

2021

Reproductive Characteristics Differ in Two Invasive Populations of Blue Catfish

Vaskar Nepal
Virginia Institute of Marine Science

Mary C. Fabrizio
Virginia Institute of Marine Science

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Aquaculture and Fisheries Commons](#)

Recommended Citation

Nepal, Vaskar and Fabrizio, Mary C., Reproductive Characteristics Differ in Two Invasive Populations of Blue Catfish (2021). *North American Journal of Fisheries Management*, 41((Special Issue 1)), S180-S194.
DOI: 10.1002/nafm.10611

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

SPECIAL ISSUE: CATFISH 2020—THE 3RD INTERNATIONAL CATFISH SYMPOSIUM

Reproductive Characteristics Differ in Two Invasive Populations of Blue Catfish

Vaskar Nepal*  and Mary C. Fabrizio 

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

Abstract

The management of invasive Blue Catfish *Ictalurus furcatus* in Chesapeake Bay tributaries is hindered by the lack of information on its reproductive biology, which is a key component of population models used to forecast abundance. We quantified and compared the reproductive traits of female Blue Catfish from two populations from the tidal reaches of the James and York River subestuaries during 2015–2017. In these systems, Blue Catfish matured between the ages of 6 and 10 years and spawned between May and July, with larger fish spawning earlier in the season. During spawning events, Blue Catfish produced 2,613–68,356 eggs, with larger and older fish producing more eggs. Fish in the more densely populated James River matured at a marginally older age but a significantly smaller size than fish in the York River, but James River fish allocated more energy to reproduction. Fish in the James River also had greater mean values of the gonadosomatic index, relative fecundity, egg organic content, and proportion of organic content in the eggs. Relative fecundity of Blue Catfish decreased with fish size, contrary to observations in most other fishes. Based on the observed variability in reproductive traits and the size dependence of relative fecundity, we recommend incorporation of population-specific reproductive rates into stock assessment models for invasive Blue Catfish.

The reproductive strategy and potential of a fish are important factors that influence the success of a species in a novel environment (Winemiller 2005; García-Berthou 2007). In such environments, the quantity and quality of propagules (i.e., eggs) may affect the dispersal and range expansion of species (Winemiller 2005). For example, fish egg size and quality are often positively related to survival of the offspring (Moran and McAlister 2009). Parental care of eggs and larvae also increases the probability of offspring survival (Stearns 1992; Winemiller and Rose 1992; Jørgensen et al. 2011). Similarly, characteristics such as a larger body size, high fecundity, a long spawning season, and a long reproductive life span increase the total number of eggs produced by a fish over its lifetime, thus increasing the potential individual fitness (Wootton and Smith 2015). Species that possess these characteristics are likely to be more successful invaders (Morris and Whitfield 2009; Lockwood et al. 2013; Liu et al. 2017).

One highly successful invasive species in the Chesapeake Bay region is the Blue Catfish *Ictalurus furcatus*

(Fabrizio et al. 2021, this special issue), the males of which guard nests. Native to large rivers in the Midwestern United States, the Blue Catfish is a large (>50 kg), long-lived (>25 years) freshwater fish that was introduced into Virginia tidal rivers of the Chesapeake Bay during the 1970s and 1980s to create a recreational fishery. Since then, the species' range has expanded and Blue Catfish now occupy many subestuaries of the Chesapeake Bay (Schloesser et al. 2011; Nepal and Fabrizio 2019). Populations in the Virginia tributaries, such as the James and York rivers, remain genetically distinct stocks with little mixing (Higgins 2006). Blue Catfish densities have also increased greatly in many systems throughout the Chesapeake Bay region (Schloesser et al. 2011; Tuckey and Fabrizio 2019) such that this species now supports commercial, recreational, and nationally recognized trophy fisheries in some subestuaries (Fabrizio et al. 2021). However, owing to the potential negative impacts of competition and predation on native species, such as White Catfish *Ameiurus catus*, river herring *Alosa* spp., blue crab

*Corresponding author: vaskarnepal@gmail.com
 Received February 10, 2020; accepted March 1, 2021

Callinectes sapidus, and native mussels (Schloesser et al. 2011; Schmitt et al. 2019), the Blue Catfish has become a significant nuisance species in many Atlantic slope estuaries. Unfortunately, Blue Catfish management in the Chesapeake Bay region is complicated by multiple conflicting objectives, including population control, maintenance of trophy and recreational fisheries, and expansion of commercial fisheries (Fabrizio et al. 2021). Stock assessment models are needed to optimize harvest strategies to meet these goals, yet the development of management plans is hindered by the lack of information on key population rates (ICTF 2014). Recently, progress has been made toward this end. Population size (Fabrizio et al. 2018), growth rate (Nepal et al. 2020; Hilling et al. 2021, this special issue), salinity tolerance (Nepal and Fabrizio 2019, 2020b), feeding ecology (Schloesser et al. 2011; Schmitt et al. 2019), and energetic demands (Nepal et al. 2021) of Blue Catfish are now known, at least for some populations in the Chesapeake Bay region.

Reproduction is a key process affecting subsequent population size, and reproductive rates are critical components of stock assessment models used to designate biological reference points and ultimately to set harvest policies. Some of the commonly used assessment models incorporate a stock–recruitment relationship and assume that the effective reproductive potential of a population is directly proportional to spawning stock biomass (Beverton and Holt 1957). Measurement error in reproductive potential, however, can obscure any stock–recruit relationship, negatively affecting the perception of a stock’s productivity. Two other assumptions of stock–recruitment models—that the proportion of females and relative fecundity (i.e., number of eggs per unit biomass) remain constant per unit biomass and over time—also do not hold for many exploited species (Marshall 2016). For example, in species with dimorphic growth, the proportion of females can change considerably over time and with age if the harvest is size selective. Relative fecundity is likewise known to be positively correlated with female condition (Lloret et al. 2013) and size in most species (Hixon et al. 2014). Use of spawning stock biomass as a proxy for total egg production, therefore, ignores the reproductive variability commonly observed among individuals and potentially leads to unreliable biological reference points and inappropriate fishery management actions (Lloret et al. 2013; Hixon et al. 2014; Marshall 2016). Total egg production, incorporating the effects of maternal age, size, and/or experience on offspring size and quality, is expected to provide a better foundation for stock–recruitment models in support of reliable harvesting strategies (Morgan 2008; Marshall 2016). Although stock assessments for Blue Catfish in the Chesapeake Bay are needed to inform management, the reproductive traits of Blue Catfish are poorly known

from both their native (Graham 1999) and nonnative (ICTF 2014) ranges.

In this paper, we provide a quantitative assessment of the reproductive potential and characteristics of Blue Catfish populations in the James and York River subestuaries of the Chesapeake Bay. In these tidal rivers, Blue Catfish demonstrate density-dependent growth, with faster somatic growth and greater body condition in the less densely populated York River compared with the James River (Nepal and Fabrizio 2020a; Nepal et al. 2020; Hilling et al. 2021); the York River also has a shorter invasion history compared with the James River. Density-dependent growth can affect lifetime fecundity via alterations in age and size at maturity or by modifying the proportion of energy allocated to reproduction (Winemiller 2005). This adaptive response to intraspecific competition—and, more generally, to the fish’s biotic and abiotic environments—can affect reproductive traits and output (Stearns 1992; Green 2008), which in turn can influence the invasion success of a species in novel environments (Winemiller 2005; García-Berthou 2007; Gutowsky and Fox 2012; Lockwood et al. 2013). If the reproductive biology of Blue Catfish varies between the two populations, then population and stock–recruit models for Blue Catfish populations must reflect these differences. Based on the predictions of life history theory (Stearns 1992; Ward et al. 2017), we expected to observe plasticity in reproductive traits: fish from the more densely populated James River were expected to show higher age at maturity, lower size at maturity, and a lower investment in reproductive tissues (e.g., egg size and egg quality) relative to fish from the York River. These variations in reproductive characteristics will ultimately affect the productivity of the two populations and will inform management strategy evaluations in support of Blue Catfish management in the Chesapeake Bay region.

METHODS

Sample collection.—All animal capture and handling procedures were approved by the Institutional Animal Care and Use Committee at William & Mary (protocols IACUC-2015-06-15-10382-mcfabr and IACUC-2017-05-22-12111-tdtuck). Blue Catfish were captured from the tidal portions of the James and York rivers during February–August 2015–2017 in habitats that ranged in salinity between 0‰ and 5‰ (Figure 1). These months were expected to encompass the prespawning and spawning seasons in these subestuaries (Graham 1999). The majority of fish were captured by a commercial fisher using a low-frequency DC electrofishing system. Because the commercial fisher did not operate before June of each year, we supplemented our samples during April and May with fish

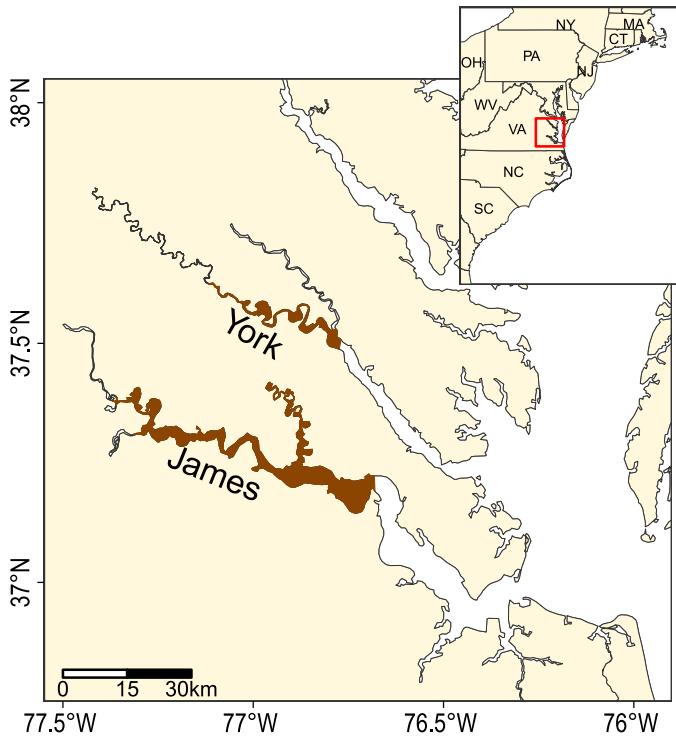


FIGURE 1. Sampling locations for Blue Catfish from the James and York River subestuaries of the Chesapeake Bay. Dark polygons represent Blue Catfish capture locations during 2015–2017.

collected by the Virginia Department of Wildlife Resources' Electrofishing Survey and the Virginia Institute of Marine Science (VIMS) Juvenile Fish Trawl Survey (hereafter, VIMS Trawl Survey). We took care to ensure random sampling of Blue Catfish across broad spatial areas throughout the tidal James and York rivers (Figure 1). Fish were usually collected weekly, returned to VIMS on ice, and processed on the day of capture.

Blue Catfish were measured (mm FL) and weighed (g) individually. We determined sex of the fish by gross examination of the gonads: testes are thin and tubular in small males and lobate in larger males (Sneed and Clemens 1963), whereas paired ovaries are saccular (V. Nepal, personal observation). We also collected lapillus otoliths for aging, and we processed the left otolith to obtain a thin (~0.5-mm) section through the nucleus. The processed otoliths were read independently by two readers, and the number of dark bands (annuli) was recorded as the age (years) of the fish. When the readers did not agree on the age of an individual, the final age was determined by consensus. We disregarded samples for which consensus could not be reached.

Gonadosomatic index.—Both size at maturity and spawning season can be inferred accurately with gonadosomatic index (GSI; Schemmel et al. 2016). We removed

both ovaries from all females and weighed them together (to the nearest 0.01 g) to calculate the GSI ($\text{GSI} = [\text{ovary weight}/\text{fish weight}] \times 100$). We assessed size- and age-specific differences in the mean GSI of Blue Catfish among months and between populations by using generalized least-squares (GLS) models (Zuur et al. 2009). We modeled GSI as a function of month, population, and either FL or age. To determine whether the effect of size or age on GSI varied within the spawning season, we also included the $\text{FL} \times \text{month}$ or $\text{age} \times \text{month}$ interaction in the model (Table 1, models 1 and 2). Despite the covariation between size and age, both FL and age were considered because variability in size at age (Nepal et al. 2020) may result in different relationships between reproductive characteristics and either FL or age; therefore, this approach allowed us to quantify the relative strength of the two predictors (Green 2008). We used fish collected during June and July, as these were the only months when sufficient numbers of gravid females of comparable size and age ranges were available. Because preliminary graphical analysis of GSI data indicated that the variance differed between populations, we configured the GLS models to estimate population-specific GSI variances (Zuur et al. 2009).

Maturation rates.—We used the GSI approach developed by Fontoura et al. (2009) to assess maturity status. In this approach, females with a GSI greater than 5% of the maximum GSI are considered mature (Fontoura et al. 2009). When identifying mature females, care was taken to include only females that were captured between April 1 and June 1 because mature active females during this period had high GSI values (see results below). After spawning starts in late May, the GSI declines in some of the mature females due to egg deposition; hence, these females may be categorized incorrectly as immature (Fontoura et al. 2009). To evaluate the effect of designating the end of the prespawning season as June 1, we reclassified fish by using May 20 or June 10 as the end date. Because the results for these alternative dates were qualitatively similar to those obtained with the original June 1 date, we used June 1 as the end of the prespawning period for subsequent analyses.

We used logistic regression to develop maturity ogives for Blue Catfish from the James and York River subestuaries. Maturity status (mature or immature) based on GSI was modeled as a function of population (James or York River population) and FL or age using the binomial distribution and the logit link (Table 1, models 3 and 4). The resulting models were used to estimate the FL or age at which 50% of the fish are mature (hereafter, mean length or age at maturity). We used bootstrap sampling (2,000 bootstrap replicates; Efron and Tibshirani 1993) to estimate the 95% confidence limits (CLs) of the mean length at maturity and mean age at maturity for each population. We subsequently calculated the two-tailed *P*-value for the

difference in mean length at maturity for the two populations as twice the proportion of instances in which the length at maturity for York River fish was greater than that for James River fish (Efron and Tibshirani 1993). The P -value for the difference in mean age at maturity was similarly calculated as twice the proportion of instances in which the age at maturity for James River fish was greater than that for York River fish. We did not model age or size at maturity as functions of fish weight or body condition, as these varied at intrayear timescales.

Fecundity and lifetime fecundity modeling.—We estimated fecundity using the standard gravimetric method. We obtained and weighed three systematic subsamples (4–50% of total ovary weight) from the right ovary of gravid females that were sampled in 2015–2016. We used subsampling because the size and density of ova can vary within an ovary (West 1990). For fish collected in 2017, we subsampled only the middle portion of the right ovary. Ovarian sections were fixed in 10% buffered formalin for at least 72 h and were transferred to 70% ethanol. To estimate annual fecundity, we counted the number of eggs in each subsample and scaled up the number by the total weight of both ovaries:

$$\text{Fecundity} = \frac{\sum_i \left(\frac{o_i}{w_i} \right)}{n} \times W, \quad (1)$$

where o_i is the number of eggs in subsample i , w_i is the weight of subsample i , n is the number of subsamples, and W is the weight of both ovaries. Relative fecundity was calculated as the number of eggs per kilogram of body weight (i.e., relative fecundity = fecundity/wet weight).

We compared mean egg size from the anterior, middle, and posterior sections of the ovary to determine whether the number of eggs per gram of ovary varied among the three sections. We used a GLS model with mean egg diameter (mm) as the response and ovary section as the independent factor (Table 1, model 7). Because we measured egg size multiple times from the same fish, we fitted a model with a compound symmetric correlation structure among the three measurements: anterior, middle, and posterior (Zuur et al. 2009). In subsequent analyses of population-, age-, and size-specific effects on fecundity, we used mean egg diameters from the middle section of the ovary because we did not detect a statistical difference in mean egg diameters among the ovarian sections (see results below). Both fecundity and relative fecundity were modeled as additive functions of population and either FL or age by using generalized linear models with a gamma distribution and a log link (Table 1, models 5–8; Zuur et al. 2009).

We developed a simple quantitative model to assess the effects of population and fish size on the lifetime fecundity of female Blue Catfish. To do this, we chose to use the

fecundity–FL relationship (model 5) instead of the fecundity–age relationship (model 6) because the former relationship was more precise (as described below). Nonetheless, we estimated fecundity for ages 1–25 by using predicted mean lengths at age from von Bertalanffy growth curves (Nepal et al. 2020) and the size-specific maturation probability (Table 1, model 1) and size-specific fecundity relationship we describe here (Table 1, model 5). Growth models for Blue Catfish in 2015–2017 (from Nepal et al. 2020) are

$$\text{FL} = 918.2 \times [1 - e^{-0.050 \times (\text{age} + 3.0)}] \text{ for James River females} \quad (2)$$

and

$$\text{FL} = 750.0 \times [1 - e^{-0.093 \times (\text{age} + 1.2)}] \text{ for York River females.} \quad (3)$$

For each age-class, we first calculated the mean FL at age and subsequently calculated the fecundity based on the fecundity–FL relationship. Estimated fecundity was multiplied by the corresponding population-specific maturation probability to reflect differences in the maturation schedules between fish from the two populations. Finally, we calculated the cumulative fecundity over the lifetime of each female, assuming successful spawning each year.

Egg characteristics.—Egg size (oocyte diameter and ash-free dry weight [AFDW]) and composition (the relative proportion of ash weight and AFDW in the egg) influence the probability of fertilization and the viability of fish embryos and larvae (Green 2008). Therefore, we assessed three egg characteristics from Blue Catfish: (1) mean oocyte diameter, (2) AFDW, and (3) proportion of ash. To determine mean oocyte size, oocytes from preserved egg samples were teased apart and the diameters of at least 10 oocytes were measured under a stereomicroscope using imaging software. In addition, we obtained mean fresh oocyte diameters from 144 spawning-capable fish both immediately after dissection and after preservation to assess the effect of preservation on egg size. The relationship between mean fresh and preserved oocyte diameters for the 144 fish was given by

$$\text{Fresh diameter} = 1.937 \times (\text{preserved diameter})^{0.461}. \quad (4)$$

We used this relationship to correct the mean oocyte diameter of preserved samples for shrinkage due to preservation. Subsequently, we tested for the effects of FL, age, sampling month, and population on mean egg diameter determined from the middle section of the ovary by using multiple regression models (Table 1, models 10 and 11).

We measured AFDW of egg samples as an index of energy content in the eggs. Egg samples from spawning-capable fish were stored in individual 20-mL scintillation

TABLE 1. Statistical models used to examine the reproductive biology of Blue Catfish collected from the James and York rivers during 2015–2017. All independent variables have linear relationships with the corresponding response, except for $s(\text{Age})$, which represents a third-degree restricted cubic spline relationship (GSI = gonadosomatic index; GLS = generalized least squares; GzLM = generalized linear model; AFDW = ash-free dry weight).

Model	Response	Response data type	Model type	Independent variables	Comments
1	Maturity	Binomial (mature/immature)	Logistic regression	FL, Population	Fixed effect of population on each parameter
2	GSI	Continuous, positive proportion	GLS model	Age, Population	Fixed effect of population on each parameter
3				FL, Population, Month, FL \times Month	Response exponentiated to meet the normality assumption; separate variance estimates for each population
4				Age, Population, Month, Age \times Month	Response exponentiated to meet the normality assumption; separate variance estimates for each population
5	Fecundity	Discrete, positive	Gamma GzLM with log link	FL, Population	FL mean-centered for better interpretability of the model
6	Relative fecundity	Continuous, positive	Gamma GzLM with log link	Age, Population	Age mean-centered for better interpretability of the model
7				FL, Population	FL mean-centered for better interpretability of the model
8				Age, Population	Age mean-centered for better interpretability of the model
9	Mean egg diameter	Continuous, positive	GLS model	Section	Compound symmetric correlation structure to account for multiple observations from a single fish
10	Mean egg diameter	Continuous, positive	Linear regression	Age, Month, Population	Using middle section of the ovary
11				FL, Month, Population	Using middle section of the ovary
12	Mean AFDW	Continuous, positive	GLS model	FL, Population	Compound symmetry
13				$s(\text{Age})$, Population	Compound symmetry
14				FL, Population	Compound symmetry; separate variance estimates for each population
15	Mean egg ash proportion	Continuous, positive proportion		Age, Population	Compound symmetry; separate variance estimates for each population

vials at -80°C . From each vial, we obtained three 20-egg subsamples, which we dried at 60°C for 72 h. These were weighed prior to combustion in a muffle furnace. We thus obtained ash weight from each sample and calculated AFDW as the difference between ash weight and dry weight. We determined the mean AFDW of a single egg by dividing the total AFDW by 20. To ascertain whether mean egg quality varied between populations, we calculated the mean proportion of ash in the eggs by dividing

the ash weight by the dry weight of each sample. Eggs of higher quality are expected to have a lower proportion of ash and, hence, a greater proportion of organic matter (i.e., higher AFDWs and higher AFDW proportions; Johnston 1997).

We modeled mean AFDW as the dependent variable using a GLS model with population and either age or FL as the independent variables. A compound symmetric correlation structure was used to account for multiple

measurements (i.e., three subsamples) from the same individual. Fork length was linearly related to egg AFDW, but age had a nonlinear relationship with egg AFDW. We therefore modeled the relationship between AFDW and age using a restricted cubic spline with four internal knots (Zuur et al. 2009; Table 1, model 13). Finally, we assessed potential population-, size-, and age-specific variation in the proportion of ash in the dry mass of eggs by using GLS models with a compound symmetric correlation structure and separate variance estimates for each population, as described above (Table 1, models 14 and 15).

Statistical analyses were conducted in R version 3.6.0 using the packages “nlme” (version 3.1-139) and “stats” with a significance level α of 0.05. We included only those sizes, ages, and months for which observations were available from both populations.

RESULTS

We assessed 875 Blue Catfish from the James River (382 males, 493 females) and 765 Blue Catfish from the York River (438 males, 327 females). Sex ratio did not differ from 1:1 in either of the populations ($\chi^2_{1,James} = 0.56$, $P = 0.45$; $\chi^2_{1,York} = 3.02$, $P = 0.08$). Females ranged from 112 to 1,055 mm FL and from 1 to 29 years of age.

Gonadosomatic Index

The GSI of female Blue Catfish ranged between 0.04% and 21.83% and varied with fish size and season (Figure 2). In general, mean GSI was lowest in fall and winter and highest in May–July, suggesting that spawning occurs during May–July. Larger Blue Catfish (>600 mm FL) achieved peak GSI values earlier in the spawning season than smaller fish (<400 mm; Figure 2). Similar relationships occurred with fish age, such that the GSI of older females peaked during May. Mean GSI of ovigerous females also varied with fish size and population but not with fish age (Table 2). Mean GSI decreased significantly with FL ($\chi^2_1 = 24.58$, $P < 0.001$) but was not significantly different in June versus July (i.e., months during which ovigerous females were collected from both populations; $\chi^2_1 = 1.25$, $P = 0.26$). The mean GSI for the average-sized fish (486 mm FL) was significantly greater in the James River (mean GSI = 13.8%; 95% CLs = 13.2%, 14.5%) compared with the York River (mean GSI = 12.6%; 95% CLs = 11.9%, 13.3%; $\chi^2_1 = 9.21$, $P = 0.002$). Age, month, and the age \times month interaction did not have significant effects on mean GSI ($F_{age} = 0.19$; $F_{month} = 0.43$; $F_{age \times month} = 0.90$; $P > 0.05$). At the mean age (11.4 years), however, mean GSI was significantly greater in the James River fish (mean = 14.2%; 95% CLs = 13.5%, 14.9%) compared with the York River fish (mean = 12.4%, 95% CLs = 11.6%, 13.2%; $\chi^2_1 = 19.181$, $P < 0.001$).

Maturity Schedules

The mean length at maturity was significantly lower for Blue Catfish in the James River (mean = 343 mm FL; 95% CLs = 334, 352 mm) than for fish in the York River (mean = 382 mm, 95% CLs = 367, 396 mm; bootstrap $P = 0.001$; Figure 3). In contrast, the mean age at maturity was marginally higher for the James River population (mean = 7.7 years; 95% CLs = 7.3, 8.0 years) than for the York River population (mean = 7.0 years, 95% CLs = 6.5, 7.6 years; bootstrap $P = 0.058$; Figure 3). These differences in size and age at maturity reflect variation in the reproductive rates of these populations.

Fecundity and Lifetime Fecundity Modeling

Fecundity varied between 2,613 and 68,356 eggs/fish (grand mean = 15,060 eggs/fish). Fecundity increased significantly with FL ($R^2 = 0.77$; $\chi^2_1 = 980.42$, $P < 0.001$). At the mean FL, fecundity was greater for James River fish (mean = 14,377 eggs/fish; 95% CLs = 13,775, 15,014 eggs/fish) than for York River fish (mean = 12,568 eggs/fish; 95% CLs = 12,036, 13,131 eggs/fish; $\chi^2_1 = 17.21$, $P < 0.001$; Figure 4). Similar to FL, fecundity increased significantly with fish age ($\chi^2_1 = 77.22$, $P < 0.001$), although the fit was characterized by greater uncertainty ($R^2 = 0.41$; Figure 4) compared with the fecundity–fish size relationship. However, at the mean age, fecundity was marginally lower for the James River fish (mean = 13,660 eggs/fish; 95% CLs = 12,604, 14,839 eggs/fish) compared with the York River fish (mean = 15,326 eggs/fish; 95% CLs = 14,132, 16,657 eggs/fish; $\chi^2_1 = 3.75$, $P = 0.053$; Figure 4). Relative fecundity ranged between 3,995 and 15,947 eggs/kg of fish (grand mean = 8,863 eggs/kg). Mean relative fecundity was significantly greater for James River Blue Catfish, and mean relative fecundity declined significantly with FL ($\chi^2_1 = 39.79$, $P < 0.001$) and age in both populations ($\chi^2_1 = 14.13$, $P < 0.001$; Table 2; Figure 5).

At any given size, Blue Catfish in the James River had greater fecundity than those in the York River, but owing to faster growth rates and earlier maturation, the latter had higher annual fecundity up to age 19 (Figure 6A). Mean cumulative fecundity increased at different rates for fish from the two populations, with fish in the James River exhibiting higher cumulative fecundity at size but lower cumulative fecundity at age until age 24 (Figure 6B). A 25-year-old female Blue Catfish from the James River could potentially produce 453,000 eggs over her lifetime, and a 25-year-old female from the York River could potentially produce 443,000 eggs over her lifetime (Figure 6B).

Egg Characteristics

Mean fresh egg diameter ranged from 1.57 to 4.03 mm (grand mean = 3.14 mm) and did not differ significantly among the anterior, middle, and posterior sections of the ovary ($\chi^2_2 = 1.52$, $P = 0.47$). We observed similar results for

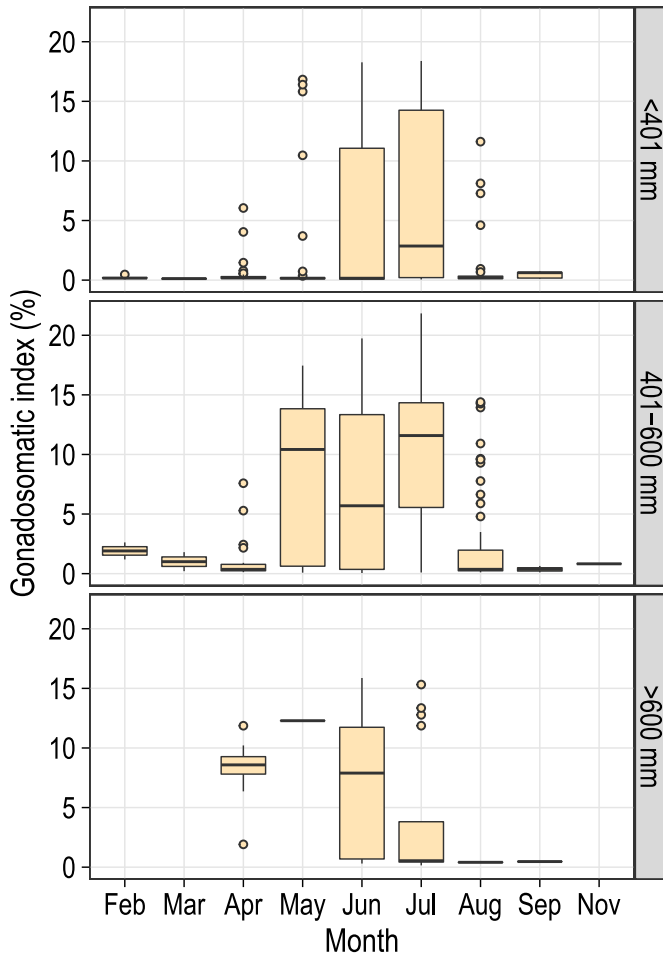


FIGURE 2. Box plots of monthly gonadosomatic indices for three size-groups of female Blue Catfish collected from the James and York rivers during 2015–2017. In each box plot, the lower, middle, and upper horizontal lines correspond to the first, second (i.e., median), and third quartiles; the lower whisker (vertical line) extends to the smallest value at most $1.5 \times$ IQR from the first quartile (where IQR is the interquartile range); the upper whisker extends to the largest value no further than $1.5 \times$ IQR; circles correspond to outliers (i.e., data beyond the end of whiskers).

preserved egg diameters ($\chi^2_2 = 1.51$, $P = 0.47$). Subsequent assessment of mean egg diameters from the middle section of the right ovary revealed no significant differences across the range of fish lengths (model 10: $F_{1, 303} = 0.52$, $P = 0.47$) or ages (model 11: $F_{1, 299} = 0.48$, $P = 0.49$) considered. We did not detect significant differences in mean egg diameters between June and July (model 10: $F_{2, 303} = 1.82$, $P = 0.17$; model 11: $F_{2, 299} = 2.18$, $P = 0.12$) or between populations (model 10: $F_{1, 303} = 0.36$, $P = 0.55$; model 11: $F_{1, 299} = 0.22$, $P = 0.64$) when size or age was included in the model.

Mean egg AFDW ranged from 2.18 to 12.94 mg/egg (grand mean = 6.60 mg/egg) and did not vary with fish size for either James River or York River Blue Catfish (model 12: $\chi^2_1 = 2.52$, $P = 0.11$). The relationship of egg AFDW to fish age was nonlinear such that AFDW

increased during the first few years after maturity before stabilizing at older ages ($\chi^2_1 = 16.23$, $P = 0.001$; Figure 7). Post hoc contrasts indicated that after age 10, mean age-specific AFDW was not significantly different among ages ($P > 0.05$). Mean AFDW was significantly greater in James River fish (mean = 6.87 mg/egg) compared with York River fish (mean = 6.27 mg/egg; $\chi^2_1 = 3.91$, $P = 0.048$; Figure 7). Across all samples, ash comprised 1.6–8.5% of egg dry mass. The proportion of ash in eggs did not vary with fish length (model 14: $\chi^2_1 = 0.08$, $P = 0.78$) or with age (model 15: $\chi^2_1 = 0.34$, $P = 0.56$) but was significantly greater for the York River population (mean = 5.1%) than for the James River population (mean = 4.1%; model 14: $\chi^2_1 = 46.55$, $P < 0.001$; model 15: $\chi^2_1 = 48.20$, $P < 0.001$).

DISCUSSION

To our knowledge, ours is the first study to quantify the reproductive biology of wild Blue Catfish from their nonnative range. Blue Catfish exhibit many “equilibrium” life history traits (sensu Winemiller and Rose 1992), such as a long reproductive life span, a large egg size, and a relatively small number of eggs per batch that are guarded by males. However, their large body size and long life span suggest that Blue Catfish also have some traits that are representative of “periodic” strategists. Population-specific differences in reproductive traits highlight the ability of Blue Catfish to shift along the continuum between different life history strategy endpoints as the species passes through different stages of invasion. Increasingly, researchers have found that the ability to tailor life history traits to prevailing environmental conditions may be more important than specific traits in ensuring successful invasion by fishes (Fox et al. 2007; Feiner et al. 2012; Copp et al. 2016; Masson et al. 2016; Liu et al. 2017). Management efforts to control the spread and population size of Blue Catfish will undoubtedly need to recognize this plasticity in reproductive traits that occurs in response to environmental conditions and potentially to harvest activities.

Maturation Rates and Life History Tactics

Blue Catfish in the more densely populated James River (Tuckey and Fabrizio 2019) matured at a smaller size but older age compared with those in the York River. Maturity at smaller sizes and older ages at high population densities has been reported in other fishes, including the Vendace *Coregonus albula* (Karjalainen et al. 2016), Rainbow Trout *Oncorhynchus mykiss* (Ward et al. 2017), Walleye *Sander vitreus* (Venturelli 2009), and Guppy *Poecilia reticulata* (Auer 2010), and was expected for these Blue Catfish populations based on their reported polyphasic growth (Nepal et al. 2020). Our observations for invasive Blue Catfish are in line with predictions from life history theory concerning maturation rates and fecundity

TABLE 2. Type III ANOVA or analysis of deviance results for models assessing reproductive characteristics of invasive Blue Catfish in two Chesapeake Bay subestuaries. Model numbers and abbreviations are defined in Table 1. N is the sample size for each model, ϕ is the dispersion parameter for the gamma generalized linear model, and ρ is the correlation coefficient for the compound symmetric correlation structure.

Model	Response	N	Parameter	Statistic	df	P	Comments
1	Maturity	728	FL	$\chi^2 = 483.6$	1	<0.001	
			Population	$\chi^2 = 18.4$	1	<0.001	
2	Maturity	698	Age	$\chi^2 = 600.9$	1	<0.001	
			Population	$\chi^2 = 3.70$	1	0.055	
3	GSI	261	FL	$\chi^2 = 24.58$	1	<0.001	
			Month	$\chi^2 = 2.14$	1	0.143	
			Population	$\chi^2 = 9.21$	1	0.002	$SD_{York} = 0.036$; $SD_{James} = 0.033$
			FL \times Month	$\chi^2 = 1.25$	1	0.263	
4	GSI	260	Age	$\chi^2 = 0.19$	1	0.665	
			Month	$\chi^2 = 0.43$	1	0.514	
			Population	$\chi^2 = 19.18$	1	<0.001	$SD_{York} = 0.039$; $SD_{James} = 0.033$
			Age \times Month	$\chi^2 = 0.90$	1	0.342	
5	Fecundity	299	FL	$\chi^2 = 980.42$	1	<0.001	$\phi = 0.07$
			Population	$\chi^2 = 17.21$	1	<0.001	
6	Fecundity	299	Age	$\chi^2 = 77.22$	1	<0.001	$\phi = 0.21$
			Population	$\chi^2 = 3.75$	1	0.053	
7	Relative fecundity	299	FL	$\chi^2 = 39.79$	1	<0.001	$\phi = 0.07$
			Population	$\chi^2 = 22.42$	1	<0.001	
8	Relative fecundity	299	Age	$\chi^2 = 14.13$	1	<0.001	$\phi = 0.07$
			Population	$\chi^2 = 42.83$	1	<0.001	
9	Mean egg diameter	159	Intercept	$\chi^2 = 47,730.3$	1	<0.001	$\rho = 0.55$
			Section	$\chi^2 = 1.52$	2	0.468	
10	Mean egg diameter	308	Intercept	$F = 2,575.21$	1	<0.001	
			FL	$F = 0.52$	1	0.470	
			Month	$F = 1.82$	2	0.165	
			Population	$F = 0.36$	1	0.551	
			Residuals		303		
11	Mean egg diameter	304	Intercept	$F = 3,586.79$	1	<0.001	
			Age	$F = 0.48$	1	0.490	
			Month	$F = 2.18$	2	0.115	
			Population	$F = 0.22$	1	0.639	
			Residuals		299		
12	Mean egg AFDW	324	Intercept	$\chi^2 = 33.73$	1	<0.001	$\rho = 0.699$
			FL	$\chi^2 = 2.52$	1	0.113	
			Population	$\chi^2 = 3.96$	1	0.046	
13	Mean egg AFDW	324	$s(\text{Age})$	$\chi^2 = 16.23$	3	0.001	$\rho = 0.674$
			Population	$\chi^2 = 3.91$	1	0.048	
14	Egg ash proportion	324	FL	$\chi^2 = 0.08$	1	0.782	$\rho = 0.613$
			Population	$\chi^2 = 46.55$	1	<0.001	$SD_{York} = 0.009$; $SD_{James} = 0.007$
15	Egg ash proportion	324	Age	$\chi^2 = 0.34$	1	0.559	$\rho = 0.613$
			Population	$\chi^2 = 48.20$	1	<0.001	$SD_{York} = 0.009$; $SD_{James} = 0.007$

(Stearns 1992; Winemiller and Rose 1992). In newly established populations, relative densities and intraspecific competition are low, resulting in low mortality and rapid somatic growth (Lockwood et al. 2013). Under these conditions, individual fitness is maximized by achieving

maturity at large sizes and young ages (Fox 1994; Masson et al. 2016). As population densities increase, however, fish maximize their individual fecundity by achieving maturity at larger body sizes (Stearns 1992); thus, fish may remain immature until an older age. Mortality constraints often

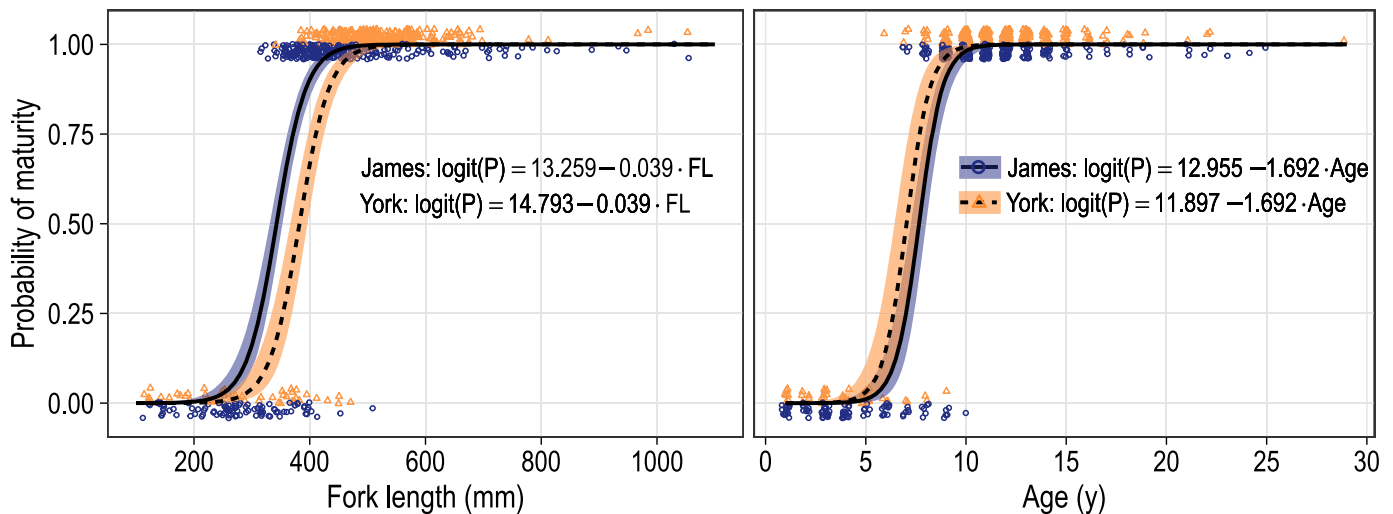


FIGURE 3. Maturity ogives for female Blue Catfish collected from the James (circles, solid lines; $n=493$) and York (triangles, dashed lines; $n=438$) rivers during 2015–2017. Raw data are jittered to improve visibility. Lines represent the model-predicted values, and shaded polygons represent the corresponding 95% confidence bands.

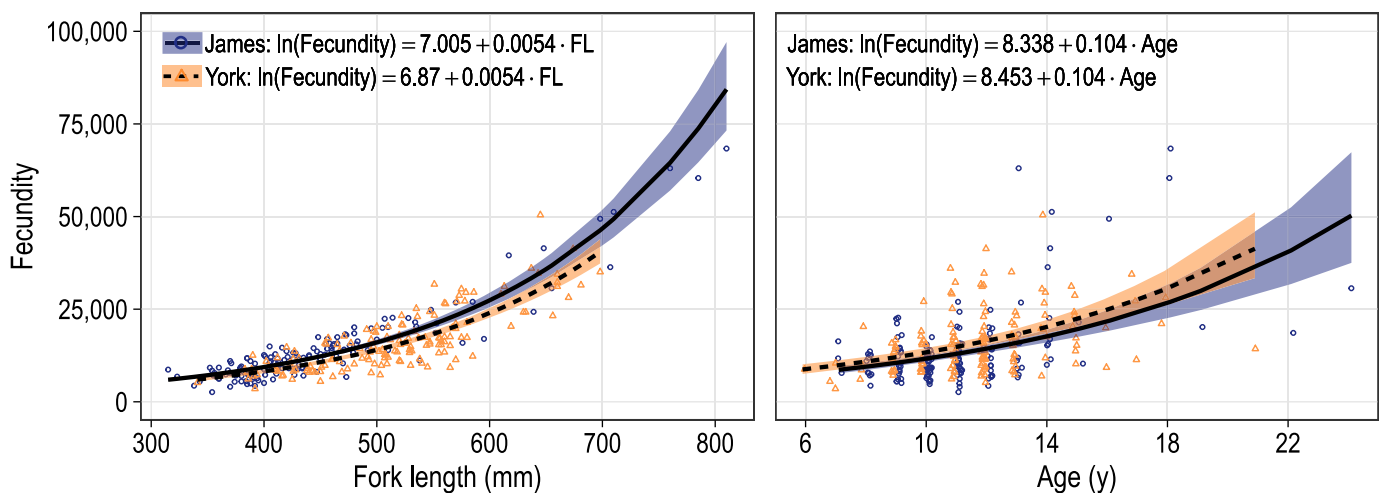


FIGURE 4. Relationships between the fecundity (eggs/fish) and FL (mm) or age (years) of Blue Catfish collected from the James (circles, solid lines) and York (triangles, dashed lines) rivers during 2015–2017. Lines represent model-predicted values, and shaded polygons represent the corresponding 95% confidence bands.

dictate that lifetime reproductive output will be maximized when maturity occurs at a suboptimal size, and this appears to describe the tactics of female Blue Catfish in the James and York rivers.

Blue Catfish from the James and York rivers mature at an older age and smaller size compared with conspecifics from their native range, where population densities tend to be lower. The relatively high densities of Blue Catfish in Chesapeake Bay waters (Tuckey and Fabrizio 2019; Fabrizio et al. 2021) account for some of the differences in maturity schedules of fish from native and nonnative waters. Specifically, the sizes at maturity of individuals

from the James and York rivers (mean = 343–382 mm FL) are at the lower end of the range reported for native populations (350–722 mm; Perry and Carver 1973; Hale and Timmons 1989). Conversely, the ages at maturity of Chesapeake Bay Blue Catfish (mean = 7.0–7.7 years) are closer to the upper range for fish from native waters (4–7 years; Graham 1999). A potential reason for the discrepancy may be methodological, however. Ages at maturity for native Blue Catfish populations were determined from ages inferred from length-frequency distributions and not from otoliths, as we did here. Thus, the results reported by Graham (1999) are likely less reliable than what we

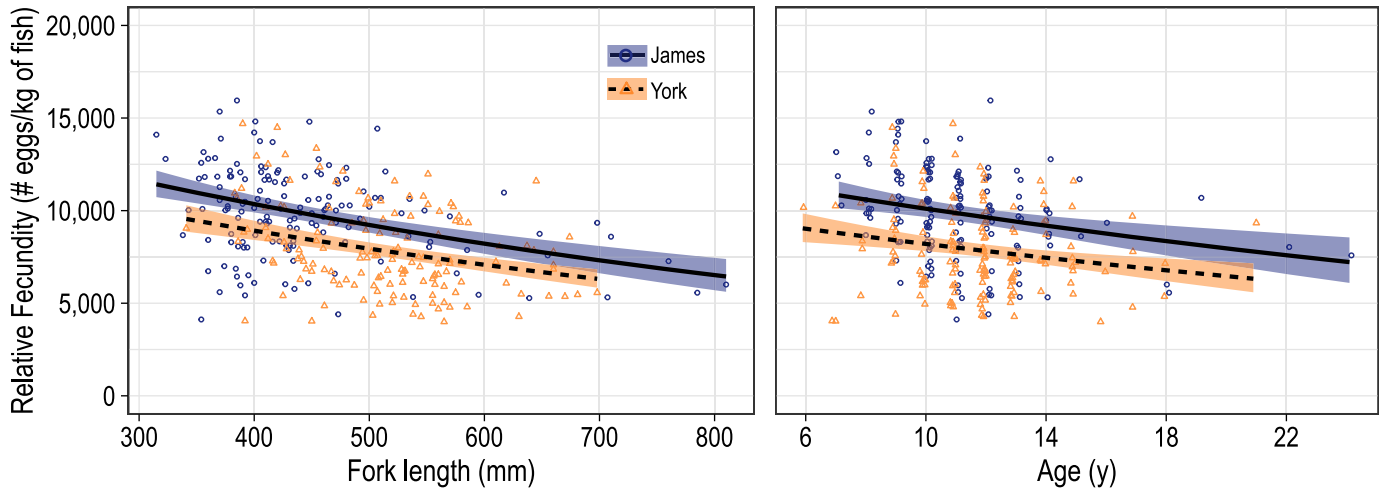


FIGURE 5. Relationships between relative fecundity (eggs/kg) and FL (mm) or age (years) of Blue Catfish collected from the James (circles, solid lines) and York (triangles, dashed lines) rivers during 2015–2017. Lines represent model-predicted values, and shaded polygons represent the corresponding 95% confidence bands.

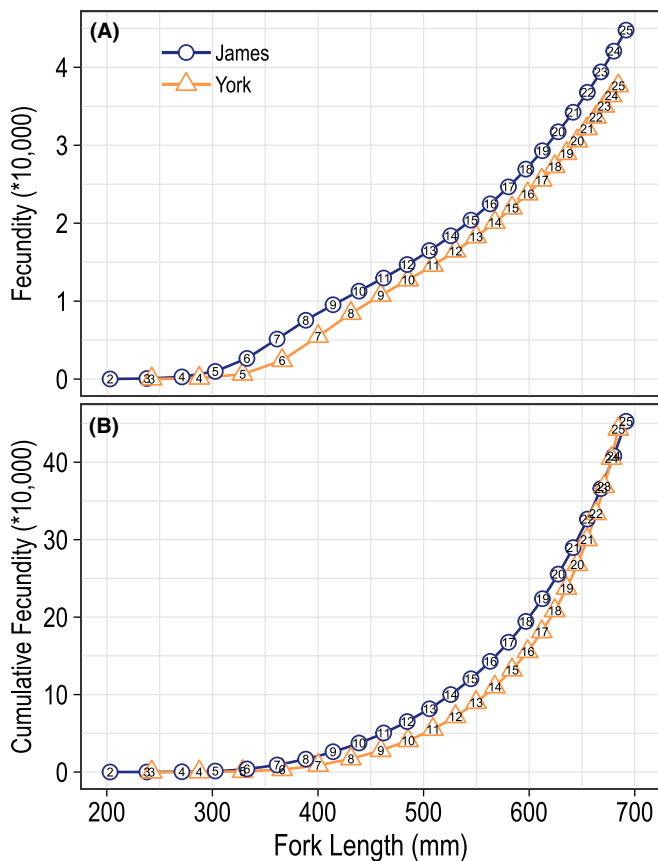


FIGURE 6. Predicted fecundity (eggs/fish) and cumulative lifetime fecundity for female Blue Catfish at ages 5–25 from the James (darker circles and lines) and York (lighter triangles and lines) rivers. Numbers within the symbols represent fish age (years).

report. The only other report of Blue Catfish maturity with age determined from hard structures was from Colehour (2009), who did not calculate the mean age at maturity but reported that the youngest mature Blue Catfish collected from the middle Mississippi River was 7 years old.

Higher GSI, relative fecundity, and egg AFDW suggest that Blue Catfish in the James River allocated a greater proportion of energy into reproduction compared with fish in the York River, contrary to our expectations based on life history theory and empirical observations of other fish populations (e.g., Hutchings 1993; Post et al. 1999; Fox et al. 2007; Auer 2010). Given these results, we expected mature Blue Catfish in the James River to grow slower and remain smaller; indeed, we found that mean FLs at ages 7–15 were consistently lower for James River fish than for York River fish (results not shown). Although it is generally preferable to grow larger, which generally decreases predation pressure and increases reproductive output in fishes (Stearns 1992; Hixon et al. 2014), Blue Catfish in the James River seem to employ novel tactics to maintain positive fitness. We propose that the imperative to grow large before maturation is low for Blue Catfish in the James River for three reasons. First, Blue Catfish—particularly larger individuals (>300 mm FL)—have few predators in the Chesapeake Bay region. Second, for a given size, Blue Catfish in the James River produce more and higher-quality eggs (i.e., eggs with greater organic content and a lower proportion of ash) compared with those in the York River; higher-quality eggs generally confer greater survivability to the larval stage (Johnston

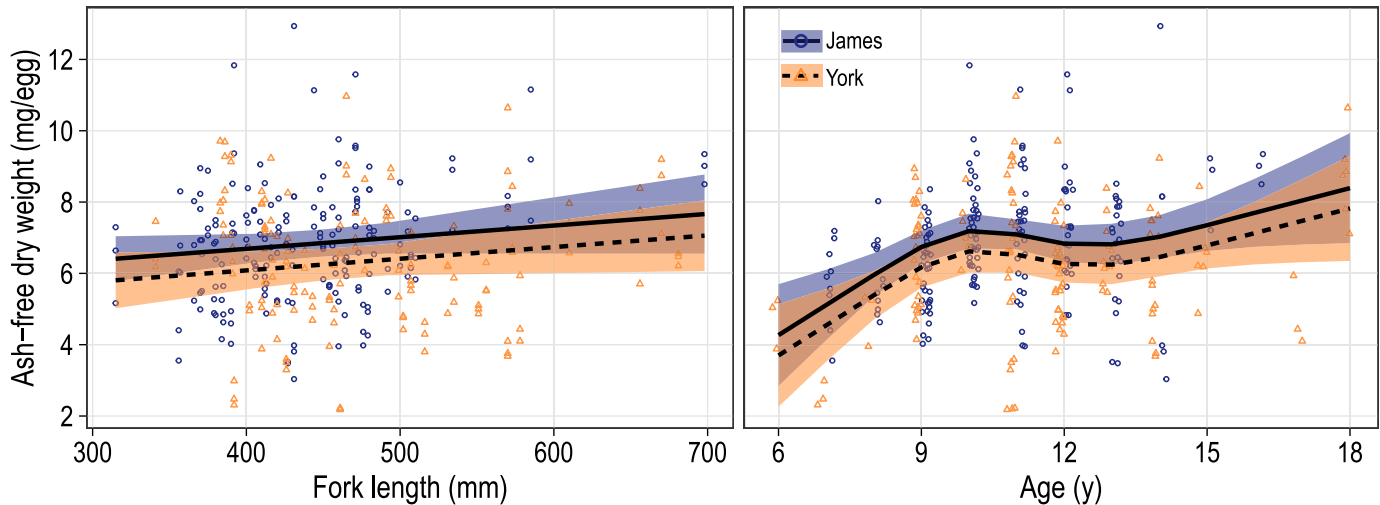


FIGURE 7. Relationships between the mean ash-free dry weight of eggs (mg/egg) and FL (mm) or age (years) of Blue Catfish collected from the James (circles, solid lines) and York (triangles, dashed lines) rivers during 2015–2017. Lines represent model-predicted values, and shaded polygons represent the corresponding 95% confidence bands.

1997). Finally, the lower rate of inbreeding in the James River Blue Catfish population (Higgins 2006) may result in higher survival of eggs because the hatchability of eggs is negatively affected by inbreeding depression in fishes (e.g., Su et al. 1996). Together, these factors suggest that the production of juvenile Blue Catfish in the York River may be lower than expected based on fecundity alone; thus, the lifetime fitness of fish from the two populations may be similar even though egg quality and cumulative fecundity differ.

Maternal Effects

Larger Blue Catfish spawned earlier during the spawning season, as has been reported for many fish species (see Hixon et al. 2014 and references therein). Size and age had strong positive effects on the number of eggs produced, although size had a greater influence. This information can be used to identify the optimal harvest seasons for Blue Catfish in systems where managers wish to support a trophy fishery. For example, regulations that protect large individuals, particularly during the early part of the spawning season, would maintain the trophy fishery for Blue Catfish and achieve high reproductive rates to sustain recruitment. This strategy will also permit substantial harvests of medium-size or medium-age fish and may thereby reduce overall population abundance (Ng et al. 2016).

We found some discrepancies between our observations and those reported in the literature. For example, the relative fecundity of Blue Catfish in the James and York rivers (mean = 8,863 eggs/kg) was considerably greater than values previously reported for this species (5,600 eggs/kg; Dunham and Argue 2000; 3,156 eggs/kg; Vo 2013) but

relatively similar to that reported in the middle Mississippi River (7,938 eggs/kg; Colehour 2009). These differences were likely due to study-specific differences in inclusion or exclusion of oocytes that were not fully developed or in the size range of sampled fish. Fecundity of Blue Catfish was more strongly correlated with FL than with age, in agreement with observations in other fishes (reviewed by Green 2008). Fecundity was higher in large but younger fish than in small but older fish. Similar results were observed in European Bullhead *Cottus gobio* (Abdoli et al. 2005) and Atlantic Cod *Gadus morhua* (Folkvord et al. 2014). This suggests that within the same population, faster immature growth coupled with a larger size at maturity may result in greater female fitness. Access to optimal nursery habitats with a high availability of food during juvenile stages may therefore greatly affect the immature growth rate, size at maturity, and ultimately the lifetime reproductive output of an individual fish.

Fish size negatively affected GSI and relative fecundity in Blue Catfish, contrary to observations in most other fish species (Green 2008; Hixon et al. 2014). Our results are consistent with observations of larger Blue Catfish (range = 552–1,111 mm TL) collected from the middle Mississippi River (Colehour 2009), suggesting that the patterns we observed persist throughout the size range of Blue Catfish. Similar results have been reported for other catfishes, including European Bullhead (Abdoli et al. 2005), Flathead Catfish *Pylodictis olivaris* (Colehour 2009), and Channel Catfish *Ictalurus punctatus* (Brauhn and McCraren 1975). Such results may be due to reproductive senescence, which has also been observed in other fishes, such as the Largemouth Bass *Micropterus salmoides* (Kelley 1962) and Turquoise Killifish *Nothobranchius furzeri* (Žák

and Reichard 2020). In young mature females (age 6–10), egg organic mass increased significantly with age, highlighting the importance of spawning experience in females. Physiological machinery for reproduction may not be well developed in first-time spawners (likely 6–7 years old), resulting in fewer eggs or eggs of lesser quality than repeat spawners (>10 years old; Green 2008).

Management Implications and Future Directions

Our results can inform management decisions regarding invasive Blue Catfish in the Chesapeake Bay region as well as Blue Catfish populations throughout the nonnative range of the species. In particular, our estimates of length at maturity can be used to inform the minimum size limits for specific management goals in the James and York rivers. If the management goal is to maintain sustainable populations of Blue Catfish, then regulations such as minimum size limits that exceed the size at maturity will allow fish to spawn at least once before being harvested, thus preventing recruitment overfishing. This is particularly relevant for Blue Catfish because relative fecundity is highest in the smallest spawners. Removals may also be restricted during May–July, when spawning occurs, thus helping to further avoid recruitment overfishing. One of the management goals considered for some of the Blue Catfish populations in the Chesapeake Bay region is the maintenance of a trophy fishery; our results suggest that protection of trophy fish will allow for high reproductive output from these individuals. However, the negative relationship between relative fecundity and body size suggests that the contribution of these individuals will not be as high as might be expected from the usual assumptions of constant relative fecundity (Marshall 2016) or of disproportionately greater fecundity for the largest females (Hixon et al. 2014). Conservation goals, such as decreasing the population size and limiting the range expansion of this invasive species, are also desired for Blue Catfish in the Chesapeake Bay region (ASMFC 2011); such goals may benefit from the disruption of spawning events or the removal of spawning fish. Our results can be used to inform size-based trade-offs in removals of mature fish.

Development of specific and effective management regulations (e.g., slot limits, inverse slot limits, one above memorable size, etc.) in light of conflicting management interests requires quantitative models that can identify the magnitude of removals and the size-classes to target for removal (Fabrizio et al. 2021). Unfortunately, most of these models rely on simplifying assumptions, such as constancy of relative fecundity and sex ratios over time (Beverton and Holt 1957), as well as the assumption of direct proportionality between fecundity and fish weight (Hixon et al. 2014). As we have shown, such assumptions are not reasonable for Blue Catfish in the James and York rivers. A stock assessment model is currently under development

for the Blue Catfish population in the James River (C. Hilling, Virginia Tech, personal communication) and may benefit from the information we report. Importantly, we identified considerable differences in reproductive characteristics of Blue Catfish from the two populations; these differences must be incorporated into assessments to best inform management strategies in the region. Population-specific differences in life history traits have prompted other researchers to also call for population-specific regulations for Blue Catfish (Stewart et al. 2016). Finally, many populations of Blue Catfish in Atlantic slope drainages, including those in the upper portion of the Chesapeake Bay, likely form metapopulations, which can contribute recruits to nearby systems (Higgins 2006; Nepal and Fabrizio 2019). The influence of such metapopulation dynamics on management recommendations needs to be considered. To do so, it is imperative to quantify the reproductive biology of Blue Catfish in each of the contributing and receiving systems.

Our study suggests a few avenues for future research. First, histological analyses may increase the accuracy of maturity designations and allow study of the presence and effects of seasonal atresia and skipped spawning on growth and fecundity dynamics (Lowerre-Barbieri et al. 2011). Atresia and skipped spawning may affect both the age-specific and lifetime reproductive output of fish. Second, the effects of salinity on spawning and the reproductive biology of Blue Catfish should be evaluated. Although traditionally considered a freshwater fish, Blue Catfish have been collected from salinities up to 21.8‰ in the Chesapeake Bay (Fabrizio et al. 2018). Blue Catfish are unlikely to survive at salinities greater than 15‰ for extended periods (Nepal and Fabrizio 2019), but sublethal effects on growth and reproduction have not been measured. Reproduction has been proposed not to occur at salinities over 2‰ (Perry 1973), but this hypothesis has not been tested. At least one freshwater fish species, the Eurasian Minnow *Phoxinus phoxinus*, is known to spawn in brackish waters up to 6‰ in the Baltic Sea, where this species is invasive (Svirgsden et al. 2018). Finally, the carryover effects of parental experience in brackish waters on reproduction and the viability of eggs also have not been studied but could be instrumental in determining population size and potential range expansion of Blue Catfish throughout the Chesapeake Bay region.

Conclusions

Blue Catfish exhibit several characteristics supportive of successful invasion: parental care, large eggs, a long reproductive life span, and a large size. In the James and York rivers, this species demonstrated considerable flexibility in reproductive tactics. However, despite population-specific differences, female Blue Catfish in the James and York

rivers may have similar lifetime fitness, depending on mortality and recruitment rates in these systems. Our findings provide quantitative information that is applicable to management both directly (e.g., through regulating seasonal harvest) and indirectly (through inputs to stock assessment or general population models) and highlight the need to consider the plasticity of populations when developing management strategies. The failure of fisheries management strategies to meet intended goals can often be traced to inaccuracies in input variables (e.g., Zemeckis et al. 2014). A lack of accurate biological information often necessitates simplifying assumptions. Incorporation of population-specific reproductive rates in stock assessment models will lead to better estimates of recruitment and production and, hence, more reliable reference points (Morgan 2008; Marshall 2016) for invasive Blue Catfish populations in the James and York rivers.

ACKNOWLEDGMENTS

We thank commercial fisher G. Trice, former Virginia Department of Wildlife Resources biologist A. Bunch, members of the American Shad and River Herring Monitoring Program, and past and present members of the VIMS Trawl Survey crew for assistance with collection of Blue Catfish for this study. We also appreciate help from volunteers, technicians, and interns in processing the fish samples. This manuscript benefited from discussions with and comments from R. Brill, W. Vogelbein, R. Mann, and two reviewers. V. Nepal was supported by graduate fellowships from the VIMS Office of Academic Studies and a graduate research fellowship from Virginia Sea Grant; the trawl survey was funded by the Virginia Marine Resources Commission and the U.S. Fish and Wildlife Service. This is contribution 4006 of the Virginia Institute of Marine Science, William & Mary. 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>

REFERENCES

- Abdoli, A., D. Pont, and P. Sagnes. 2005. Influence of female age, body size and environmental conditions on annual egg production of the Bullhead. *Journal of Fish Biology* 67:1327–1341.
- Auer, S. K. 2010. Phenotypic plasticity in adult life-history strategies compensates for a poor start in life in Trinidadian Guppies (*Poecilia reticulata*). *American Naturalist* 176:818–829.
- Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Her Majesty's Stationery Office, London.
- Brauhn, J. L., and J. McCraren. 1975. Ovary maturation in Channel Catfish. *Progressive Fish-Culturist* 37:209–212.
- Colehour, J. D. 2009. Fecundity of Flathead Catfish and Blue Catfish from the Mississippi River between Hannibal and Cape Girardeau, Missouri. Master's thesis. University of Central Missouri, Warrensburg.
- Copp, G. H., A. S. Tarkan, G. Masson, M. J. Godard, J. Koščo, V. Kováč, A. Novomeská, R. Miranda, J. Cucherousset, G. Pedicillo, and B. G. Blackwell. 2016. A review of growth and life-history traits of native and non-native European populations of Black Bullhead *Ameiurus melas*. *Reviews in Fish Biology and Fisheries* 26:441–469.
- Dunham, R. A., and B. J. Argue. 2000. Reproduction among Channel Catfish, Blue Catfish, and their F₁ and F₂ hybrids. *Transactions of the American Fisheries Society* 129:222–231.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall/CRC Press, New York.
- Fabrizio, M. C., V. Nepal, and T. D. Tuckey. 2021. Invasive Blue Catfish in the Chesapeake Bay region: a case study of competing management objectives. *North American Journal of Fisheries Management*. DOI:10.1002/nafm.10552.
- Fabrizio, M. C., T. D. Tuckey, R. J. Latour, G. C. White, and A. J. Norris. 2018. Tidal habitats support large numbers of invasive Blue Catfish in a Chesapeake Bay subestuary. *Estuaries and Coasts* 41:827–840.
- Feiner, Z. S., D. D. Aday, and J. A. Rice. 2012. Phenotypic shifts in White Perch life history strategy across stages of invasion. *Biological Invasions* 14:2315–2329.
- Folkvord, A., C. Jørgensen, K. Korsbrekke, R. D. M. Nash, T. Nilsen, and J. E. Skjæraasen. 2014. Trade-offs between growth and reproduction in wild Atlantic Cod. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1106–1112.
- Fontoura, N. F., A. S. Braun, and P. C. C. Milani. 2009. Estimating size at first maturity (L₅₀) from gonadosomatic index (GSI) data. *Neotropical Ichthyology* 7:217–222.
- Fox, M. G. 1994. Growth, density, and interspecific influences on Pumpkinseed sunfish life histories. *Ecology* 75:1157–1171.
- Fox, M. G., A. Vila-Gispert, and G. H. Copp. 2007. Life-history traits of introduced Iberian Pumpkinseed *Lepomis gibbosus* relative to native populations. Can differences explain colonization success? *Journal of Fish Biology* 71:56–69.
- García-Berthou, E. 2007. The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* 71:33–55.
- Graham, K. 1999. A review of the biology and management of Blue Catfish. Pages 37–49 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm Jr., and T. Coon, editors. *Catfish 2000: proceedings of the international ictalurid symposium*. American Fisheries Society, Symposium 24, Bethesda, Maryland.
- Green, B. S. 2008. Maternal effects in fish populations. Pages 1–105 in D. W. Sims, editor. *Advances in marine biology*, volume 54. Elsevier, London.
- Gutowsky, L. F. G., and M. G. Fox. 2012. Intra-population variability of life-history traits and growth during range expansion of the invasive Round Goby, *Neogobius melanostomus*. *Fisheries Management and Ecology* 19:78–88.
- Hale, R. S., and T. J. Timmons. 1989. Comparative age and growth of Blue Catfish in the Kentucky portion of Kentucky Lake between 1967 and 1985. *Transactions of the Kentucky Academy of Science* 50:22–26.
- Higgins, C. B. 2006. Invasion genetics of the Blue Catfish (*Ictalurus furcatus*) range expansion into large river ecosystems of the Chesapeake Bay watershed. Master's thesis. Virginia Commonwealth University, Richmond.
- Hilling, C. D., Y. Jiao, A. J. Bunch, R. S. Greenlee, J. D. Schmitt, and D. J. Orth. 2021. Growth dynamics of invasive Blue Catfish in four subestuaries of the Chesapeake Bay, USA. *North American Journal of Fisheries Management*. DOI:10.1002/nafm.10506.

- Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71:2171–2185.
- Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74:673–684.
- ICTF (Invasive Catfish Task Force). 2014. Final report of the Sustainable Fisheries Goal Implementation Team Invasive Catfish Task Force. National Oceanic and Atmospheric Administration, Chesapeake Bay Program Office, Annapolis, Maryland.
- Johnston, T. A. 1997. Within-population variability in egg characteristics of Walleye (*Stizostedion vitreum*) and White Sucker (*Catostomus commersoni*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:1006–1014.
- Jørgensen, C., S. K. Auer, and D. N. Reznick. 2011. A model for optimal offspring size in fish, including live-bearing and parental effects. *American Naturalist* 177:E119–E135.
- Karjalainen, J., O. Urpanen, T. Keskinen, H. Huuskonen, J. Sarvala, P. Valkeajärvi, and T. J. Marjomäki. 2016. Phenotypic plasticity in growth and fecundity induced by strong population fluctuations affects reproductive traits of female fish. *Ecology and Evolution* 6:779–790.
- Kelley, J. W. 1962. Sexual maturity and fecundity of the Largemouth Bass, *Micropterus salmoides* (Lacépède), in Maine. *Transactions of the American Fisheries Society* 91:23–28.
- Liu, C., L. Comte, and J. D. Olden. 2017. Heads you win, tails you lose: life-history traits predict invasion and extinction risk of the world's freshwater fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27:773–779.
- Lloret, J., G. Shulman, and R. M. Love. 2013. Condition and health indicators of exploited marine fishes. John Wiley & Sons, Chichester, UK.
- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. *Invasion ecology*, 2nd edition. John Wiley & Sons, Chichester, UK.
- Lowerre-Barbieri, S. K., N. J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. M. Wyanski, and F. Saborido-Rey. 2011. Emerging issues and methodological advances in fisheries reproductive biology. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:32–51.
- Marshall, C. T. 2016. Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. Pages 438–464 in T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. *Fish reproductive biology: implications for assessment and management*, 2nd edition. John Wiley & Sons, Chichester, UK.
- Masson, L., J. W. Brownscombe, and M. G. Fox. 2016. Fine scale spatio-temporal life history shifts in an invasive species at its expansion front. *Biological Invasions* 18:775–792.
- Moran, A. L., and J. S. McAlister. 2009. Egg size as a life history character of marine invertebrates: is it all it's cracked up to be? *Biological Bulletin* 216:226–242.
- Morgan, M. J. 2008. Integrating reproductive biology into scientific advice for fisheries management. *Journal of Northwest Atlantic Fishery Science* 41:37–51.
- Morris, J. A., and P. E. Whitfield. 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum NOS-NCCOS-99.
- Nepal, V., and M. C. Fabrizio. 2019. High salinity tolerance of invasive Blue Catfish suggests potential for further range expansion in the Chesapeake Bay region. *PLOS (Public Library of Science) ONE* [online serial] 14(11):e0244770.
- Nepal, V., and M. C. Fabrizio. 2020a. Density-dependence mediates the effects of temperature on growth of juvenile Blue Catfish in nonnative habitats. *Transactions of the American Fisheries Society* 149:108–120.
- Nepal, V., and M. C. Fabrizio. 2020b. Sublethal effects of salinity and temperature on non-native Blue Catfish: implications for establishment in Atlantic slope drainages. *PLOS (Public Library of Science) ONE* [online serial] 15(12):e0244392.
- Nepal, V., M. C. Fabrizio, and R. W. Brill. 2021. Effects of food limitation on growth, body condition and metabolic rates of non-native Blue Catfish. *Conservation Physiology* 9:coaa129.
- Nepal, V., M. C. Fabrizio, and W. J. Connelly. 2020. Phenotypic plasticity in life-history characteristics of invasive Blue Catfish. *Ictalurus furcatus*. *Fisheries Research* 230:105650.
- Ng, E. L., J. P. Fredericks, and M. C. Quist. 2016. Population dynamics and evaluation of alternative management strategies for nonnative Lake Trout in Priest Lake, Idaho. *North American Journal of Fisheries Management* 36:40–54.
- Perry, W. G. 1973. Notes on spawning of Blue and Channel catfish in brackish water ponds. *Progressive Fish-Culturist* 35:164–166.
- Perry, W. G., and D. C. Carver. 1973. Length at maturity and total length-collarbone length conversions for Channel Catfish, *Ictalurus punctatus*, and Blue Catfish, *Ictalurus furcatus*, collected from the marshes of southwest Louisiana. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 26:541–553.
- Post, J. R., E. A. Parkinson, and N. T. Johnston. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecological Monographs* 69:155–175.
- Schemmel, E., A. Friedlander, P. Andrade, K. Keakealani, L. Castro, C. Wiggins, B. Wilcox, Y. Yasutake, and J. Kittinger. 2016. The development of coastal fisheries monitoring methods to support local management. *Ecology and Society* [online serial] 21(4):article 34.
- Schloesser, R. W., M. C. Fabrizio, R. J. Latour, G. C. Garman, R. S. Greenlee, M. Groves, and J. Gartland. 2011. Ecological role of Blue Catfish in Chesapeake Bay communities and implications for management. Pages 369–382 in P. H. Michaletz and V. H. Travnichek, editors. *Conservation, ecology, and management of catfish: the second international symposium*. American Fisheries Society, Symposium 77, Bethesda, Maryland.
- Schmitt, J. D., B. K. Peoples, L. Castello, and D. J. Orth. 2019. Feeding ecology of generalist consumers: a case study of invasive Blue Catfish *Ictalurus furcatus* in Chesapeake Bay, Virginia, USA. *Environmental Biology of Fishes* 102:443–465.
- Sneed, K. E., and H. P. Clemens. 1963. The morphology of the testes and accessory reproductive glands of the catfishes (Ictaluridae). *Copeia* 1963:606–611.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York.
- Stewart, D. R., J. M. Long, and D. E. Shoup. 2016. Simulation modeling to explore the effects of length-based harvest regulations for *Ictalurus* fisheries. *North American Journal of Fisheries Management* 36:1190–1204.
- Su, G.-S., L.-E. Liljedahl, and G. A. E. Gall. 1996. Effects of inbreeding on growth and reproductive traits in Rainbow Trout (*Oncorhynchus mykiss*). *Aquaculture* 142(3):139–148.
- Svirgsden, R., M. Rohtla, A. Albert, I. Taal, L. Saks, A. Verliin, and M. Vetemaa. 2018. Do Eurasian Minnows (*Phoxinus phoxinus* L.) inhabiting brackish water enter fresh water to reproduce: evidence from a study on otolith microchemistry. *Ecology of Freshwater Fish* 27:89–97.
- Tuckey, T. D., and M. C. Fabrizio. 2019. Estimating relative juvenile abundance of ecologically important finfish in the Virginia portion of Chesapeake Bay (1 July 2018–30 June 2019). Virginia Institute of Marine Science, William & Mary, F-104-R-23, Gloucester Point.
- Venturelli, P. A. 2009. Life history, maternal quality and the dynamics of harvested fish stocks. Doctoral dissertation. University of Toronto, Toronto.
- Vo, K. M. 2013. Reproduction of Channel \times Channel, Channel \times Blue, and Blue \times Blue catfish as influenced by morphological characteristics and behavior. Master's thesis. Auburn University, Auburn, Alabama.

- Ward, H. G. M., J. R. Post, N. P. Lester, P. J. Askey, and T. Godin. 2017. Empirical evidence of plasticity in life-history characteristics across climatic and fish density gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 74:464–474.
- West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research* 41:199–222.
- Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 62:872–885.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196–2218.
- Wootton, R. J., and C. Smith. 2015. Reproductive biology of teleost fishes. John Wiley & Sons, Chichester, UK.
- Žák, J., and M. Reichard. 2020. Reproductive senescence in a short-lived fish. *Journal of Animal Ecology* 90:492–502.
- Zemeckis, D. R., M. J. Dean, and S. X. Cadrin. 2014. Spawning dynamics and associated management implications for Atlantic Cod. *North American Journal of Fisheries Management* 34:424–442.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.