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Spatial Variability and Macro-Scale Drivers of Growth for Native and Introduced Flathead Catfish Populations

Danielle L. Massie*

Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 413 Forest Resources Building, University Park, Pennsylvania 16802, USA

Geoffrey D. Smith

Pennsylvania Fish and Boat Commission, Bureau of Fisheries, Division of Fisheries Management, 1601 Elmerton Avenue, Harrisburg, Pennsylvania 17106, USA

Timothy F. Bonvechio

Georgia Department of Natural Resources, Wildlife Resources Division, Post Office Box 2989, Waycross, Georgia 31502-2089, USA

Aaron J. Bunch

Virginia Department of Game and Inland Fisheries, 3801 John Tyler Memorial Highway, Charles City, Virginia 23030, USA

David O. Lucchesi

South Dakota Department of Game, Fish, and Parks, 4500 South Oxbow Avenue, Sioux Falls, South Dakota 57106, USA

Tyler Wagner

U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, 402 Forest Resources Building, University Park, Pennsylvania 16802, USA

Abstract
    Quantifying spatial variability in fish growth and identifying large-scale drivers of growth are fundamental to many conservation and management decisions. Although fish growth studies often focus on a single population, it is becoming increasingly clear that large-scale studies are likely needed for addressing transboundary management needs. This is particularly true for species with high recreational value and for those with negative ecological consequences when introduced outside of their native range, such as the Flathead Catfish *Pylodictis olivaris*. This study quantified growth variability of the Flathead Catfish across a large portion of its contemporary range to determine whether growth differences existed between habitat types (i.e., reservoirs and rivers) and between native and introduced populations. Additionally, we investigated whether growth parameters varied as a function of latitude and time since introduction (for introduced populations). Length-at-age data from 26 populations across 11 states in the USA were modeled using a Bayesian hierarchical von Bertalanffy growth model. Population-specific growth trajectories revealed large variation in Flathead Catfish growth and relatively high uncertainty in growth parameters for some populations. Relatively high uncertainty was also evident when comparing populations and when quantifying large-scale patterns. Growth parameters (Brody growth coefficient [K] and theoretical maximum average length [L_∞]) were not different (based on

overlapping 90% credible intervals) between habitat types or between native and introduced populations. For populations within the introduced range of Flathead Catfish, latitude was negatively correlated with K. For native populations, we estimated an 85% probability that L_∞ estimates were negatively correlated with latitude. Contrary to predictions, time since introduction was not correlated with growth parameters in introduced populations of Flathead Catfish. Results of this study suggest that Flathead Catfish growth patterns are likely shaped more strongly by finer-scale processes (e.g., exploitation or prey abundances) as opposed to macro-scale drivers.

The growth of individuals is fundamental for ecological processes related to survival, reproductive potential, life span, and population dynamics (Hoenig 1983; Lester et al. 2004; Charnov 2008; Charnov et al. 2013). Knowledge on the growth of fishes is therefore essential for understanding the productivity and dynamics of populations (Quinn and Deriso 1999) and can be used to help evaluate the efficacy of different management strategies (Isermann et al. 2007). Because growth is a function of a variety of abiotic influences (e.g., temperature), biotic influences (e.g., prey availability), and evolutionary processes (Conover et al. 2005), it is common for intraspecific spatial variability in growth to occur (Helser and Lai 2004). Identifying the drivers of spatial variability could help to predict how species and ecosystems may respond to environmental change. In addition, the introduction of fishes across the landscape is increasingly common and often has negative ecological consequences for native aquatic communities (Echelle and Connor 1989; Zambrano et al. 1999; Green et al. 2012; Love and Newhard 2012). Quantifying the spatial variability in growth of a species within both its native and introduced ranges and understanding large-scale growth patterns may provide further insight into how a species might respond to future introductions or range expansions made possible by changing environmental conditions.

Flathead Catfish *Pylodictis olivaris* are native to the Mississippi River, Mobile River, and Rio Grande drainages and the Laurentian Great Lakes region (Fuller et al. 1999; Jackson 1999). Flathead Catfish are popular among anglers due to their aggressive nature, potential to reach large sizes, and pleasing taste (Layher and Boles 1980; Jackson 1999). These fish have been introduced into many Atlantic coast rivers and areas of the western USA (Fuller 2017). Flathead Catfish are, in most cases, intentionally stocked by state agencies or illegally introduced by anglers. However, some speculate that migrations into new areas have occurred (e.g., Apalachicola River, Florida; Fuller et al. 1999). Once introduced, Flathead Catfish are usually able to establish viable populations outside their native range (Guier et al. 1984; Dobbins et al. 1999; Fuller et al. 1999). The species' characteristics, such as its long life span, early maturation, high salinity tolerance, and lack of predators, often contribute to success in new territories (Munger et al. 1994; Bringolf et al. 2005;

Marshall et al. 2009; Bonvechio et al. 2016). Introduced Flathead Catfish populations often have detrimental effects on native fauna (Guier et al. 1984; Thomas 1995; Pine et al. 2007; Bonvechio et al. 2009), even more so than introduced Blue Catfish *Ictalurus furcatus* (Guier et al. 1984; Schmitt et al. 2017). In fact, Fuller et al. (1999) suggested that Flathead Catfish introductions were the "most biologically harmful of all fish introductions in the US." Diet studies have revealed that Flathead Catfish are primarily piscivorous as adults (Minckley and Deacon 1959; Jolley 2005; Schmitt et al. 2017); this, coupled with their ability to reach large sizes, creates a complex problem for managers interested in preserving native fauna.

Understanding growth variation of Flathead Catfish is especially important given their popularity as a sport fish, widespread introduction outside their native range, and negative effects on native fish populations. Numerous studies have quantified the species' growth rates; however, those studies only focused efforts on single populations (Mayhew 1969; Grabowski et al. 2004; Daugherty and Sutton 2005; Marshall et al. 2009) or multiple populations from a limited spatial extent of their contemporary geographic range (Young and Marsh 1990; Kwak et al. 2006; Sakaris et al. 2006; Kaesar et al. 2011; Bonvechio et al. 2016). Previous studies of Flathead Catfish have shown that growth is variable among populations (Kwak et al. 2006; Sakaris et al. 2006; Kaesar et al. 2011; Rypel 2011; Bonvechio et al. 2016). For example, introduced populations are generally thought to grow faster than native populations (Kwak et al. 2006; Sakaris et al. 2006). However, it is unclear whether latitudinal gradients in growth exist for native and introduced Flathead Catfish populations, since latitude can be used to index temperature, which is one of the most influential variables affecting fish growth (Jobling 1981). Although primarily a riverine species, Flathead Catfish are also found in lentic or reservoir habitats (Jackson 1999). Several studies have evaluated Flathead Catfish growth differences between lentic and lotic waterbodies, with varying results (Kwak et al. 2006; Jolley and Irwin 2011; Rypel 2011). Kwak et al. (2006) found that reservoir populations grew faster than river populations, while Rypel (2011) found no difference between lentic and lotic populations.

The goal of this study was to quantify the spatial variability in Flathead Catfish growth rates throughout a large

portion of its contemporary range. By increasing the spatial extent of the area being studied and synthesizing data from multiple populations, meta-analysis results can highlight broad-scale growth patterns that can be used to help guide fisheries management and conservation efforts. Only a few large-scale studies of fish growth have occurred (e.g., Largemouth Bass *Micropterus salmoides*: Helser and Lai 2004; various catfish: Rypel 2011; Southern Flounder *Paralichthys lethostigma*: Midway et al. 2015), and currently no studies have quantified Flathead Catfish growth across much of the species' present geographic range. Our specific objectives were to (1) describe spatial variability in growth between river and reservoir populations; (2) describe spatial variability in growth between native and introduced populations; and (3) investigate potential drivers of spatial variability, including latitudinal gradients and time since introduction (for introduced populations).

METHODS

Data Collection

Length-at-age data (TL [mm] and age [years]) for 26 Flathead Catfish populations were compiled from peer-reviewed literature and state agency surveys (Table 1). The data assemblage included information from 18 rivers and 8 reservoirs across 11 states in the USA (Figure 1). Of the 26 populations, 13 populations were within the native range and 13 populations were from waterbodies outside the native range (hereafter, "introduced range"; Fuller et al. 1999). The Mississippi River, Mississippi, and James River, Virginia, populations were sampled at multiple locations that are geographically isolated, and, in the case of the James River, exhibit different salinity regimes. Therefore, data from these two rivers were treated separately and split into "upper" and "lower" populations. Flathead Catfish were sampled with a variety of gear types; however, the majority of studies used electrofishing (Table 1). All fish were aged using pectoral spines or lapillus otoliths (Long and Stewart 2010). Although otoliths have been shown to provide better age estimates for older fish (≥5 years; Nash and Irwin 1999), we presumed that studies using pectoral spines provided reasonable age estimates (Jackson et al. 2008). Furthermore, only about 15% of the fish were aged using pectoral spines. The number of fish sampled from each population ranged from 13 to 1,518 individuals, and sampling took place between 1996 and 2017.

Growth Modeling

To quantify spatial variability in Flathead Catfish somatic growth, we utilized methods similar to those of Midway et al. (2015). The von Bertalanffy growth equation was incorporated into a Bayesian nonlinear

hierarchical modeling framework as follows:

$$y_{ij} = L_{\infty j}\left[1 - e^{(-K_j(t_{ij} - t_{0j}))}\right] + \epsilon_{ij}, \qquad \epsilon_{ij} \sim N\left(0, \sigma^2\right)$$

$$\log\begin{pmatrix} L_{\infty j} \\ K_j \end{pmatrix} \sim \text{BVN}(\mu, \Sigma),$$

$$\mu = \log(\overline{L}_\infty, \overline{K}),$$

$$t_{0j} \sim N(\overline{t}_0, \sigma_{t_0}^2),$$

where y_{ij} is the TL for fish i from population (i.e., river or reservoir) j; t_{ij} is the observed age for fish i from population j; and $L_{\infty j}$, K_j, and t_{0j} are the population-specific von Bertalanffy growth parameters. The parameter L_∞ refers to the asymptotic length or theoretical maximum average length; K is the Brody growth coefficient (hereafter, "growth coefficient"), which describes how quickly mean lengths at age approach L_∞; and t_0 is the hypothetical age (years) when length is equal to zero. Growth parameters K and L_∞ were estimated on the loge scale in order to reduce scale differences between parameters, thus improving model convergence, and were assumed to come from a bivariate normal distribution (BVN) with a grand mean μ and a variance–covariance matrix Σ; t_{0j} was assumed to come from a normal distribution with mean $\overline{t}_0$ and among-population variance $\sigma_{t_0}^2$. The population average parameters $(\overline{L}_\infty, \overline{K}, \text{and } \overline{t}_0)$ describe the growth curve across the entire data set. The residual error term ϵ_{ij} was assumed to come from a normal distribution with a mean of zero and a variance σ^2. In an effort to explain spatial variability in L_∞ and K, we added covariates as follows:

$$\log\begin{pmatrix} L_{\infty j} \\ K_j \end{pmatrix} =$$

$$\begin{pmatrix} \gamma_0^{L_\infty} + \gamma_1^{L_\infty} \times Covariate_j + \cdots \gamma_n^{L_\infty} \times Covariate_n \\ \gamma_0^K + \gamma_1^K \times Covariate_j + \cdots \gamma_n^K \times Covariate_n \end{pmatrix},$$

where γ_0^x and γ_1^x are the intercepts and slopes, respectively, of the growth parameter–covariate relationship. All continuous covariates were standardized prior to analysis.

Models were fitted using JAGS version 3.3.0 software (Plummer 2003) called from the programming environment R (R Development Core Team 2017) via the "r2-jags" package (Su and Yajima 2012). Three Markov chains were run, beginning at different starting values. The chains ran for 100,000 iterations, 50,000 of which were discarded as burn-in. Diffuse normal priors were used for slope and intercept parameters ($\overline{t}_0$, γ_0^x, and γ_1^x), and a diffuse uniform prior was used for σ and σ_{t0}. The variance–covariance matrix Σ was modeled using the scaled inverse-Wishart distribution (Gelman and Hill 2007). Model convergence was visually assessed through posterior distribution trace plots but was also confirmed through the use

TABLE 1. Description of populations used in the Flathead Catfish growth meta-analysis (ID = index number for the population [corresponds to population number in Figure 1]; status = native or introduced [introduced populations include the year of estimated introduction in parentheses]; n = number of fish sampled; gear type = sampling gear used [STE = standard electrofishing; LFE = low-frequency electrofishing; TRL = trotlines; REA = recreational angling; HPN = hoop nets; BKP = bank poles; GLN = gill nets]; aging method = structure used to age fish).

ID	Waterbody	State	Status	n	Sample year(s)	Gear type	Aging method	Range of TLs (mm)	Age range (years)
1	Altamaha River	GA	Introduced (1980[a])	262	2000	STE	Otoliths	122–1,299	1–16
2	Apalachicola River	FL	Introduced (1982[b])	474	2005–2006	REA	Otoliths	390–1,070	3–15
3	Cedar River	IA	Native	1,017	2004–2009	TRL, HPN, BKP, LFE	Otoliths	69–821	1–8
4	Des Moines River	IA	Native	866	2004–2009	TRL, HPN, BKP, LFE	Otoliths	64–945	1–8
5	Iowa River	IA	Native	1,518	2004–2009	TRL, HPN, BKP, LFE	Otoliths	87–840	1–8
6	Kansas River	KS	Native	571	2005–2006	LFE	Spines	118–1,191	1–21
7	Lake Buchanan	TX	Native	13	2000	GLN	Spines	433–771	2–9
8	Lake Lyndon B. Johnson	TX	Native	14	2000	GLN	Spines	380–620	1–4
9	Lake Marion	SC	Introduced (1964[c])	39	2004–2006	GLN, LFE	Otoliths	173–1,060	1–26
10	Lake Meredith	TX	Native	14	2000	GLN	Spines	490–920	4–15
11	Lake Mitchell	SD	Introduced (2007[d])	259	2013–2015	LFE	Spines	140–978	1–13
12	Lake Moultrie	SC	Introduced (1964[c])	47	2004–2006	GLN, LFE	Otoliths	193–1,094	2–19
13	Lake Palestine	TX	Native	194	2014	LFE	Otoliths	215–1,312	1–32
14	Lake Travis	TX	Native	15	2000	GLN	Spines	400–893	2–9
15	Little Pee Dee River	SC	Introduced (1980[e])	295	2014–2015	LFE	Otoliths	70–1,192	1–26
16	Llano River	TX	Native	55	2014–2015	STE	Otoliths	145–1,018	1–13
17	Lower James River	VA	Introduced (1977[f])	584	1997–2015	LFE	Otoliths	96–1,096	1–15
18	Lower Mississippi River	MS	Native	239	1996–2000	LFE, HPN	Spines	193–848	1–11
19	Lumber River	NC	Introduced (1995[g])	36	2005–2006	LFE	Otoliths	124–965	0–12
20	Northeast Cape Fear River	NC	Introduced (1975[g])	94	2005–2006	LFE	Otoliths	123–1,150	1–17
21	Neuse River	NC	Introduced (1985[g])	114	2005–2006	LFE	Otoliths	150–1,165	1–14
22	North Raccoon River	IA	Native	905	2004–2009	TRL, HPN, BKP, LFE	Otoliths	67–920	1–8
23	Satilla River	GA	Introduced (1994[h])	549	2014–2015	LFE	Otoliths	133–1,215	1–12
24	Susquehanna River	PA	Introduced (2002[i])	135	2016–2017	HPN	Otoliths	386–1,115	2–17
25	Upper James River	VA	Introduced (1983[f])	244	2015	LFE	Otoliths	126–1,060	1–28
26	Upper Mississippi River	IA	Native	456	2000–2009	LFE	Spines, otoliths	107–1,143	1–30

[a] Thomas (1995).
[b] Dobbins et al. (1999).
[c] Stevens (1964).
[d] Lucchesi et al. (2017).
[e] Bonvechio et al. (2016).
[f] Jenkins and Burkhead (1994).
[g] Kwak et al. (2006).
[h] Sakaris et al. (2006).
[i] Brown et al. (2005).

of the Brooks–Gelman–Rubin statistic ($\hat{R}$), with values less than 1.1 indicating convergence. We defined an important relationship as occurring when the 90% credible interval (CI) of differences between parameters did not overlap zero (i.e., when comparing categorical variables) or when the 90% CI for slope estimates (relationship between
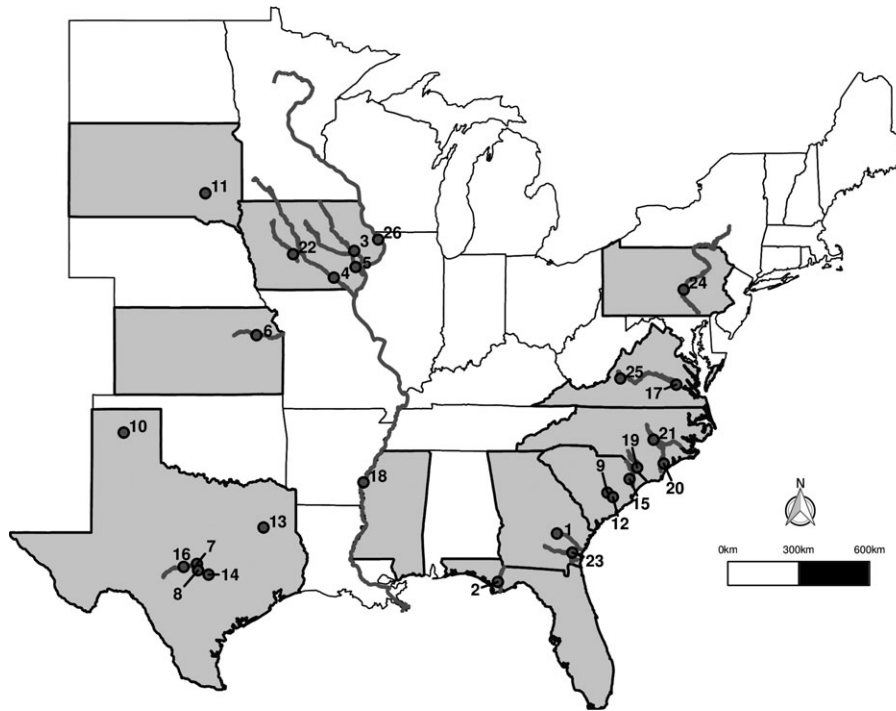
FIGURE 1. Map of populations used in the Flathead Catfish meta-analysis. Each population is labeled with a number corresponding to the population description in Table 1.

growth parameters and covariates) did not overlap zero. Since relying on overlapping CIs with zero introduces an arbitrary cutoff for "significance" (e.g., 90% CI), we also calculated the probability that the relationships between growth parameters (either K or L_∞) and covariates were in the same direction as the posterior mean. This allowed for a simple representation of uncertainty in the posterior distributions of parameter estimates and a more objective means to determine potential biological significance (Filstrup et al. 2014). The following three models were fitted to address our specific research objectives.

Model 1: reservoirs versus rivers.— We first evaluated whether growth parameters varied between reservoir and river populations. If they did not differ, we would use this to justify pooling these waterbody types when fitting model 2. We chose this approach, as opposed to including waterbody type in model 2 explicitly, because reservoir populations were primarily located at southern latitudes, which would have prevented investigating waterbody type × latitude interactions. Therefore, this model only included the predictor variable of waterbody type.

Model 2: native versus introduced and latitude.— To assess how Flathead Catfish growth differed between native and introduced populations, as well as with latitude, we fitted a hierarchical model with the covariates of status (i.e., native or introduced), latitude, and an interaction between status and latitude. The interaction term allowed for determining whether native or introduced

populations differed in their growth parameter relationships with latitude. Latitudes from the midpoint of the sampling area were estimated using Google Maps (Google Maps 2017). We hypothesized that growth would differ between native and introduced populations, with introduced populations having greater K and L_∞, and that the growth parameters K and L_∞ would be negatively correlated with latitude for both native and introduced populations. We hypothesized this negative relationship between growth parameters and latitude since temperature influences fish growth and is the most likely mechanism affecting latitudinal growth variation (Helser and Lai 2004).

Model 3: introduced populations: time since introduction.— We expected growth in introduced populations to vary as a function of time since introduction. Specifically, we predicted that K would be negatively correlated and L_∞ would be positively correlated with time since introduction. The year of Flathead Catfish introduction was determined for each population based on published peer-reviewed literature (Table 1). If the literature reported a range of years (e.g., James River; Jenkins and Burkhead 1994), the latest year was used. By taking the difference between the sampling year and the estimated year of introduction, we were able to estimate how long Flathead Catfish were established prior to sampling for each population.

The hierarchical formulation of the von Bertalanffy growth model allows for growth parameters to be

estimated for all populations, even those with small sample sizes. Because the uncertainty in estimated growth parameters for low-sample-size populations is propagated throughout the analysis, the inclusion of these populations should have minimal effects on inferences. However, to directly assess the sensitivity of our inferences to the inclusion of populations with relatively few sampled fish, we refitted models 1 and 2 using only those populations with a sample size greater than 20 fish. Model 3 was not refitted because limiting the analysis to populations with more than 20 sampled fish only removed native populations.

RESULTS

Individuals collected from the North Raccoon River, Iowa, were not included in growth analyses because this population demonstrated linear growth patterns, which resulted in unrealistic growth parameter estimates (specifically, the L_∞ estimate was over 1,800 mm). The remaining data included information from 25 populations, with a total sample size of 8,104 fish. The compiled data covered a wide variety of TLs (range = 64–1,312 mm) and age-classes (range = 0–32 years). The average fish age was 4.4 years (SD = 3.2), and average length was 460.8 mm (SD = 238.1). Limiting the data set to populations with over 20 sampled fish resulted in the loss of four native populations (all located in Texas; see Table 1 for sample sizes).

Model 1: Reservoirs versus Rivers

Growth parameters were estimated between reservoir ($n = 8$) and river ($n = 17$) populations. The mean maximum average length for reservoir populations ($L_\infty = 1,023.2$ mm) was larger than that of river populations ($L_\infty = 983.0$ mm); however, the 90% CI of the difference between these estimates overlapped zero (90% CI = −0.25 to 0.17). Exclusion of populations with low sample sizes generated similar results: no differences in L_∞ were observed between reservoir and river populations (90% CI for difference between estimates = −0.4 to 0.14). Growth coefficients for reservoir and river populations were roughly the same ($K_{reservoir} = 0.167$ versus $K_{river} = 0.173$). Similar to the L_∞ estimates, the 90% CIs of the differences for posterior estimates of K (90% CI = −0.31 to 0.37) overlapped zero, indicating that growth parameters did not differ among waterbody types. Again, exclusion of low-sample-size populations resulted in similar inferences (90% CI for difference between estimates = −0.13 to 0.64). Consequently, data from both rivers and reservoirs were pooled for inclusion in model 2.

Model 2: Native versus Introduced and Latitude

Twelve native and 13 introduced populations with latitudes ranging from 30°N to 43°N were included in the model. The population average growth parameters, across all populations, were estimated as follows: L_∞ was 941.8 mm (90% CI = 811.1–1,085.1), K was 0.17/year (90% CI = 0.13–0.21), and t_0 was 0.72 years (90% CI = 0.56–0.90). There was substantial variability in growth parameters among populations, with population-specific growth curves showing different growth trajectories (Figure 2). The exclusion of the four low-sample-size populations did not alter the population-specific growth estimates (Supplementary Figure S1 available in the online version of this article).

Population-specific L_∞ posterior mean estimates ranged from 607 to 1,411 mm (Table 2). Flathead Catfish in the Northeast Cape Fear River, North Carolina, were found to reach the greatest maximum average length ($L_\infty = 1,411$ mm). Northern populations in the species' native range had L_∞ estimates below average. Furthermore, the L_∞ estimates for these native northern populations were lower than that of the most northerly population in the introduced range (Iowa River, Iowa [$L_\infty = 607$ mm] versus the Susquehanna River, Pennsylvania [$L_\infty = 989$ mm]). Population-specific K ranged between 0.08/year (Lake Mitchell, South Dakota) and 0.38/year (Satilla River, Georgia). The Satilla River and the Apalachicola River, Florida ($K = 0.27$/year), had growth coefficients nearly double the population average estimate ($K = 0.17$/year).

Growth coefficients decreased with increasing latitude for populations in both the native and introduced ranges (Figure 3). The 90% CIs of the effect of latitude on K for introduced populations did not overlap zero (effect of latitude on K: introduced = −0.24; 90% CI = −0.48 to −0.003; 95% probability of a negative effect). However, the 90% CI for the effect of latitude on K for native populations overlapped zero (effect of latitude on K: native = −0.08; 90% CI = −0.29 to 0.12; 74% probability of a negative effect). Exclusion of the four low-sample-size native populations resulted in a slight positive relationship between latitude and K for native populations; however, the 90% CI still overlapped zero (Figure S2). In addition, the CI for the difference in native and introduced slopes of K versus latitude contained zero (90% CI = −0.17 to 0.48), indicating that the effect of latitude on growth coefficients between native and introduced populations was not different.

The slopes (effect) of the L_∞–latitude relationships for native and introduced populations differed in direction (Figure 3). Average maximum size decreased with increasing latitude for populations within the native range (effect of latitude on L_∞: native = −0.08; 90% CI = −0.21 to 0.05; 85% probability of a negative effect), while average maximum size increased with increasing latitude for introduced populations (effect of latitude on L_∞: introduced = 0.05; 90% CI = −0.11 to 0.21; 69% probability of a positive effect). The exclusion of the four
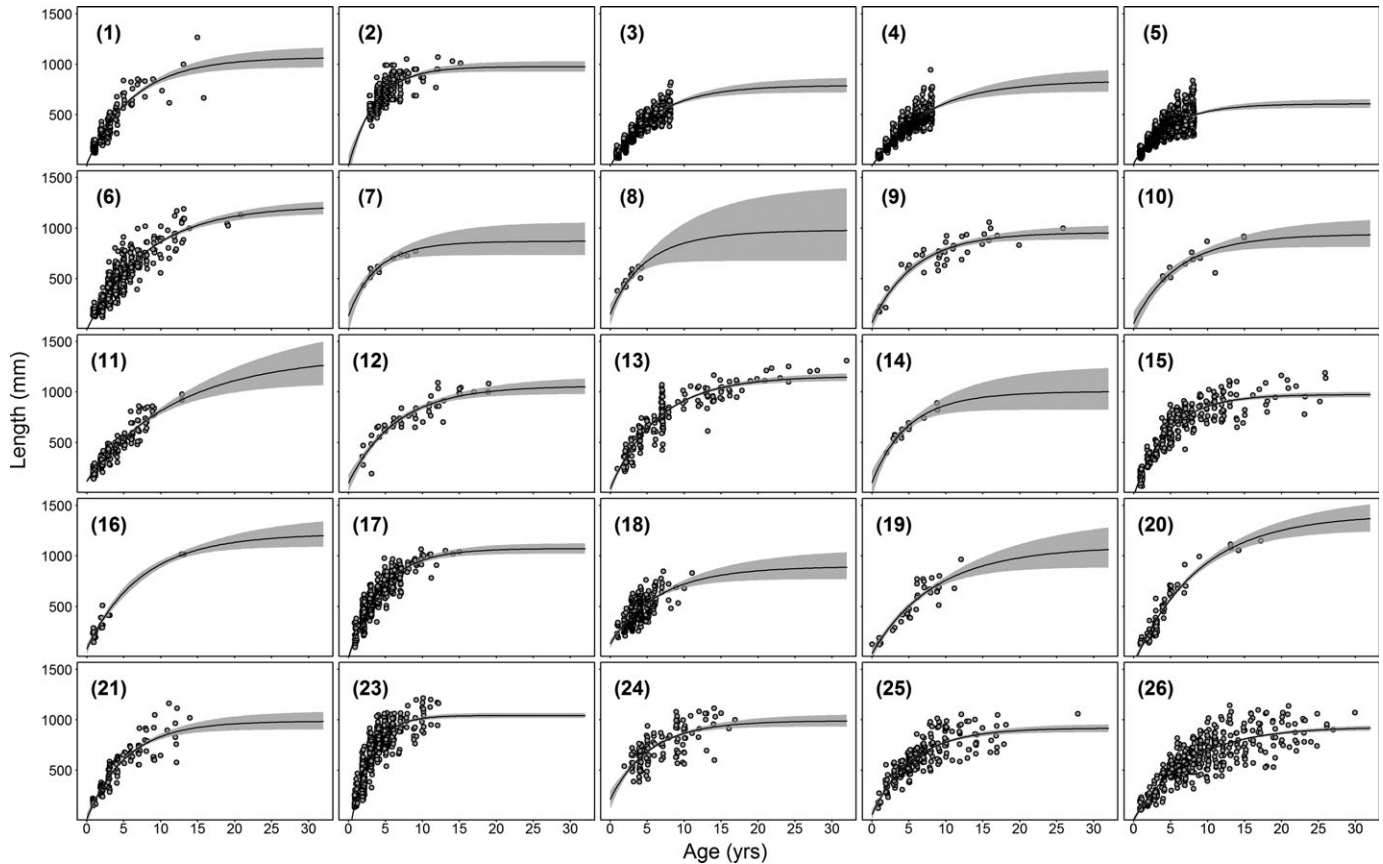
FIGURE 2. Fitted von Bertalanffy growth curves for 25 Flathead Catfish populations (North Raccoon River [population 22] was excluded from analyses; see text). All plots are labeled with numbers referring to the population descriptions in Table 1. Observed ages (years) and TLs (mm) of Flathead Catfish are represented with black dots. Thin black lines represent the posterior means of the population-specific fitted growth curves; the 90% credible intervals are depicted by the shaded regions.

low-sample-size native populations resulted in a slightly stronger negative relationship between L_∞ and latitude for populations within the native range (probability of a negative effect = 93% versus 85% when all populations were included; Figure S2). Similar to the relationship observed for K, the effect of latitude on L_∞ values did not differ between native and introduced populations, as the 90% CI of the difference in slopes contained zero (90% CI = −0.34 to 0.07).

Model 3: Introduced Populations: Time Since Introduction

Data from 13 introduced populations (3 reservoir populations and 10 river populations) were included in model 3. Time since introduction ranged from 6 to 42 years (mean = 24.7 years; SD = 8.8). The K-values showed a weakly positive relationship with time since introduction (slope = 0.08; 90% CI = −0.17 to 0.36; 71% probability of a positive effect), while L_∞ estimates illustrated a weak negative relationship (slope = −0.02; 90% CI = −0.19 to 0.13; 61% probability of a negative effect;

Figure 4). The 90% CIs for both relationships, however, overlapped zero.

DISCUSSION

Understanding macro-scale patterns in fish growth and identifying potential macro-scale drivers can be important for fisheries conservation and management. We performed a meta-analysis of Flathead Catfish growth across 25 populations in the species' native and introduced ranges and found that the von Bertalanffy growth parameters K and L_∞ varied considerably among populations. Although there was substantial uncertainty in attempting to identify macro-scale drivers, some spatial patterns were observed.

Model 1: Reservoir versus Rivers

Researchers have suspected that Flathead Catfish in reservoirs grow more rapidly than those in riverine habitats (Guier et al. 1984; Kwak et al. 2006; Lucchesi et al. 2017), although relatively few studies have tested this hypothesis. Jolley and Irwin (2011) compared catfish

TABLE 2. Posterior means for population-specific growth parameters for Flathead Catfish (ID = index number for the population [corresponds to population number in Figure 1]; L_∞ = asymptotic average maximum length [mm]; K = Brody growth coefficient [per year]; t_0 = hypothetical age [years] at which length is zero). Values in parentheses are 90% credible intervals.

ID	Waterbody	L_∞	K	t_0
1	Altamaha River	1,067 (970–1,179)	0.16 (0.13–0.19)	0.91 (0.76–1.0)
2	Apalachicola River	975 (926–1,030)	0.27 (0.22–0.33)	1.0 (0.60–1.5)
3	Cedar River	789 (721–872)	0.17 (0.14–0.20)	1.1 (0.91–1.2)
4	Des Moines River	835 (730–972)	0.14 (0.10–0.17)	1.1 (0.88–1.0)
5	Iowa River	607 (567–654)	0.21 (0.18–0.24)	0.85 (0.70–1.0)
6	Kansas River	1,221 (1,151–1,299)	0.12 (0.11–0.14)	1.0 (0.90–1.2)
7	Lake Buchanan	870 (732–1,058)	0.27 (0.16–0.42)	0.55 (0.18–1.1)
8	Lake Lyndon B. Johnson	982 (674–1,423)	0.24 (0.11–0.43)	0.47 (0.19–0.86)
9	Lake Marion	955 (888–1,035)	0.17 (0.13–0.22)	0.67 (0.35–1.1)
10	Lake Meredith	940 (814–1,106)	0.17 (0.11–0.24)	0.73 (0.25–1.5)
11	Lake Mitchell	1,368 (1,090–1,771)	0.08 (0.06–0.12)	0.34 (0.23–0.45)
12	Lake Moultrie	1,059 (982–1,154)	0.15 (0.12–0.19)	0.54 (0.23–0.95)
13	Lake Palestine	1,155 (1,114–1,198)	0.15 (0.14–0.17)	0.78 (0.55–1.0)
14	Lake Travis	1,006 (824–1,275)	0.21 (0.12–0.32)	0.60 (0.22–1.2)
15	Little Pee Dee River	973 (947–1,001)	0.22 (0.20–0.23)	1.1 (0.97–1.3)
16	Llano River	1,221 (1,093–1,405)	0.14 (0.09–0.19)	0.60 (0.36–0.87)
17	Lower James River	1,071 (1,022–1,126)	0.22 (0.20–0.25)	1.0 (0.86–1.2)
18	Lower Mississippi River	895 (770–1,063)	0.15 (0.11–0.21)	0.35 (0.19–0.54)
19	Lumber River	1,097 (888–1,386)	0.12 (0.08–0.17)	0.78 (0.46–1.2)
20	Northeast Cape Fear River	1,411 (1,258–1,593)	0.11 (0.09–0.14)	1.5 (1.2–1.9)
21	Neuse River	985 (904–1,085)	0.19 (0.15–0.23)	0.90 (0.61–1.2)
23	Satilla River	1,041 (1,016–1,067)	0.38 (0.35–0.41)	1.5 (1.4–1.6)
24	Susquehanna River	989 (933–1,056)	0.19 (0.14–0.23)	0.29 (0.10–0.55)
25	Upper James River	916 (878–958)	0.18 (0.16–0.21)	0.68 (0.47–0.9)
26	Upper Mississippi River	928 (900–957)	0.14 (0.12–0.15)	0.91 (0.70–1.2)

growth between reservoir and tailwater habitats along the Coosa River, Alabama, and did not find differences in growth between habitats for Channel Catfish *I. punctatus*, Blue Catfish, or Flathead Catfish. A meta-analysis by Rypel (2011) addressed this question using mean back-calculated length-at-age data from native Flathead Catfish populations across a large range of latitudes (27–47°N). Similar to Jolley and Irwin (2011), Rypel (2011) did not find a significant difference in growth parameters between lotic and reservoir habitats. We tested this hypothesis further by using individual length-at-age data from native and introduced populations. We predicted that growth parameters would be larger in riverine habitats because increased flows have been shown to positively increase Flathead Catfish foraging opportunities and to result in increased growth rates (Jones and Nolite 2007). However, our study supports the findings of Jolley and Irwin (2011) and Rypel (2011), as we did not observe differences in growth parameters between reservoir and river populations. Growth similarities between habitat types may be due to similarity of prey items available in both system types (Rypel 2011), and diet studies have revealed that Flathead Catfish are opportunistic foragers, preying on

whatever fishes are available (Layher and Boles 1980; Pine et al. 2005).

Model 2: Native versus Introduced and Latitude

Growth of introduced fish populations are often greater than that of populations located in the native range (Rypel 2014; Pusack et al. 2016), and this faster growth of introduced populations has also been shown for some Flathead Catfish populations. Sakaris et al. (2006) compared growth rates between two introduced river populations and two native river populations of Flathead Catfish and concluded that introduced populations grew substantially faster than their native counterparts. Populations in that study occurred in Alabama and Georgia, which represent a relatively small portion of the Flathead Catfish's contemporary range (Fuller 2017), reservoir habitats were excluded. Another meta-analysis by Rypel (2014) compared Flathead Catfish growth rates between native and introduced populations and concluded that growth was faster in the introduced range. However, Rypel (2014) normalized growth to account for climate effects and compared climate-neutral growth curves. In our study, K-values, on average, were not different between native
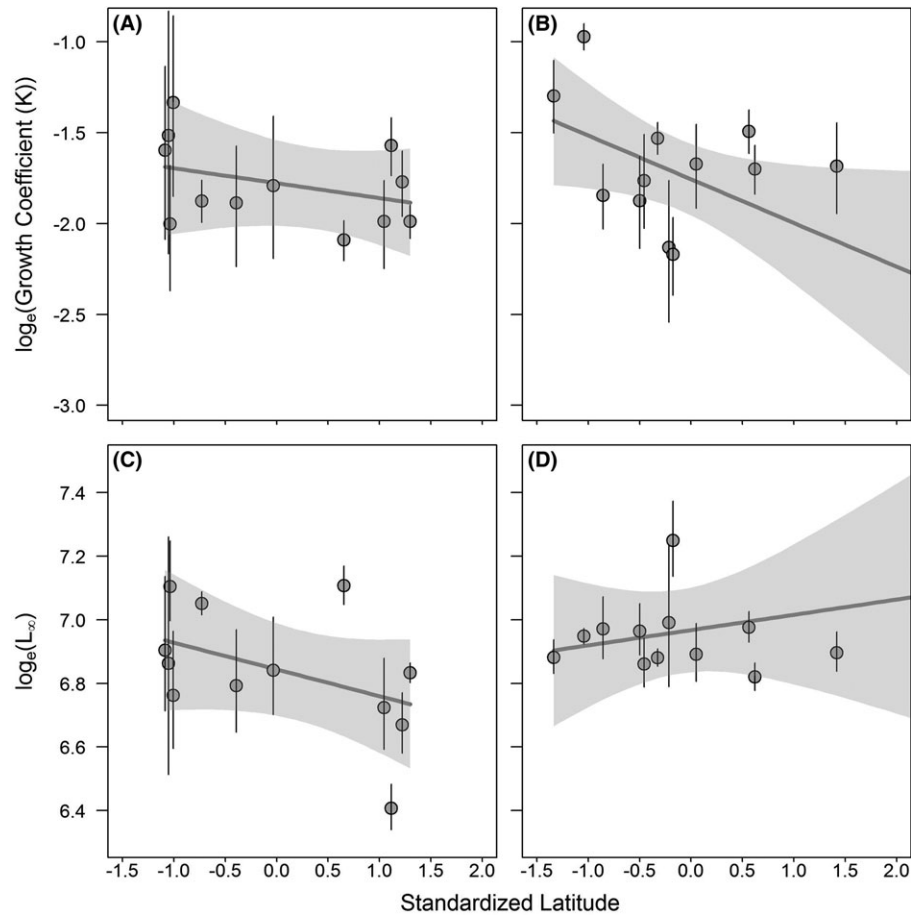
FIGURE 3. Relationships between von Bertalanffy growth parameters and latitude for 25 Flathead Catfish populations: **(A)** Brody growth coefficients (K) for native populations; **(B)** K-values for introduced populations; **(C)** theoretical maximum average lengths (L) for native populations; and **(D)** L values for introduced populations. Gray dots represent the posterior mean population-specific parameter estimates ($\pm 90\%$ credible interval). The thick gray line represents the hierarchical regression line; the shaded area depicts the 90% credible region. Growth parameters are estimated on the $\log_e$ scale, and latitude has been standardized.

and introduced populations; this lack of a difference in K could be a function of the populations included in our analysis. For example, Kaesar et al. (2011) reported that Flathead Catfish introduced into Georgia rivers experienced a decline in growth rates after 10–15 years of establishment. Seventy-six percent of the populations used in this study were established over 15 years before being sampled; therefore, the growth trends of the introduced populations may closely resemble, on average, those of native populations. Secondly, some populations (i.e., Cedar River, Iowa, and Lake Lyndon B. Johnson, Texas) were represented by a limited number of age-classes. Hierarchical models can estimate growth parameters for these data-poor populations (whereas other methods may not converge) through the ability to borrow strength from the entire data set (Raudenbush and Bryk 2002). However, shrinking data-poor populations toward the overall mean reduces growth differences among populations. This

property of the hierarchical model results in a conservative approach for elucidating differences among populations.

Growth coefficients were negatively correlated with latitude for introduced populations, suggesting the potential for slower growth of introduced populations at higher latitudes. These results are similar to findings by Kwak et al. (2006). Those authors qualitatively compared Flathead Catfish growth rates in populations that were introduced into North Carolina rivers to the results from previous studies of introduced populations located at lower latitudes, and they concluded that fishes in the northern populations grew slower than those located further south. However, for native Flathead Catfish populations, latitude was not found to be an important predictor of K. Local-scale processes (e.g., exploitation rates or prey availability; Bonvechio et al. 2011) could hinder the detection of large-scale patterns in growth. For example, the largest K-value in our study was observed for the Satilla River,
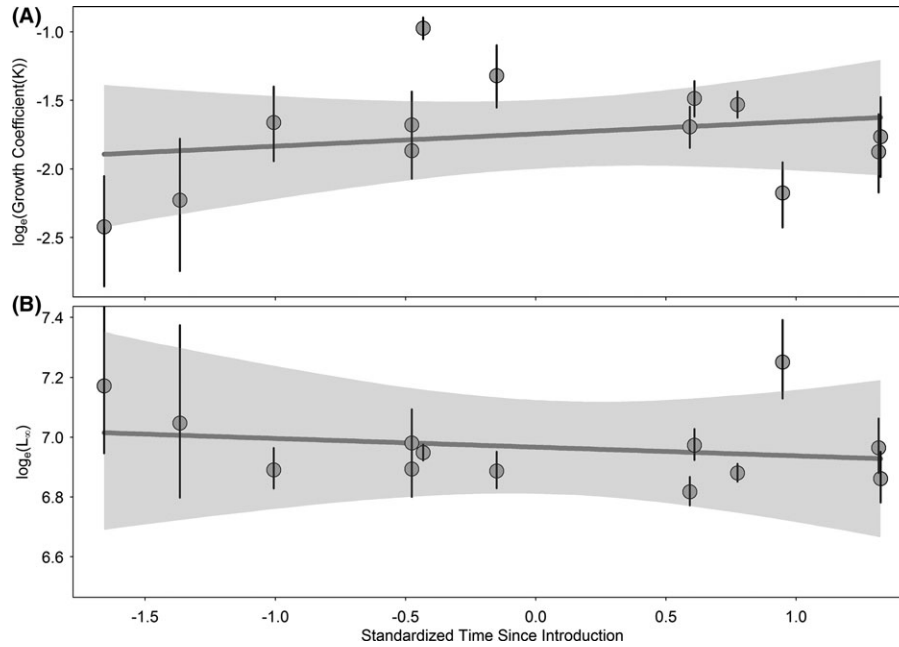
FIGURE 4. Relationships between von Bertalanffy growth parameters and time since introduction for introduced Flathead Catfish populations: **(A)** Brody growth coefficient (K); and **(B)** theoretical maximum average length (L). Gray dots represent the posterior mean population-specific parameter estimates ($\pm$90% credible interval). The thick gray line represents the hierarchical regression line; the shaded area depicts the 90% credible region. Growth parameters are estimated on the $\log_e$ scale, and time since introduction has been standardized.

which was the site of an extensive Flathead Catfish removal program that dramatically decreased the number of large individuals from the population (Bonvechio et al. 2011). Since fish have the most potential to grow from a young age, the removal of large individuals (i.e., most likely older individuals) causes the K of the population to increase (Bonvechio et al. 2011). We did find that L_∞ estimates of native populations declined, on average, with increasing latitude. A similar negative L_∞–latitude relationship has been reported for other fish species (Copp et al. 2004; Helser and Lai 2004), and temperature is the likely dominant mechanism behind this latitudinal effect (Jobling 1981).

Model 3: Introduced Populations: Time Since Introduction

Growth rates from introduced fish populations are generally thought to increase rapidly in the early stages of establishment into the new system. After a period of rapid growth, the growth rates plateau as the environmental carrying capacity is reached (Sakai et al. 2001; Lucchesi et al. 2017). Based on this and previous Flathead Catfish growth studies (Kwak et al. 2006; Bonvechio et al. 2016), we predicted that more recently introduced populations would have higher K and lower L_∞ estimates. However, we did not find time since introduction to be an important predictor of growth parameters. Researchers have reported differing periods of sustained growth in Flathead Catfish.

Kaesar et al. (2011) reported that Flathead Catfish in the Flint and Altamaha River systems, Georgia, were capable of sustained growth for 10–15 years, while Sakaris et al. (2006) estimated this period to be as long as 20–25 years after initial introduction in the Ocmulgee and Satilla rivers, Georgia. The lack of very recently introduced populations in our study (time since introduction ranged from 6 to 42 years; mean = 24.7 years) and the uncertainty in the year of introduction for some populations may have affected our ability to detect an effect of time since introduction.

Conclusions

This study quantified macro-scale variability in growth and identified important covariates of growth for native and introduced Flathead Catfish populations. Of the covariates we were able to examine, latitude was negatively correlated with K for introduced populations (95% probability of declining K with increasing latitude), and there was a high probability (85%) that L_∞ declined with increasing latitude for native populations. Because latitude was used as a proxy for temperature, these results suggest that changing climate conditions that affect thermal habitat may influence the growth dynamics of both introduced and native populations of Flathead Catfish.

Our study was limited to landscape predictors that were available for all study populations, thus limiting the number of covariates we could investigate. In addition, we had

to rely on landscape predictors that were proxies for more biologically relevant properties that would directly influence growth. Direct measurements of more biologically relevant attributes of the fish habitats would likely be useful for future macro-scale investigations into fish growth. By quantifying spatial variability and identifying large-scale patterns in growth, this study provides information that managers can use in decision-making processes during the development of conservation and harvest policies.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.