



Growth dynamics of invasive Blue Catfish in four subestuaries of the Chesapeake Bay, USA

Journal:	<i>North American Journal of Fisheries Management</i>
Manuscript ID	UJFM-2020-0001.R1
Manuscript Type:	Special Section
Keywords:	Age and Growth, Life History, Mixed Models, Non-Indigenous Species, Spatiotemporal Variability
In Press, August 9, 2020	

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Manuscripts

1 Suggested Running Head: Invasive Blue Catfish Growth Dynamics

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31 <A>Abstract

32 Biological invasions occur as a multi-stage process and life history traits can change during the
33 invasion process. Blue Catfish *Ictalurus furcatus* were introduced in three Virginia tidal
34 tributaries of the Chesapeake Bay in the 1970s and 1980s, but have expanded their range to
35 almost all large tributaries of the Bay. Understanding the species' growth is important to
36 understand impacts on other resident species and population dynamics. Virginia Blue Catfish
37 exhibited wide variability in individual growth, prompting testing of six alternative hypotheses
38 (similar growth across space and time, as well as variable growth by: river systems, sampling
39 years, cohorts and both river systems and time) on its growth dynamics within four Virginia tidal
40 rivers (James, Mattaponi, Pamunkey, and Rappahannock) over the period 2002–2016. Blue
41 Catfish growth in Virginia was best explained by a model considering cohort and river as
42 random effects. The Rappahannock River was the first in Virginia to receive Blue Catfish and
43 had slower growth than other systems during the observation period. Growth rates declined for
44 all ages examined in the James, Mattaponi, and Pamunkey rivers, but only ages 7, 10, and 13 in
45 the Rappahannock. We did not generally observe synchronous growth responses among rivers,
46 supporting that more fine scale factors may be influencing growth rates. This work supports that
47 growth rates of non-native species may decline over time and comparisons of non-native growth
48 may be most useful when variability over space and time is considered.

49 <A>Introduction

50 Life history traits can shift during the invasion process from opportunistic to equilibrium
51 strategies (Feiner et al. 2012). Newly introduced invaders or individuals at the invasion front
52 tend to grow faster than those from previously established populations and can invest more
53 energy in growth than reproduction (Bøhn et al. 2004; Brandner et al. 2013; Azour et al. 2015;
54 Kornis et al. 2017). Individual growth is an important life history trait to understand population
55 biology of fishes. Growth parameters are related to other life history traits (e.g., natural mortality
56 and reproductive characteristics; Jensen 1996) and affect vulnerability to predation and fisheries
57 (Kerns and Lombardi-Carlson 2017). Growth rates of fishes are influenced by activity level,
58 population density and environmental conditions, including food availability, food quality, and
59 environmental factors such as temperature (Kitchell et al. 1977; Jones 1986; Jenkins et al. 1999;
60 Grant and Imre 2005; Jiao et al. 2010). Life history variation in non-native populations has been

61 attributed to differences in intraspecific competition, adaptive selection, or epigenetic changes
62 (Prentis et al. 2008; Phillips et al. 2010; Richards et al. 2012; Liebl et al. 2013; Azour et al. 2015;
63 Masson et al. 2016). However, few studies of non-native species' life history feature long time
64 series or large spatial ranges (e.g., Tarkan et al. 2012; Copp et al. 2016), thus understanding
65 spatial, temporal, and environmental factors may provide insights for ecology and management
66 of widespread or established invaders.

67 Blue Catfish *Ictalurus furcatus* are native to many large North American rivers of the
68 Gulf of Mexico drainages, but have been widely introduced beyond their native range in the
69 United States to provide fishing opportunities (Greenlee and Lim 2011; Schloesser et al. 2011).
70 Consequently, the species now ranges from California to the Atlantic coast states from Florida to
71 New Jersey (Fuller and Neilson 2019). Studies on non-native Blue Catfish have reported high
72 abundances (Fabrizio et al. 2018), low natural mortality rates (Hilling et al. 2018), reductions in
73 native species' abundances (Bonvechio et al. 2011b; Homer and Jennings 2011; Schloesser et al.
74 2011), and predation on at-risk and economically important species (Moran et al. 2016; Aguilar
75 et al. 2017; Schmitt et al. 2017, 2019a). However, Jennings et al. (2018) found diets were
76 dominated by Asian clams *Corbicula fluminea* and reported that Blue Catfish were unlikely to
77 harm sportfish communities. Life history traits of Blue Catfish can be exceptionally plastic
78 including food habits (Schmitt et al. 2019b), growth rates (Boxrucker and Kuklinski 2006), and
79 movement patterns (Tripp et al. 2011; Tuckey et al. 2017). Further, this freshwater species has
80 been noted to tolerate relatively high salinities with records in Chesapeake Bay in water as saline
81 as 21.8 psu and can thrive in estuaries (Fabrizio et al. 2018; Nepal and Fabrizio 2019). More
82 research on life history traits across the non-native range of Blue Catfish is needed. For example,
83 the food habits of this species are size-dependent, where the prevalence of fish in the diet
84 increases with Blue Catfish size (Schloesser et al. 2011; Schmitt et al. 2017, 2019a, 2019b).
85 Studies on individual growth dynamics over space and time can help managers prioritize control
86 efforts to areas where fish quickly or regularly reach sizes conducive to predation on species of
87 economic and ecological importance (e.g., blue crab *Callinectes sapidus* and *Alosa* spp.).

88 Studies suggest that while native Blue Catfish populations exhibit fast individual growth
89 (Graham 1999), fish from non-native populations can grow exceptionally fast (Bonvechio et al.
90 2011b; Greenlee and Lim 2011). Further, Blue Catfish have exhibited highly variable growth in

91 Virginia subestuaries of Chesapeake Bay (Greenlee and Lim 2011). Many studies on growth of
92 invasive species have compared growth of native and non-native populations with mixed results
93 (Kwak et al. 2006; Sakaris et al. 2006; Rypel 2014; Copp et al. 2016; Massie et al. 2018). These
94 mixed results may stem from temporal differences in growth as populations progress through the
95 process of invasion. The primary objective of this study was to evaluate how growth variability
96 is partitioned over space and time for an established invader. With an incomplete 15-year time
97 series of length-at-age observations, we examined growth of non-native Blue Catfish in four
98 rivers with different introduction histories. We evaluated six candidate models to improve our
99 understanding of growth variability, based on alternative hypotheses (Table 1) of growth
100 similarity over space and time, as well as differences over space, time, and space and time. We
101 hypothesized Blue Catfish growth would decline over time as the species became established.
102 Further, we assessed whether patterns in mean length-at-age were synchronous among river
103 systems. Another objective was to assess growth over time in comparison to native and non-
104 native populations to determine if inferences changed depending on which point in time was
105 used for comparisons. We expected growth would be faster than most populations early in the
106 time series, but closer to average as populations matured. We expand upon previous work by
107 Greenlee and Lim (2011) as we add eight years to the time series, examine growth variability
108 from a model selection approach, examine synchrony among rivers, and compare to other
109 populations. Other previous work examining growth rates in Virginia tributaries of Chesapeake
110 Bay have ignored spatial differences (Hilling et al. 2018) or focused on age-0 fish (Nepal and
111 Fabrizio 2020).

112 <A>Methods

113 *Study area.*—The Chesapeake Bay estuary is the largest in the United States and supports
114 numerous recreational and commercial fisheries, providing economic benefits to the region
115 (Houde 2006). However, nutrient pollution, heavy fishing pressure, habitat alteration, and
116 disease contributed to fishery collapses throughout the 1900s (Houde 2006; Schulte 2017).
117 Introductions of Blue Catfish in Virginia subestuaries of the Chesapeake Bay began in 1974 in
118 the Rappahannock River to provide new fisheries and later in the James (1975) and Mattaponi
119 (1985) rivers (Figure 1, Jenkins and Burkhead 1994). In the late 1980s, the species presumably
120 colonized the Pamunkey River from the Mattaponi River via their confluence that forms the

121 York River, which ultimately flows into Chesapeake Bay. After stockings ceased in the 1980s,
122 these populations showed a prolonged period of invasion reaching highest densities in the mid-
123 late 2000s (Orth et al. 2017; Bunch et al. 2018). Over the course of the invasion, individuals have
124 expanded to many other Chesapeake Bay tributaries in Virginia and Maryland (Schloesser et al.
125 2011; Bunch et al. 2018; Nepal and Fabrizio 2019).

126 *Data collection.*—We analyzed length-at-age data collected by Virginia Department of Game
127 and Inland Fisheries (VDGIF) from 2002 to 2016 to examine trends and variability in Blue
128 Catfish individual growth in the James, Mattaponi, Pamunkey, and Rappahannock rivers.
129 Personnel from VDGIF collected Blue Catfish using low-frequency electrofishing or high-
130 frequency electrofishing to monitor populations and collect biological data. All electrofishing
131 was conducted using a Smith-Root 9.0 GPP boat-mounted electrofishing unit. Low-frequency
132 electrofishing (15 pulses/sec, 340 or 680 V) was used to sample catfishes from late July to early
133 September in some years, but usually entirely in August to avoid reduced gear efficiency at
134 lower temperatures (Bodine and Shoup 2010). Fixed sampling sites were selected using a
135 modified-predator approach to target areas where large Blue Catfish were known to exist
136 (Vokoun and Rabeni 1999; Greenlee and Lim 2011). River bends associated with large drop offs
137 were selected for fixed sites as early surveys suggested they were preferred habitat for large Blue
138 Catfish. Sites selected were generally within the freshwater to oligohaline sections of these tidal
139 rivers, but salinities during sampling were as high as 11.8 psu. Sites were sampled from 2002 to
140 2016 for age information with not all rivers and sampling sites within rivers sampled annually.
141 Some sites were not sampled in all years due to reduced effectiveness of sampling gear due to
142 low ($< 100 \mu\text{S}/\text{cm}$) or high conductivity ($> 18,000 \mu\text{S}/\text{cm}$). A new electrofishing unit was used in
143 2014 collections that was prone to overloading when salinity exceeded approximately 2 psu. The
144 original electrofishing units were repaired for use in 2016 to avoid conductivity issues. High
145 frequency electrofishing (60–120 pulses/sec, 340–680 V) within the same time frames
146 supplemented low-frequency collections from the Rappahannock River, providing additional
147 large fish (Table 2). The total length (L_T , mm) of captured fish was measured and lapillar otoliths
148 were extracted to estimate ages (Long and Stewart 2010). A subsampling procedure was used to
149 reduce the number of fish within size groups for age analysis. Biologists randomly selected fish
150 from two size groups < 600 mm and fish ≥ 600 mm at each sampling site to reduce sample sizes
151 to a manageable number for laboratory procedures given high abundances of Blue Catfish in

152 these systems (Bunch et al. 2018; Fabrizio et al. 2018). A random subsample of fish < 600 mm
153 (generally $n = 30$) were sacrificed per site, as well as 25 to 100% of fish ≥ 600 mm, depending
154 on how many large fish were collected in an individual sampling run. The purpose of this
155 subsampling procedure was to ensure large individuals were well-represented in the sample due
156 to observed growth variability (Greenlee and Lim 2011). Otoliths were processed via the
157 protocol developed by (Buckmeier et al. 2002) with modifications described by Greenlee and
158 Lim (2011). We calculated the year class for all aged fish using assigned ages and collection
159 year.

160 *Data analysis.*— We examined growth dynamics in Virginia Blue Catfish using both growth
161 modeling in an information theoretic framework and hypothesis testing based on length-at-age
162 observations. We extended the von Bertalanffy growth function (VBGF) to nonlinear mixed
163 effect models to examine Blue Catfish growth during over a 15-year period in Virginia's tidal
164 rivers during the establishment and expansion phases of the invasion. Nonlinear mixed effects
165 models feature fixed and random effects with nonlinear parameters of the underlying model. We
166 used the three-parameter version of the von Bertalanffy growth function (Quinn and Deriso
167 1999; Haddon 2011). Because variance in length-at-age increases with age, we assumed length-
168 at-age (L_t) followed a multiplicative error structure (i.e., the natural logarithm of the model
169 produces normally-distributed, additive errors) as

$$170 \quad L_t = L_\infty(1 - e^{-k(t-t_0)})e^\varepsilon, \varepsilon \sim N(0, \sigma^2),$$

171 where L_∞ is the average maximum length, k is the Brody growth coefficient describing how
172 quickly L_∞ is reached, t is the age, and t_0 is the theoretical age when length is zero, and σ^2 is the
173 variance of the model residuals which are assumed to follow a normal distribution (Quinn and
174 Deriso 1999; Haddon 2011). We estimated L_∞ on a \log_e -scale to reduce the scale differences
175 among parameters to ease model convergence.

176 The VBGF as presented above can be extended to nonlinear mixed effect models to
177 incorporate variability over space and time (Ma et al. 2017). We used random effects to describe
178 growth within cohorts, sampling years, and rivers (Vincenzi et al. 2014), providing a convenient
179 methodology to efficiently estimate parameters that vary among numerous years and locations.
180 Further, preliminary exploration of the dataset suggested differences in growth exist among

181 cohorts through time. Length-at-age observations from single collection years show unusual
182 growth patterns due to seemingly faster growing older cohorts. The inclusion of random effects
183 in modeling efforts permitted grouping of correlated length-at-age observations. Further, this
184 provided an opportunity to develop multiple hypotheses and candidate models to explain growth
185 within and among these populations over time.

186 We developed six alternative hypotheses and corresponding models to better understand
187 the patterns in Blue Catfish growth over space and time (Table 1). We fitted Model 0 (assuming
188 similar growth over space and time) using nonlinear least squares regression. We fitted nonlinear
189 mixed effects models corresponding to alternative hypotheses using the nlmer function in the
190 lme4 package (Bates et al. 2015) in R version 3.1.3 (R Core Team 2015). Six candidate models
191 were examined with random effects of river, collection year, and cohort on L_{∞} and k (Table 1).
192 The t_0 parameter was not allowed to vary via random effects as we assumed differences in size
193 early in life among populations and over time were likely negligible. The VBGF fitted to all
194 length-at-age observations undifferentiated with respect to time and space (Model 0) was
195 compared to nonlinear mixed effects models. Model adequacy was assessed using the Akaike
196 Information Criterion with the small-sample-size correction (AICc), providing a criterion to rank
197 models (Hurvich and Tsai 1989; Burnham and Anderson 2002). Models were compared based on
198 AICc, where models with lower AICc values were considered superior to those with larger AICc
199 values (Guthery 2008).

200 Uncertainty surrounding von Bertalanffy parameters of nonlinear mixed effects models
201 was assessed using nonparametric bootstrapping (Thai et al. 2014). We sampled the original
202 dataset with replacement 500 times and fit nonlinear mixed effect models to the resampled
203 datasets. The 500 estimates for each parameter were summarized to estimate standard deviation,
204 95% confidence intervals (percentile method; Carpenter and Bithell 2000), and the coefficient of
205 variation for parameter estimates. Bootstrap sample sizes within random effects groupings were
206 based on sample sizes of the original data to ensure estimated of uncertainty were not influenced
207 by differences in the numbers of samples within groupings across bootstrap iterations.

208 As we used an information theoretic approach to determine which model best explained
209 variability in length-at-age, we wanted to statistically determine if trends existed over the study
210 period. We tested for trends in mean length-at-age over time using simple linear regression for

211 the ages 1, 4, 7, 10, and 13. This analysis allowed us to examine differences in length at like ages
212 for cohorts over time. We also examined the spatial synchrony of growth responses by
213 examining residuals from the linear trend test models discussed above. Using the residuals
214 allowed us to examine growth among rivers with the overall trends removed. Spatial synchrony
215 was assessed using the Pearson rank correlation test via pairwise river comparisons of residuals
216 from the regression of mean length-at-age and collection years. We were unable to examine
217 synchrony of age-1 growth in the James and Rappahannock rivers due to differences in sampling
218 schedules and a lack of age-1 fish in some years. Significance was assessed at $\alpha = 0.05$.

219 We examined growth differences between native and non-native Blue Catfish populations
220 to understand if non-native populations grow faster and how non-native Virginia populations
221 compare over time. We included studies based on otolith ages (as spines may underestimate
222 ages, Nash and Irwin 1999; Buckmeier et al. 2002; Olive et al. 2011) that presented fitted von
223 Bertalanffy growth models or mean length-at-age data from which a von Bertalanffy growth
224 model could be fitted. Excluding spine-based studies and those with different data types, we
225 examined 12 native populations and 3 non-native populations (Table 3), in addition to the 4 non-
226 native Virginia populations examined in the present study. Non-native populations from
227 Altamaha River, Georgia, USA and Lake Norman, North Carolina, USA were sampled 5 and
228 42–44 years after Blue Catfish was first reported, respectively. Records for Blue Catfish
229 introductions in Badin Lake, North Carolina, USA were unavailable (Dorsey et al. 2011). We
230 plotted the fitted models to see how interpretation of native and non-native growth comparisons
231 may differ over time for Virginia Blue Catfish.

232 <A>Results

233 A total of 9,650 Blue Catfish was sampled for age analysis from the James, Mattaponi,
234 Pamunkey, and Rappahannock rivers from 2002 to 2016. We analyzed the growth of 9,650 fish
235 from these four river systems over the 15-year period. Observed L_T ranged from 20 to 1330 mm.
236 The maximum observed age in the whole dataset was 25 years, but varied by river and year.
237 Maximum observed age within rivers increased over the sampling period in the James (simple
238 linear regression, $F = 113.6$, $df = 1,5$, $P < 0.001$), Mattaponi ($F = 245.2$, $df = 1,6$, $P < 0.001$), and
239 Pamunkey ($F = 337.2$, $df = 1,7$, $P < 0.001$) rivers, but not the Rappahannock River ($F = 0.7656$,
240 $df = 1,6$, $P = 0.4152$). Length-at-age was variable, differing by as much as 700 mm for individual

241 ages among the rivers examined. Sample sizes from respective rivers and sampling years are
242 provided in Table 2.

243 The best model describing established Blue Catfish growth patterns in Virginia's tidal
244 rivers featured river and cohort as random effects on the parameters L_{∞} and k (Model
245 River:Cohort), supporting hypothesis H₅. Hypothesis H₄ had the second most support, but the
246 corresponding model (Model River:Year) had a large Δ AICc when compared to the best model
247 (Δ AICc = 824.7). Models considering spatial and temporal differences in growth simultaneously
248 were superior to models considering spatial or temporal differences only (Table 4). The VBGF
249 without random effects (Model 0, hypothesis H₀) was inferior to all other models based on AICc
250 (more than 5,000 AICc units from the best model). Correlations in parameters from fitted models
251 indicated a negative correlation in L_{∞} and k .

252 We observed a decline in mean length-at-age through time, and greater variability for
253 older age classes (Figure 2). Similarly, predicted length-at-age from Model River:Year decreased
254 over time, and fit data well (Figure 3). Predicted length-at-age seemed to be similar at early ages
255 and diverged at older ages. However, seemingly random variability among cohorts was evident
256 when mean length-at-age is compared within ages within rivers (Figure 2). A decrease in L_{∞}
257 existed in the James River when examining cohorts, although temporal fluctuations were evident.
258 Other river systems exhibited modest declines. Estimates of k for Model River:Cohort tracked L_{∞}
259 as the two were generally negatively correlated. Older cohorts grew faster than more recent
260 cohorts leading to growth patterns with unreasonable estimates of L_{∞} . Further, truncated age
261 structures for more recently established populations (e.g., Pamunkey in 2003) or low sample
262 sizes (e.g., Rappahannock in 2004) could also contribute to large L_{∞} estimates. An increase in L_{∞}
263 toward the end of the time series for Model River:Cohort was likely an artifact of sampling fish
264 not yet old enough to exhibit ontogenetic declines in individual growth rate, whereas increases
265 early in the time series likely indicate greater availability of larger fish in subsequent years as
266 populations matured.

267 The trend analysis using simple linear regression revealed significant negative trends in
268 length-at-age for most ages and rivers from 2002–2016 (Table 5). Mean length-at-age declined
269 significantly for all ages examined (1,4,7, 10, and 13) in the James, Mattaponi, and Pamunkey
270 rivers. However, we did not detect significant declines for ages 1 and 4 in the Rappahannock

271 River. We made 28 pairwise comparisons to assess synchrony among rivers. Due to differences
272 in sampling schedules, correlations were based on 4 to 7 years of data points depending on the
273 rivers compared. Synchrony was only detected in a few cases (James/Rappahannock-age 4,
274 Mattaponi/Rappahannock-age 4, Pamunkey/Rappahannock-age 7, Mattaponi/Pamunkey-age 10,
275 Pamunkey/Rappahannock-age 10).

276 Visual examination of native and non-native Blue Catfish fitted von Bertalanffy models
277 indicated substantial variability existed among native populations (Figure 4). Non-native
278 populations exhibited growth trajectories in the middle of the native population range or greater.
279 The Rappahannock River in 2016 exhibited the slowest growth among non-native populations
280 examined. Non-native populations from the Altamaha River and Badin Lake grew faster than
281 most native populations and generally faster than Virginia non-native populations. Lake Norman,
282 however, appears to have unremarkably fast or slow growth compared to other populations.

283 <A>Discussion

284 Growth of Blue Catfish differed among cohorts and rivers with some significant declines
285 in length-at-age during the establishment and expansion phases of the invasion. Consequently,
286 comparing growth of invasive species within their native and non-native range appears to be
287 more complicated than often presented. Frequently, scientists are interested in whether non-
288 native populations grow more quickly than those in the native range. In some cases, non-native
289 species grow faster than native species (Kwak et al. 2006, Sakaris et al. 2006) and other cases
290 native populations grow faster (Copp et al. 2004; Copp et al. 2016) or there is no difference
291 (Rypel 2014). Changes in growth over time may make comparisons only applicable during the
292 time period in which data were collected and contribute to the mixed results observed. In the
293 present study, growth transitioned from being faster than many native populations to a state
294 where it was average or below average compared to native populations. Kwak et al. (2006)
295 reported slower growth from more recent cohorts of Flathead Catfish *Pylodictis olivaris* and
296 suggested declines in growth may be related to resource depletion during establishment.
297 Conversely, Kaeser et al. (2011) observed differences in growth over time with faster growth
298 later in their study period. Massie et al. (2018) reported no influence of time since introduction
299 on Flathead Catfish growth, but suspected their study lacked populations that were introduced
300 recently enough to observe a difference. Considering the time since introduction of populations

301 may be important when comparing growth of invasive species to avoid making conclusions that
302 may not apply over time. However, this topic requires further study to understand interactions of
303 growth dynamics, environmental factors, and native status.

304 We found a reduction in length-at-age as populations matured in the James, Mattaponi
305 and Pamunkey rivers. Our results are consistent with other studies examining non-native species,
306 where growth and body sizes were reduced in older populations (Young et al. 2010; Gutowsky
307 and Fox 2011; Feiner et al. 2012; Brandner et al. 2018). Density dependent factors are known to
308 reduce growth rates of fishes (Ryman and Myers 1992; Bohlin et al 2002) and may contribute to
309 the observed declines in the present study. Two studies in Virginia tidal rivers reported Blue
310 Catfish growth was negatively correlated with indices of relative abundance (Greenlee and Lim
311 2011; Nepal and Fabrizio 2020). Mean length-at-age appears to level off for ages 4, 7, and 10
312 around the time estimated biomass stabilized in an unpublished study by Orth et al. (2017).
313 However, a study on Channel Catfish *Ictalurus punctatus* reported growth was density
314 independent when controlling for environmental factors in Mississippi, USA floodplain rivers
315 (Shephard and Jackson 2009). Fishing can also influence growth as populations optimize life
316 history traits in response to elevated mortality rates (van Walraven 2010; Enberg et al. 2012).
317 Reported commercial catfish harvest in Virginia has doubled since 1993 to over 1000 tonnes in
318 2016 (Orth et al. 2017). However, opportunities to evaluate the role of exploitation are limited as
319 available harvest data lack size information, estimates of recreational harvest, and species
320 reporting prior to 2010. Further, as sampling was conducted in habitats preferred by large
321 individuals, study-induced mortality from otolith collection may also present a selective
322 pressure. It seems plausible that density dependence, as well as fishing and study-induced
323 mortality has contributed to the observed changes in growth, but currently available data lack
324 utility to evaluate their influences. As we generally were unable to detect synchrony in growth
325 dynamics among rivers, system-specific factors may be more influential than region-scale
326 environmental processes. Spatial growth dynamics may be related to differences in population
327 demographics due to differences in introduction history.

328 We detected declines in growth over time, as well as differences among rivers. The
329 Rappahannock River was the only system to have age classes where significant declines in
330 growth rates were not detected. Examination of biomass estimates supported that biomass

331 stabilized earliest in the Rappahannock among the James, Rappahannock, and York rivers (Orth
332 et al. 2017). The Rappahannock generally had the slowest growth among the four rivers
333 examined. For many of the temporal comparisons of younger age classes, mean length-at-age in
334 the James, Mattaponi, and Pamunkey rivers stabilized following the mid-2000s, when it is
335 believed abundances peaked in the James River (Bunch et al. 2018). Differences among rivers
336 may also be related to river productivity, however, the Rappahannock River is more productive
337 than the York River (Nesius et al. 2007). The Chesapeake Bay and many of its tributaries are
338 highly productive due to human land use practices leading to eutrophication (Kemp et al. 2005)
339 and likely contributed to Blue Catfish's successful establishment (Bauer 2012). However, more
340 productive rivers (Rappahannock and James, Nesius et al. 2007) were stocked first and have the
341 highest abundances (Orth et al. 2017), making disentangling biotic and abiotic influences on
342 Blue Catfish growth difficult.

343 We observed wide variability in individual growth among and within cohorts. For
344 instance, length ranged more than 500 mm for age-12 Blue Catfish from the 1998 cohort in the
345 James River. Other studies have also observed wide variability in Blue Catfish growth among
346 and within populations (Mauck and Boxrucker 2004; Boxrucker and Kuklinski 2006). Wide
347 variability in length-at-age prompted Greenlee and Lim (2011) to declare that age-length keys
348 were not valuable for these populations. Variability in growth could stem from several factors
349 including sex, dietary variability or habitat. In terms of sex, male Blue Catfish have been
350 reported to grow larger than females (Marshall et al. 2009). Diets of Blue Catfish are highly
351 variable, as the species appears to function as an opportunistic omnivore in these subestuaries
352 (Schmitt et al. 2017, 2019b). Further, tidal rivers are dynamic systems at the interface of
353 freshwater and marine environments (Hoitnik and Jay 2016) and habitats with flowing currents
354 and optimal temperatures may promote greater growth rates (Rypel 2011). In addition, stress
355 from increased salinity during summertime may reduce growth in fish occupying downstream
356 reaches of these rivers. Electrofishing's reduced effectiveness in high conductivity water limited
357 the present study to less saline portions of these subestuaries (Warry et al. 2013; Schmitt et al.
358 2019a), so we could not assess growth differences within rivers. Understanding growth patterns
359 over this gradient of environmental conditions could improve our understanding of factors
360 influencing Blue Catfish growth. However, Blue Catfish are highly mobile with variable
361 movement patterns among individuals (Timmons 1999; Garrett and Rabeni 2011; Tripp et al.

2011; Tuckey et al. 2017) and inferences based on collection site conditions may be confounded by conditions at other utilized habitats. Future work should consider tag-recapture studies to explore drivers and consequences of individual variation in growth (Punt et al. 2016).

This study adds to the literature base on invader life history over time by considering growth differences over space and time for populations with different introduction histories. The time series and spatial extent of this study exceeds those of many other studies on non-native life history changes. We recommend consideration of introduction history when comparing native and non-native life history traits, as life history characteristics for non-native populations appear to vary temporally. We recommend evaluations of invasive species control measures include sensitivity analyses, as life history may change during establishment or in response to control strategies (Bonvechio et al. 2011a). Further, future work would benefit from estimates of abundance, as well as collection of more detailed information on harvest (commercial, recreational, or removal efforts) and environmental variables to improve our understanding of invasion ecology and shifts in life history during an invasion.

<A>Acknowledgements

We thank Virginia Department of Game and Inland Fisheries for funding this project and their efforts to collect and organize data. We thank Virginia Sea Grant for student support of C.D. Hilling through a Graduate Research Fellowship. We also thank P. L. Angermeier, M. C. Fabrizio, P. H. Michaletz, T. J. Kwak, the associate editor, and two anonymous reviewers for their thoughtful comments that vastly improved the quality of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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665 TABLE CAPTIONS

666 TABLE 1. Alternative hypotheses and associated candidate models describing variability in
 667 growth for Blue Catfish *Ictalurus furcatus* collected from 2002 to 2016 in four tidal tributaries of
 668 the Chesapeake Bay in Virginia. Candidate models are the von Bertalanffy growth model
 669 (VBGF) extended to nonlinear mixed-effect models, where random effects (RE) of collection
 670 year (year), cohort, and river on parameters of the VBGF (L_{∞} and k) are used to examine growth
 671 differences over space and time.

Hypothesis	Explanation	Model	Model description
H ₀	Similar growth over space/time	Model 0	No RE
H ₁	Growth varies by river	Model River	River as RE of L_{∞} & k
H ₂	Growth varies by year	Model Year	Year as RE of L_{∞} & k
H ₃	Growth varies by cohort	Model Cohort	Cohort as RE of L_{∞} & k
H ₄	Growth varies by river & year	Model River:Year	Year & river as RE of L_{∞} & k
H ₅	Growth varies by river & cohort	Model River:Cohort	Cohort & river as RE of L_{∞} & k

672

673 TABLE 2. Rivers and years sampled for Blue Catfish *Ictalurus furcatus* otoliths from four
 674 Virginia tidal rivers from 2002 to 2016. Numbers indicate sample sizes, whereas the number of
 675 sampling sites are given in parentheses. Blue Catfish were collected exclusively using low-
 676 frequency electrofishing, except where an * indicates low-frequency samples were supplemented
 677 with high-frequency electrofishing.

Year	James	Mattaponi	Pamunkey	Rappahannock
2002	330 (11)	178 (6)	150 (7)	245* (6)
2003	0	175 (9)	362 (10)	0
2004	216 (5)	130 (4)	187 (4)	126* (2)
2005	0	0	300 (7)	410* (6)
2006	536 (11)	304 (7)	333 (9)	0
2007	0	0	0	230* (6)
2008	470 (10)	266 (7)	287 (9)	0
2009	0	0	0	383* (7)
2010	445 (11)	0	357 (10)	0
2011	0	254 (7)	0	355 (9)
2014	372 (9)	207 (7)	422 (10)	307 (10)
2016	458 (13)	266 (7)	284 (8)	305 (9)

679

680 TABLE 3. Blue Catfish *Ictalurus furcatus* populations considered in examination of range-wide
 681 growth. Parameters from the von Bertalanffy growth model (L_{∞} mm, k yr⁻¹, and t_0 yr) taken from
 682 listed references (or estimated from mean total length-at-age as Bonvechio *et al.* 2011).

Location	Status	L_{∞}	k	t_0	Reference
Eufaula Lake, OK	Native	622	0.091	-2.526	Boxrucker and Kuklinski 2006
Hugo Lake, OK	Native	512	0.214	-0.677	Boxrucker and Kuklinski 2006
Kaw Lake, OK	Native	853	0.136	-0.151	Boxrucker and Kuklinski 2006
Keystone Lake, OK	Native	860	0.133	-0.919	Boxrucker and Kuklinski 2006
Lake Ellsworth, OK	Native	898	0.063	-0.665	Boxrucker and Kuklinski 2006
Lake Texoma, OK	Native	964	0.077	-1.843	Boxrucker and Kuklinski 2006
Waurika Lake, OK	Native	1050	0.095	0.114	Boxrucker and Kuklinski 2006
Ft. Loudoun Reservoir, TN	Native	1105	0.044	-1.227	Stewart et al. 2009
Kentucky Lake, TN	Native	940	0.126	-1.217	Stewart et al. 2009
Lake Barkley, TN	Native	1115	0.110	-0.693	Stewart et al. 2009
Mississippi River, TN	Native	830	0.145	-1.019	Stewart et al. 2009
Lake Wilson, AL	Native	1303	0.081	-0.243	Holley et al. 2009
Altamaha River, GA	Non-native	745	0.238	-0.367	Bonvechio et al. 2011
Badin Lake, NC	Non-native	1028	0.138	-0.239	Dorsey et al. 2011
Lake Norman, NC	Non-native	939	0.094	-0.880	Dorsey et al. 2011

683
 684 TABLE 4. Model rankings using Akaike information criterion (AICc) for the von Bertalanffy
 685 growth function (Model 0) and its extension to nonlinear mixed models with random effects of
 686 river, collection year, and cohort fitted to 9,377 Blue Catfish *Ictalurus furcatus* total length-at-
 687 age observations in four Virginia tidal rivers collected from 2002 to 2016.

Rank	Model	AIC _c	ΔAIC _c
1	Model River:Cohort	-6844.6	0
2	Model River:Year	-6019.9	824.7
3	Model Year	-3888.5	2956.1
4	Model River	-3621.5	3223.1
5	Model Cohort	-2845.6	3999.0
6	Model 0	-1570.1	5274.5

688
 689 TABLE 5: Slopes and P-values from simple linear regression examining trends in length-at-age
 690 (ages 1, 4, 7, 10, and 13) over collection years (2002–2016) for Blue Catfish *Ictalurus furcatus* in
 691 four Virginia subestuaries of the Chesapeake Bay.

Age	James	Mattaponi	Pamunkey	Rappahannock

1	-1.28, $P = 0.006$	-2.53, $P < 0.001$	-1.77, $P < 0.001$	-0.47, $P = 0.165$
4	-2.04, $P = 0.005$	-2.79, $P < 0.001$	-6.34, $P < 0.001$	0.60, $P = 0.270$
7	-8.47, $P < 0.001$	-11.83, $P < 0.001$	-14.70, $P < 0.001$	-3.09, $P = 0.026$
10	-15.23, $P < 0.001$	-18.35, $P < 0.001$	-18.99, $P < 0.001$	-11.34, $P < 0.001$
13	-15.03, $P < 0.001$	-23.30, $P < 0.001$	-26.67, $P < 0.001$	-7.49, $P = 0.061$

693

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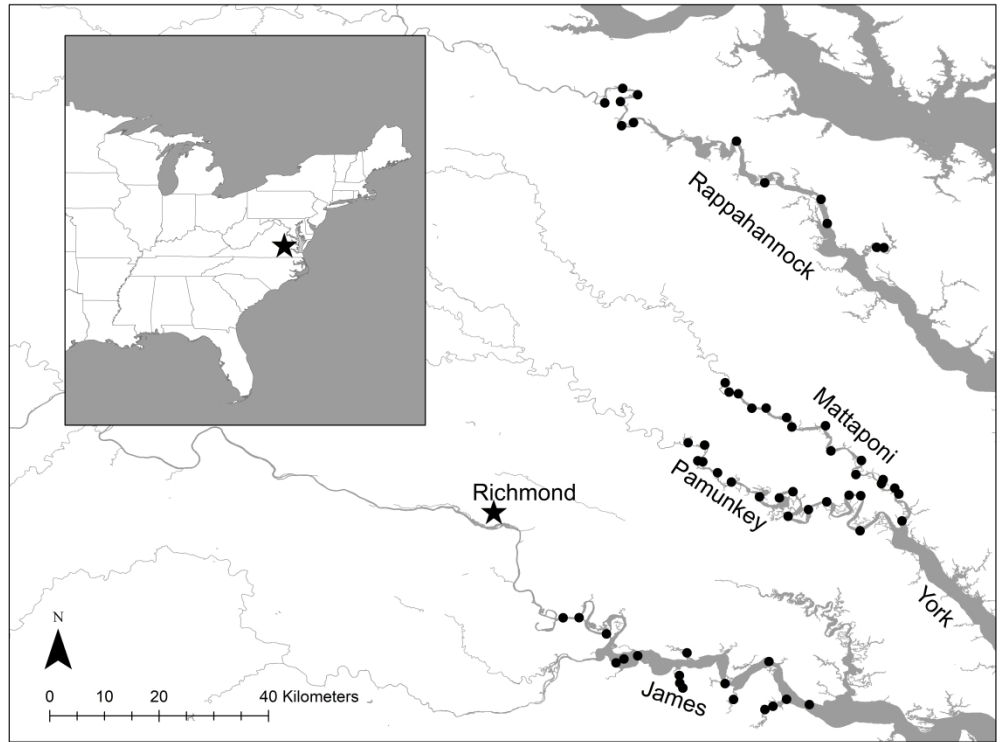


FIGURE 1. Major Chesapeake Bay tributaries in Virginia with electrofishing sites for Blue Catfish *Ictalurus furcatus* otolith collections (black circles) from 2002 to 2016. The inset depicts where the study area is located in the eastern United States related to Richmond, Virginia (black star).

304x228mm (600 x 600 DPI)

Hilling_et_al_Figure 2

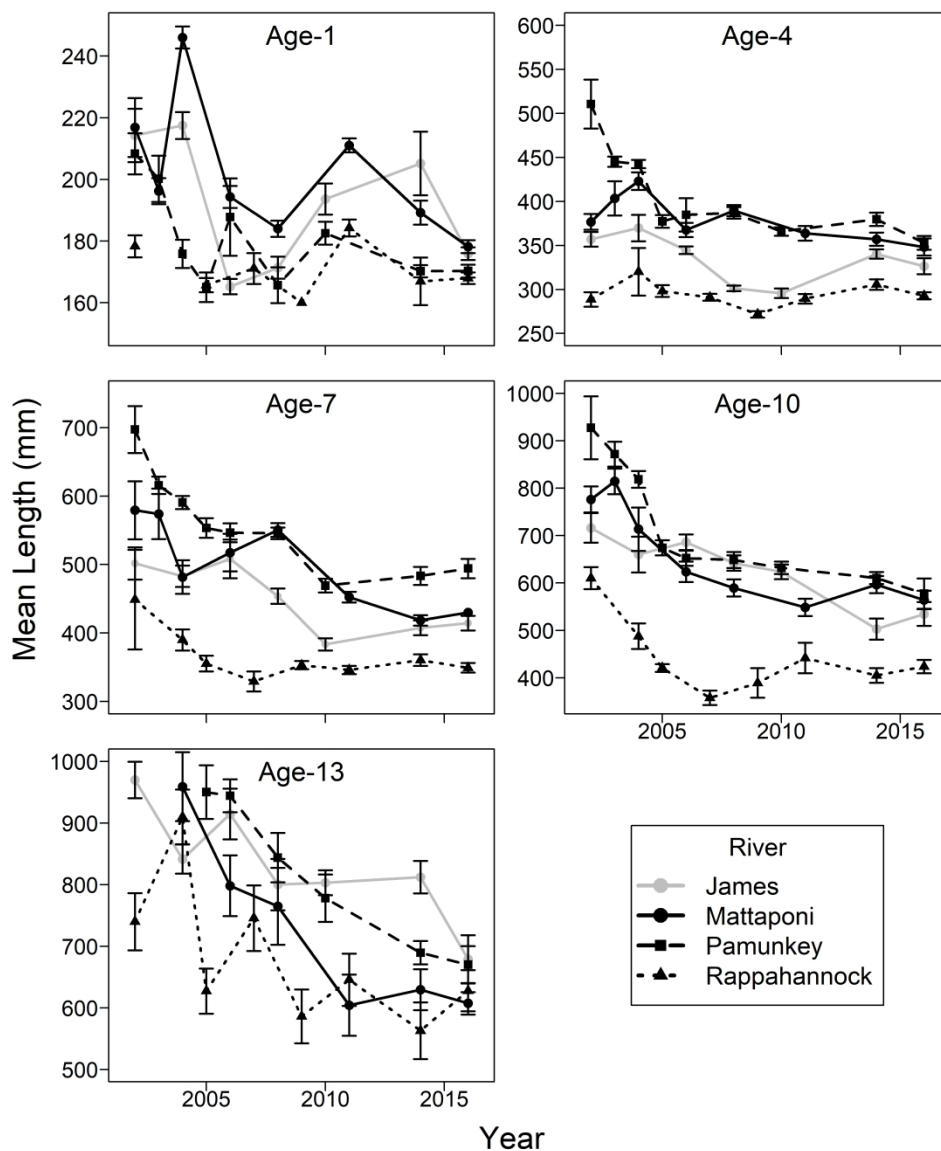
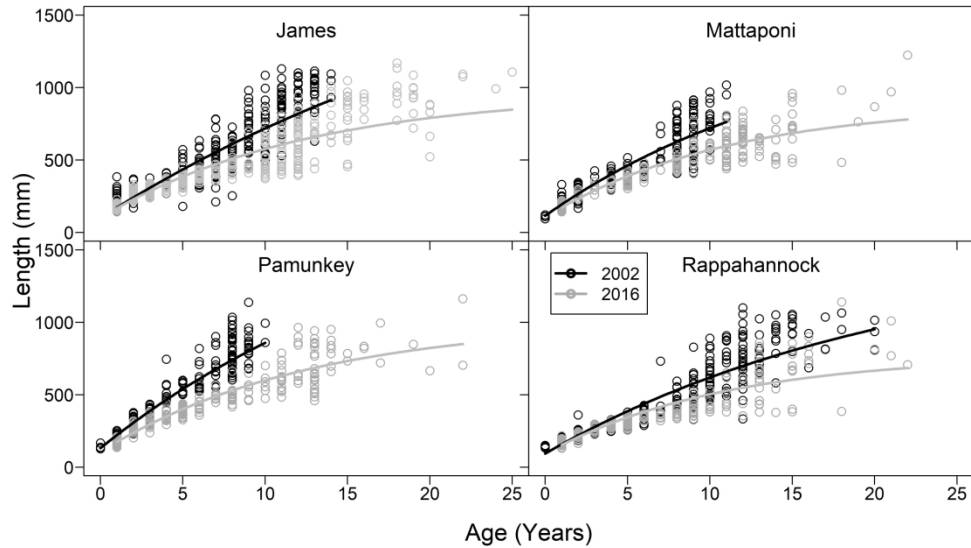


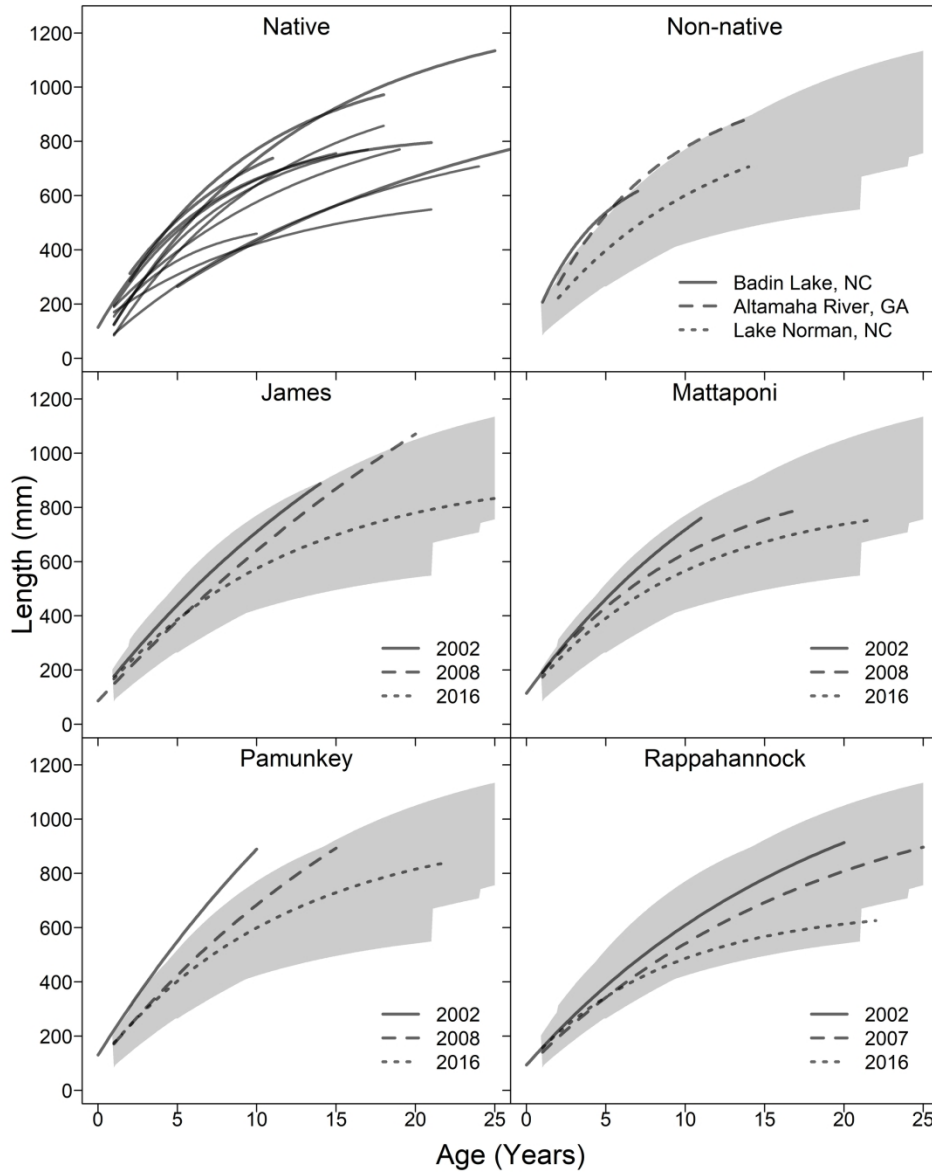
FIGURE 2. Mean total length-at-age for Blue Catfish *Ictalurus furcatus* collected using boat electrofishing from 2002 to 2016 in four Virginia, USA tidal rivers for ages 1, 4, 7, 10, and 13. Ages were assigned from sectioned otoliths. Error bars represent standard errors.

190x228mm (600 x 600 DPI)



Predicted Blue Catfish *Ictalurus furcatus* total length-at-age (lines) and individual length-at-age observations (circles) for four Virginia, USA tidal rivers using a von Bertalanffy growth model extended to nonlinear mixed-effect model with random effects of river and year from fish collected in 2002 and 2016. Horizontal extent of lines reflects observed ages.

247x139mm (300 x 300 DPI)



Comparison of Blue Catfish *Ictalurus furcatus* total length-at-age among native, non-native, and Virginia, USA non-native populations over time (James, Mattaponi, Pamunkey and Rappahannock rivers). Lines represent fitted von Bertalanffy models within the extent of observed ages. Shaded area indicates the range of fitted curves from the native populations.

203x254mm (300 x 300 DPI)