Population Dynamics of Introduced Flathead Catfish in Two Atlantic Coastal Plain Rivers Under Differing Management Strategies

Timothy F. Bonvechio, *Georgia Department of Natural Resources, Wildlife Resources Division P.O. Box 2089, Waycross, GA 31502-2089*

Jason E. Marsik, *South Carolina Department of Natural Resources, 295 S. Evander Drive, Florence, SC 29506*

Carl W. Bussells, *South Carolina Department of Natural Resources, 305 Black Oak Road, Bonneau, SC 29431*

Abstract: We described and compared population dynamics of introduced flathead catfish (*Pylodictis olivaris*) between the Satilla River, Georgia, and the Little Pee Dee River, South Carolina. Both of these Atlantic coastal plain rivers are blackwater, low productivity systems that historically supported popular redbreast sunfish (*Lepomis auritus*) fisheries. Flathead catfish have been established in the Little Pee Dee River since the late 1970s or early 1980s, whereas the species was introduced into the Satilla River in the mid 1990s. Both populations are managed differently by their respective state fisheries agencies with an intensive annual flathead catfish removal program on the Satilla River beginning in 1996 and a more recent, less intensive removal program on the Little Pee Dee River that began in 2011. Results from this study indicate the Satilla River flathead catfish population was characterized as having high relative abundance, high mortality, fast growth rates, and a truncated size and age structure containing mostly younger fish with a maximum age of 12. The Little Pee Dee River population of flathead catfish was also characterized as having a high relative abundance but with slow growth rates and a more balanced size and age structure, containing fish up to age 26. This study expands our population dynamics knowledge of introduced flathead catfish populations along the Atlantic coastal plain and provides a few examples of how agencies in the southeastern United States have met the challenge of managing an introduced apex predator.

Key words: *Pylodictis olivaris*, redbreast sunfish, removal, stocking

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The flathead catfish (*Pylodictis olivaris*) is a large apex predator found in lotic environments and is native to Gulf Coast drainages from the Mobile to the Rio Grande basins (Jackson 1999). Anglers within the native range of flathead catfish consider them to be a desirable game fish due to their large maximum size attained, strong fighting ability and excellent table fare (Layher and Boles 1980, Weller and Geihsler 1999). As a result, flathead catfish have been widely introduced by anglers and state resource agencies throughout the southeastern United States (Weller and Geihsler 1999). In South Carolina, flathead catfish are non-native and were first stocked into the Santee-Cooper Lake system in 1964 (Stevens 1964). Flathead catfish subsequently spread to other lotic systems in South Carolina over the next several decades and are believed to have been present in the Little Pee Dee River since the late 1970s or early 1980s (Bulak et al. 1998). In Georgia, flathead catfish are native to the Mobile and Tennessee drainages of the northwestern corner of the state (Boschung and Mayden 2004). The first introduction of this species in Georgia was in the Flint River in the early 1950s (Quinn 1988), followed by the Ocmulgee River in the early 1970s (Evans 1991, Probst 1991), and in the downstream Altamaha River by the late 1980s (Thomas 1995). One of the latest introductions was in the Satilla River in the mid-1990s (Sakaris et al. 2006, Bonvechio et al. 2009) where year classes have been traced back to 1994 (Bonvechio et al. 2011). As a result, the Satilla River flathead catfish population was assumed to be about 20 years old in 2014.

Despite the popularity of flathead catfish among anglers, there have commonly been public and state agency concerns about the potential detrimental effects that these fish have on native riverine fish species (Thomas 1995, Cailteux et al. 2003, Cailteux and Dobbins 2005, Pine et al. 2005). Documented impacts have occurred on native species such as brown bullhead (*Ameirus nebulosus*; Thomas 1995), redbreast sunfish (*Lepomis auritus*; Thomas 1995, Sakaris et al. 2006, Bonvechio et al. 2009), largemouth bass (*Micropterus salmoides;* Bonvechio et al. 2009) and spotted bullhead (*A. serracanthus*; Cailteux and Dobbins 2005). Additionally, this species has been found to prey on juvenile sturgeons, leading to concerns regarding their impacts on anadromous fish restoration programs (Ashley and Buff 1987, Brown et al. 2005, Pine et al. 2005, Flowers et al. 2011).

Historically, the Satilla River has been known as one of the premier sunfish fisheries in Georgia, with redbreast sunfish being the preferred species (Georgia Department of Natural Resources, unpublished data). Sammons and Maceina (2009) found that the fastest growth rates for redbreast sunfish in 12 Georgia rivers occurred in the Satilla River, reaching 203 mm total length (TL) in only 3.6 yrs. The Little Pee Dee River, South Carolina, has a similar reputation as a popular redbreast sunfish fishery (Crochet and Sample 1993). Angler surveys in the early 1990s revealed that sunfish were the most caught and harvested species in terms of numbers and total weight. Similar to what Thomas (1995) described on the Altamaha River, Georgia, predation by introduced flathead catfish is believed to have caused dramatic declines in the abundances of native fishes in the Satilla River by the early 2000s (Bonvechio et al. 2009). Following flathead catfish establishment, declines in the redbreast sunfish population were also noted in the Little Pee Dee River (Crochet and Sample 1993).

When flathead catfish become established in new waters and subsequent declines in abundance of native fish populations are observed, state agencies have few management options to deal with the introduced apex predator. The Georgia Department of Natural Resources (GADNR) has conducted flathead catfish removal using boat electrofishing on the Satilla River beginning in 1996; this effort has been intensified since 2006, with a full-time biologist and a seasonal removal crew dedicated solely to the removal program (Bonvechio et al. 2011). Direct removal of an exotic species can be unpopular with segments of the public (Weller and Geihsler 1999) and may also be ineffective (Moser and Roberts 1999, Grabowski et al. 2004). However, the GADNR flathead catfish removal program successfully increased the total annual mortality of the Satilla River population, resulting in truncated size and younger age structure in the flathead population (Bonvechio et al. 2011). In recent years, declines in the redbreast sunfish populations across SouthCarolina, possibly due to flathead catfish, resulted in the South Carolina Department of Natural Resources (SCDNR) receiving political and public pressure to increase redbreast sunfish populations (R. Self, SCDNR, personal communication). As a result, SCDNR has stocked approximately 2.77 million redbreast sunfish into Little Pee Dee River from 2010–2014, approximately 14,350 sunfish per river km. Some targeted removal activities of flathead catfish have also occurred on the Little Pee Dee River by SCDNR from 2011–2014 but not to the scale of removal efforts on the Satilla River by GADNR. Thus, the objectives of this study were to describe the population dynamics of introduced flathead catfish occurring in two similar Atlantic coastal plain blackwater rivers that have contrasting invasion histories and management strategies.

Study Areas

The Little Pee Dee River begins near Laurinburg, North Carolina, and flows 187 km joining the Great Pee Dee River near Yauhannah, South Carolina (Crochet and Sample 1993). The Satilla River begins in southeastern Georgia, near the town of Fitzgerald and flows 362 km to the Atlantic Ocean at St. Andrews Sound. Both watersheds are heavily forested, containing bald cypress (*Taxodium distichum*) swamps, sweetgums (*Liquidambar styraciflua*) oaks (*Quercus*), and tupelos (*Nyssa* spp.) and other lowland tree species, resulting in tannic, blackwater streams (Sandow et al. 1974 Marshall et al. 2005). Both rivers have acidic pH, ranging between 4.5 to 6.0 in the Satilla River (Sandow et al. 1974), and between 5.5 and 6.8 in the Little Pee Dee River (U.S. Geological Survey gage 02135000). Both rivers have primarily sand substrates and woody debris cover. The Satilla River has a mean annual discharge of 2170 cfs (1931–2014) (U.S. Geological Survey gage 0222800), while the Little Pee Dee River has a discharge of 2918 cfs (1942–2015) (U.S. Geological Survey gage 02135000).

Methods

On the Satilla River, flathead catfish removal was conducted using low-amperage pulsed DC electrofishing range (200–1000 volts at 18 pulses sec^{-1} and >1 A of output) during daylight hours in a downstream direction from either a 3.7- or 5.1-m aluminum johnboat equipped with either a Smith-Root model 12B backpack electrofisher or model LR-24 backpack electrofisher (Thomas 1995). Both of these boxes had special after-market modifications performed on them by Smith-Root in an effort to maximize efficiency in low conductivity systems. This gear was also used to collect fathead catfish in the Little Pee Dee River, along with a Smith-Root boat mounted GPP-5.0 electrofisher with pulsed DC, operated (50–250 volts), at 15 pulses sec^{-1} and 1–2 A output. A chase boat was always used to increase sampling efficiency (Cunningham 2004, Daugherty and Sutton 2005) used during age and growth collections but only on the Little Pee Dee River. Sampling occurred on both rivers in the summer between 7 May and 7 October when water temperatures exceeded 21 C and rivers were within their banks. Although transects were not standardized by time, sampling time was recorded for each transect and used to calculate relative abundance (fish h^{-1}).

In 2014, flathead catfish were collected for this study from both rivers using similar methods as those described above. All flathead catfish collected were brought back to the lab and measured for total length (TL mm) and weight (kg). Fish were grouped into length categories defined by Neumann et al. (2012) [substock <356 mm TL), stock (356–509 mm TL), quality (510–709 mm TL), preferred (710–859 mm TL), memorable (860–1010 mm TL), and trophy (>1020 mm TL)]. Due to the large number of fish in our samples, we used a chi-square test to test for differences in the size distribution between rivers (Neumann and Allen 2007). Fish condition was also calculated using relative weight (W_r). Length-specific standard weights (W_s) for flathead catfish ≥ 140 mm TL were derived from the standard weight equation given in Neumann et al. (2012) and averaged for each length category. We used an analysis of variance (ANOVA) to compare the mean relative weight between rivers and among these size groups. We included a river-size group interaction term and, when appropriate, used the LSMEANS procedure to separate out means.

Otoliths (lapilli; Long and Stewart 2010) were removed from 5 fish per 20-mm group < 700 mm total length (TL) and all fish > 700 mm TL. Two independent readers estimated ages following methods described by Bonvechio et al. (2011). An age-length key was used from the aged fish extrapolated to the entire sample (Ricker 1975). The instantaneous (Z) and total (A) rates of annual mortality were estimated for age-2 and older fish using weighted catch-curves in the Fishery Analysis and Modeling Simulator software (Slipke and Maceina 2014). Slopes of the catch-curve regressions were compared between rivers for age-2 to age-12 fish (i.e., ages that overlapped between rivers) using an Analysis of Covariance (ANCOVA; SAS Institute 2011). Age, growth, and mortality parameters for flathead catfish in both rivers were compared to other populations in Atlantic coastal plain drainages; data were obtained only from studies that aged fish with otoliths to avoid the documented biases resulting from use of other structures (Nash and Irwin 1999, Buckmeier et al. 2002, Maceina and Sammons 2006). Mean growth of age-2 to age-7 flathead catfish (i.e., ages where $n > 10$ fish per age group for both rivers) was compared between rivers using an ANCOVA (SAS Institute 2011). All statistical tests were considered significant at $P < 0.05$.

Results

Because of the different sampling and management objectives of South Carolina DNR and Georgia DNR, total electrofishing effort, number, and biomass of flathead catfish removed from the two study rivers has differed considerably over time. For 18 years (1996–2014), GADNR has been removing flathead catfish from the Satilla River with 59,517 flathead catfish with an aggregate weight of 56,533 kg removed as of 2014. From 2011–2014, 2935 flathead catfish totaling 6094 kg were removed from the Little Pee Dee River (Table 1). Over the same time period, GADNR biologists removed 27,736 flathead catfish totaling 17,386 kg from the Satilla River. These removals were accomplished with a total of 122.8 and 673.5 h of electrofishing effort in the Little Pee Dee and Satilla rivers, respectively (Table 1).

Relative abundance (fish h^{-1}) appeared to be relative similar between rivers in 2014, but mean biomass (kg h^{-1}) removed was markedly higher in the Little Pee Dee River than the Satilla River (Table 2). There were large differences in the sample size of fish collected and the size structure of the flathead catfish populations between the two rivers (Figure 1). In the Little Pee Dee River, a total of 1969 flathead catfish were collected; fish ranged in size from 60 to 1140 mm TL and had a mean total length of 407 mm TL. In the Satilla River, 16,681 flatheads were collected in 2014 and they ranged in size from 60 to 1202 mm TL with a mean total length of 307 mm TL. The majority (57%) of the Little Pee Dee River population was > 355 mm TL compared to only 25% of the Satilla River population (Figure 1). In addition, 27% and 10% of the flathead catfish population was > 510 mm TL in the Little Pee Dee and Satilla rivers, respectively. Accordingly, the mean size of flathead catfish removed was 2.6 times larger in the Little Pee Dee River than in the Satilla River (Table 2). All size structure indices of flathead catfish were higher in the Little Pee Dee River than in the Satilla River (Table 2). Results of the chi square test revealed significant differences in the length-frequency distributions in all six size groups ($\chi^2 = 998.2$, $P < 0.0001$). The interaction term was significant ($F = 8.25$, df = 5, 18,328, $P < 0.001$), so individual comparisons were made using the LSMEANS procedure. Mean W_r of substock and stock size fish was significantly higher in the Little Pee Dee River than the Satilla River (LSMEANS, $t_1 = 4.424$ to 8.206, $P < 0.001$; Figure 2). Mean W_r was similar between rivers for quality, preferred and trophy size fish (LSMEANS, $t_1 = 0.090$ to 1.568, $P = 0.117$ to 0.928). However, mean W_r of memorable size fish was greater in the Satilla River than in the Little Pee Dee River (LSMEANS, $t_1 = 2.513$, $P = 0.012$).

Table 1. Summary statistics for the flathead catfish removal efforts on the Satilla River, Georgia, and the Little Pee Dee River, South Carolina, from 2011 to 2014. Electrofishing effort is expressed as h of pedal time, and number and aggregate weight of flathead catfish removed from each river are given for each year.

	Satilla				Little Pee Dee			
	2011	2012	2013	2014	2011	2012	2013	2014
Effort (h)	186.4	149.0	116.0	222.0	23.0	42.3	35.5	22.0
Number	3469	2861	4725	16,681	95	360	511	1969
Weight (kg)	4211	1623	1668	9884	277	1429	1612	2776

Table 2. Total annual mortality (A), total instantaneous mortality (Z), proportional size distribution for quality (PSD), preferred (PSD-P), and memorable-sized (PSD-M) fish, mean weight (wt), catch-per-unit-effort (CPUE) and biomass-per-unit-effort (BPUE) of flathead catfish sampled from the Satilla River, Georgia, and the Little Pee Dee River, South Carolina, in 2014. Standard errors are in parentheses.

	A	Z	PSD	PSD-P	PSD-M	Mean wt (kg)	CPUE (fish h^{-1})	BPUE (kg h^{-1})
Satilla	0.62	0.582	41	7	2	0.59	75.1 (6.7)	44.5 (4.5)
Little Pee Dee	0.31	0.362	47	11	3	1.55	89.3 (10.4)	126.0 (18.9)

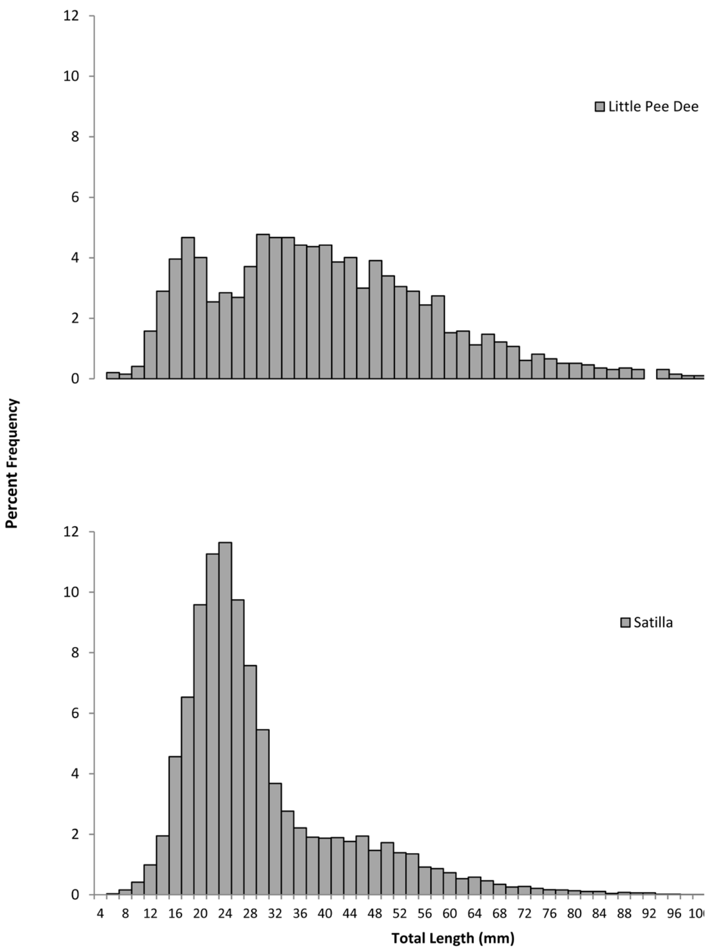

Figure 1. Length-frequency distributions (2-cm length groups, shaded bars) of flathead catfish collected in the Little Pee Dee River ($n = 1969$), South Carolina, and the Satilla River, Georgia ($n = 16,681$) for 2014.

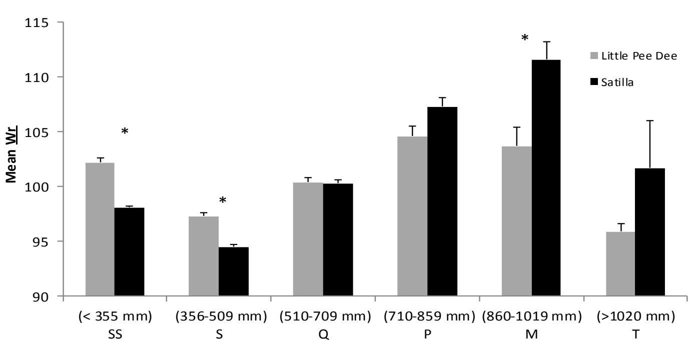

Figure 2. Graph representing the mean relative weight (*Wr*) of flathead catfish in six size categories listed by Neumann et al. (2012) from two Atlantic coastal plain rivers. Asterisk denotes differences between mean *Wr* between rivers within each size category. Error bars on each size group for each river indicate SE. Note: abbreviations of the six size categories (SS = substock, S = stock, Q = quality, P = preferred, M = memorable, and T = trophy).

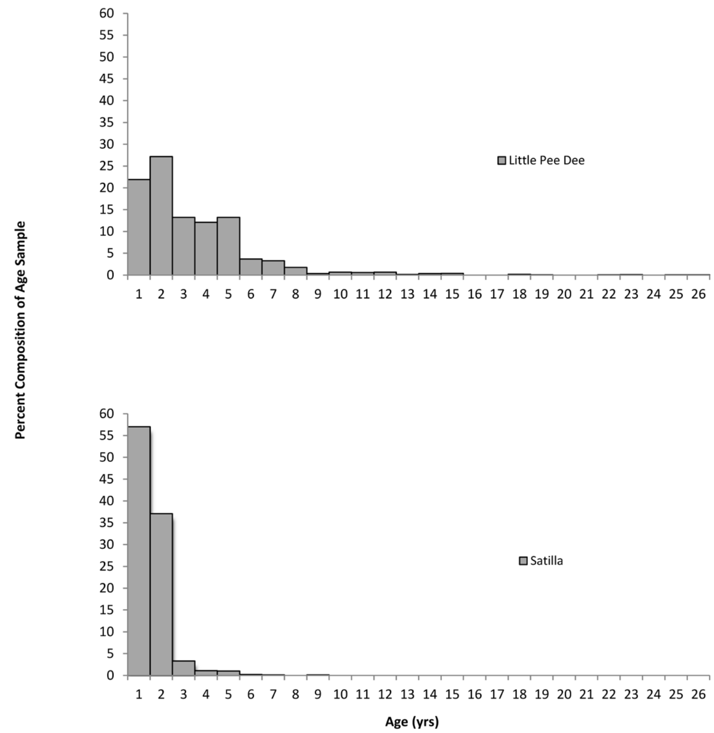

Figure 3. Age-frequency distributions of flathead catfish collected in the Little Pee Dee River, South Carolina ($n = 277$), and the Satilla River, Georgia ($n = 279$) during 2014. Notice the varying scales on the Y-axes.

In both the Little Pee Dee and the Satilla Rivers, age was estimated for 556 flatheads and between-reader agreement was 91%, but all aging discrepancies were subsequently resolved by concert reads. The age composition of flathead catfish was noticeably older in the Little Pee Dee River compared to the Satilla River (Figure 3). Age-1 and age-2 fish composed 49% of the sample in the Little Pee Dee River but 94% in the Satilla River. Maximum age in the Little Pee Dee River was 26 years, whereas the oldest fish collected in the Satilla River was only 12 years old. Of the fish aged, there was considerable variation in length at age but noticeably more scatter was observed among the Little Pee Dee River samples likely due to more old fish. As a result, catch-curve analysis found that Z was 0.375 in the Little Pee Dee River ($r^2 = 0.88$, $P = 0.01$) and 0.981 in the Satilla River ($r^2 = 0.95$, $P = 0.01$), conferring an A of 0.31 and 0.63 in the Little Pee Dee and Satilla rivers, respectively. The ANCOVA revealed that annual mortality of flathead catfish from age 2 to age 12 was higher in the Satilla River ($F = 58.48$, df = 3, 17, $P < 0.0001$).

The von Bertalanffy equation for the Little Pee Dee River flathead catfish was solved as $TL = 1140\ (1 - e^{-0.088[age - 2.17]})$ and estimated that fish reached preferred size (710 mm TL) in 9 yrs and trophy size (1020 mm TL) in 23 yrs (Figure 4). For the Satilla River,

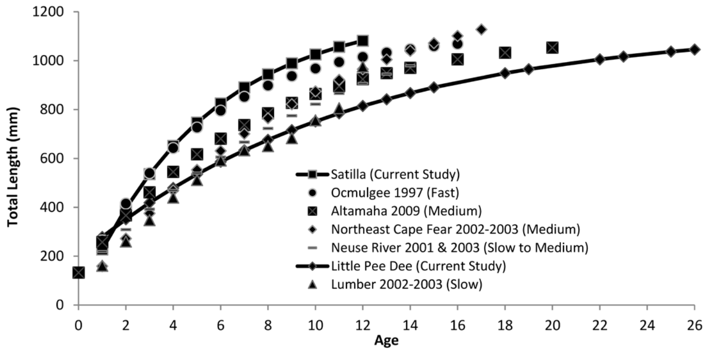

Figure 4. Von Bertalanffy growth curves obtained from predicted mean total length (TL)-at age estimates for the Little Pee Dee River and Satilla River and observed mean TL estimates for the Little Pee Dee River and Satilla River. Populations were compared to other introduced coastal plain populations that were classified as either fast, medium, or slow growing populations from the Ocmulgee River, Georgia (Nash 1999, Sakaris et al. 2006), Altamaha River, Georgia (Kaeser et al. 2011), and the Northeast Cape Fear, Neuse, and Lumber rivers of North Carolina (Kwak et al. 2006).

growth was solved as $TL = 1202\ (1 - e^{-0.19[age - 1.061]})$, and it was estimated that fish reached preferred size (710 mm TL) in 4.5 yrs and trophy size (1020 mm TL) in only 10 yrs. Accordingly, the ANCOVA revealed that growth of age-2 to age-7 flathead catfish was higher in the Satilla River ($F = 55.34$, df = 3, 8, $P < 0.0001$).

Discussion

As in other studies of flathead catfish (Kwak et al. 2006), we observed a large range in sizes at each age in our age-length key among the two rivers sampled. For example, the total length of age-7 fish ranged from 420 to 900 mm TL on the Little Pee Dee River while the Satilla River fish ranged from 660 to 1020 mm TL. Large variation in lengths at age could be due to differential growth or mortality rates among the same year-class. Sample sizes were not believed to be an issue, but we note that larger age samples are recommended by Coggins et al. (2013) in systems that have recruitment issues. The authors were conscious of the substantial overlap in lengths among ages from previous flathead catfish studies noted in Alabama, Georgia, Kansas, North Carolina, and Oklahoma (Layher and Boles 1980, Winkelman 2002, Grabowski et al. 2004, Kwak et al. 2006, Marshall et al. 2009); as a result, the study design specifically called for aging a larger proportion of adult flathead catfish (> 700 mm TL), where wide ranges of lengths within ages could bias the age-length key. Recruitment failure has been cited as a cause for the overlapping lengths among age classes in crappie (*Pomoxis* spp.; Sammons et al. 2000, Bonvechio et al. 2014). However, catch curves of flathead catfish in these two systems appeared to have fairly constant recruitment and good fit (high r^2) with few missing year-classes in the age-composition up to age-10 for both populations examined. Accuracy and precision of growth and mortality parameter estimates are likely influenced by the life history and the exploitation history of the stock in question (Coggins et al. 20013). In the Satilla River, we noted some length-at-age overlap presumably due to a high level of mortality that has occurred due in the long-standing removal program.

The fast growth rates observed on the Satilla River were similar to Sakaris et al. (2006) findings on the Ocmulgee River, Georgia. Likewise, von Bertalanffy growth parameters were similar between data collected on the Satilla River in this study (2014) and those presented by Sakaris et al. (2006) for data collected 10 years earlier (i.e., Linf : 1202 vs 1229 and K: 0.19 and 0.20). Slower growth rates have been documented for introduced populations in the Altamaha River, Georgia (Kaeser et al. 2011), and the Northeast Cape Fear River, North Carolina (Kwak et al. 2006). The slow growth rates on the Little Pee Dee River were very similar to what Kwak et al. (2006) found on the Neuse and Lumber rivers, North Carolina; fish reached preferred size in 8–10 years in all three rivers.

As an introduced population expands and reduces its initial food supply, growth is likely to slow due to intraspecific competition and other density-dependent factors (Kwak et al. 2006, Greenlee and Lim 2011). Our findings confirm observations by Sakaris et al. (2006) that rapid growth in an introduced population can be sustained for at least 20–25 years. They documented fast growth rates from systems with the youngest introduced populations at the time that the samples were collected. Kaeser et al. (2011) reported moderate growth rates in a 22-yr-old flathead catfish population. Our study found slow growth rates of flathead catfish in the Little Pee Dee River, a population that was believed to be approximately 35 yrs old at the time of sampling (Bulak et al. 1998). Kwak et al. (2006) found slower growth rates in the North Carolina populations of the Northeast Cape Fear River and that population exceeded 35 years at the time of the sample. Guier et al. (1981) documented fast growth of flathead catfish in this same population when it was 13 years old.

It is unknown if growth rates on the Satilla will continue to be rapid, but if so, they may be perpetuated by the increased level of exploitation due to the ongoing removal. It has been speculated that a population's growth rate may vary depending on how close the population is to carrying capacity and upon which individuals are removed (Benton et al. 2006, Zipkin et al. 2009). Condition of substock- and stock-sized (juveniles) flathead catfish was poorer in the Satilla River than in the Little Pee Dee River, but the opposite was true for memorable- and trophy-sized fish. Population bottlenecks have been found to regulate mortality and growth in juvenile largemouth bass (Olson 1996, Ludsin and DeVries 1997) and bluegills (*Lepomis macrochirus*; Cargenelli and Gross 1996).

The removal appears to be forcing a bottleneck of poorer condition at smaller sizes on the Satilla or a ontogenetic diet change may be occurring (Olson 1996), because the majority of the population is competing for the same food resources, but at this point it is doesn't appear to be affecting overall growth patterns. Slaughter and Jacobson (2008) demonstrated that flathead catfish have an extremely large gape and are predominantly piscivorous at sizes (> 500 mm TL). Although an ontogenetic shift may be occurring at the juvenile stage before they reach 500 mm TL, a diet study was beyond the scope of this management study.

Longevity is fairly well documented in several studies. The 26-year-old flathead aged in our study from the Little Pee Dee River is the oldest documented age in the literature for an introduced population (Kaeser et al. 2011). Marshall et al. (2009) aged a 34-yr-old flathead catfish from Lake Wilson, Alabama, which stands as the oldest reported in a native population. In general, mortality was high in our study rivers in comparison to what has been found by other studies on introduced flathead catfish populations. Estimated annual mortality of flathead catfish was highest in the Satilla River (0.63) and can be attributed to the nearly two-decade removal effort which has undoubtedly reduced the age structure to mostly younger individuals (Bonvechio et al. 2011). Estimated annual mortality of flathead catfish in the Little Pee Dee River was 0.31, similar to what Kaeser et al. (2011) found for the species in the Altamaha River, Georgia (0.36). Other studies on introduced flathead populations found lower total annual mortality rates ranging from 0.16 to 0.20 (Kwak et al. 2006, Sakaris et al. 2006).

Similar to conclusions found on the Satilla River in Bonvechio et al. (2011), the current study results suggest that flathead catfish removal in the Satilla River has caused growth over-fishing to occur. Stocking redbreast sunfish on the Little Pee Dee River has not been evaluated, but if stocking continues to occur and funding becomes available, we recommend evaluating year-class contribution of stocking through OTC batch marked fish or through genetic clips. Biologists should be aware of the plasticity range in growth observed in age-length keys for flathead catfish which could have rather large management implications, especially when setting harvest regulations. If harvest increases in a population, population dynamic rates may significantly change, rendering a management regulation ineffective.

This study expands our knowledge base on introduced flathead catfish population dynamics along the Atlantic coastal plain and provides a few examples of how agencies in the Southeast have managed a very challenging issue in regard to managing an introduced apex predator.

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Literature Cited

Ashley, K. W. and B. Buff. 1987. Food habits of flathead catfish in the Cape Fear River, North
Carolina. Proceedings of the Annual Conference Southeastern Association of Fish and
Wildlife Agencies 41:93–99.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B 273:1173–1181.

Bonvechio, T.F., D. Harrison, and B. Deener. 2009. Populations changes of sportfish following flathead catfish introduction in the Satilla River, Georgia. Proceedings of the Annual Conference of the Southeast Association Fish and Wildlife Agencies 63:133–139.

———, M.S. Allen, D. Gwinn and J. S. Mitchell. 2011. Impacts of electrofishing induced exploitation on flathead catfish population metrics in the Satilla River, Georgia. Pages 395–408 *in* P. H. Michaletz and V. H. Travnichek, editors. Conservation, ecology, and management of catfish: the second international symposium. American Fisheries Society Symposium 77, Bethesda, Maryland.

———, B. W. Baker, B. R. Bowen. 2014. Population dynamics of white crappie occurring in a small Georgia impoundment with female-only largemouth bass. Journal of the Southeastern Associated Fish and Wildlife Agencies 2:93–100.

Boschung, H. T., Jr. and R.L. Mayden. 2004. Fishes of Alabama. Pp. 334–335. Smithsonian Books, Washington, D.C.

Brown, J. J., J. Perillo, T. J. Kwak, and R. J. Horowitz. 2005. Implications of *Pylodictis olivaris* (flathead catfish) introduction in the Delaware and Susquehanna drainages. Northeastern Naturalist 12:373–384.

Buckmeier, D. L., E. R. Irwin, R. K. Betsil, and J. A. Prentice. 2002. Validity of otoliths and pectoral spines for estimating ages of channel catfish. North American Journal of Fisheries Management 22:934–942.

Bulak, J., J. Crane, J. Leitner, and A. Robb. 1998. Statewide Research-Freshwater Fisheries. South Carolina Department of Natural Resources, Division of Wildlife and Freshwater Fisheries, Annual Progress Report, Federal Aid Project F-63, Columbia.

Cailteux, R. L. and D. A. Dobbins. 2005. Population status and distribution of spotted bullhead *Ameirus serracanthus* in north Florida Rivers. Florida Scientist 68:122–169.

———, ———, and R. S. Land. 2003. Appalachicola/Ochlockonee River Investigations. Florida Fish and Wildlife Conservation Commission, Annual Report, Tallahassee.

Cargnelli, L. M. and M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill:Lepomis macrochirus). Canadian Journal of Fisheries and Aquatic Sciences 53:360–367.

Coggins, L. G., Jr., D. C. Gwinn, and M. S. Allen. 2013. Evaluation of age length key sample sizes required to estimate fish total mortality and growth. Transactions of the American Fisheries Society 142:832–840.

Crochet, D. and C. Sample. 1993. Fisheries investigations in lakes and streams, District VII. Completion Report F-31-4, South Carolina Department of Natural Resources, Columbia.

Cunningham, K. K. 2004. Efficacy of a chase boat for electrofishing flathead catfish in three Oklahoma reservoirs. North American Journal of Fisheries Management 24:1427–1430.

Daugherty, D. J. and T. M. Sutton. 2005. Use of a chase boat for increasing electrofishing efficiency for flathead catfish in lotic systems. North American Journal of Fisheries Management 25:1528–1532.

Evans, J. W. 1991. A fisheries and recreational use survey of the upper Ocmulgee River. Georgia Department of Natural Resources, Game and Fish Division, Final Report, Federal Aid Project, F-33, Social Circle.

Flowers, H. J., T. F. Bonvechio, and D. L. Peterson. 2011. Observation of Atlantic sturgeon predation by a flathead catfish. Transactions of the American Fisheries Society 140:250–252.

Grabowski, T. B., J. J. Isely, and R. R. Weller. 2004. Age and growth of flathead catfish, *Pylodictis olivaris* Rafinesque, in the Altamaha River System, Georgia. Journal of Freshwater Ecology 19:411–417.

Greenlee, R. S. and Catherine N. Lim. 2011. Searching for equilibrium: Population parameters and variable recruitment in introduced blue catfish populations in four Virginia tidal rivers systems. Pages 349–367 *in* P. H. Michaletz and V. H. Travnichek, editors. Conservation, ecology, and management of catfish: the second international symposium. American Fisheries Society Symposium 77, Bethesda, Maryland.

Guier, C. R., L. E. Nichols, and R. T. Rachels. 1981. Biological investigations of flathead in the Cape Fear River. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 35:607–621.

Jackson, D. C. 1999. Flathead catfish: biology, fisheries, and management. Pages 23–35 *in* E. R.

Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. Catfish 2000: proceedings of the internationational ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Kaeser, A., T.F. Bonvechio, D. Harrison, and R. Weller. 2011. Population dynamics of introduced flathead catfish in rivers of southern Georgia. Pages 409–422, *in* P. H.

Michaletz and V. H. Travnichek, editors. Conservation, ecology, and management of catfish: the second international symposium. American Fisheries Society Symposium 77, Bethesda, Maryland.

Kwak, T. J., W. E. Pine, and D. S. Waters. 2006. Age, growth and mortality of introduced flathead catfish in Atlantic rivers and a review of other populations. North American Journal of Fisheries Management 26:73–87.

Layher, W. G. and R. J. Boles. 1980. Food habits of the flathead catfish, *Pylodictis olivaris* (Rafinesque), in relation to length and season in a large Kansas reservoir. Transactions of the Kansas Academy of Sciences 83:200–214.

Long, J. M. and D. R. Stewart. 2010. Verification of otolith identity used by fisheries scientists for aging channel catfish. Transactions of the American Fisheries Society 139:1775–1779.

Ludsin, S. A. and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. Ecological Applications 7:1024–1038.

Maceina, M. J. and S. M. Sammons. 2006. An evaluation of different aging structures to age freshwater fish from a northeastern U. S. river. Fisheries Management and Ecology 13:237–242.

Marshall, B., M. Crockett, R. Scharf, and J. Alford. 2005. Little Pee Dee River eligibility study for the South Carolina Scenic Rivers Program. South Carolina Department of Natural Resources Land, Water, and Conservation Division, Final Report, Columbia.

Marshall, M. D., M. J. Maceina, and M. P. Holley. 2009. Age and growth variability between sexes of three catfish species in Lake Wilson, Alabama. North American Journal of Fisheries Management 29:1283–1286.

Moser, M. and S. B. Roberts. 1999. Effects of nonindigenous ictalurids and recreational electrofishing on the ictalurid community of the Cape Fear River drainage, North Carolina. Pages 479–485 *in* E. R. Irwin, W. A Hubert, C. F. Rabeni, H. Schramm, and T. Coon, editors. Catfish 2000: Proceedings of the International Ictalurid Symposium.

Nash, M. K. and E. R. Irwin. 1999. Use of otoliths versus pectoral spines for aging adult flathead catfish. Pages 309–316 *in* E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. Catfish 2000: proceedings of the international Ictalurid symposium. American Fisheries Society, Symposium 24, Bethesda, Maryland.

Neumann, R. M. and M. S. Allen. 2007. Size structure. Pages 375–421 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

———, C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637–676 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd Edition. American Fisheries Society, Bethesda, Maryland.

Olson, M. H. 1996. Ontogenetic diet shifts in largemouth bass: variability and consequences for First year growth. Ecology 77:179–190.

Pine, W. E., T. J. Kwak, D. S. Waters, and J. A. Rice. 2005. Diet selectivity of introduced Flathead catfish in coastal rivers. Transactions of the American Fisheries Society 134:901–909.

Probst, W. 1991. Evaluation of a stream sport fish monitoring program for some south Georgia streams. Georgia Department of Natural Resources, Game and Fish Division, Federal Aid Project F-29-18, Final Report, Social Circle.

Quinn, S. P. 1988. Investigations into the biology and potential fishery for the flathead catfish (Pylodictis olivaris) in the lower Flint River. Georgia Department of Natural Resources, Project F-28-15, Final Report, Albany.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191

Sakaris, P. C., E. R. Irwin, J. C. Jolley, D. Harrison. 2006. Comparison of native and introduced flathead catfish populations in Alabama and Georgia: growth, mortality and management. North American Journal of Fisheries Management 26:867–874.

Sammons, S. M., P.W. Bettoli, and D. Isermann. 2000. Crappie population dynamics and stocking success in Tennessee reservoirs. Final Report to Tennessee Wildlife Resources Agency, Nashville.

——— and M. J. Maceina. 2009. Variation in growth and survival of bluegills and redbreast sunfish in Georgia Rivers. North American Journal of Fisheries Management 29:101–108.

Sandow, J. T., D. R. Holder, and L. E. McSwain. 1974. Life history of the redbreast sunfish in the Satilla River, Georgia. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 28:270–295.

SAS Institute Inc. 2011. SAS/STAT 9.3 User's guide. SAS Institute, Cary, North Carolina. Slaughter, J. E., IV, and B. Jacobson. 2008. Gape:body size relationship of flathead catfish. North American Journal of Fisheries Management 28:198–202.

Slaughter, J. E., IV and B. Jacobson. 2008. Gape:body size relationship of flathead catfish. North American Journal of Fisheries Management 28:198–202.

Slipke, J. W. and M. J. Maceina. 2014. Fishery Analysis and Modeling Simulator (FAMS). Version 1.64. American Fisheries Society, Bethesda, Maryland.

Stevens, R. E. 1964. Investigations of Fish Populations in Reservoirs. South Carolina Wildlife Resources Department, Federal Aid Project F-1-R-11, Columbia.

Thomas, M. E. 1995. Monitoring the effects of Introduced flathead catfish on sport fish populations in the Altamaha River, Georgia. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies: 47:531–538.

Weller, R. R. and M. R. Geihsler. 1999. Angler attitudes concerning the management of the introduced flathead catfish in the Altamaha River system, Georgia. Pages 435–442 *in* E. R. Irwin, W. A Hubert, C. F. Rabeni, H. Schramm, and T. Coon, editors. Catfish 2000: Proceedings of the International Ictalurid Symposium. American Fisheries Society Symposium 24, Bethesda, Maryland.

Winkelman, D. L. 2002. Factors influencing fish populations in Oklahoma waters: evaluation of the flathead catfish population and fishery in Lake Carl Blackwell, OK, with emphasis on the effects of noodling. Oklahoma Department of Wildlife Conservation, Final Report, Project F-41-R, number 23, Oklahoma City.

Zipkin, E. F., P. J. Sullivan, E. G. Cooch, C. E. Kraft, B. J. Shuter, and B. C. Weidel. 2008. Overcompensatory response of a smallmouth bass population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Science 65:2279–2292.