

## Population Dynamics of Introduced Flathead Catfish in Rivers of Southern Georgia

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*Abstract.*—The flathead catfish *Pylodictis olivaris* is a widely successful invader of lotic ecosystems across North America. The ability of flathead catfish to grow quickly to large sizes while preying upon native fish has caused concern and spurred aggressive measures to control introduced populations in states like Georgia. Although studies have examined differences among native and introduced populations with respect to demographic factors such as age, growth, and mortality, little is known of introduced population dynamics over the long term. As a unique opportunity to improve our understanding of the trajectory and fate of introduced flathead catfish populations, we examined temporal dynamics within some of the oldest (30+ years), introduced populations in the southeastern United States, those of the Flint River and Altamaha River systems of Georgia. Flathead catfish abundance (both density and biomass) was substantially (71–88%) lower among populations recently examined relative to historical observations. A comparison of modeled growth indicated that individual growth rates of flathead catfish were also lower among contemporary populations than among those previously observed. Monitoring of relative abundance over a 22-year period in the Altamaha River revealed a distinct and recurrent population boom and decline, suggesting that equilibrium abundance of flathead catfish has either not been reached or will remain dynamic in the future in this system. Changes in the population demographics of introduced populations occurred rapidly, within a matter of years, and represented striking shifts in the abundance of flathead catfish populations in southern Georgia. An investigation of factors associated with such dynamics and their ecological consequences remain important areas for future research.

### Introduction

Among North American fish assemblages, the flathead catfish *Pylodictis olivaris* is a formidable and potent invader (Fuller et al. 1999). The native distribution of the flathead catfish is extensive (Jackson 1999), indicating the species is adapted to a wide range of environmental conditions. The flathead catfish is long-lived (Kwak et al. 2006), has a varied diet (Quinn

1987; Weller and Robbins 1999; Pine et al. 2005), and has an extremely large gape (Slaughter and Jacobson 2008). At larger sizes (>500 mm), flathead catfish become predominantly piscivorous (Guier et al. 1981; Jolley and Irwin 2003; Pine et al. 2005), and adults are often the apex predators in a system.

Because they are a popular sport fish, the flathead catfish has been widely introduced (Jackson 1999). In Georgia, flathead catfish are native only to the Coosa River system in northwestern Georgia but have been introduced into several other Georgia river systems. The earliest of these introductions occurred in the Flint River near Thomaston during

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the early 1950s (Quinn 1988a). Flathead catfish were subsequently reported downstream as early as 1972 at the Albany Dam (Quinn 1988a). Anglers also reported catching flathead catfish in Ichawaynochaway Creek, a downstream tributary to the lower Flint River, in the mid-1980s (Freeman and Freeman 1992). To the east, flathead catfish were introduced into the Ocmulgee River in the 1970s (Evans 1991) and were common downstream throughout the Altamaha River by the late 1980s (Probst 1991; Thomas 1993). More recently (mid-1990s), flathead catfish were introduced into the Satilla River (Sakaris et al. 2006).

Following establishment, flathead catfish can spread quickly throughout a system and attain very high population abundance and biomass (Guier et al. 1981; Quinn 1988b; Dobbins et al. 1999; Moser and Roberts 1999; Weller and Geihlsler 1999). Impacts of these large predators on the naïve, native fauna have been documented in Georgia (Probst 1991; Thomas 1993; Bonvechio et al. 2009) and elsewhere (Guier et al. 1981; Bart et al. 1994; Moser and Roberts 1999). In an attempt to mitigate these impacts, measures have been taken to reduce flathead catfish numbers and biomass in Georgia. Electrofishing removal efforts were conducted on the lower Ocmulgee and upper Altamaha rivers during 1997 to 2000 and are currently ongoing in the Satilla River (1996–present) (Bonvechio et al. 2011, this volume).

The objectives of this study were to assess current status and to describe long-term trends in flathead catfish dynamics among a few of the oldest (i.e., >30 years), introduced populations in the southeastern United States, those of the Flint and Altamaha River systems in Georgia. An understanding of the dynamics of introduced flathead catfish populations is important to fisheries management and relevant to invasion biology in general. Recent studies have focused on differences in growth rates between introduced and native populations (Kwak et al. 2006; Sakaris et al. 2006). Little is known, however, of the trajectories and fates of introduced populations—whether they stabilize and at what level and whether their dynamics change over time. To reveal long-term dynamics and outcomes, periodic assessment of key demographic parameters such as age, growth, mortality, and abundance must occur among introduced populations with a long history of residence in a system. Such information is not only useful for developing management strategies, but also provides the necessary foundation for topical review and synthesis.

## Methods

### *Study Systems*

To assess temporal changes in population demographics, we sampled flathead catfish in the lower Flint River, Ichawaynochaway Creek, Ocmulgee River, and Altamaha River. These streams are primarily located within the Coastal Plain physiographic province (Figure 1). The mean width of the Flint River between Albany and Newton is ~85 m, and mean daily discharge at Newton is 180 m<sup>3</sup>/s (USGS 2010; water data, gauge 02353000). We examined flathead catfish throughout the lower 124 km of the lower Flint River. Ichawaynochaway Creek is a fifth-order tributary to the lower Flint River. In its lower reaches, Ichawaynochaway Creek has a mean width of 37 m and mean daily discharge of 25 m<sup>3</sup>/s (USGS 2010; water data, gauge 02355350). We examined the lower 24 km of the creek, a reach that is wholly contained within the Joseph W. Jones Ecological Reserve at Ichauway, an 11,500-ha property with restricted public access. The Altamaha River is formed by the confluence of the Oconee and Ocmulgee rivers and flows 220 km to the Atlantic coast (Figure 1). Mean daily discharge at Doctortown, Georgia is 377 m<sup>3</sup>/s (USGS 2010; water data, gauge 02226000). We examined flathead catfish throughout the Altamaha River and throughout the lower 132 km of the Ocmulgee River.

### *Abundance*

To assess absolute abundance of flathead catfish, population estimates were made using mark–recapture techniques (Van Den Avyle and Hayward 1999) on the Flint River and Ichawaynochaway Creek in 2007 and between river kilometers 55 and 72 on the Altamaha River in 1995 and 2009. On the Flint River, we sampled flathead catfish in the 56-km reach between the cities of Albany and Newton, a reach previously studied by Quinn (1988b). Fish were collected during summer months using low-frequency (18 kHz) electrofishing gear and a crew operating two boats—one to carry the electrofishing gear and the other to collect fish (i.e., the chase boat; Daugherty and Sutton 2005c). Sampling was conducted on the lower 24 km of Ichawaynochaway Creek using canoes to facilitate navigation in shallow areas. All captured fish were measured (millimeters total length [TL]) and weighed (g), and all individuals  $\geq 305$  mm TL were marked with a fin clip and released at the site of capture. To evaluate movement of marked fish, Icha-



FIGURE 1. Map of study systems in Georgia. Study areas included the lower 122 km of the Flint River, the lower 24 km of Ichawaynochaway Creek, the lower 132 km of the Ocmulgee River, and the entire length of the Altamaha River. The entire unshaded area of the map represents the Coastal Plain physiographic province.

waynochaway Creek was subdivided into contiguous 1.5-km segments in which flathead catfish were given a unique fin clip. Recapture sampling on all streams was conducted approximately 1 week later. Population estimates were calculated using Bailey's (1951) modification of the Petersen index. Observed density (number of individuals per unit area) and biomass (kg/ha) were calculated based on the area sampled in each study river.

We assumed populations were closed during the sampling period based on radiotelemetry studies reporting limited movement and site fidelity of flathead catfish during summer (Skains and Jackson 1995; Pugh and Schramm 1999; Daugherty and Sutton 2005a), in addition to our own observations. Quinn (1988b) reported that 79% of fish recaptured in the Flint River showed no detectable movement,

and in Ichawaynochaway Creek, we recaptured 78% of fish within 3 km of their release point, a distance shorter than any of our study reaches. To generate an accurate estimate of the area sampled by Quinn (1988b), we analyzed a geographic information systems-based map of the lower Flint River; this value was used to adjust the estimate of flathead catfish density reported in Quinn (1988b).

To assess relative abundance (i.e., catch per unit effort [CPUE]) of flathead catfish in terms of fish collected per hour (CPUE number or fish/h) and biomass collected per hour (CPUE biomass or kg/h), standardized surveys were conducted annually throughout each study river as follows: Flint River (5–10 sites per year, 1996–present), Altamaha River (10 sites per year, 1987–present), and the Ocmulgee

River (10 sites per year, 1993–present). Surveys were conducted during summer using low-frequency electrofishing as described above. All sites were sampled for 1 h, and fish  $\geq 150$  mm TL were collected, measured (TL), and weighed to the nearest gram. Standardized surveys were not conducted in some years as a result of high discharge that prevented sampling, insufficient time and personnel, or equipment failures. Pearson's correlations between the two relative abundance metrics were calculated using Microsoft Excel.

#### *Age and Growth*

To obtain samples of fish for age estimation, we harvested a minimum of five fish per 25-mm length-class during the 2007 and 2009 recapture events described above. The age sample from Ichawaynochaway Creek was supplemented by fish captured during a flathead catfish fishing derby open to staff and family members of the Jones Ecological Research Center. The derby was held from April 1 to August 1, 2007. Flathead catfish harvested during the derby were not included in abundance, biomass, length-frequency, or mortality calculations. All fish were measured (TL) and weighed (g), and lapilli otoliths were removed for age estimation. Otoliths were slide-mounted using Buehler Crystalbond, and transverse sections were made using a Buehler Isomet low-speed saw. Sections were polished using 600–800 grain waterproof sandpaper and examined under a compound microscope (403) to estimate age by enumerating annuli (Nash and Irwin 1999). Otoliths were independently examined by two readers; any discrepancies in age were resolved by mutually examining the second otolith. Age data published in Quinn (1988b) and used for modeling in this study were based on an examination of the pectoral fin articulating process.

#### Von Bertalanffy growth models

$$L_t = L_\infty \left[ 1 - e^{-k(t-t_0)} \right]$$

where  $L_t$  is the predicted total length at time  $t$  in years,  $L_\infty$  is the theoretical maximum mean total length,  $e$  is the base of the natural logarithm, and  $k$  is the growth coefficient] were fitted to mean length at age data for each population (Ricker 1975) using FAST (Fisheries Analysis and Simulation Tools; Slipke and Maceina 2003). To avoid aging bias associated with the use of the pectoral fin articulating process (Nash and Irwin 1999), a growth model was fitted to observed mean length at age for ages

1 through 5 fish only from Quinn (1988b), with a fixed theoretical maximum total length of 1,016 mm—the length of the largest individual fish captured during the study and a value deemed highly representative of  $L_\infty$  for this population. To visually compare growth rates among populations, we predicted mean length at age 1 through 13 using the developed growth models. We included modeled growth data from the Ocmulgee/Altamaha River system in 2000 (Grabowski et al. 2004) and modeled growth from the Ocmulgee River in 1997 (Sakaris et al. 2006) for comparison.

Analysis of covariance (ANCOVA) was used to test for differences in the growth rates among the Flint River 2007, Ichawaynochaway Creek 2007, and Altamaha River 2009 populations. The null hypothesis of similar growth rates among all three populations was tested by examining the Type III sum-of-squares  $F$ -values associated with the two interaction terms (i.e., population\*age and population\*age<sup>2</sup>) of the covariance model using SAS (SAS Institute 2001), following the approach described by Isely and Grabowski (2007). To test for differences in growth rate between years in the Flint River (1985 versus 2007), we conducted a paired  $t$ -test of the mean length increments at each age for ages 1–5 fish only (DeVries and Frie 1996).

#### *Mortality*

Age-length keys were developed using FAST for the 2007–2009 populations sampled, and ages were assigned to all unique individuals  $\geq 150$  mm TL collected during the electrofishing sampling events described above. The natural log of the total number of fish in each age-class ( $n + 1$ ) was plotted against age, and unweighted catch curve regressions were initiated at the youngest age that appeared fully recruited to the sampling gear and extended through the oldest age-class with at least four representatives to avoid introducing bias in the mortality rate estimate (Van Den Avyle and Hayward 1999). The slopes of regression equations generated in FAST provided estimates of instantaneous total mortality ( $Z$ ). Total annual mortality ( $A$ ) was derived from the formula  $A = 1 - e^{-Z}$ . Confidence intervals for  $Z$  were calculated using the variance of the slope of the regression line (Miranda and Bettoli 2007). ANCOVA was used to test for differences in  $Z$  (i.e., the catch curve, regression line slopes) among populations (Miranda and Bettoli 2007) using SAS (SAS Institute 2001).

## Results

### Abundance

The population estimate of flathead catfish  $\geq 305$  mm TL in the Flint River was substantially lower in 2007 than observed in 1985 (Table 1). Observed density and biomass of flathead catfish in the Flint River were 83% and 88% lower, respectively, than observations made 22 years earlier by Quinn (1988b). Mean weight of fish  $\geq 305$  mm TL was also lower in 2007 (1.23 kg) than observed in 1985 (1.78 kg). Likewise, the population estimate in the Altamaha River was significantly lower in 2009 than in 1995. Density of flathead catfish was 71% lower, and biomass was 84% lower than observed in the same reach 14 years earlier. Mean weight of flathead catfish  $\geq 305$  mm TL was 3.67 kg in 1995 compared to 2.00 kg in 2009. Estimated abundance and mean weight of flathead catfish in Ichawaynochaway Creek was low and comparable to the recent Flint River and Altamaha River estimates.

The two relative abundance metrics, CPUE biomass (kg/h) and CPUE number (fish/h), were positively correlated in both the Altamaha River and Flint River (Pearson's correlation  $r = 0.79$ ,  $p < 0.0001$  and  $0.94$ ,  $p < 0.0001$ , respectively); higher catch rates of flathead catfish were associated with higher total biomass in the catch. The two metrics were uncorrelated in the Ocmulgee River case ( $r =$

$-0.19$ ,  $p > 0.4$ ). Based on CPUE biomass, abundance of flathead catfish in the Altamaha River steadily increased through 1992, peaked during 1993–1996, and thereafter declined to lower levels through 2002 (Figure 2). A second peak in abundance was observed during 2004–2006, followed again by a decline to lower levels. Relative abundance as indexed by CPUE number generally showed similar trends, although temporal variation was not as great as for CPUE biomass. Trends in CPUE biomass of flathead catfish upstream in the Ocmulgee River mirrored those of the Altamaha River with peaks in abundance in 1996 and 2005 (Figure 2). Trends in CPUE number again exhibited less variation than CPUE biomass, with the highest values occurring in the early 2000s. Long-term trends in the abundance of flathead catfish in the Flint River during the study period were indiscernible due to the imprecision of estimates for both CPUE biomass and CPUE number (Figure 2). However, relative abundance appeared to be highest from 2006 to 2009. The Flint River was not regularly monitored for flathead catfish until the mid-1990s, so interannual trends in abundance that occurred during the apparent “boom” phase of the population in the 1980s were not documented.

### Age and Growth

Flathead catfish from the Flint River ranged in age from 0 to 18 years and in length from 74 to 954 mm

TABLE 1. Flathead catfish population estimates of fish  $\geq 305$  mm total length in study systems. Estimates from different years were made in the same locations on both the Flint and Altamaha rivers. Values in parentheses represent 95% confidence intervals (CI) for estimates.

Site	Year	Fish/km (95% CI)	Fish/ha (95% CI)	Mean weight (kg) <sup>a</sup>	kg/ha <sup>b</sup>
Flint River	1985 <sup>c</sup>	153 (123–202)	18 (15–21)	1.78	32.1
Flint River	2007	27.5 (22.4–32.6)	3.1 (1.3–4.9)	1.23	3.8
Ichawaynochaway Creek	2007	13.3 (8.5–18.1)	3.6 (2.3–4.9)	1.83	6.6
Altamaha River	1995	211 (153–269)	14.7 (10.6–18.8)	3.67	54.0
Altamaha River	2009	61.1 (35.5–86.7)	4.2 (2.4–6.0)	2.00	8.4

<sup>a</sup> Mean weight is the average biomass of fish  $\geq 305$  mm in total length collected during population estimates.

<sup>b</sup> Estimates of kg/ha based on the mean weight of fish  $\geq 305$  mm in total length.

<sup>c</sup> Flint River estimates from 1985 provided by Quinn (1988a, 1988b).

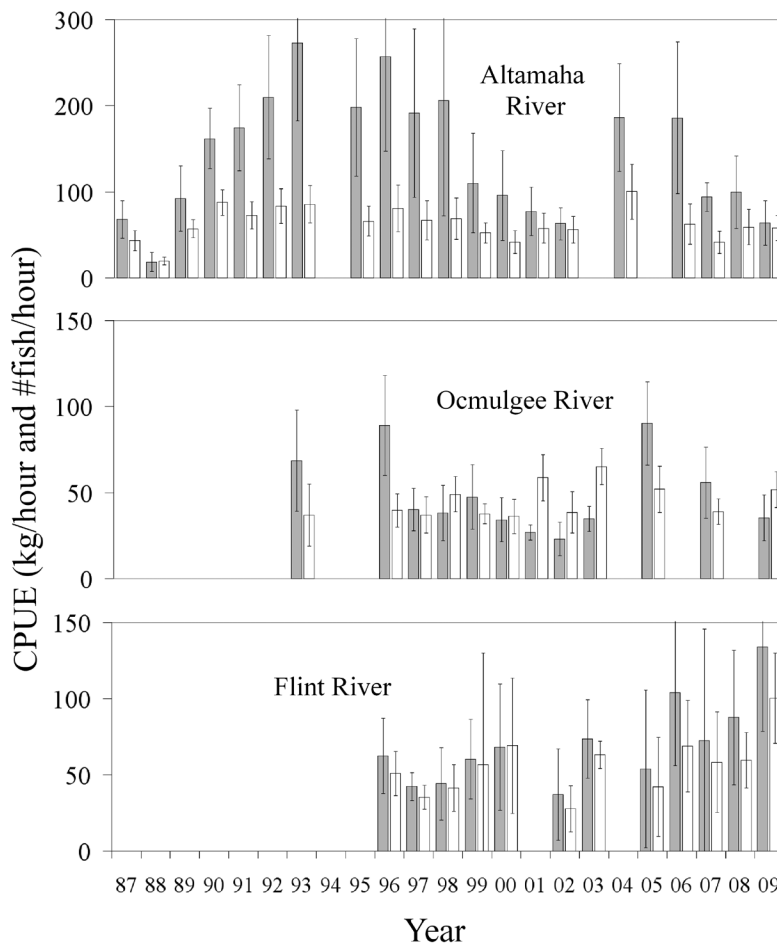


FIGURE 2. Catch per unit effort (CPUE) biomass (kg/h; gray bars) and CPUE number (# fish/h; white bars) of flathead catfish by year of observation on the Altamaha, Ocmulgee, and Flint rivers. Error bars represent 95% confidence intervals. Note difference in y-axis scales among rivers.

TL ( $n = 160$ ; Table 2). Flathead catfish from the Altamaha River ranged in age from 0 to 20 years and in length from 114 to 1080 mm TL ( $n = 191$ ). In Ichawaynochaway Creek, fish ranged in age from 1 to 20 years and ranged in length from 163 to 1,092 mm TL ( $n = 120$ ).

The Ichawaynochaway Creek fishing derby contributed 53 fish (total biomass = 218 kg) for age analysis. Most of the fish harvested (91%) during the derby were greater than 500 mm TL. A total of 17 of these fish were  $\geq 10$  years of age.

Von Bertalanffy growth models fit the data well for all populations ( $r^2 = 0.83$ – $0.99$ ; Table 3). Growth rates did not differ statistically among the Flint River 2007, Altamaha River 2009, and Ichawaynochaway Creek 2007 populations

(ANCOVA:  $F_{2,41} = 0.67$  and  $1.32$ ,  $P = 0.278$  and  $0.516$  for interaction terms). The growth coefficient ( $k$ ) for flathead catfish in the Flint River 2007 model was lower than the growth coefficient of the 1985 model (Table 3), but the difference in growth rate (ages 1–5 fish only) was not statistically significant at the  $\alpha = 0.05$  level ( $t = 1.79$ ,  $p = 0.073$ , one-tailed test). Growth models predicted that flathead catfish reached 500 mm TL (i.e., approximate size at which fish become predominantly piscivorous; Quinn 1987; Weller and Robbins 1999; Pine et al. 2005) at age 4.7 years in the Flint River, at age 5.3 in Ichawaynochaway Creek, and at age 3.6 in the Altamaha River.

A comparison of von Bertalanffy-modeled growth among years and systems indicated that in-



TABLE 2. Mean ( $\pm 1$  SD) total length (mm) of flathead catfish collected for age determination from the Flint River (2007), Ichawaynochaway Creek (2007), and Altamaha River (2009) populations.

Age	Flint River			Ichawaynochaway Creek			Altamaha River		
	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range
0	7	104 $\pm$ 18	74–132				2	167.5 $\pm$ 76	114–221
1	21	175 $\pm$ 42	110–248	9	231 $\pm$ 47	163–296	36	212 $\pm$ 49	132–321
2	14	220 $\pm$ 49	164–341	14	284 $\pm$ 45	199–351	38	377 $\pm$ 63	263–497
3	33	338 $\pm$ 71	224–493	9	343 $\pm$ 49	275–418	12	490 $\pm$ 58	410–587
4	26	434 $\pm$ 90	278–631	13	452 $\pm$ 98	274–560	24	523 $\pm$ 108	254–685
5	20	551 $\pm$ 102	335–703	8	552 $\pm$ 109	379–700	12	610 $\pm$ 86	378–725
6	17	558 $\pm$ 66	420–668	13	586 $\pm$ 81	439–718	23	636 $\pm$ 117	320–870
7	5	704 $\pm$ 66	596–759	7	550 $\pm$ 96	421–694	21	731 $\pm$ 78	580–945
8	3	750 $\pm$ 107	628–830	5	585 $\pm$ 30	540–620	6	810 $\pm$ 70	694–882
9	4	709 $\pm$ 188	490–885	11	666 $\pm$ 116	534–904	3	764 $\pm$ 53	720–823
10	4	891 $\pm$ 63	828–954	6	729 $\pm$ 96	597–831	5	901 $\pm$ 165	704–1,060
11	2	638 $\pm$ 27	619–657	1	620		2	976 $\pm$ 148	871–1,080
12	1	816		3	954 $\pm$ 119	884–1,092	1	970	
13	2	853 $\pm$ 83	794–912	6	862 $\pm$ 92	750–978	2	837 $\pm$ 36	811–862
14				5	830 $\pm$ 182	634–1,016	1	1,020	
15				1	755	755–879			
16				1	734		1	1,001	
17				2	696 $\pm$ 22	680–711			
18	1	950					1	1,045	
19				3	929 $\pm$ 86	831–967			
20				3	902 $\pm$ 165	753–1,080	1	1,050	

dividual growth rates declined over time among introduced populations (Figure 3). Modeled growth of Flint River 1985 and Ocmulgee River 1997 fish was similar and highest among the populations examined. Modeled growth of Ocmulgee/Altamaha 2000, Altamaha 2009, and Flint River 2007 fish was lower than growth predicted by earlier models from these systems. The greatest decline in modeled growth occurred in the oldest introduced population examined, that of the Flint River.

#### Mortality

Mortality rates were similar among populations. Instantaneous mortality rates were not statistically different among the 2007 Flint River ( $Z = 0.35 \pm 0.11$  confidence interval [CI]<sub>0.95</sub>), 2007 Ichawaynochaway Creek ( $Z = 0.37 \pm 0.16$  CI<sub>0.95</sub>), and 2009 Altamaha River ( $Z = 0.45 \pm 0.28$  CI<sub>0.95</sub>) populations (ANCOVA:  $F_{2,24} = 0.61$ ,  $p = 0.55$ ; Figure 4).

TABLE 3. Flathead catfish growth parameters of von Bertalanffy models fitted to mean total length at age data for the Flint River (FR) 1985 and 2007, Ichawaynochaway Creek (IC) 2007, and Altamaha River (ALT) 2009 populations.  $L_{\infty}$  = theoretical maximum total length;  $k$  = growth coefficient;  $t_o$  = hypothetical age of fish when length = 0;  $r^2$  = coefficient of determination for model fit with respect to all age-classes.

Parameter	Population			
	FR 1985	FR 2007	IC 2007	ALT 2009
$L_{\infty}$ (mm)	1,016	1,000.5	1,092.0	1,118.9
$k$	0.264	0.145	0.081	0.140
$t_o$	0.206	-0.127	-2.296	-0.670
$r^2$	0.99	0.94	0.83	0.97

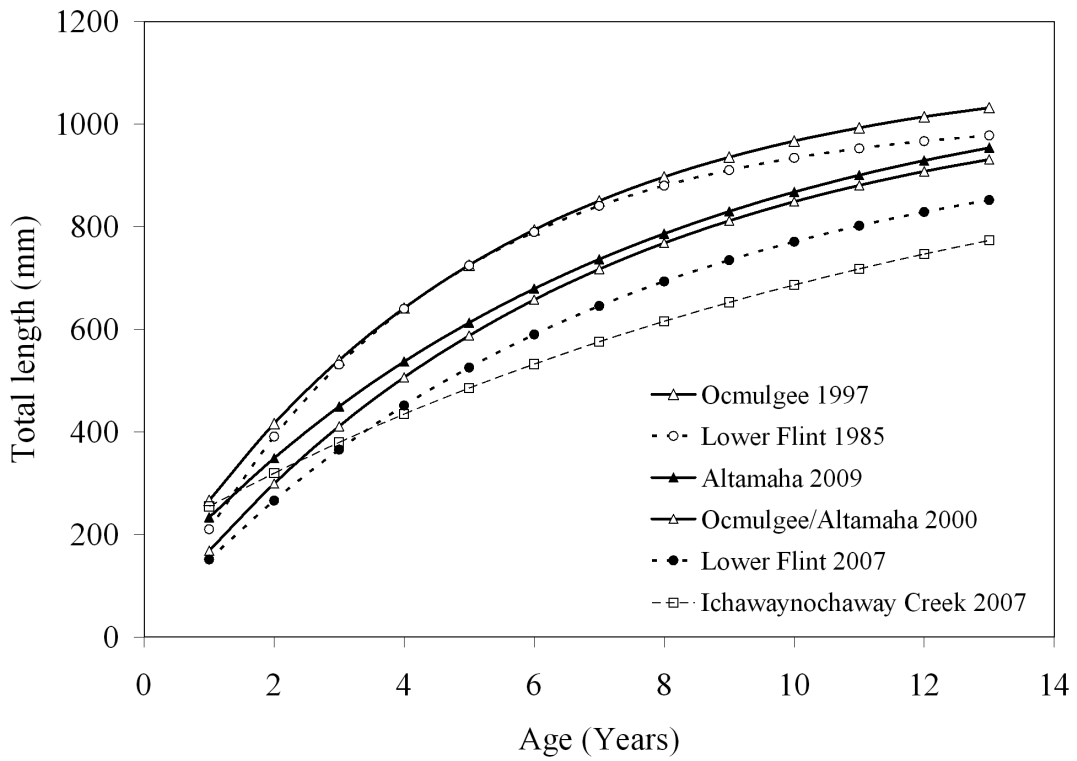


FIGURE 3. A comparison of von Bertalanffy growth curves for flathead catfish from the Altamaha and lower Flint River systems. Ocmulgee River 1997 data were obtained from Sakaris et al. (2006), lower Flint River 1985 data were obtained and reanalyzed from Quinn (1988b), and the Ocmulgee/Altamaha River 2000 data are from Grabowski et al. (2004).

## Discussion

Substantial changes have occurred among flathead catfish populations introduced into Georgia river systems more than 30 years ago. Our data indicate that these populations experienced a steady growth phase (i.e., the population boom) that culminated at peak density and biomass approximately 10–15 years after establishment. Similar population booms have been documented on rivers like the Cape Fear in North Carolina (Guier et al. 1981). Peak abundances of flathead catfish were not sustained, and introduced populations subsequently declined to lower levels. Observations of the Altamaha and Ocmulgee River populations suggest that such declines can occur rapidly after only a few years at peak abundance. The differences in flathead catfish density and biomass between peak and trough periods were profound and, to our knowledge, undocumented for introduced flathead catfish populations. Boom-and-

bust phenomena have been observed for other introduced fish populations (Loftus and Kushlan 1987; Fury and Morello 1994; Trexler et al. 2000) and, in some cases, have been rationalized as a population explosion driven by exploitation of food resources that is later checked by depletion of those resources (Welcomme 1988). The term “bust” has been used to describe both disappearance of an introduced population or persistence at low levels of abundance (Williamson 1996).

A curious ecological question springs from our observation of a recurring peak and decline in abundance of flathead catfish in the Altamaha River system, revealed only through annual monitoring efforts. Will oscillations in abundance repeat in the future, will they dampen over time, and what are the principal driving factors? Such oscillations may be the result of feedback mechanisms related to the interaction of flathead catfish abundance and environmental carrying capacity (Haddon 2001). Likewise,



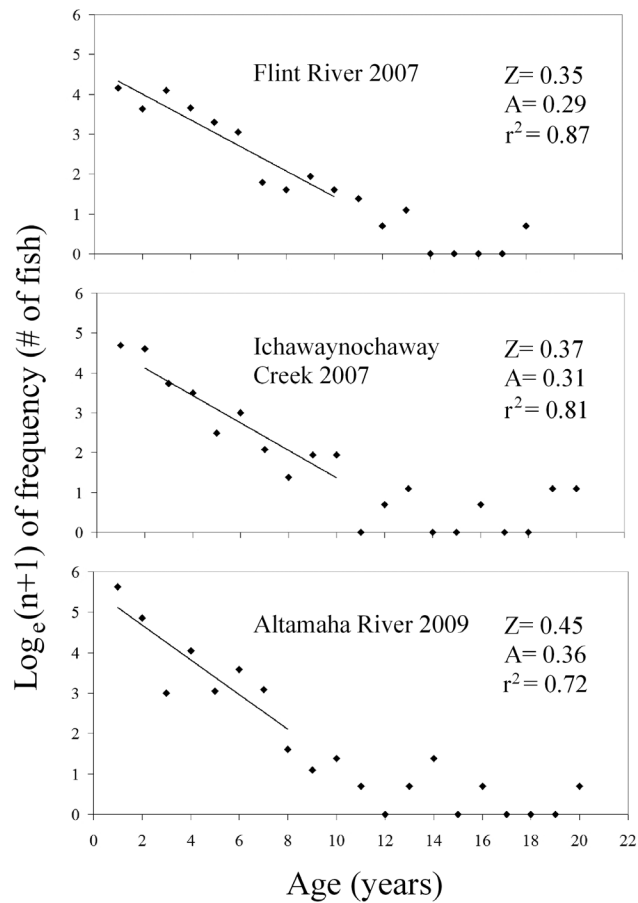


FIGURE 4. Abundance ( $\log_e[n + 1]$ ) at age and associated catch-curve regressions for flathead catfish collected from the lower Flint River in 2007 ( $n = 269$ ), Ichawaynochaway Creek in 2007 ( $n = 340$ ), and the Altamaha River in 2009 ( $n = 572$ ).

Williamson (1996) discussed the potential for introduced predators to induce predator-prey cycles that require time to reach equilibrium. An examination of driving factors and trends among prey populations of these rivers was, however, beyond the scope of this study. At the very least, these observations indicate that the long-term trajectory of flathead catfish abundance in the Altamaha River system cannot simply be characterized as a decline followed by persistence at some low level; the term “boom-and-bust” does not accurately describe flathead catfish dynamics in this system.

Although flathead catfish removal occurred on the Ocmulgee and Altamaha rivers during the period 1997–2000, we cannot attribute the coincident population decline on the Altamaha River to these efforts. The area of intensive removal was focused

primarily in lower reaches of the Ocmulgee River and upstream of 9 of the 10 survey sites on the Altamaha River (R. R. Weller, unpublished data). Given the broad geographic separation of the 10 sampling sites throughout the Altamaha River, we believe removal efforts had little to no effect on abundance in the Altamaha River. In addition, declines following recurrent peaks in abundance in both the Ocmulgee and Altamaha rivers occurred in the absence of any management-directed removal efforts. Furthermore, a decline in abundance in the Flint River occurred where no such removal efforts were undertaken. On the other hand, removal efforts may have influenced abundance in the Ocmulgee River to some degree, as we observed a precipitous decline in CPUE biomass from 1996 to 1997, followed by a distinct increase in the frequency of small flathead catfish

captured in this river in 2001 and 2003. The effects of removal may explain why we observed no correlation between the two relative abundance metrics in the Ocmulgee River.

Few population estimates of introduced flathead catfish exist in the literature, precluding a meaningful comparison of abundance among systems. Kwak et al. (2004) reported densities ranging from 1 to 8 fish/ha (4–31 fish/km; >125 mm TL) among three introduced populations in North Carolina streams similar in width to Ichawaynochaway Creek. In the oldest population examined (~30 years; northeast Cape Fear River), these authors reported lower densities (0.3–2 fish/ha, 4–9 fish/km; fish > 125 mm TL) and lower biomass (0.2–0.7 kg/ha) than observed in 2007–2009 Georgia study populations.

Unlike abundance, a large body of data on age and growth of flathead catfish exists in the literature. A summary and analysis of these data by Kwak et al. (2006) provide a foundation for comparing growth rates among native and introduced populations. In this study, Kwak et al. (2006) suggested that growth rates of introduced populations might decline over time and resemble those of native populations. Indeed, contemporary growth observed in both the Flint River and Ichawaynochaway Creek populations resembled the slower growth characteristic of native, riverine flathead catfish populations. Recent growth of Altamaha River fish falls between the averages reported for native and introduced river populations and resembles the growth reported for similarly aged, introduced populations like those of the northeast Cape Fear River in North Carolina (Kwak et al. 2006) and the Great Pee Dee River in South Carolina (Bulak and Leitner 1999).

Interestingly, a decline in individual growth rate in the Ocmulgee/Altamaha population occurred over a short time frame (1997 to 2000) and coincided with observed declines in the abundance of flathead catfish in this system. Although the growth of flathead catfish in Ichawaynochaway Creek or the Altamaha River was not determined within 10–15 years of introduction, we suspect that growth was high during this period and closely resembled that of neighboring populations. If so, then growth declines among populations in these rivers have also occurred. Sakaris et al. (2006) questioned whether high growth rates, such as observed for the Flint River in 1985 and the Ocmulgee River in 1997, could be maintained over long periods of time. Our findings indicate that high growth rates do not persist among introduced populations in southern

Georgia and that these rates can change over the span of a few years.

Kwak et al. (2006) postulated that the growth rates of introduced flathead catfish populations would decline over time due to intraspecific competition and other density-dependent factors as populations expanded and depleted their food resources. Quite intriguingly, we observed higher growth rates during periods of peak flathead catfish abundance (i.e., when flathead catfish density and presumably competition were highest) and lower growth rates during periods of lower abundance in both the Flint and Altamaha River systems. One plausible explanation for this phenomenon may involve lasting changes in prey assemblages occurring as a result of flathead catfish predation. Flathead catfish have been described as opportunistic predators that feed nonselectively on a variety of prey species (Pine et al. 2005). At first introduction, a native prey assemblage is naïve to this new predator and its behavior. As the abundance of flathead catfish increases, it stands to reason that these predators could exert significant pressure on an existing prey assemblage. Indeed, Thomas (1993) documented changes in prey species (e.g., sunfishes *Lepomis* spp. and bullhead catfish *Ameiurus* spp.) during the period of peak flathead catfish abundance in the Altamaha River. If heavy predation depleted the food resources available, and prey assemblages were slow or failed to recover as predation pressure subsided (i.e., during periods of declining flathead catfish abundance), then individual growth rates of flathead catfish might thereafter remain depressed, as observed in this study. A rotenone study conducted in 1981 documented that brown bullhead *Ameiurus nebulosus*, snail bullhead *A. brunneus*, and flat bullhead *A. platycephalus* once constituted ~20% of the total fish biomass in the Altamaha River (Hottell et al. 1983). Recent monitoring data from the Altamaha River indicates that these species have been virtually eliminated from the system and, thus, no longer serve as available prey items (Georgia Department of Natural Resources, unpublished data).

If changes in the trophic resources of study systems provide one possible explanation for trends in growth and abundance, the influence of exploitation provides perhaps another explanation for changes in abundance only. Mortality rates observed in this study were somewhat higher than reported for other introduced populations. Sakaris et al. (2006) observed an instantaneous mortality rate of  $Z = 0.227$  in the 1997 Ocmulgee River population. Kwak et al. (2006) reported instantaneous mortality rates rang-

ing from 0.170 to 0.221 among three introduced populations in North Carolina. Alternatively, when using an analysis approach similar to that taken in this study (i.e., using only age-classes with  $\geq$  five individuals), Kwak et al. (2004) reported a higher instantaneous mortality rate (0.6264;  $A = 0.47$ ) among flathead catfish in the Northeast Cape Fear River and attributed higher mortality in this system to higher exploitation. Although reasons for our observations of higher mortality rates are unclear at this point, we likewise suggest that fishing mortality is one plausible factor.

Fishing for and harvest of flathead catfish is popular on both the Flint River and Altamaha River, and a variety of gears in addition to traditional hook and line are used (Quinn 1993; Weller and Geihlsler 1999). Bush hooks or limb lines are numerous along both rivers (A. J. Kaeser, personal observation). Assuming that recruitment to a recreational fishery occurs at  $\sim$ 500 mm TL, as supported by our Ichawaynochaway Creek derby results, our age and growth data indicate that flathead catfish

recruit to the fishery of the Flint River between ages 4 and 5 and recruit a full year earlier (between ages 3 and 4) on the Altamaha River, where we observed the highest mortality rate. The proportion of fish greater than 500 mm TL (11–21%) and rarity of older fish in our 2007–2009 collections suggests that these populations experience a moderate level of exploitation (Figure 5; Table 2; Daugherty and Sutton 2005b).

Data gathered during the Ichawaynochaway Creek fishing derby importantly provide insight on both the level of mortality that can occur as a result of exploitation and the realized effects of exploitation on standing biomass of flathead catfish. The flathead catfish population of Ichawaynochaway Creek typically experiences low fishing pressure as a consequence of restricted public access; we expected this population to exhibit a lower mortality rate than observed among flathead catfish in the Flint River. The mortality rate we observed, however, was at least partially influenced by the harvest of 53 fish  $\geq$  305 mm TL from the population during the

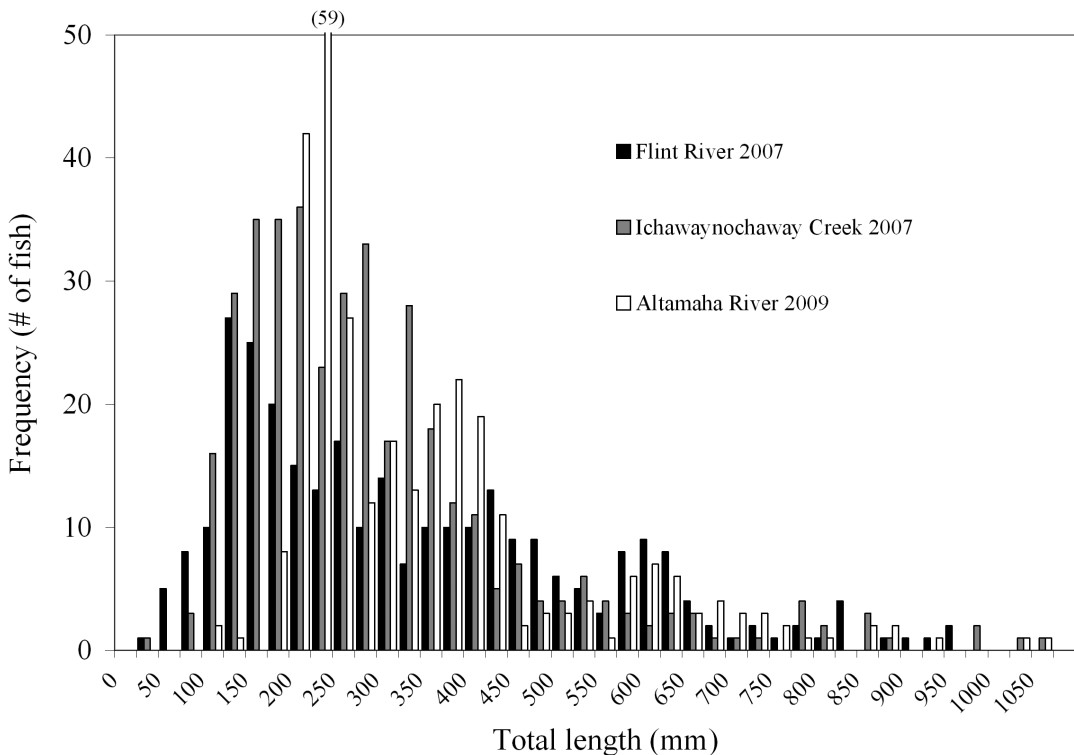


FIGURE 5. Length-frequency histogram of flathead catfish collected during mark-recapture sampling from study rivers. Bars show total number of fish collected from 25-mm length-groups.

derby and prior to our electrofishing sampling for population and mortality estimation. Assuming that harvested fish would have remained in the population, the exploitation rate attributable to this organized fishing event was ~15% ( $u = 0.15$ ). This level of exploitation greatly exceeded what would be expected during a typical season on Ichawaynochaway Creek, thereby increasing the mortality rate estimate. Interestingly, our estimate of 15% exploitation attributable to the derby was similar to an estimate of 14–25% annual exploitation for 1985 in the Flint River (Quinn 1993). At an exploitation rate of 15%, roughly half of the expected annual mortality for the Ichawaynochaway Creek population ( $A = 0.309$ ) can be attributed to harvest.

Several studies have proposed that exploitation may serve as an effective mechanism for reducing the overall biomass of an introduced flathead catfish population (Sakaris et al. 2006; Pine et al. 2007; Bonvechio et al. 2011). A model by Sakaris et al. (2006) of flathead catfish dynamics in the Ocmulgee River (based on 1997 population data) predicted that modest levels of exploitation ( $u = 0.05$ – $0.15$ ) would reduce maximum biomass in this population by 25–50% over a 1-year period. At an exploitation rate of 15% in Ichawaynochaway Creek, we observed a 27% reduction in standing biomass over a 4-month period. This observation lends some empirical support to the model predictions of Sakaris et al. (2006) and Pine et al. (2007) and provides confirmation that anglers can impact flathead catfish population biomass at modest levels of exploitation.

This study represents the first assessment of long-term dynamics among introduced populations of flathead catfish. Flathead catfish have persisted for decades in rivers of southern Georgia, and it would appear that eradication is unlikely. We observed several common trends in the dynamics of introduced populations and have provided evidence that growth, biomass, and abundance of introduced flathead catfish can change dramatically over time following establishment in Georgia rivers. Observations in the Altamaha River system suggest that a decline and persistence at low levels of abundance is not necessarily a characteristic outcome of flathead catfish invasions. Whether these trends apply generally to other introduced populations will require additional long-term investigations in other geographic regions. In light of these findings, attempts to characterize and compare the dynamics of introduced and native flathead catfish populations should consider time since establishment an influential fac-

tor. Our findings raise additional questions related to mechanisms driving the dynamics of introduced flathead catfish; the extent to which factors such as food availability or exploitation drive observed patterns in abundance remains an important area of future investigation. The long-term ecological impact of introduced flathead catfish and the potential for recovery of prey species cannot be addressed with the data presented in this study and also remain subjects for future investigation.

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