.00
GDD + subestuary + adult + age-0 + GDD:subestuary + GDD:adult	13	6.4	0.04
GDD + subestuary + age-0 + adult + GDD:subestuary + GDD:age-0	13	15.8	0.00
GDD + subestuary + adult + age-0 + GDD:subestuary + GDD:adult + GDD:age-0	14	0	0.91

TABLE 2. The parameter estimates for the best linear mixed model describing the growth of age-0 Blue Catfish in the James, York, and Rappahannock River subestuaries. The best model is provided in bold in Table 1. Interactions between two independent variables are denoted with a colon between the variables. “Age-0” and “adult” refer to the abundance indices for those age groups.

Parameter	Estimate	Lower CL	Upper CL
Fixed effects			
GDD	25.7	24.5	26.9
SubestuaryJames	124.6	120.6	128.7
SubestuaryRappahannock	128.1	122.9	133.3
SubestuaryYork	117.6	111.9	123.3
Adult	-4.0	-6.6	-1.5
Age-0	-2.7	-6.6	1.1
GDD:subestuaryRappahannock	4.8	2.0	7.6
GDD:subestuaryYork	-4.0	-6.9	-1.1
GDD:adult	-2.0	-3.2	-0.9
GDD:age-0	-1.4	-2.5	-0.3
Random effects			
SD_{cohort}	8.1		
$SD_{\text{cohort:tow}}$	12.3		
SD_{residual}	12.8		

assuming mean observed densities of Blue Catfish. Such findings have implications for the effect of continued warming on the growth of Blue Catfish and the future of the species in the Chesapeake Bay watershed. Changes in thermal regimes are expected to foster growth of temperate fish species, like Blue Catfish, which tend to have a wide tolerance to temperatures (Pörtner and Peck 2010; Rypel 2014). Provided that other environmental and genetic factors remain unchanged, the growth rates and individual weights of Blue Catfish will likely increase in the future as the Chesapeake Bay region accumulates more GDDs. In particular, the accelerated warming of the bodies of water in the Chesapeake Bay during winter

(Wingate and Secor 2008) will potentially benefit Blue Catfish growth by increasing the cumulative GDD and overall length of the growing season.

We observed considerable variation between subestuaries in GDD accumulation and size of age-0 Blue Catfish. Growing degree-day accumulations were lowest in the Rappahannock River (the subestuary that is at the highest latitude) and highest in the York and James rivers. Such observations conform to general patterns of latitudinal variation in water temperature. However, contrary to expectation, the growth rate of Blue Catfish was highest in the Rappahannock River and lowest in the York River. These contradictions could be due to the underlying

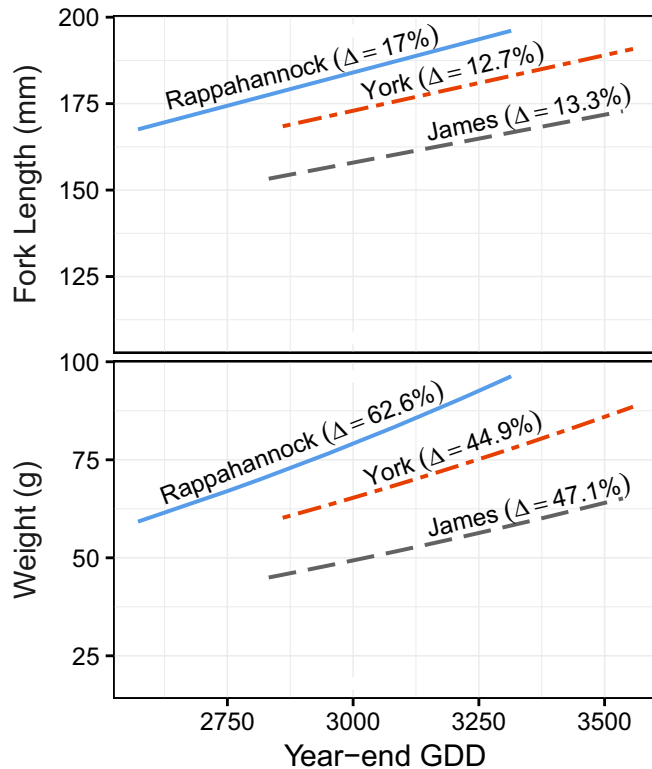


FIGURE 5. The predicted mean FL (mm) and wet weight of Blue Catfish at the end of the first year as a function of cumulative GDDs in the James, York, and Rappahannock River subestuaries during different years. For each river, the percent difference in FL and weight with respect to the coolest year are also shown. Note that the y-axes do not start at zero. [Color figure can be viewed at afs.journals.org.]

genetic differences in the populations in these three subestuaries; the York River population is the most inbred of the three populations, probably due to the smaller founder population size compared with the others (Higgins 2006). Such inbreeding depression has been shown to have negative impacts on the growth rates of many fishes, including Rainbow Trout *Oncorhynchus mykiss* (Su et al. 1996) and Channel Catfish (Bondari and Dunham 1987). Countergradient variation in growth (Conover 1990) may also contribute to increased growth rates in northern subestuaries, as reported for Blue Catfish across its latitudinal range (Rypel 2011). However, we suspect that this contribution is likely insignificant, owing to small differences in the latitudes of these subestuaries compared with the overall geographic range of Blue Catfish (from South Dakota to Mexico, Guatemala, and Belize: Graham 1999). Finally, subestuary characteristics such as dissolved oxygen, productivity, depth, and availability of refugia can greatly affect the growth and behavior of fishes (e.g., Pörtner and Peck 2010; Blair et al. 2013; Andersen et al. 2017). For example, low productivity in a system may

lead to higher competition for resources, and therefore a decline in the growth rate of fish (Andersen et al. 2017). The lower growth rates observed in juvenile Blue Catfish from the York River might, in part, be a result of the lower productivity in this subestuary compared with the others (Nesius et al. 2007). Rutherford et al. (1995) also found that the growth of age-1 Blue Catfish in the Mississippi River was higher during years that exhibited higher total organic carbon, suggesting that growth may be positively influenced by primary productivity of the system. We did not include these variables in our model because data for many of these variables were incomplete, and when available, were statistically confounded with the effect of subestuary.

Density- and temperature-dependent changes in growth rates have been observed in many aquatic animals. For example, the growth rates of hatchery-spawned juvenile Sockeye Salmon *Oncorhynchus nerka* that were released into two lakes were positively influenced by temperature and negatively influenced by conspecific density (Reed et al. 2010). Another study on experimentally stocked populations of Rainbow Trout reported similar results (Ward et al. 2017). Unsurprisingly, the positive effects of temperature on growth have also been observed in other ectothermic taxa such as freshwater mussels (Kendall et al. 2010). Many predators (e.g., Blue Catfish) and their prey (e.g., mollusks, crustaceans, and other fishes; Schloesser et al. 2011; Schmitt et al. 2019) in the Chesapeake Bay region will likely experience faster growth rates in the future due to global climate change. Because larger Blue Catfish have a greater salinity tolerance compared with those that are smaller in size (Nepal and Fabrizio 2019), faster growth could allow more individuals to expand in range into higher salinity waters in these subestuaries. Together these results highlight the potential for substantial changes in the ecological interactions and food-web structures that are likely to unfold in the future in Chesapeake Bay waters. Predictions of changes to food-web structures will require complex ecosystem models, but we contend that our results can provide essential input toward the development of such models.

Our growth model explained a large proportion of the variation (85%) in the length of Blue Catfish during their first year of life. The residual variation unexplained by the model is likely due to the necessary simplifying assumptions that we made in this study. First, the model assumed that individuals in a subestuary respond similarly to GDD accumulation and to their abundance, and thus did not incorporate individual variations due to genetic or environmental differences. Second, the movement of individuals within the subestuary was not considered in this model. For example, an individual may experience temperatures outside those recorded within the sampling area during vertical migration within the water

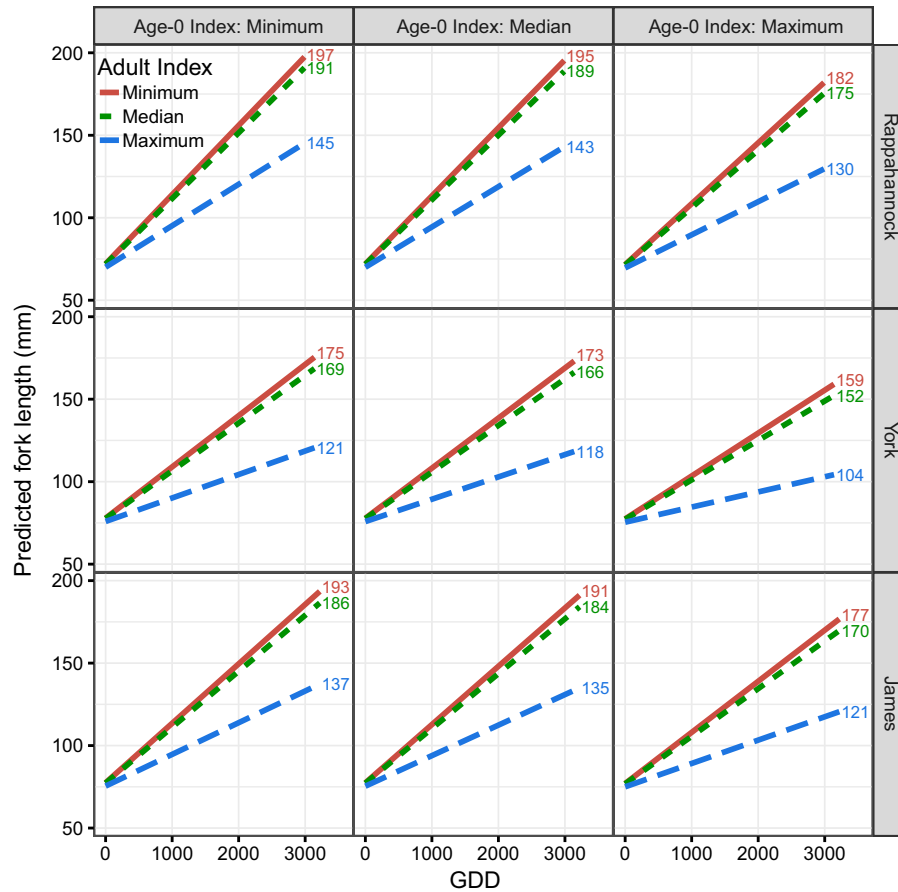


FIGURE 6. The predicted mean FL (mm) as a function of cumulative GDDs for age-0 Blue Catfish collected during 1996–2017 from the James, York, and Rappahannock River subestuaries under three density scenarios. The minimum, median, and maximum abundance indices for age-0 fish were respectively 0.00, 2.61, and 18.89, and those for adults were respectively 0.00, 17.18, and 137.30. The lengths at the end of age-0 are given by numbers at the end of each line. Note that the rivers accumulated different numbers of cumulative GDDs. [Color figure can be viewed at afsjournals.org.]

column, excursions to different mesohabitats for food or shelter, or seasonal migration into or away from the sampling area. In particular, individuals in tidal freshwater habitats may move upriver and experience different conditions. Such movement can offset or exacerbate the density-dependent effects on growth (Marco-Rius et al. 2013; Freshwater et al. 2017). Finally, the model assumes that all temperatures above the base temperature of 9°C contribute positively and linearly to growth. This is true for temperatures between 9°C and the optimal temperature, where growth rate is expected to be maximized. At temperatures greater than the optimum, the metabolic scope of fish is truncated such that less energy is available for processes beyond the maintenance of homeostasis, thus the growth rate declines and may cease at these temperatures (Schoolfield et al. 1981; Honsey 2018). The optimal growing temperature for Blue Catfish is reported to be approximately 24°C (Collins 1988), though this information has not yet been rigorously tested. In our

study, 43% of the individuals were captured at temperatures >24°C. We suspect that some of these individuals, particularly those that experienced temperatures >30°C for prolonged periods of time, experienced slower growth than that predicted by our model.

The GDD model presented here describes the effect of temperature and conspecific abundance on apparent growth, i.e., the growth of survivors. Size- or age-selective mortality of age-0 Blue Catfish could also lead to the observed patterns. For example, smaller age-0 fish are less likely to survive the first winter due to energy depletion (Biro et al. 2004), resulting in only larger individuals surviving to be sampled and therefore producing an appearance of faster growth (Walters and Post 1993). Such size-selective mortality could also result from changes in metabolic rates associated with density- or size-specific competitive interactions (Walters and Post 1993). However, the effects of age- or size-selective mortality could not be separated from apparent growth with the available

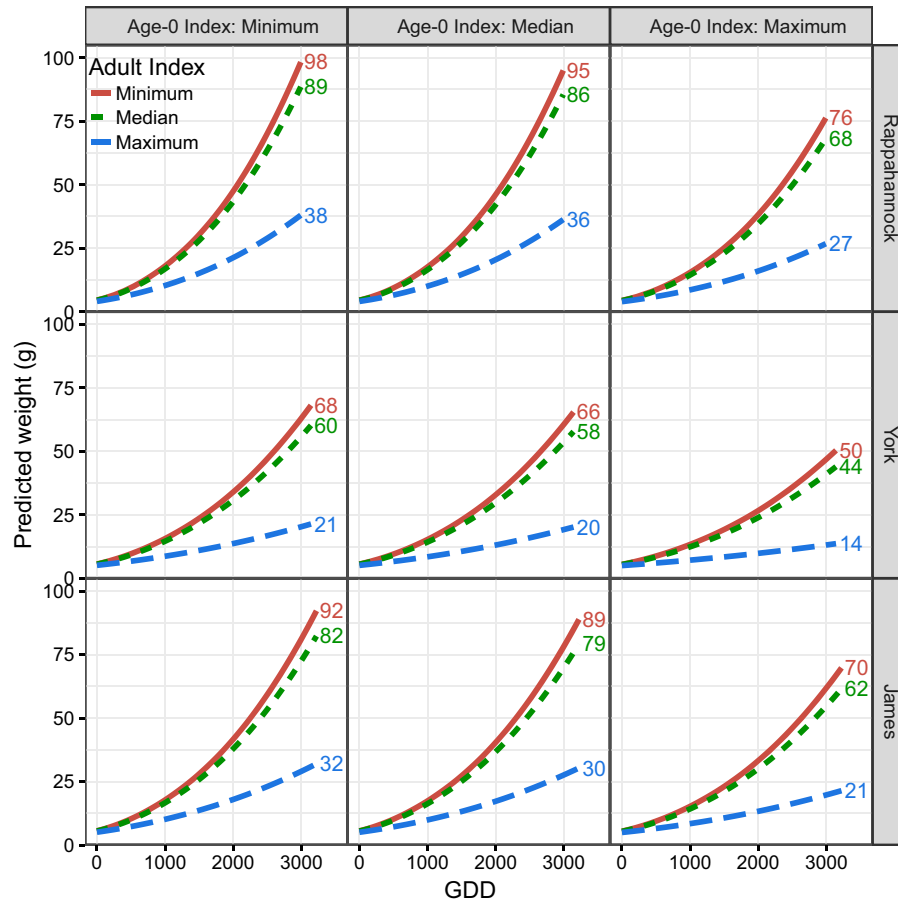


FIGURE 7. The predicted mean wet weight (g) as a function of cumulative GDDs for age-0 Blue Catfish collected during 1996–2017 from the James, York, and Rappahannock River subestuaries under three density scenarios. The minimum, median, and maximum abundance indices for age-0 fish were respectively 0.00, 2.61, and 18.89, and those for adults were respectively 0.00, 17.18, and 137.30. The weights at the end of age-0 are given by numbers at the end of each line. [Color figure can be viewed at afs.journals.org.]

data. Information on hatch-dates of the individuals may be useful in assessing actual growth instead of apparent growth, and may increase the accuracy, precision, and predictive ability of our model.

Predictions of Blue Catfish population dynamics and their effects on native species of Chesapeake Bay subestuaries must take into account the role of local conditions such as food availability, density dependence, and invasion history on the resulting dynamics. Given our findings, the removal of adult or juvenile Blue Catfish from local populations will likely be somewhat offset by a reciprocal increase in the growth rates of juvenile fish, as has been demonstrated for the Flathead Catfish *Pylodictis olivaris* (Bonvecchio et al. 2011), suggesting that high levels of removal might be needed to control population biomass. Yet, the required level of harvest is currently unknown and needs directed research (Fabrizio et al. 2018). Targeted harvests from known nursery areas could be beneficial toward efforts to disrupt the recruitment of this species.

ACKNOWLEDGMENTS

We thank the past and present members of the Virginia Institute of Marine Science Juvenile Fish Trawl Survey for collecting the fish samples and temperature data, and the Virginia Estuarine and Coastal Observing System staff for generously providing additional temperature data. Thanks also to Manisha Pant, Patrick Kilduff, Troy Tuckey, and Kevin Weng for thoughtful discussions and comments on earlier drafts of the manuscript. This manuscript benefitted from the comments and suggestions of two anonymous reviewers and the associate editor. V. Nepal was supported by a research fellowship from Virginia Sea Grant, and the trawl survey was funded by the Virginia Marine Resources Commission and the U.S. Fish and Wildlife Service. There is no conflict of interest declared in this article.

ORCID

Vaskar Nepal  <https://orcid.org/0000-0001-9155-7768>

Mary C. Fabrizio  <https://orcid.org/0000-0002-6115-5490>

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