Phenotypic plasticity in life-history characteristics of invasive blue catfish, *Ictalurus furcatus*

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ABSTRACT

Blue catfish, *Ictalurus furcatus*, are an invasive species in the Chesapeake Bay region, where they negatively impact native species of ecological, economic and cultural value. Management of blue catfish is, however, hindered by a lack of information on their population dynamics. We studied decadal changes in growth and body condition and made inferences about maturity schedules of blue catfish in two Chesapeake Bay subestuaries (James and York rivers). Specifically, we quantified the dynamic responses of these populations to biotic and abiotic characteristics experienced by fish during two stages of invasion (1998−2000 or "early" period and 2015−2017 or "recent" period). In general, somatic growth rate, body condition and reproductive allocation were greater in the early, less dense populations, which also exhibited larger mean size-at-maturity. We observed sexual dimorphism in growth patterns where males reached larger asymptotic sizes than females in both rivers. Such sex-specific and density-dependent responses in life-history characteristics provide information critical for the development of quantitative models and deployment of effective management plans. Our results highlight the need for management plans to consider dynamic feedback mechanisms: efforts to decrease population density may diminish the negative impacts of blue catfish on native species, but this will be offset by increased growth rates and higher reproductive output.

1. Introduction

Fisheries managers directly rely on population metrics such as length-at-age, age-at-maturity and body condition to optimize management strategies (Hilborn and Walters, 1992). Traditional fisheries management approaches consider these metrics as time-invariant; but there is increasing recognition that spatiotemporal differences in these characteristics can be substantial (Lorenzen, 2016). Changes in resource availability, temperature or density often engender concomitant changes in growth rates and maturation schedules of fishes (Enberg et al., 2012; Masson et al., 2016). Such changes are particularly relevant for non-native species because they experience novel and dynamic environmental conditions as they pass through different stages of invasion.

During establishment, an opportunistic life-history strategy (*sensu* Winemiller and Rose, 1992) promotes the survival of an invasive species (Hutchings, 1993; Olden et al., 2006; Fox et al., 2007). An opportunistic life-history strategy is characterized by rapid growth (especially in juveniles), early maturation and a high reproductive investment. As the invasive species establishes, resources may become limiting due to an increase in inter- and intra-specific competition. Under such conditions of density dependence, the traits most favorable for survival include slow growth, late maturation and low reproductive investment that are typical of the equilibrium life-history strategy (Winemiller and Rose, 1992; Hutchings, 1993; Fox et al., 2007). The ability of an organism to adapt its life-history characteristics in response to environmental conditions such as food supply, temperature and population density is termed phenotypic plasticity (Lorenzen, 2016). High levels of phenotypic plasticity of life-history traits enable invasive species to maximize their fitness in new habitats (Sakai et al., 2001). Potentially high phenotypic plasticity in invasive species necessitates that management plans for such species consider plasticity in key life-history characteristics for optimal and adaptive management of these fishes.

Management of invasive blue catfish, *Ictalurus furcatus*, in Chesapeake Bay could greatly benefit from knowledge of spatio-temporal differences in growth and condition dynamics of the fish. Blue catfish is a freshwater fish native to the Mississippi, Missouri and Ohio river basins throughout the central and southern United States (Graham et al., 1999). Because of their fame as a recreationally and

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commercially important species in their native range, blue catfish have been introduced into river systems throughout the United States. During the 1970s and 1980s, blue catfish were introduced into the tidal freshwater regions of the Rappahannock, York and James rivers in the Chesapeake Bay (Schloesser et al., 2011). Since then, blue catfish population densities and range have increased throughout the riverine and estuarine areas of the Chesapeake Bay (Schloesser et al., 2011; Fabrizio et al., 2018; Nepal and Fabrizio, 2019). Blue catfish have now been reported from all major Chesapeake Bay subestuaries (Nepal and Fabrizio, 2019) from salinities as high as 21.8 practical salinity units (psu; Fabrizio et al., 2018). Blue catfish support a nationally-acclaimed trophy fishery as well as a burgeoning commercial fishery in the region; resource managers are, however, concerned about the negative impacts of blue catfish on species such as blue crab, *Callinectes sapidus*, river herring, *Alosa* sp., American eel, *Anguilla rostrata* and Atlantic sturgeon, *Acipenser oxyrhynchus* (Schloesser et al., 2011; ICTF, 2014; Schmitt et al., 2019). Blue catfish are now considered an invasive species in the Chesapeake Bay region, and coordinated management will be undoubtedly necessary to minimize their ecological and economic harm (ICTF, 2014). The development of management plans has, however, been hindered by a poor understanding of their population dynamics.

Biological data on length, weight and age are key components of population and ecosystem models that inform management of fish stocks. Many researchers have studied growth of blue catfish in both the native and non-native ranges, but most of these studies are based on a narrow range of ages (e.g., Connelly, 2001; Greenlee and Lim, 2011; Latour et al., 2013) and lack information on sex-specific differences (e.g., Hilling et al., 2018). Information regarding body condition and estimated time to sexual maturity is limited. Yet, these population characteristics directly contribute to the relative abundance, distribution and ecological impacts of the fish. For example, larger and more robust (i.e., higher body condition) individuals of blue catfish have a greater salinity tolerance than smaller, less robust fish (Nepal and Fabrizio, 2019). Individuals with rapid growth rates will therefore contribute disproportionately to dispersal, colonization and range expansion of the species. The situation is analogous to that of European anchovy, *Engraulis encrasicolus*, where individuals with higher body conditions are better prepared for migration and better able to migrate to more suitable winter habitats (Shulman, 2002).

Our objective was to assess plasticity in life-history traits of blue catfish across two stages of invasion in two tidal rivers of Virginia, United States. Blue catfish populations in the James and York rivers differ in several ways (Table 1). For example, blue catfish were introduced earlier into the James River (1973–1977) than the York River (1985) at different stocking densities (Higgins, 2006). The relative abundance and recruitment of blue catfish remain greater in the James River (Greenlee and Lim, 2011; Tuckey and Fabrizio, 2018), potentially due to inter-population differences in growth rates, body condition, and time to maturity. We examined the variability in growth patterns and life-history traits during two decades in the James and York rivers. We hypothesized that older, established populations will have lower mean

somatic condition and growth rate, but greater age-at-maturity owing to higher density and intra-specific competition compared with the more recently established populations (Masson et al., 2016). We thus, sought to provide critical information for the formulation of population and ecosystem models needed to develop management strategies for blue catfish in the Chesapeake Bay region.

2. Methods

2.1. Specimen collection

We examined blue catfish from the James and York rivers (Fig. 1) and from two periods (1998 − 2000 or "early" period and 2015 − 2017 or "recent" period). These two periods were chosen because they represent different stages of blue catfish invasion and because relevant data were available from these periods. Fish from the early period provided data on sex, fork length (FL), weight and age of fish. During the early period, 364 blue catfish (290 from the James and 74 from the York) were collected using Virginia Institute of Marine Science Juvenile Fish Trawl Survey (hereafter, "VIMS Trawl Survey"). We also collected samples opportunistically from the VIMS Striped Bass Seine Survey, anchor gillnets, and the Virginia Department of Game and Inland Fisheries (VDGIF) Electrofishing Survey (Connelly, 2001).

In the recent period, we collected data from 1726 blue catfish from the James and York rivers. Most fish were collected with the help of a commercial fisher using low frequency DC electrofishing technique at salinities < 5 psu. We also obtained fish from the VDGIF Electrofishing Survey and VIMS Trawl Survey during April and May when the commercial fisher did not operate. Our goal was to obtain random samples of blue catfish from the James and York rivers. We measured fork lengths (FL) to the nearest mm and fish mass to the nearest 0.1 g. We identified sex of each fish by macroscopic examination of the gonads, although sex could not be determined or was not recorded for 16.6% of the fish. All collection, fish handling, and euthanasia procedures followed institution-approved protocols. During the recent period, we followed William & Mary Institutional Animal Care and Use Committee (IACUC) protocol # IACUC-2015-06-15-10382-mcfabr; the IACUC did not exist at William & Mary during the early period.

2.2. Age estimation

We removed lapillus otoliths, which were then dried and stored in labelled plastic vials. We sectioned the left otolith perpendicular to the longitudinal axis to obtain a thin (~ 0.5 mm) section through the nucleus. These were mounted on a glass slide using CrystalBond™, and sanded on 320-grit sandpaper until the annuli were clearly visible (Latour et al., 2013). The section was then covered with a thin layer of CrystalBond™ to further increase clarity. Processed lapilli were read independently by two readers using a stereomicroscope. The total number of dark bands (annuli) represented the estimated age (in years) of each individual. Because annuli form during May–July in blue catfish

Table 1

Period-specific characteristics of James and York rivers, demonstrating the history of blue catfish introduction and relevant environmental conditions. For characteristics that do not change between the periods, values are provided in only one column. USGS NWIS = United Stated Geological Survey National Water Information System; VECOS = Virginia Estuarine and Coastal Observing System.

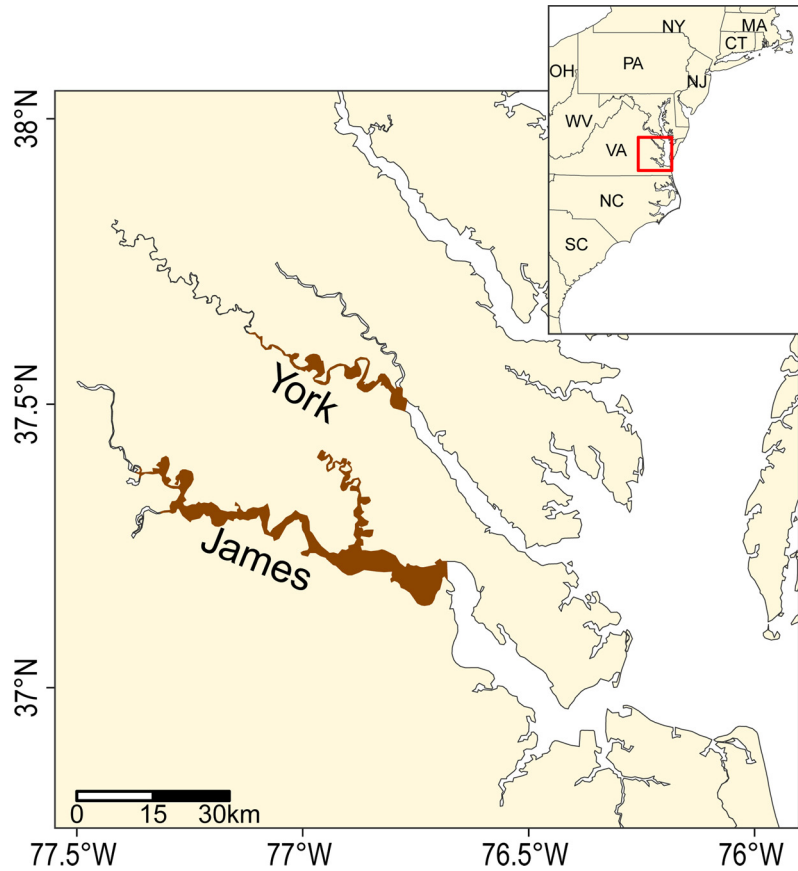|	Early (1998 − 2000)		Recent (2015 − 2017)		Source
	James	York	James	York	
Founder population size	115,614	1850			Table 1 in Higgins (2006)
Inbreeding coefficient F	0.22	0.27			Table 4 in Higgins (2006)
Mean annual discharge (m³ s⁻¹)	193.5	30.7			Data from USGS NWIS website
Years since initial introduction	23 − 25	13 − 15	40 − 43	30 − 33	Table 1 in Higgins (2006)
Mean chlorophyll a (μg l⁻¹)	21.7	6.5	16.1	5.5	Annual mean, data from VECOS
Mean relative density	23.8	0.01	43.4	4.4	Random Stratified Index; data from Tuckey and Fabrizio (2018)

Fig. 1. Map of blue catfish collection locations (dark shaded region) in the tidal James and York rivers during early (1998–2000) and recent (2015-2017) periods.

(Connelly, 2001), we adjusted the age of the fish based on the date of capture. For instance, if we captured the fish between July and December, we assigned an age equal to the number of dark bands. But if we captured the fish between January and June, we assigned an age equal to the number of bands if the edge of the otolith was dark (i.e., annulus for that year was forming or had formed by the time of capture), or the number of bands plus one if a dark band was absent from the edge (i.e., the specimen was captured prior to annulus formation for that year). If the two readers did not agree on the age of an individual, the readers aged the otolith together to arrive at a consensus. Otoliths were discarded if the readers could not reach a consensus (6.06% of the total cases). Our age estimation protocol was consistent between the two periods.

We checked for systematic differences in assigned ages between the two readers using a modified age-bias plot (Ogle et al., 2019) and the McNemar test of symmetry (Hoenig et al., 1995). We assessed the precision of the ages between the readers using the average coefficient of variation (ACV, Chang, 1982).

$$ACV = \frac{\sum_{j=1}^{n} \frac{s_j}{\bar{x}_j}}{n} \times 100 \tag{1}$$

where s_j is the standard deviation of the age estimates for the jth fish, $\bar{x}_j$ is the mean age for the jth fish, and n is the number of aged fish in the sample. We considered an ACV $< 5\%$ to be acceptable.

2.3. Size- and age-at-maturity

To estimate the size- and age-at-maturity from the length-at-age data, we used Lester's biphasic growth model (LM, Lester et al., 2004; Quince et al., 2008). The basic form of the LM assumes that immature growth is linear because surplus energy (i.e., the energy beyond that

needed for homeostasis) is invested solely in somatic growth. Mature growth is assumed to be asymptotic because energy is invested in both somatic growth and reproduction. We contend that LM is suitable for addressing questions related to life-history strategies and phenotypic plasticity because it is grounded in life-history theory. It also allows estimation of life-history traits such as juvenile growth rate, length-at-maturity, asymptotic length, natural mortality rate and the cost to somatic growth of maturity (Quince et al., 2008).

In LM, the length at age t (l_t) is given by

$$l_t = l_0 + ht, \ t \leq T \ \text{for juveniles} \tag{2}$$

$$l_t = l_\infty (1 - e^{-k(t-t_0)}), \ t > T \ \text{for adults} \tag{3}$$

where l_0 is the theoretical length at age 0 (mm), h is the somatic growth rate (mm y^{-1}), T is the LM parameter for age at maturity (y), l_∞ is the asymptotic length (mm), k is the von Bertalanffy (VB) growth coefficient (y^{-1}), and t_0 is the hypothetical age at length 0 based on the VB growth curve for adults (y). These quantities are related to t_1, the hypothetical age at length 0 for immature fish (y), and g (the cost to somatic growth of maturity) as:

$$h = -\frac{l_0}{t_1} = \frac{g l_\infty}{3} \tag{4}$$

$$k = \ln\left(1 + \frac{g}{3}\right) \tag{5}$$

$$t_0 = T + \ln\left(1 - \frac{g(T - t_1)}{3}\right) \Big/ \ln\left(1 + \frac{g}{3}\right) \tag{6}$$

We used a likelihood-based approach to infer age- and length-at-maturity from LM for blue catfish following Honsey et al. (2017). In brief, we fitted LM on length-at-age data with age-at-maturity (T) allowed to vary between two and 10 years in increments of 0.1 year (i.e.,

81 models corresponding to 81 potential values of T for each population). For each of the 81 models, we maximized the model likelihood using the optim function in R version 3.6.0 (R Core Team, 2019). For each river, we selected the most parsimonious model, which was the one that resulted in the highest maximum likelihood among the 81 alternative models. LM parameter estimates for each river were based on the final (selected) model. Following Honsey et al. (2017), we assessed the goodness of model fit based on the shape of the likelihood profile: a good fit has a single likelihood peak and a likelihood interval ≤ 2 y. We also calculated precision in length at age for each population because precision can affect the goodness of fit of the LM models (Honsey et al., 2017). Precision was calculated as the average of the inverse of the coefficient of variation in length at each age across all ages, weighted by sample size at age.

We used bootstrap techniques to estimate 95% confidence intervals for each parameter (Efron and Tibshirani, 1993). Specifically, we obtained 1000 bootstrap resamples, and estimated LM parameters for each resample. Lower and upper confidence limits for each parameter were estimated as the 2.5th and 97.5th percentile of the 1000 estimates for the parameter. We calculated bootstrap-based two-tailed p-values to compare statistically the parameter estimates between populations (Efron and Tibshirani, 1993). We followed the standard approach of fitting LM only on female blue catfish because increased investment of energy into reproduction after maturity is reasonable for females but not for males (Ward et al., 2017; Honsey et al., 2017). In addition, the "early" period had a low sample size and the model did not fit well. We therefore fit the LM only for observations from the "recent" period.

Model fit was validated by comparing LM model estimates with empirical estimates based on observation of gonads by Perry and Carver (1977), who report the maturity status (mature or immature) along with the size bins of fish (bin width = 50 mm total length (TL)) for female blue catfish in southwest Louisiana. We modeled the effect of size on maturity status of the fish using a logistic regression:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \mu + \beta TL \tag{7}$$

where p_i is the probability of fish i being mature, $\ln\left(\frac{p_i}{1-p_i}\right)$ is the log-odds of being mature, μ is the overall mean log-odds of being mature, β is the regression coefficient, and TL is the mean of the corresponding length class. We used the logistic regression model to estimate the mean size-at-maturity (l_{50}) for the population. For accurate comparison with the l_{50} estimate from the LM model, we converted the l_{50} estimate from the logistic regression from TL (cm) to FL (cm) using the equation FL = $-3.944 + 0.862TL + 7.933 \times 10^{-5}TL^2$. This equation was based on FL and TL data from 659 blue catfish collected from Chesapeake Bay during 2015−2017 (V. Nepal and M. Fabrizio, unpublished data). Perry and Carver (1977) did not age the fish used for maturity analysis, but estimated the age-at-maturity for female blue catfish to be ~ 5 y based on visual examination of length frequency distributions. Maturation schedules of blue catfish are not yet available from the James and York rivers.

2.4. Growth in the recent period (2015−2017)

Most published reports on growth of blue catfish (and other fishes, in general) use VB growth function to characterize length-at-age throughout the observed age range (e.g., Marshall et al., 2009; Hilling et al., 2018). In contrast, the LM we described in the previous section considers VB growth only for mature female fish. We also modeled length-at-age during the recent period with the VB model to allow direct comparisons with previous studies and to explicitly characterize sexual dimorphism in growth of blue catfish. We did not fit the VB growth model to observations from the early period because of poor model fit, stemming from the fact that few individuals were greater than 12 years old (Connelly, 2001). As a result, we could not estimate

l_∞ or k.

The basic formulation of the VB growth equation, presented in Eq. (3), was modified in two ways. First, we applied Eq. (3) to the entire age range for both sexes, instead of just the mature female fish. Second, we used a multiplicative error structure to account for higher variation in FL at older ages and to aid model fitting (Kimura, 2008). We used non-linear regression with river (York and James) and sex (male and female) as covariates in the VB growth model following the approach outlined by Kimura (2008). The length-at-age model included two dummy variables, s_i and r_i, indicating sex and river of origin of fish i:

$$l_{ti} = (\beta_{0l_\infty} + s_i\beta_{1l_\infty} + r_i\beta_{2l_\infty})(1 - e^{-(\beta_{0k}+s_i\beta_{1k}+r_i\beta_{2k})(t_i-(\beta_{0t_0}+s_i\beta_{1t_0}+r_i\beta_{2t_0}))}) \tag{8}$$

where $s_i = 0$ for females and $s_i = 1$ for males, and $r_i = 0$ for James River and $r_i = 1$ for York River. We estimated the 95% confidence interval for all model parameters by bootstrapping the residuals 1000 times (Efron and Tibshirani, 1993). River- and sex-specific differences in VB parameters were assessed by calculating bootstrap-based p-values as described previously.

2.5. Immature growth rate

To assess spatiotemporal differences in the growth rates of blue catfish, we compared growth of immature blue catfish between the two rivers and the two periods using a growing degree-day (GDD) model because river- and period-specific differences in growth rate may be influenced by differences in temperature (Nepal and Fabrizio, 2020). We controlled for the effects of temperature on the size of immature blue catfish (≤ 4 y old; see results below) using the GDD approach, which is based on the idea that temperatures above a minimum threshold are conducive to growth of ectotherms, including fishes (Neuheimer and Taggart, 2007). As an index of thermal energy, GDD is known to influence growth rates in fishes (Neuheimer and Taggart, 2007; Venturelli et al., 2010). Note from Section 2.3 that LM yielded immature growth rates for blue catfish during the recent period only, and from Section 2.4 that the growth coefficient k in the VB growth models does not represent the growth rate, but rather the rate of approaching l_∞ (Hilborn and Walters, 1992). We used June 1 of the first year of life as the first day of GDD accumulation for all individuals because of the absence of hatch-date information and because June 1 is the peak of blue catfish spawning in Virginia waters (V. Nepal and M. Fabrizio, unpublished data). Because GDD represents the cumulative thermal energy experienced by an individual over its lifetime, GDD was calculated up to the day of capture for each fish. Therefore, number of GDDs accumulated by fish i was calculated as:

$$GDD_i = \sum_{t=1}^{N} \overline{T}_{ti} - T_b, \ \overline{T}_{ti} > T_b \tag{9}$$

where N is the number of days between June 1 of first year of life ($t = 1$) and the day of capture for fish i, $\overline{T}_{ti}$ is the mean temperature experienced by fish i on day t, and T_b is the base temperature below which growth ceases. We used T_b of 9°C as reported for blue catfish in the Chesapeake Bay region (Nepal and Fabrizio, 2020).

We compared the immature growth rate of blue catfish during the two periods using a generalized least squares model of the form

$$L_{irp} = \mu + River_r + Period_p + \beta GDD + \varepsilon_{irp} \tag{10}$$

where L_{irp} is the FL of fish i in river r during period p, μ is the overall mean FL, $River_r$ and $Period_p$ are the fixed effects of river and period respectively, β is the regression coefficient for GDD, and ε_{irp} is the random unexplained error. We also included two-way interactions of GDD with river and period in the model. We did not include sex of the fish in the model because (1) we did not have this information for many fish, and (2) graphical analysis showed that growth rates of immature males and immature females were similar. For immature fish, all energy in excess of that needed for homeostasis is channeled into growth, not

reproduction, regardless of the sex of the fish (Lester et al., 2004). We initially considered including an index of relative abundance as a covariate to assess the effect of conspecific density on growth of blue catfish. We could not, however, include this variable in the model because relative abundance was confounded with period and river (Table 1). Graphical analysis showed increasing variance in FL (i.e., heteroscedasticity) with GDD. In addition, the heteroscedasticity was greater in the York River compared with the James River. We therefore explicitly modeled the heteroscedasticity in FL using a variance function of the type "constant plus power," which allows variance in each river to increase as a power function of the covariate GDD (Pinheiro and Bates, 2000). Analysis of residuals showed that this variance function was appropriate.

2.6. Body condition

We used fish body condition to assess spatiotemporal differences in health of individual blue catfish in the Chesapeake Bay region. Specifically, we calculated the scaled mass index (SMI; Peig and Green, 2009) as a morphometric index of body condition. We chose SMI as the measure of body condition for two reasons. First, SMI has been shown to be one of the most accurate morphometric indices of body condition in fishes (Wuenschel et al., 2018). Second, unlike most morphometric indices of body condition, the scaling relationship used in the SMI approach acknowledges that natural variability due to growth affects both weight and length. It thus acknowledges that there may be measurement error not only in weight but also in length (Peig and Green, 2009).

SMI of fish i was calculated as

$$\hat{SMI}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

(11)

where M_i and L_i are respectively the body mass and FL of fish i; b_{SMA} is the scaling exponent estimated by the standardized major axis (SMA) regression of M on L; L_0 is an arbitrary L to which all individuals of blue catfish are standardized; and $\hat{SMI}_i$ is the predicted eviscerated body mass for individual i when FL is standardized to L_0. We used median FL (420 mm) as L_0, and report this value to allow comparison among studies. We used the two-step procedure suggested by Peig and Green (2009) to compute b_{SMA}. First, we identified and subsequently removed strong outliers based on a bivariate plot of M and L ($n = 6$; 0.3% of the total observations). Second, we fit an SMA regression to log-transformed M and L values to obtain b_{SMA}, which is the slope of the regression. The SMA regression approach acknowledges the natural and measurement variability in both M and L, and is therefore preferred over ordinary least-squares approaches (Peig and Green, 2009). Because the size range of fish differed between periods, we restricted SMI calculation to fish between 110 and 765 mm to allow comparisons between periods.

We modeled the effects of river, sampling period and sex of fish on mean SMI using a linear mixed model:

$$SMI_{irpsm} = \mu + River_r + Period_p + Sex_s + s(FL) + Month_m + \varepsilon_{irpsm}$$

(12)

where SMI_{irpsm} is the SMI of the ith blue catfish from the rth river, pth period, sth sex and mth month, μ is the overall population mean of the response variable SMI, $River_r$, $Period_p$ and Sex_s are the fixed effects of river, period and sex respectively, $Month_m$ is the random effect of month, and ε_{irpsm} is the random unexplained error. Preliminary graphical analysis showed that SMI changed in a slightly non-linear fashion with FL. This violates a key requirement for a condition index, that a condition index should not covary with body size (Peig and Green, 2009). We therefore detrended SMI across FL to control for the effect of period-specific differences in FL distributions. As such, our model included FL as a cubic B-spline function with three degrees of freedom, represented as $s(FL)$ in Eq. (12). Graphical analyses showed

that the spline function was adequate in detrending SMI across the FL distribution. We included the random effect of month in the model to account for potential seasonal differences in body condition, particularly for females as a result of gonadal development during spring and summer in preparation for spawning. We also considered two- and three-way interactions among river, period and sex in the model. To assess whether the random effect of month was important in the model, we compared the mixed model (Eq. (12)) with a reduced linear model without the random effect using a simulation-based likelihood ratio test. As with the model for immature growth rates (Eq. (10)), we did not include mean annual abundance index as a predictor variable because abundance indices were confounded with river and period. We did, however, calculate Pearson's correlation between the predicted mean SMI and abundance index based on the VIMS Trawl Survey to assess whether mean SMI was lower in rivers or periods with higher blue catfish densities.

We performed all statistical analyses in R version 3.6.0 using packages FSA version 0.8.4 for ageing bias and precision analysis (Ogle et al., 2019), nlme version 3.1–137 for generalized least squares model (Pinheiro and Bates, 2000), smatr version 3.4–8 for SMA regression (Warton et al., 2012) and lme4 version 1.1–21 for linear mixed-effects models (Bates et al., 2015). Generalized least squares models and linear mixed-effects models were fitted using the restricted maximum likelihood approach.

3. Results

3.1. Sample characteristics

During the early period, blue catfish FL ranged between 28 and 938 mm, body mass between 78.6 and 19,750 g and age estimates between 0 and 15 y. In contrast, in the recent period, blue catfish were slightly larger (35 and 1125 mm FL), had a more variable body mass (15.9 and 29,610 g) and attained older ages (0 and 29 y). Of the 1726 blue catfish from the recent period that were aged by two readers, 87.6% ($n = 1512$) of the otolith readings agreed, and an additional 11.0% ($n = 189$) agreed within one year (Fig. 2). The ACV was 1.2%, and there was no systematic bias in ageing between the two readers (McNemar's $\chi_1^2 = 0.92$; $p = 0.34$). Graphical analysis also showed that the coefficient of variation was consistently less than 3.5% throughout the age or FL ranges.

3.2. Size- and age-at-maturity in the recent period

During the recent period, immature female blue catfish in the York River grew significantly faster ($h = 51.8$ mm y^{-1}; 95% Confidence
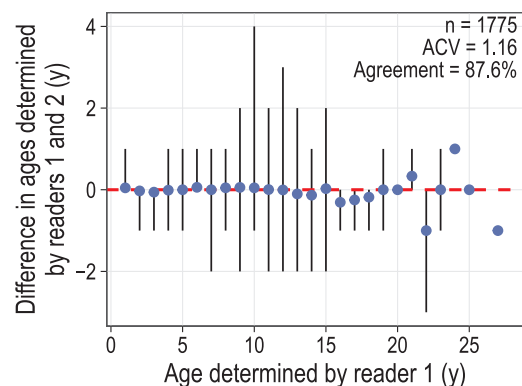

Fig. 2. A modified age-bias plot for blue catfish aged blindly by two readers. The dot indicates the mean difference in age estimates of the two readers, and the vertical line indicates the range of discrepancies. ACV is the average coefficient of variation.

Table 2
Primary and derived parameter estimates for Lester's biphasic growth model fitted on length-at-age data on female blue catfish in the James and York rivers during 2015–2017. Two-tailed p-values for difference in parameter estimates between York and James rivers are also provided.

Parameter	York	James	p
g	0.168	0.099	0.080
h	51.8	39.9	0.002
T	5.2	3.6	0.002
l_0	80.6	111.5	0.006
t_1	−1.6	−2.8	0.002
l_∞	924.1	1210.2	0.228
k	0.055	0.032	0.074
t_0	−3.5	−3.7	0.746
L_{50}	349.9	255.2	< 0.001
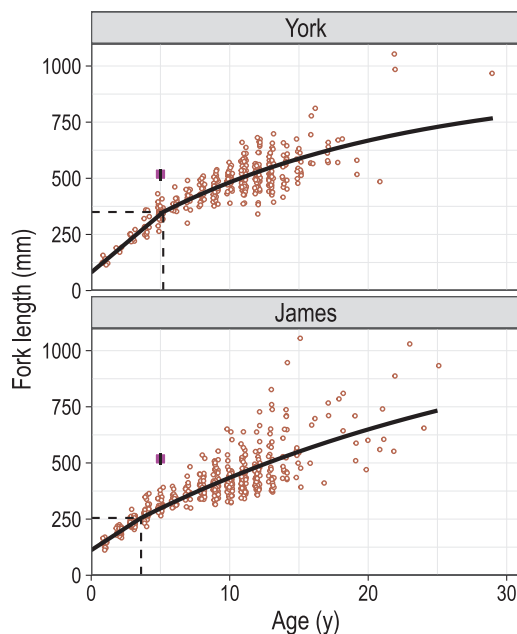
Fig. 3. Growth of female blue catfish from the James and York rivers, 2015–2017, based on Lester's biphasic growth model. Maturity occurs at the point of inflection, where the growth changes from linear to von Bertalanffy; the two stages are delineated in the graph by the horizontal and vertical dashed lines. Points are jittered to show detail. Purple square with the error bar shows the estimated mean length at maturity and corresponding 95% confidence interval for female blue catfish based on data from Perry and Carver (1977). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Limits [CI]: 45.8 and 58.8) than those in the James River (h = 39.9 mm y^{-1}; CI: 34.3 and 45.5; p = 0.002; Table 2). Fish in the York River also began allocating energy towards reproduction at a larger mean size (l_{50} = 350 mm FL; CI: 317 and 403) and greater mean age (T = 5.2 y; CI: 4.3 and 6.3) compared with those in the James River (l_{50} = 255 mm; CI: 228 and 278; p < 0.001; T = 3.6 y; CI: 3.0 and 4.1; p = 0.002; Table 2; Fig. 3). Note that these l_{50} estimates are lower than those reported for a Louisiana population (l_{50} = 518 mm FL; CI: 491 and 540); T estimate for the Louisiana population (5 y) is greater than that for James, but comparable to that for York river (Fig. 3). Further, fish in the York River allocated a marginally larger fraction of energy towards reproduction (York = 0.17; CI$_{York}$: 0.11 and 0.23; g $_{James}$ = 0.10; CI$_{James}$: 0.04 and 0.15; p = 0.08) but attained a mean asymptotic size ($l_{\infty York}$ = 924 mm; CI$_{York}$: 756 and 1267; $l_{\infty James}$ = 1210 mm; CI$_{James}$: 885 and 2440; p = 0.23) comparable to fish from the James River. Model fit was excellent for York River fish with a single likelihood peak that spanned < 2 y. The fit for James river fish was poorer with a single

Table 3
Parameter estimates for sex-specific von Bertalanffy growth curves for non-native blue catfish from two Virginia rivers during 2015–2017. For each parameter, p values for river-specific differences for each sex are given in the right column (p_{River}) and those for sex-specific differences within each river are given below the parameter estimates (p_{sex}).

Parameter	Sex	York	James	p_{River}
l_∞	Male	821.5	990.7	0.036
	Female	750.0	918.2	0.036
		p_{sex} = 0.002	p_{sex} = 0.002	
k	Male	0.092	0.049	< 0.001
	Female	0.093	0.05	< 0.001
		p_{sex} = 0.397	p_{sex} = 0.411	
t_0	Male	−0.9	−2.6	< 0.001
	Female	−1.2	−3.0	< 0.001
		p_{sex} = 0.002	p_{sex} = 0.002	

likelihood peak, but spanning 5 y. Precision estimates for length at age for the James and York River blue catfish were respectively 8.8 and 9.6.

3.3. Growth in the recent period

Blue catfish growth during 2015−2017 was characterized by the following equations:

$$FL = 990.7(1 − e^{−0.049(t+2.6)}) \text{ for males in the James River}$$

$$FL = 918.2(1 − e^{−0.050(t+3.0)}) \text{ for females in the James River}$$

$$FL = 821.5(1 − e^{−0.093(t+0.9)}) \text{ for males in the York River}$$

$$FL = 750.0(1 − e^{−0.093(t+1.2)}) \text{ for females in the York River}$$

Female asymptotic sizes were significantly smaller than those of males in both the James and York rivers (p_{James} = 0.002; p_{York} = 0.002) but females and males approached asymptotic sizes at comparable rates (p_{James} = 0.411; p_{York} = 0.397; Table 3). When comparing the blue catfish populations in the two rivers, fish in the York River reached smaller mean asymptotic sizes (p_{Male} = 0.036; p_{Female} = 0.036) but approached the asymptotic sizes significantly faster than those in the James River (p_{Male} < 0.001; p_{Female} < 0.001; Table 3; Fig. 4). Blue catfish growth in the Chesapeake Bay region is lower than those of most native and non-native populations examined to date (Fig. 5).

3.4. Immature growth

Immature blue catfish (estimated age $\leq$ 4 y) grew linearly with accumulation of GDD, but demonstrated period- and river-specific differences in growth rates (Fig. 6). During both periods, the mean size of newly hatched blue catfish in the James River (i.e., the intercept) was higher than that in the York River (p < 0.05; Fig. 6), in agreement with our LM results (Fig. 3). Immature blue catfish grew faster in the York River compared with the James River (GDD × River: Wald χ_1^2 = 41.6; p < 0.001). Within river, immature blue catfish grew faster during the early period than during the recent period (GDD × Period: Wald χ_1^2 = 17.6; p < 0.001; Fig. 6).

3.5. Body condition

SMI was highly variable and ranged between 618.2 and 1652.5 g for a 420 mm fish. Sex, river and period had interactive effects on mean SMI of blue catfish (sex × river × period: $F_{1,1742.55}$ = 5.06; p = 0.025). In general, fish in the recent period had lower mean body condition (i.e., lower SMI) compared with the early period. The decline in body condition through time was, however, particularly evident for male blue catfish in the York River (Fig. 7). Interestingly, mean SMIs were similar for males and females in both rivers during both periods, except for the York River during the early period, when females had
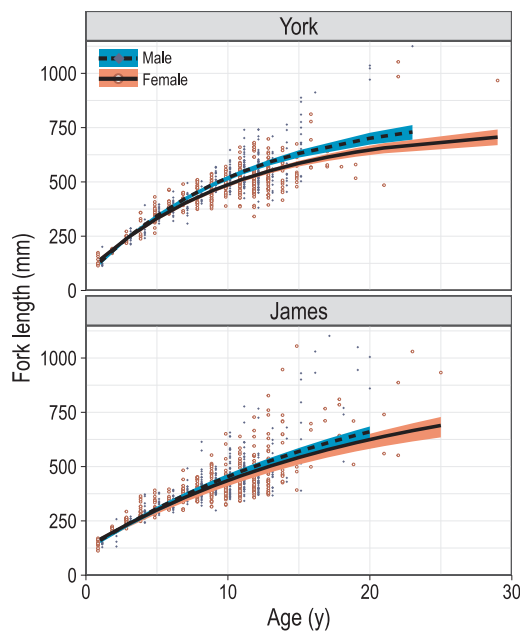
Fig. 4. von Bertalanffy growth curves for blue catfish from the James and York rivers, 2015–2017. Males are represented by blue diamonds and dashed lines, and females by empty red circles and solid lines. Shaded polygons around the predicted von Bertalanffy curves represent the 95% confidence bands. Points are slightly offset to show detail. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
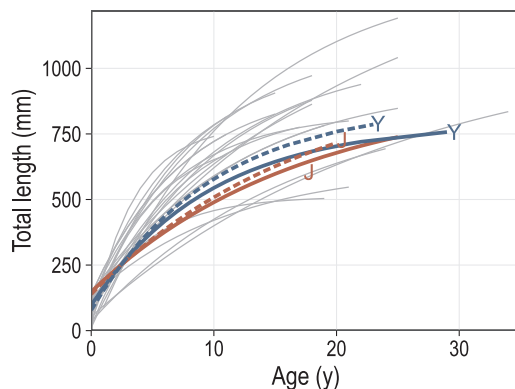

Fig. 5. von Bertalanffy growth curves for 19 blue catfish populations from native and non-native ranges (thin gray lines). Thicker lines show corresponding curves for male (dashed lines) and female (solid lines) blue catfish from the James (marked with "J", red) and York (marked with "Y", blue) rivers collected during 2015–2017. To allow valid comparisons with other populations, we show von Bertalanffy growth curves for James and York rivers based on total length (estimated based on fork length: TL = 2.477 + 1.169 × FL − 0.00012 × FL^2). Note, however, that the curves for the total length-age relationships provided here are for illustration purposes only and do not depict the equations given in the text, which are based on fork length. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

considerably lower mean SMI compared with males (Fig. 7). The likelihood ratio test comparing the mixed model with a reduced fixed-effect model was significant (χ^2 likelihood ratio = 65.86; $p < 0.001$), suggesting considerable intra-annual variation in SMI: mean SMI was higher than average during May and June, and lowest during February (Fig. 8). Mean SMI was negatively correlated with the relative abundance index, but the relationship was weak and not significant ($r = -0.37$; $t_{10} = -1.24$; $p = 0.24$).
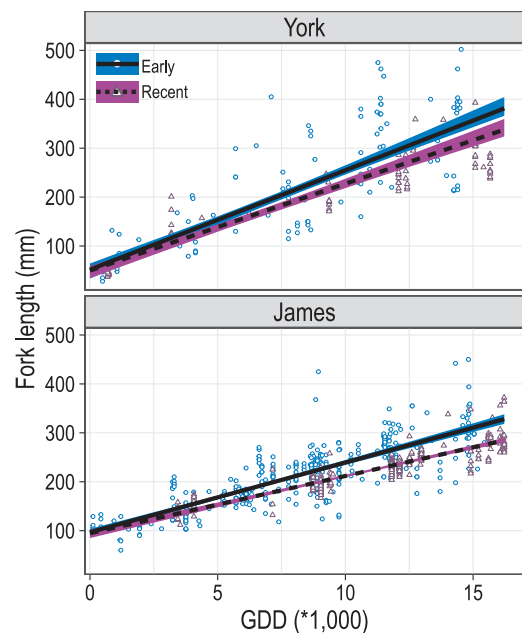
Fig. 6. Fork length as a function of cumulative growing degree days (GDD) for immature blue catfish (≤4 y) collected from the James and York rivers during early (blue circles and solid lines; 1998-2000) and recent (purple triangles and dashed lines; 2015–2017) periods. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
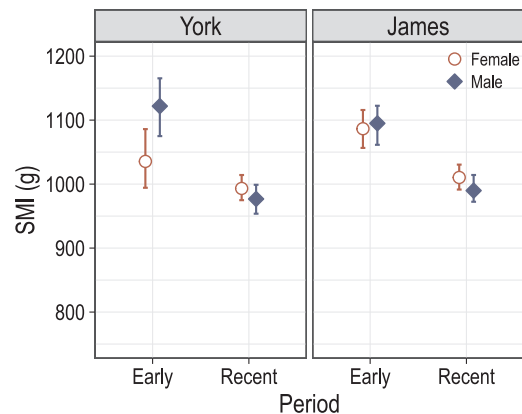
Fig. 7. Marginal mean scaled mass index (SMI, g) for a 420 mm FL blue catfish collected during early (1998-2000) and recent (2015-2017) periods from the James and York rivers. Females are represented by open red circles, and males by filled blue diamonds. Error bars represent 95% confidence intervals for the predicted SMI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Invasive populations of blue catfish in the James and York rivers demonstrated considerable plasticity in life-history characteristics during two decades. Populations established for longer periods (i.e., recent period and James River) generally exhibited higher densities, smaller size-at-maturity, slower growth rates and lower body condition. These results showcase the expected changes in vital rates that characterize the population dynamics of an invasive species during two stages of invasion (Bøhn et al., 2004; Masson et al., 2016). As such, they emphasize the need to consider sex-, population- and period-specific rates in the development of management strategies for invasive species (Lorenzen, 2016).
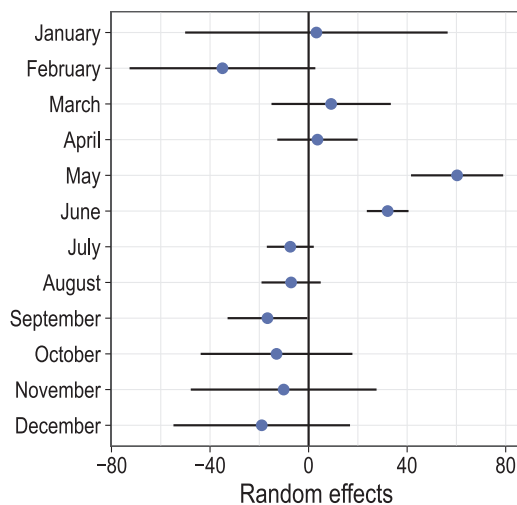
Fig. 8. Conditional modes and the corresponding 95% confidence intervals for the random effect of month in the linear mixed-effects model on scaled mass index of blue catfish in two rivers.

We observed a greater number (and proportion) of older fish in the recent period compared with the early period. Indeed, the maximum ages observed for blue catfish populations in the James and York rivers are higher than those reported for many other populations (Graham, 1999; Stewart et al., 2016). The presence of older fish allowed us to use the VB model as an appropriate representation of blue catfish growth in the Chesapeake Bay. Connelly (2001), Greenlee and Lim (2011) and Latour et al. (2013) fit linear growth models due to lack of older (> 15 y) individuals in their samples. Elsewhere, Homer et al. (2015) could not fit VB model for a non-native population of blue catfish in Georgia because the population lacked older, larger fish. Recently, Hilling et al. (2018) fit VB growth models to blue catfish populations in Virginia. Compared to the estimates by Hilling et al. (2018), who based their model on composite data collected between 2002–2016, our temporally explicit approach shows generally faster growth during the early period and slower growth in the recent period. Fish in the recent period also achieved smaller asymptotic sizes, further highlighting the need to consider plastic changes in growth dynamics when modeling this species. The growth patterns and VB growth parameters in our model were within the range reported from other populations throughout the native and non-native ranges (Graham, 1999; Stewart et al., 2016; Hilling et al., 2018). In general, the growth rates and mean asymptotic sizes of blue catfish from the James and York rivers during 2015−2017 are lower than many native populations, including that studied by Perry and Carver (1977), likely due to higher density dependence in the James and York rivers.

We observed a shift in life-history strategy from "opportunistic" to "equilibrium" (Winemiller and Rose, 1992), as blue catfish populations progressed through stages of invasion. Our findings are consistent with the predictions of life-history theory where individuals in established, more dense populations grow more slowly, mature at a smaller size, and allocate more energy towards reproduction (Bowen et al., 1991; Walters and Post, 1993). Similar results have been reported for other invasive fishes such as round goby, *Neogobius melanostomus* (Masson et al., 2016), vendace, *Coregonus albula* (Bøhn et al., 2004) and white perch, *Morone americana* (Feiner et al., 2012). Individuals in established populations would also be expected to mature later (e.g., Feiner et al., 2012; Masson et al., 2016), although we did not observe this. A reason for this might come from the relatively poor LM fit for the James River population. Somewhat low precision in length-at-age and low reproductive allocation for James River fish resulted in poorer model fits, as evidenced by large confidence intervals for the g and l_∞ parameters of the model. Honsey et al. (2017) found that their implementation of

LM was less accurate in predicting maturity in such scenarios. Gear selectivity is also likely to affect LM estimates, though the precise nature of the effects is not yet clear. We did not consider gear selectivity in our model, but future implementations of LM might benefit from incorporating gear selectivity.

Observed decreases in growth rates and body condition in the recent period reflect resource limitations and density-dependent effects. Similar results have been observed in invasive bigheaded carp, *Hypophthalmicthys* sp. (Coulter et al., 2018) and Indo-Pacific red lionfish, *Pterois volitans* (Dahl et al., 2019). Many other river-specific factors likely contributed to the observed plasticity in growth rates, maturation rates and body condition of blue catfish. Despite the higher primary productivity and low inbreeding in the James River population, fish grew slower than those in the York River. Moreover, the discrepancy in length-at-maturity between the Chesapeake Bay populations and the Louisiana population likely results from higher water temperature, lower density and considerably faster growth in the latter. This suggests that several spatiotemporally variable biotic and abiotic factors act together to determine the growth dynamics of fish; quantification of such dynamics for population assessment purposes needs to consider these plastic changes.

Declines in growth rate and body condition has mixed implications for management. The negative impacts on native fishes due to predation are likely to decrease because smaller blue catfish are less likely to prey upon other fishes (Schmitt et al., 2019). Further, smaller and less robust (i.e., lower body condition) individuals are less tolerant of elevated salinities than larger, more robust individuals (Nepal and Fabrizio, 2019). Therefore, dispersal, colonization and range expansion into high salinity habitats may decrease. Slower growth rates imply, however, that small individuals may accumulate higher concentrations of contaminants such as mercury and polychlorinated biphenyl (PCB; Luellen et al., 2018). High contaminant loads in small, but older fish will negatively impact raptors that prey on blue catfish, such as bald eagle, *Haliaeetus leucocephalus*, and osprey, *Pandion haliaetus*, (Viverette et al., 2007). High contaminant loads also have implications for the safe human consumption of blue catfish. Because smaller blue catfish feed at lower trophic levels (Schmitt et al., 2019), negative impacts due to competition may increase on some fishes (such as juvenile striped bass, *Morone saxatilis*, and Atlantic croaker, *Micropogonias undulatus*) and invertebrates (such as freshwater mussels and blue crabs).

Recreational and commercial harvests have been suggested as a management measure to ameliorate the negative impacts of blue catfish (Fabrizio et al., 2018). Our results show, however, that such declines may release the remaining individuals from density-dependent mechanisms currently suppressing individual growth rates. This will, in turn, cause compensatory changes in demographic characteristics including mean growth rates, body condition and age-at-maturity. These effects have been observed in other teleost fishes, but are most common among long-lived fishes with high fecundity (Rose et al., 2001). We argue that blue catfish will demonstrate such compensatory mechanisms because they are long-lived (maximum age > 25 y) and have relatively high fecundity for a nest-guarding species (> 40,000 eggs per fish for large individuals, V. Nepal and M. Fabrizio, unpublished data). Increased growth rates would also increase predation on native fishes because large blue catfish consume a high proportion of fishes (Schmitt et al., 2019). Our conclusions are bolstered by the observations of higher recruitment and earlier maturation in response to increased exploitation in flathead catfish, *Pylodictis olivaris* (Bonvechio et al., 2011), another non-native ictalurid catfish now present in the Chesapeake Bay region. These findings are also consistent with predictions from life-history theory that an increase in adult mortality rate due to exploitation will select for earlier age at maturity and higher reproductive investment (Lester et al., 2014).

Blue catfish from the James and York rivers show sexually dimorphic growth, where males grow faster and attain larger sizes, a pattern consistent with observations in a native population in Alabama

(Marshall et al., 2009). Because male blue catfish exhibit nest guarding behavior and provide parental care for eggs and fry (Graham, 1999), larger males have a reproductive advantage in aggressive confrontations. There would thus be a positive selection pressure towards larger males (Parker, 1992). Sexual dimorphism in growth of blue catfish has important management implications. Because harvest efforts typically remove larger individuals (> 500 mm), a larger proportion of males will be removed, thus allowing a large proportion of females to continue reproduction. Harvesting strategies that differentially remove larger male fish may enhance recruitment, at least until males become limiting. Management actions to successfully curtail the reproductive output of blue catfish will, therefore, need to ensure removal of a sufficient number of large females.

Our findings also bring to light avenues for future research. First, we assessed plasticity in age- and size-at-maturity based on Lester's model fitted to length-at-age data for female blue catfish. For increased accuracy and a more complete treatment, however, maturity schedules should be based on examination of gonads. Second, we did not explicitly study the size-at-age of blue catfish at different densities observed throughout the invasion history. A more thorough analysis should relate year-specific density to corresponding incremental growth of blue catfish during that year via mark-recapture techniques or otolith increment analysis (Lorenzen, 2016). Finally, future studies should expand the spatiotemporal domain of study; we focused on two subestuaries in two periods, the earlier of which encompassed a period 15–25 y after introduction. With documented range expansion of blue catfish throughout the Chesapeake Bay watershed (Nepal and Fabrizio, 2019), managers and conservation biologists would benefit from knowing the likely colonization pathways and characteristics of populations in newly invaded tributaries. Range expansions during wet seasons may lead to periodic supply of propagules and potentially the development of metapopulations, inducing novel spatiotemporal differences in population dynamics of invasive blue catfish populations in the Chesapeake Bay region.

Management plans for invasive species need to consider the sex-and population-specific life-history traits in a dynamic context. In other words, management plans need to take into account the phenotypic plasticity and compensatory feedbacks that are likely to occur in response to management actions. Towards this end, our findings provide baseline information needed for the development of management plans for blue catfish. Our findings also provide a template for expected changes in life-history strategies of blue catfish populations in more recently invaded systems in the Chesapeake Bay region (e.g., Nanticoke River) and elsewhere in the tidal rivers in Maryland, Pennsylvania and Delaware. With the expected range expansion of blue catfish in the Chesapeake Bay region over the next decades (Nepal and Fabrizio, 2019), vigilant monitoring and proactive management plans are crucial in determining the status and ultimately the impacts of this invasive species on the ecology of this region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Vaskar Nepal: Conceptualization, Data curation, Formal analysis, Visualization, Writing - original draft, Funding acquisition. **Mary C. Fabrizio:** Conceptualization, Supervision, Writing - review & editing, Funding acquisition, Resources. **William J. Connelly:** Data curation, Formal analysis.

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