

EFFECTS OF HYDROLOGIC VARIATION ON DYNAMICS OF CHANNEL
CATFISH AND FLATHEAD CATFISH POPULATIONS IN REGULATED
AND UNREGULATED RIVERS IN THE SOUTHEAST USA

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AND UNREGULATED RIVERS IN THE SOUTHEAST USA

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EFFECTS OF HYDROLOGIC VARIATION ON DYNAMICS OF CHANNEL
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VITA

Peter Constantine Sakaris, son of Chris Sakaris and Barbara (Luglio) Sakaris, was born June 28, 1977, in Smithtown, Long Island, New York. He graduated from Smithtown High School in 1995. He attended Stony Brook University (SUNY) and graduated cum laude from the Honors College with a Bachelor of Science degree in Biology in May 1999. In August 1999, he entered Graduate School at the University of Maryland Eastern Shore and graduated with a Master of Science degree in Fisheries Science in May 2002. In June 2002, he entered Graduate School at Auburn University in the Department of Fisheries and Allied Aquacultures and received a Research Assistantship at the Alabama Cooperative Fish and Wildlife Research Unit.

DISSERTATION ABSTRACT

EFFECTS OF HYDROLOGIC VARIATION ON DYNAMICS OF CHANNEL
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AND UNREGULATED RIVERS IN THE SOUTHEAST USA

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Altered flow regimes resulting from dam construction can have negative impacts on growth and recruitment of fishes in regulated river systems. The effects of hydrologic variation on channel catfish *Ictalurus punctatus* and flathead catfish *Pylodictis olivaris* populations were examined in regulated and unregulated river systems. The objectives of this dissertation were to: 1) develop and validate methods for daily aging age-0 channel catfish, 2) examine the effects of hydrologic variability on growth and hatching success

of age-0 channel catfish in regulated and unregulated reaches of the Tallapoosa River Basin, Alabama, and 3) incorporate the effects of variable hydrology on recruitment and variable mortality as stochastic factors influencing the population growth of native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers.

In validation studies, mean daily ring counts from sagittal otoliths and known ages of channel catfish were strongly related, indicating that daily ring deposition occurred in the otoliths of age-0 channel catfish. Daily ring counts were accurate for 107 - 119 days post-hatch. In the Tallapoosa River System, growth of age-0 channel catfish was generally highest among age-0 fish from unregulated sites in the Coastal Plain, intermediate among fish from regulated sites in the Piedmont, and lowest among fish from unregulated sites in the Piedmont. All age-0 fish that hatched in September originated from the regulated site, indicating that fish in the regulated reach had a protracted spawning season. Multiple regression models indicated that positive relations existed between growth of age-0 channel catfish and hydrologic variables including mean discharge, minimum discharge, number of high pulses, and rise rate. In addition, growth was negatively affected by high fall rates. Age-0 channel catfish typically hatched during periods with low and stable flow conditions.

Size classified matrix models were constructed for native and introduced flathead catfish populations from the Coosa (Alabama, USA) and Ocmulgee (Georgia, USA) rivers, respectively. Recruitment of flathead catfish in the Coosa River was positively related to mean spring discharge and November low flow. In the Ocmulgee River, year-class strength was negatively related to mean March discharge and positively related to

June low flow. Incorporation of variable hydrology as a stochastic factor in the matrix model had a negative effect on population growth in the Coosa River. In contrast, incorporation of hydrologic variation as a stochastic factor resulted in stable population growth in the Ocmulgee River. By variably decreasing the mortality of flathead catfish with the highest reproductive values, population growth improved over a 50-year period in the Coosa River. Simulation of increased mortality of harvestable sized flathead catfish in the Ocmulgee River resulted in a substantial decline in population size.

Managers are encouraged to use models described in this dissertation as tools in adaptive-flow management programs in the Alabama River System. Specifically, these models can be used to prescribe flow regimes in regulated river systems. Researchers should continually improve models by collecting more data and closely monitoring responses of fish populations to variable flow conditions in regulated river systems.

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I. INTRODUCTION

Hydrologic alterations resulting from dam construction have negatively impacted fish diversity and productivity in rivers worldwide (Pringle et al. 2000). Alterations have included habitat fragmentation, conversion of lotic to lentic habitat, variable flow and thermal regimes, degraded water quality, altered sediment transport processes, and changes in timing and duration of floodplain inundation (Cushman 1985; Pringle 2000). Specifically, dams have impeded migration of diadromous and potamodromous species (e.g., salmonids and white sturgeon, *Acipenser transmontanus*), which has severely reduced their reproductive success (Wunderlich et al. 1994; Beamesderfer et al. 1995). In the Alabama River system (USA), flow-modification in regulated reaches has resulted in losses of river-dependent fish species, and distributions of federally listed species have been restricted by main stem impoundment (Freeman et al 2004). Several researchers have documented major changes in fish assemblage structure following dam construction (Paragamian 2002; Quinn and Kwak 2003; Gillete et al. 2005). Quinn and Kwak (2003) reported that long-term changes in the fish assemblage after dam construction on the White River (Arkansas, USA) included a shift from warmwater to coldwater species, a substantial decrease in fluvial specialists, and dramatic reductions in species richness.

Altered flow regimes below dams have typically produced unfavorable conditions for recruitment of fishes (Fraley et al. 1986; Brouder 2001; Freeman et al. 2001;

Wildhaber et al. 2000; Propst and Gido 2004). Freeman et al. (2001) reported that juvenile fish abundances were strongly related to the persistence of shallow habitats in a regulated reach of the Tallapoosa River, Alabama. However, habitat persistence was severely reduced by rapid flow fluctuations resulting from hydropeaking operations (Freeman et al. 2001). In a regulated section of the Neosho River (Kansas), the reduction of minimum flows below John Redmond Dam reduced the availability of riffle habitats that were suitable for Neosho madtoms (*Noturus placidus*, Wildhaber et al. 2000). Furthermore, hypolimnial-release of coldwater from dams will generally slow growth and development and alter physiology of fish during early life stages; whereas, the release of warm water from small, surface release dams may result in reduced densities of coldwater fish species (Clarkson and Childs 2000; Lessard and Hayes 2003).

Recruitment of fishes has been related to hydrology in freshwater ecosystems; however, most studies have been conducted in reservoirs (Maceina and Stimpert 1998; Buynak et al. 1999; Sammons and Bettoli 2000; Schultz et al. 2002). Few studies have examined relations between hydrology and recruitment of fishes in regulated river sections. In a regulated section of the Roanoke River (North Carolina), Rulifson and Manooch (1990) reported that striped bass *Morone saxatilis* recruitment was highest when river flows were low to moderate (142 – 283 m³/s) during the spawning season. During the years when recruitment was highest, flows typically resembled pre-impoundment flow conditions (Rulifson and Manooch 1990). Striped bass required a specific flow regime for successful transport of eggs and larvae to nursery habitats, which was altered by hydropower operations (Rulifson and Manooch 1990). Recruitment of sunfishes *Lepomis* spp. and black basses *Micropterus* spp. has also been related to

hydrology in rivers (Bonvechio and Allen 2005). Bonvechio and Allen (2005) hypothesized that high flows in the fall would increase access to floodplain habitats, thereby increasing prey availability (i.e., invertebrates) for adult sunfishes before the spawning season. As a result, sunfish would consume more prey and allocate more energy towards reproduction (i.e., fecundity), increasing the likelihood of a stronger, future year class. Few studies have evaluated relations between flow variability and fish growth in regulated rivers below dams (Freeman et al. 2001).

Studies investigating relations between hydrology and recruitment of catfishes have been very limited in regulated rivers. Irwin et al. (1999) reported that riffle habitats (i.e., shallow-fast and shallow coarse) were utilized by juvenile channel catfish *Ictalurus punctatus* and flathead catfish *Pylodictis olivaris*. However, persistence of these habitats may decrease in highly regulated systems (Bowen et al. 1998), thereby negatively influencing the recruitment of catfishes. Holland-Bartels and Duval (1988) suggested that variation in channel catfish productivity was related to river discharges. A decrease in age-0 channel catfish abundance was attributed to a sharp increase in river discharge that likely disrupted spawning activity and flushed young from nests (Holland-Bartels and Duval 1988).

Growth of catfishes may also be related to hydrology in river systems. Quist and Guy (1998) suggested that increased growth of channel catfish in the Kansas River resulted from floodplain inundation. Inundation of the floodplain typically provides more shallow, prey-rich habitats for fishes (Welcomme 1979). In addition, floodplain inundation probably influenced the growth of flathead catfish in the lower Mississippi River system (Mayo and Schramm 1999). However, Mayo and Schramm (1999)

hypothesized that growth of flathead catfish was also influenced by water temperature during the growing season, in addition to the number of flood days. Rutherford et al. (1995) determined that growth of age-0 channel catfish in the Mississippi River was related to the length of the growing season.

In the Alabama River system, four hydropower dams have been constructed on the main stem of the Tallapoosa River (Boschung and Mayden 2004). In the Northern Piedmont, flows have rapidly fluctuated between extremely low and high flows as a result of hydropeaking operations downstream of Harris Dam on the Tallapoosa River (Irwin and Freeman 2002). These extreme fluctuations in discharge during a period of only four to 6 hours have generated a highly variable flow regime that has potentially threatened the persistence of several native fishes (i.e., fluvial specialists) below the dam (Irwin and Freeman 2002). Irwin and Freeman (2002) reported that significant changes in hydrology occurred after construction of Harris Dam in 1982, which included increases in high-pulse frequency, low-pulse frequency, fall rate, and the number of flow reversals. On the Tallapoosa River in the East Gulf Coastal Plain, a minimum continuous flow of 34 m³/s was established below Thurlow Dam (i.e., the terminal dam) as part of a re-licensing agreement in 1991. Although diversity of fishes increased approximately 3 km downstream of the dam (Travnichek et al. 1995), Thurlow Dam has still exhibited high annual variability in discharge that often exceeds dam capacity, which has typically resulted in prolonged periods of high flow (> 283 m³/s).

The Coosa River is also a highly regulated system in the Alabama River system. Mitchell Dam, one of six hydroelectric facilities on the main stem of the Coosa River, has exhibited high variation in average seasonal flows and annual high and low pulse

frequencies. In general, most of the free-flowing habitats in the Alabama River system have been converted to unimpounded main stem river sections (Freeman et al. 2004). A better understanding of how hydrologic alteration has affected growth and recruitment of catfishes is needed below hydropower dams throughout the system.

Few studies have been conducted to evaluate changes in fish productivity or diversity after flow regimes were prescribed or modified in regulated river sections below dams (Travnichek et al. 1995; Propst and Gido 2004). Propst and Gido (2004) attempted to partially mimic the natural flow regime in a regulated reach of the San Juan River (Colorado). Densities of native fishes typically increased in years with high spring discharges (Propst and Gido 2004). Wildhaber et al. (2000) evaluated relations between Neosho madtom densities and flows in the Neosho River Basin below John Redmond Dam and suggested that higher minimum flows be prescribed in the river to improve densities of Neosho madtoms and other ictalurids. Although regulated rivers can never be fully restored to natural conditions, flows below dams should be managed to best represent natural flow conditions (i.e., the natural flow regime; Poff et al. 1997).

An adaptive approach for managing regulated river systems has recently been implemented in the Tallapoosa River below Harris Dam (i.e., adaptive-flow management; Irwin and Freeman 2002). Managers are attempting to restore rivers similar to their natural flow regimes while still providing needed resources for society (Irwin and Freeman 2002). The main goal of adaptive-flow management is to continually improve management as uncertainty about a river system is reduced, which requires cooperation and commitment among natural resource personnel, private industry, landowners, and other stakeholders. Adaptive flow management can be described as an iterative process

with a series of steps that include 1) prescription of a flow/management regime, 2) monitoring and evaluation of the flow regime's effect on habitat and biota, and 3) the recommendation of a new and improved management regime. By quantifying relations between hydrology and growth and recruitment of fishes in regulated rivers, models can be developed to predict responses of fish populations to the prescription of flow regimes. These models can be continually improved as we learn more about the effects of hydrologic variability on the dynamics of fish populations.

My objectives were to: 1) develop and validate techniques for using otoliths to daily age age-0 channel catfish, 2) assess the effects of hydrology on growth and hatching success of young-of-the-year channel catfish in regulated and unregulated reaches within the Tallapoosa River system, 3) quantify relations between hydrology and recruitment of native and introduced flathead catfish in regulated and unregulated river systems in Alabama and Georgia, respectively, 4) develop stochastic population matrix models for flathead catfish to predict how effects of hydrologic variability on recruitment and variable mortality will ultimately affect the growth of populations, and 5) using these findings, recommend or prescribe flow regimes for managing catfishes in regulated river sections of the Tallapoosa and Coosa rivers.

II. VERIFICATION OF DAILY RING DEPOSITION IN THE OTOLITHS OF AGE-0 CHANNEL CATFISH

Abstract. – I developed and validated methods for daily aging age-0 channel catfish, *Ictalurus punctatus*. Two clutches of channel catfish eggs were hatched in the laboratory; subsequently, one was stocked in a 0.046-acre earthen nursery pond and the other in a 200-g, outdoor circular tank. Prior to stocking, a sub-sample of fish was collected at swim-up and 3 d post swim-up to evaluate early ring formation. Fish were sampled from the pond and tank on eight occasions ranging from 30 to 119 days post hatch. Distinct differences in early ring formation were found between yolk-sac and free-swimming larval stages. Mean ring count and known age were closely related for tank and pond-raised fish, indicating that daily ring deposition occurred in the otoliths of age-0 channel catfish. In general, daily ring counts were reasonably accurate for 107 - 119 days after hatch. However, tank-raised fish were aged more accurately than pond-raised fish, which I attributed to ring compression resulting from slower growth among pond-raised fish after 30 days. Fish length was positively related to otolith size for tank and pond-raised fish; however, slopes of relations between fish length and otolith radius were different between treatments. Therefore, I could not confirm that the relation between fish length and otolith size was directly proportional for age-0 channel catfish. I conclude that

otoliths from age-0 channel catfish can provide reliable estimates of hatch and swim-up dates and back-calculated lengths at age (i.e., up to 120 days after hatch). Differences in early ring formation will allow researchers to estimate dates of hatch and swim-up for age-0 channel catfish. I encourage researchers to use this aging technique to determine how abiotic and biotic factors influence early life history characteristics of catfishes.

Introduction

Methodology for daily aging using otoliths has been developed for various freshwater and estuarine fish species (Barkman 1978; Miller and Storck 1982; Secor and Dean 1992; Dicenzo and Bettoli 1995; Ahrenholz et al. 2002). Researchers have aged larval fish to back-calculate hatch dates, estimate mortality rates, and determine early growth histories, which have been related to abiotic and biotic factors (e.g., hydrology and climatic conditions; Crecco and Savoy 1987; water temperature and zooplankton abundance; Limburg et al. 1999; hydrology and zooplankton abundance; Sammons et al. 2001). Daily ring deposition has been verified with known-age fish for numerous fish species (Miller and Storck 1982; Davis et al. 1985; Graham and Orth 1987; Sweatman and Kohler 1991; Parrish et al. 1994; Paragamian et al. 1992; Dicenzo and Bettoli 1995); however, methods have not been adequately validated for catfishes.

Holland-Bartels and Duval (1988) attempted to verify the hypothesized 1:1 relation of age to ring count in the otoliths of larval channel catfish, *Ictalurus punctatus*, up to 60 days in the laboratory. Although increments were observed up to 18 d post-hatch, difficulties with ring resolution were apparent after 20 d (Holland-Bartels and Duval 1988). This inability to easily resolve rings after 20 days may have been attributed to rearing fish in an aquarium at constant water temperature versus a more natural setting

(e.g., a nursery pond) with variation in photoperiod and temperature. However, Holland-Bartels and Duval (1988) did not report a resolution problem when aging wild fish, indicating that fish could be aged beyond 20 days post-hatch.

Annulus formation has been verified in otoliths of adult channel catfish and researchers have suggested that otoliths be the primary structures for aging catfishes (Nash and Irwin 2001; Buckmeier et al. 2002). However, the small size of otoliths (e.g., radii = 0.11 – 0.69 mm, 9 – 107 d post-hatch) from age-0 catfish presents major challenges for development of a successful daily aging technique. Traditional daily aging techniques have typically involved the mounting of otoliths in thermoplastic cement and, in most cases, sectioning in the sagittal or longitudinal planes (Miller and Storck 1982; Davis et al. 1985; Sweatman and Kohler 1991; Parrish et al. 1994; Diczynski and Bettoli 1995; Bestgen and Bundy 1998; Roberts et al. 2004). However, these traditional techniques may not be appropriate for aging ictalurids, due to differences in size and structure of otoliths between catfishes and other species (e.g., centrarchids).

Although Holland-Bartels and Duval (1988) aged age-0 channel catfish by sectioning otoliths in the sagittal plane, other researchers have successfully aged adult catfishes by sectioning otoliths in the transverse plane (Buckmeier et al 2002; Nash and Irwin; Grabowski et al. 2004; Kwak et al. 2006). In addition, alternative daily aging techniques have involved embedding otoliths in epoxy and sectioning along the transverse plane (e.g., striped bass, *Morone saxatilis*; Limburg et al. 1999). Therefore, daily aging of catfishes may be more successful using transverse sections versus sagittal sections of otoliths. In this study, my objectives were to: 1) develop an alternative

method for daily aging of age-0 channel catfish, 2) determine if ring deposition occurs daily in the otoliths of this species, and 3) verify when daily ring deposition begins.

Methods

Two clutches of channel catfish eggs were hatched at 28°C in the laboratory on 17-18 May 2005 and 30-31 May 2005, respectively. After eggs were hatched, yolk-sac larvae from the first clutch were held in a 10-g aquarium (at 28°C) equipped with aeration and water flow until they reached swim-up stage on 23 May 2005 (i.e., 5-6 days post-hatch). At swim-up, larvae were stocked in an outdoor, circular tank (~ 200 gallons) that continually received inflow from a large reservoir in a flow-through system. Although the fish potentially received natural prey items from the reservoir, channel catfish larvae were trained to eat pelleted food and were fed once daily to satiation (i.e., offered food until they no longer accepted it). Larvae from the second clutch were held in a 10-g aquarium (at 28°C) until they were successfully trained to eat dry food on 8 June 2005 (i.e., three days after reaching swim-up stage). Larvae were then transferred to a 0.046-acre earthen nursery pond where they were fed once daily to satiation. Water temperature was monitored in the tank and pond with Optic StowAway© loggers (Onset© Computer Corporation, Bourne, Massachusetts) that recorded temperature every 24 min. Fish were exposed to natural variation in temperature and photoperiod after they were transferred to the tank and pond.

Larvae were collected from the circular tank at swim-up stage and three days after swim-up to determine if daily ring deposition differed between yolk-sac and free-swimming larval stages. Age-0 channel catfish were also collected from the tank on eight occasions (i.e., 30, 45, 58, 72, 90, 105, 112, and 119 days post-hatch). Pond-raised

channel catfish were collected at stocking (nine days post-hatch) and on eight other occasions (i.e., 36, 45, 53, 59, 67, 77, 85, and 107 days post-hatch). In all cases, approximately 20 – 30 age-0 fish were collected on each occasion. Five fish were randomly chosen from each sample for daily aging. Fish were measured to the nearest 1.0 mm TL and weighed to the nearest 0.01 g. Otoliths were extracted using fine-tipped forceps with a dissecting microscope and stored dry prior to preparation.

Otolith preparation and aging

For larvae sampled from the tank at swim-up and three days post swim-up, otoliths were mounted with thermoplastic cement on a microscope slide. Otolith sizes at swim-up stage (sagittal radii \approx 0.1 mm) presented major challenges for preparing transverse sections, so sagittal sections were prepared (Secor et al. 1992). Otoliths were lightly polished with three-micron aluminum oxide Fibrmet® sheets (Buehler®, Lake Bluff, Illinois) until otolith cores were visible. Otolith sections were closely examined for daily ring deposition before and after swim-up. If rings were present, any differences in ring formation before and after swim-up were noted. Data from these otolith sections were not used for statistical purposes.

Otoliths from the remaining fish were embedded in a clear epoxy resin and were fixed with thermoplastic cement in a position perpendicular to the plane of a microscope slide. Otoliths were slowly ground with ultra fine (600-grit) sandpaper and routinely viewed under a compound microscope (at 400X magnification) until the core and rings were visible. The otolith was then inverted and ground slowly on the other side until a thin, transverse section was obtained. In most cases, the section would have to be

inverted and polished several times with aluminum oxide Fibrmet® sheets before otolith cores and rings were clearly visible.

Without reference to known ages, otoliths were read independently three times in random order, and no two counts of the same otolith were made consecutively (Miller and Storck 1982; DiCenzo and Bettoli 1995). Otolith rings were counted from the outer edge to the core at 400X magnification. The mean of the three counts for each otolith was used for analyses. Otolith radii were measured from the center of the core to the outer edge (to the nearest μm) using an image analysis system (Image-Pro® Plus, Media Cybernetics, Inc., Silver Spring, Maryland). I also used line profile analysis to plot intensity level (i.e., gray level) along transects from cores to outer edges of otolith sections (Image-Pro® Plus, Media Cybernetics, Inc., Silver Spring, Maryland). Changes in intensity level and peak formation, specifically from yolk-sac to free-swimming larval stages, were evaluated along transects.

Statistical analysis

Linear regression analyses were used to evaluate relations between the following variables: 1) mean ring count and known age (d), 2) fish length (mm total length - TL) and known age (d), and 3) fish length (mm TL) and otolith radius (OR – converted to mm). I tested null hypotheses that slopes and intercepts of regressions between mean ring count and known age equaled one and zero, respectively (*t*-tests). Mean deviance of mean ring count from known age was calculated for each age group from tank and pond samples. Analysis of covariance (ANCOVA) was used to compare slopes of TL-to-age regressions between tank and pond samples. I also used ANCOVA to compare slopes of

TL-to-OR regressions between tank and pond samples. Significance was set at $\alpha=0.05$, and all statistics were conducted using Statistical Analysis System software (SAS 1990).

Results

I aged 45 fish from the pond and 40 fish from the tank. In general, fish growth in the tank was more variable than growth in the pond (Table 1). Water temperature varied on a diel basis, but did not vary greatly over time in either the tank or pond (tank mean temperature: $28.5^{\circ}\text{C} \pm 1.4$ – S. D.; pond mean temperature: $28.3^{\circ}\text{C} \pm 2.5$ – S. D.).

Ring deposition was apparent before and after swim-up. However, ring formation before swim-up appeared irregular with rings tightly spaced together (Figure 1). After larvae reached swim-up stage, rings appeared to be regularly deposited and were more distinct than rings formed during the yolk-sac stage (Figure 1). In addition, line profile analysis indicated that intensity level and peak formation differed considerably along transects between yolk-sac and free-swimming larval stages; however, a transition period (≈ 5 d) was apparent between these stages (Figure 2). Careful inspection of otolith cores and line profiles indicated that the first ring formed on the day of hatch.

Mean ring count was closely related to known age of tank-raised fish ($r^2 > 0.99$, $P < 0.01$; Figure 3a); slope (= 0.96) and intercept (= 1.75) of the regression were not different from one and zero, respectively (slope: $df = 6$, $t = 1.36$, $P > 0.20$; intercept: $df = 6$, $t = 0.78$, $P = 0.47$). Mean ring count was also closely related to known age of pond-raised fish ($r^2 > 0.99$, $P < 0.01$; Figure 3b), and the intercept (= 2.53) of the regression was equal to zero ($df = 6$, $t = 2.00$, $P = 0.08$). However, the slope (= 0.93) was different from one for pond-raised fish ($df = 6$, $t = 3.42$, $P < 0.05$). Mean deviance from known age was minimal ($-1.6 \leq D \leq 2.5$) up to 105 days after hatch for tank-raised fish. Age

was underestimated by only 3.1 days after 119 days (Figure 4a). In contrast, age of pond-raised fish was underestimated by 6.3 days at 107 days after hatch (Figure 4b).

Slope of the TL-to-age regression for tank-raised fish (slope = 0.78) was higher than the slope for pond-raised fish (slope = 0.55), indicating that tank-raised fish grew faster than pond-raised fish after 30 days (ANCOVA: $t = 2.39$, $P = 0.03$; Figure 5). Fish length was positively related to otolith size (Tank: $r^2 = 0.96$, $P < 0.01$; Pond: $r^2 = 0.92$, $P < 0.01$; Figures 6a-b). However, slope of the TL-to-OR regression for tank-raised fish (slope = 165) was higher than the slope for pond-raised fish (slope = 130; ANCOVA: $t = 4.21$, $P < 0.01$).

Discussion

Daily ring deposition occurred in otoliths of age-0 channel catfish, and these daily rings can be enumerated for 107 - 119 days after hatch. Similar findings have been reported for centrarchids (Miller and Storck 1982; DiCenzo and Bettoli 1995; Roberts et al. 2004). Miller and Storck (1982) raised larval largemouth bass, *Micropterus salmoides*, for 150 days after hatch and determined that age estimation using otoliths was accurate for 80-100 days after swim-up phase. Redspotted sunfish, *Lepomis miniatus*, were successfully aged through 119 d (Roberts et al. 2004), and ages of age-0 white crappie, *Pomoxis annularis*, were accurately estimated up to 100 d after hatch (Sweatman and Kohler 1991).

I observed distinct differences in daily ring formation before and after swim-up phase. These differences will allow researchers to estimate hatch and swim-up dates for age-0 channel catfish. Ring formation appeared irregular for approximately four to five

days after swim-up, but this may be attributed to stress associated with transfer from the aquarium to the pond or tank.

Underestimation of age was more prevalent for pond-raised channel catfish than for tank-raised fish after 80 d. Pond-raised fish exhibited slower growth rates than tank-raised fish after 30 d, which resulted in the compression of daily rings near the edges of otolith sections. Faster growth rates among tank-raised fish resulted in wider daily increments near edges of otolith sections, thereby facilitating the reading and interpretation of ages of older fish. DiCenzo and Bettoli (1995) reported that slow growth resulted in the compression of daily rings and the underestimation of ages for spotted bass, *M. punctulatus*, after 94 days. Ages of largemouth bass were also underestimated after 100 days, which was attributed to declining growth rates at lower water temperatures (Miller and Storck 1982). I postulate that slow growth was likely the cause for low resolution of rings in the otoliths of laboratory-reared channel catfish after 20 d post-hatch in Holland-Bartels and Duval's (1988) study.

I observed strong relations between fish length and otolith size. Similar relations have been observed for other species, such as largemouth bass and redspotted sunfish (Miller and Storck 1982; Roberts et al. 2004). After finding a strong relation between fish length and sagitta radius, Miller and Storck (1982) reported that lengths of age-0 largemouth bass could be back-calculated at any age. However, I could not confirm that relations between channel catfish size and otolith size were directly proportional. If a directly proportional relation existed for channel catfish, slopes of TL-to-OR regressions would have been equal between pond and tank samples.

Studies have indicated that otoliths continue to grow at a linear rate when somatic growth is negligible (Secor and Dean 1992; Bestgen and Bundy 1998). Bestgen and Bundy (1998) reported that otoliths from Colorado squawfish, *Ptychocheilus lucius*, continued to grow for 15 days although growth in body length ceased. Secor (1992) observed a similar response in larval striped bass, *Morone saxatilis*, and determined that otoliths grew at a linear rate even when larvae experienced negative somatic growth. Therefore, back-calculation methods for determining growth histories may be more accurate if they involve multiple regression or quadratic response models that incorporate other factors that predict length-at-age in addition to otolith size (Secor 1992). More studies are needed to investigate relations between otolith growth and somatic growth of larval fishes.

I conclude that otoliths from age-0 channel catfish can provide reliable estimates of hatch and swim-up dates (i.e., up to 120 days after hatch) as well as early growth histories. For fish exhibiting substantial growth rates, these estimates could potentially be valid up to 150 days after hatch. I encourage researchers to use this aging technique to determine how abiotic and biotic factors influence early life history characteristics and, ultimately, the population dynamics of catfishes.

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Table 1. Mean (S.D.), minimum and maximum total lengths (mm) of age-0 channel catfish that were aged from the pond and tank.

Sample	Day	N	Total Length	Min/Max
<i>Pond</i>	9	5	15 (2.6)	15/16
	36	5	48 (1.9)	45/52
	45	5	53 (2.5)	50/55
	53	5	50 (3.1)	47/54
	59	5	50 (8.6)	47/54
	67	5	57 (4.2)	51/72
	77	5	65 (5.3)	61/72
	85	5	68 (5.5)	61/74
	107	5	88 (2.6)	82/96
	<i>Tank</i>	30	5	31 (2.9)
45		5	36 (4.8)	31/41
58		5	52 (7.2)	41/59
72		5	60 (8.1)	49/69
90		5	78 (6.4)	67/82
105		5	86 (19.0)	53/100
112		5	84 (10.7)	75/101
119		5	105 (6.6)	98/113

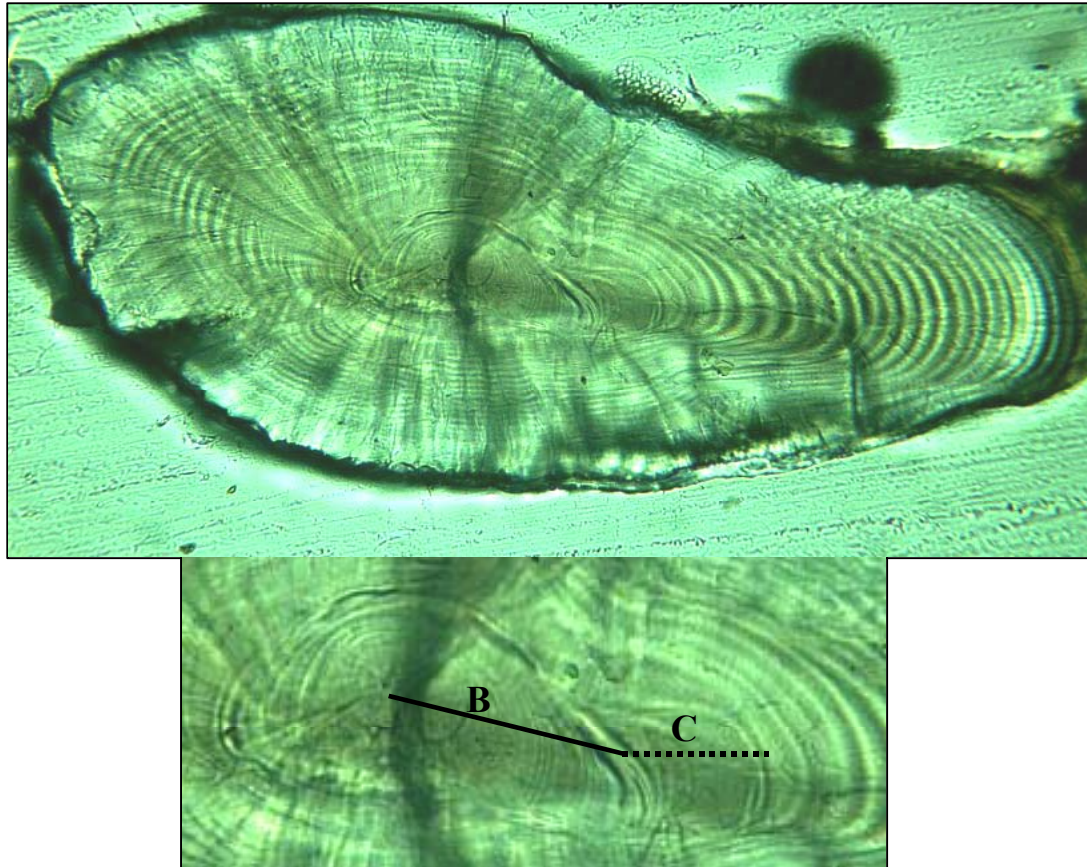


Figure 1. Transverse section of an otolith extracted from a 36 day old fish revealing the A) otolith core, B) rings formed before swim-up, and C) the transition to regular ring formation after swim-up.

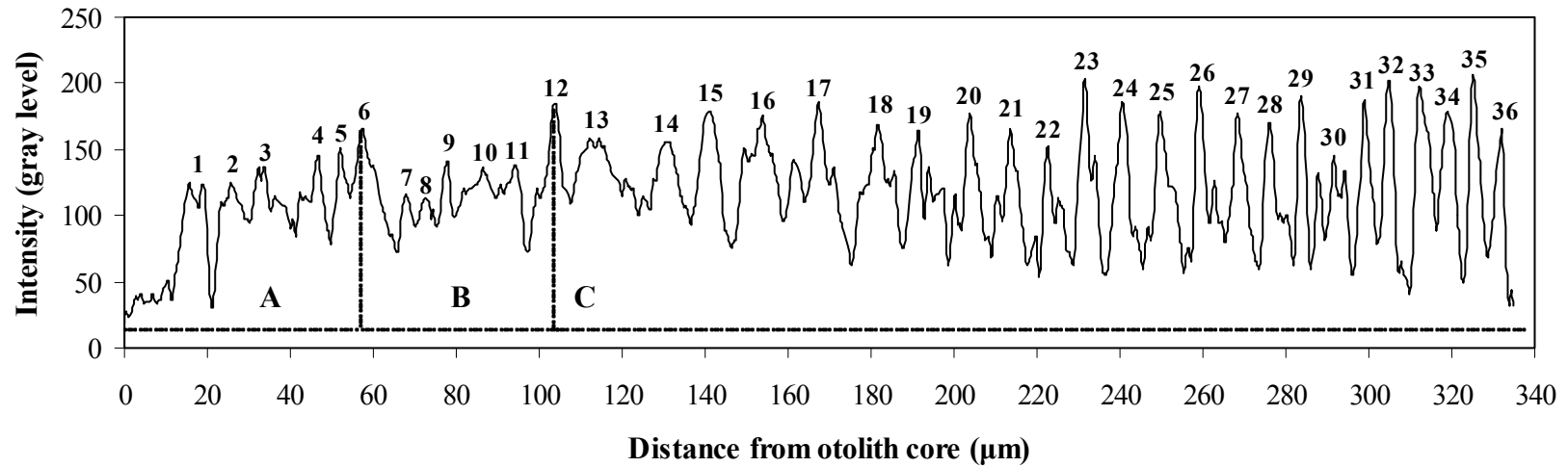


Figure 2. Line profile along a transect from the core to the outer edge of an otolith extracted from a 36 day old fish indicating intensity levels A) before swim-up, B) during a transition period, and C) after swim-up. Peaks that represent the intensity of a daily ring are labeled with the appropriate day number.

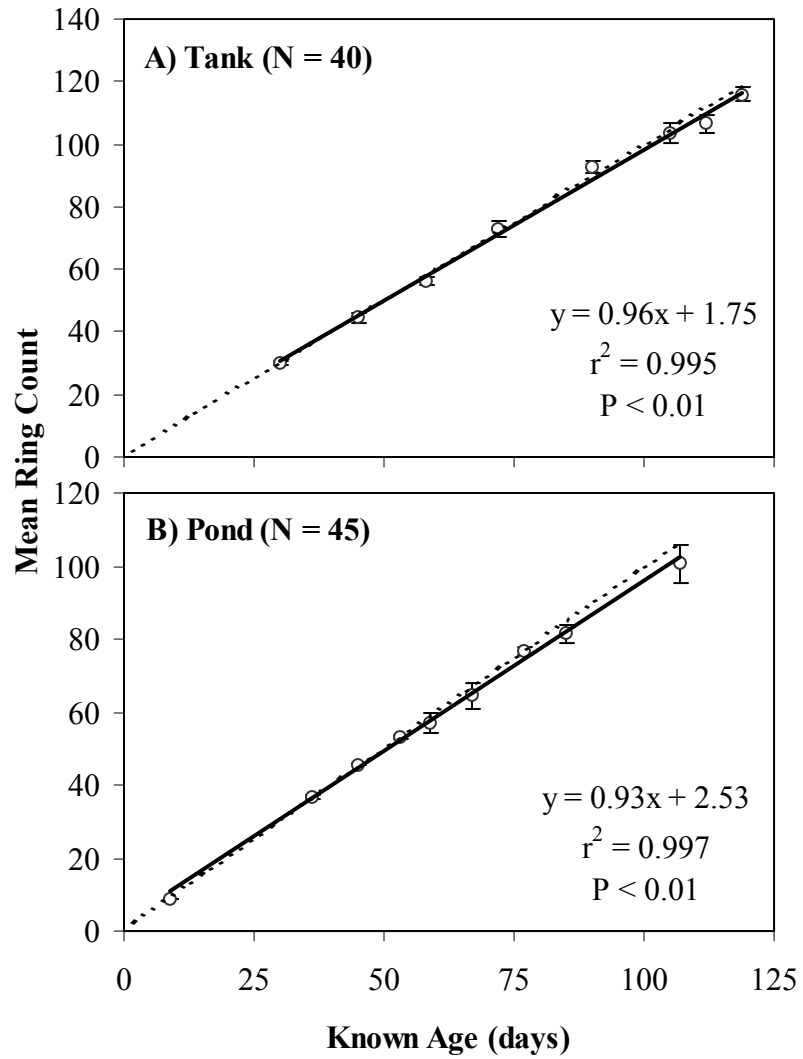


Figure 3. Relations between mean ring count and known age for age-0 channel catfish that were raised in the tank (A) and pond (B) (Error bars = S.D.; dashed lines represent 1:1 relationships).

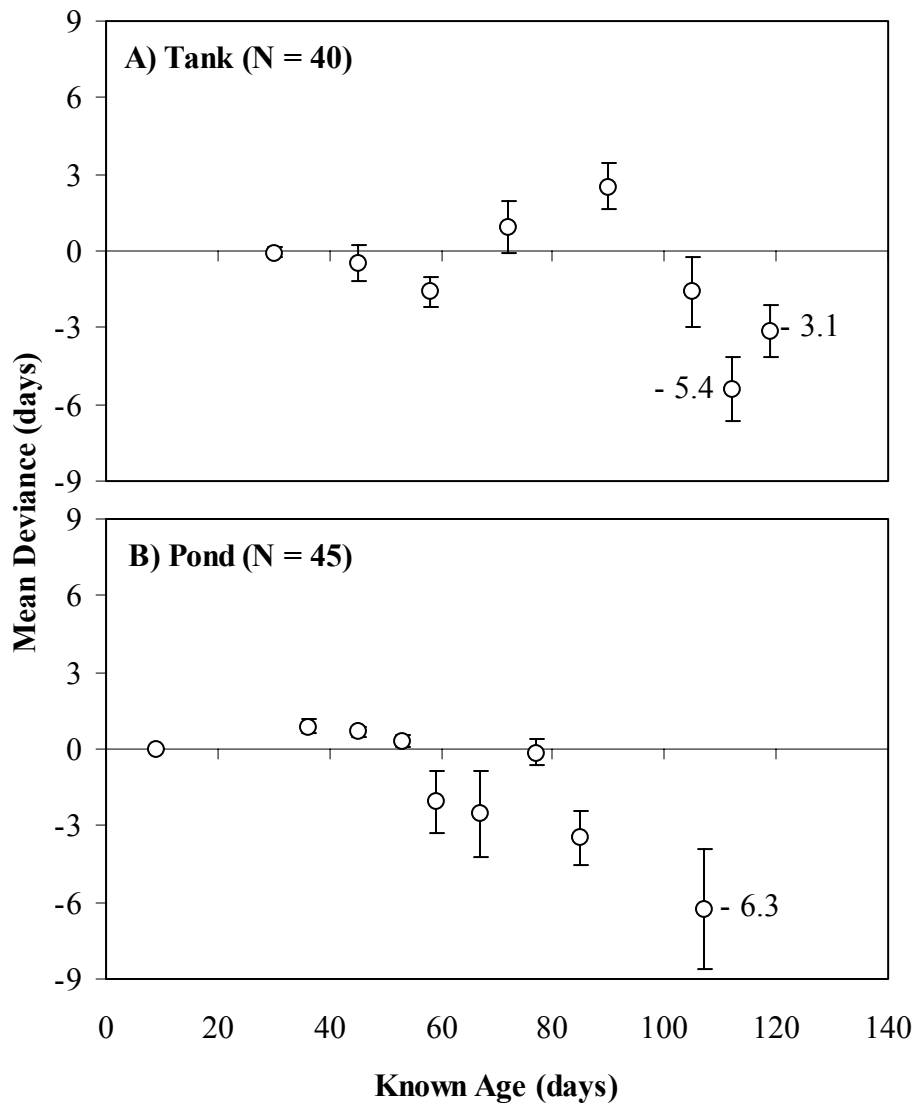


Figure 4. Deviance of mean ring count from known age for age-0 channel catfish that were raised in the tank (A) and pond (B) (Error bars = S.E.).

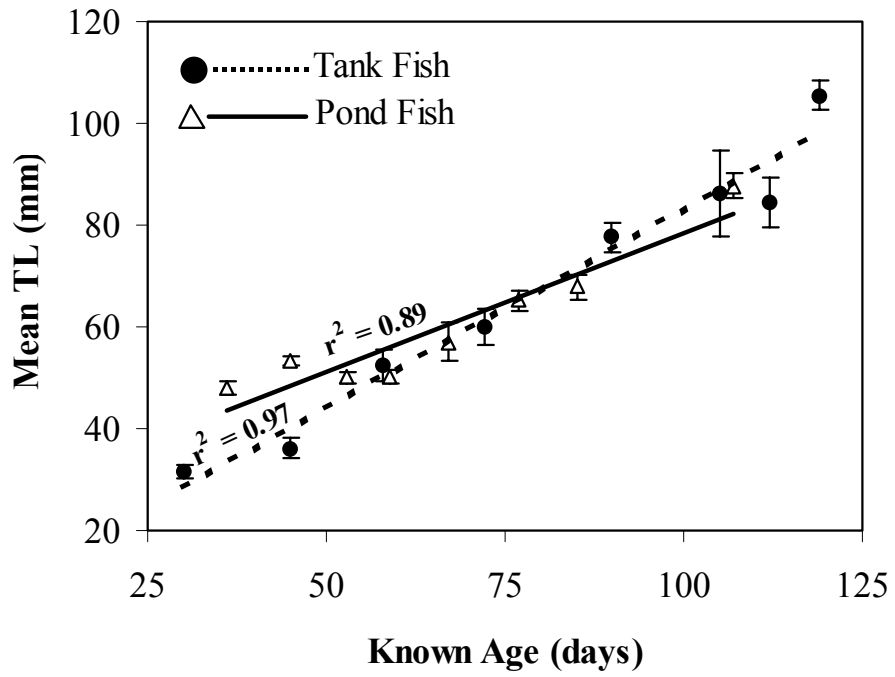


Figure 5. Relations between total length (TL) and known age for age-0 channel catfish (≥ 30 days old) that were raised in the tank and pond (Error bars = S.E.).

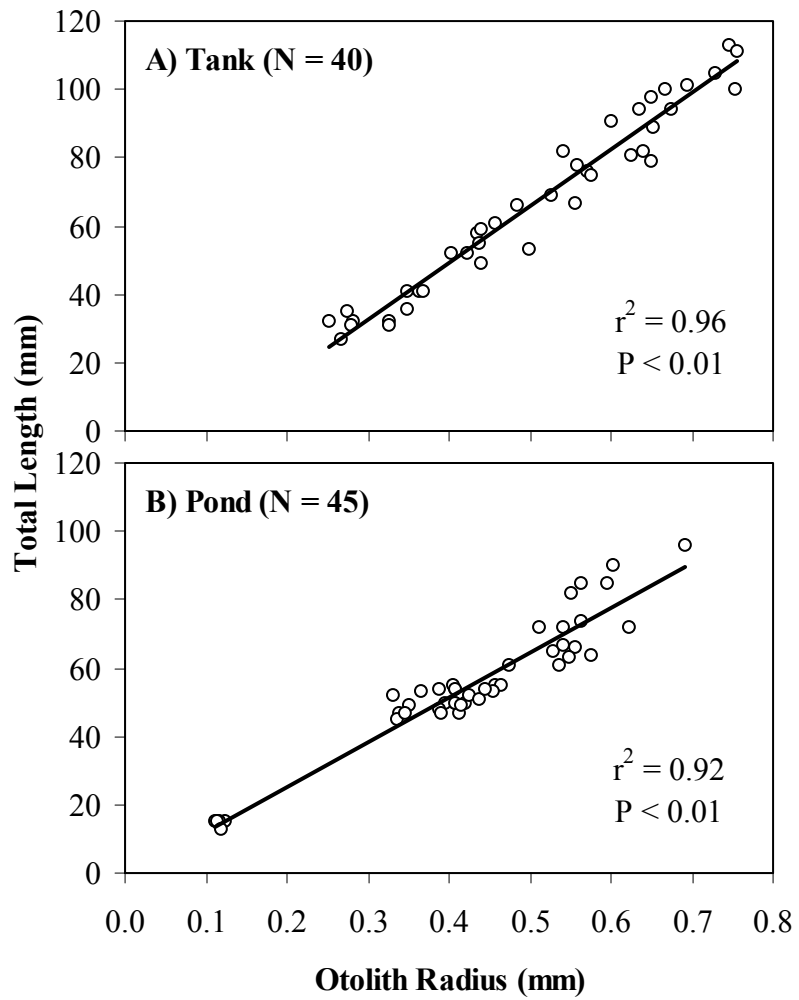


Figure 6. Relations between total length and otolith radius for age-0 channel catfish that were raised in the tank (A) and pond (B).

III. HYDROLOGIC EFFECTS ON GROWTH AND HATCHING SUCCESS OF AGE-0 CHANNEL CATFISH IN THE TALLAPOOSA RIVER BASIN: IMPLICATIONS FOR MANAGEMENT IN REGULATED SYSTEMS

Abstract. –I examined the effects of hydrology on growth and hatching success of age-0 channel catfish in regulated and unregulated reaches of the Tallapoosa River Basin, Alabama. Age-0 channel catfish (N = 91) were collected from sites in the Coastal Plain and Piedmont in fall 2003 and fall 2005, respectively. Fish were assigned daily ages using otoliths. Hatch dates of fish were back calculated, and growth histories were estimated every 20-d post-hatch from otolith sections using incremental growth analysis. Age-0 channel catfish from the Coastal Plain hatched from 7 June to 27 August 2003, whereas fish from the Piedmont hatched from 8 June to 15 Sept 2005. Ages and growth rates of age-0 channel catfish ranged from 20 to 126 d and 0.60 to 1.5mm/d, respectively. In general, growth was highest among age-0 fish from unregulated sites in the lower Coastal Plain, intermediate among fish from regulated sites in the Piedmont, and lowest among fish from unregulated sites in the upper Piedmont. All age-0 fish that hatched in fall originated from the regulated site, indicating that fish in the regulated reach had a protracted spawning season. Generally, positive relations existed between growth of age-0 channel catfish and hydrologic variables including mean discharge, minimum

discharge, number of high pulses, and rise rate. However, several relations between growth of age-0 channel catfish and hydrologic variables were non-linear and were best described by second-degree polynomial regressions. In addition, fish growth was negatively affected by high fall rates. Successful hatching of age-0 channel catfish typically occurred during periods with low and stable flow conditions. Based on these findings, I prescribed a flow regime that would potentially enhance growth and recruitment of age-0 channel catfish in a regulated reach of the Tallapoosa River.

Introduction

Regulation of river flow alters physical, chemical, and biological conditions in freshwater ecosystems (Cushman 1985). Hydropower operations can potentially reduce fish productivity as a result of rapidly fluctuating flows (e.g.; hydropeaking) that alter stream habitat and reduce temperatures (Poff et al. 1997). Freeman et al. (2001) reported that habitat stability was necessary for successful fish reproduction and young-of-the-year survival in regulated rivers. However, few studies have examined the influence of hydrology on fish growth and recruitment in regulated rivers below dams (Freeman et al. 2001). Quantifying the effects of hydrologic alteration on fish populations would assist managers in developing fishery and dam licensing plans, given that most rivers in the Southeast (USA) are regulated. Specifically, models relating hydrology to fish growth and reproductive success can be used to prescribe flow regimes that may potentially improve fish productivity in regulated systems within an adaptive flow management framework (Irwin and Freeman 2002).

Hydrologic alteration in regulated rivers may have negative impacts on catfish productivity. High flow variability may alter riffle habitat utilized by juvenile channel

catfish *Ictalurus punctatus* and flathead catfish *Pylodictis olivaris* (Irwin et al. 1999). Other studies have indicated that floodplain inundation and water temperature may influence the growth of catfishes (Mayo and Schramm 1999; Quist and Guy 1998). Inundation of the floodplain typically provides fishes with more shallow, prey-rich habitat (Welcomme 1979); however, the frequency and timing of floodplain inundation may be altered by hydropower operations (Cushman 1985; Pringle et al. 2000). Coldwater from hypolimnial-release dams may dramatically lower spring and summer tailwater temperatures, which may slow growth and development and alter physiology during early life stages of fishes (Clarkson and Childs 2000).

Holland-Bartels and Duval (1988) studied the spatial and temporal variation in abundances of young-of-the-year channel catfish in the upper Mississippi River and hypothesized that variation in productivity was partially related to river discharges. In 1984, a decrease in age-0 channel catfish production was observed and attributed to a sharp increase in river discharge that likely disrupted spawning activity and flushed young fish from nests (Holland-Bartels and Duval 1988). Rutherford et al. (1995) examined relations between physicochemistry and growth of young channel catfish (\leq age-2) in the Mississippi River and determined that growth of age-0 channel catfish was related to the length of the growing season. No studies have investigated relations between hydrology and daily growth of recently hatched age-0 channel catfish in regulated or unregulated river systems. In addition, general information about the early life history of channel catfish in river systems is limited.

In Alabama, discharges below Harris Dam on the middle Tallapoosa River have rapidly fluctuated between extremely low and high flows as a result of hydropeaking

operations (Irwin and Freeman 2002). This extreme fluctuation in river flow during a period of only four to 6 hours has produced unstable flow conditions that have potentially threatened the persistence of several native riverine species below the dam (Irwin and Freeman 2002). Irwin and Freeman (2002) reported that significant changes in hydrology occurred after construction of Harris Dam in 1982, which included increases in high-pulse frequency, low-pulse frequency, fall rate (i.e., mean or median of all negative differences between consecutive daily values), and the number of flow reversals (i.e., number of times that flow switches between rising and falling periods). A better understanding of how hydrologic alteration has affected daily growth of age-0 fish and reproductive success is needed below Harris Dam.

On the lower Tallapoosa River, a minimum continuous flow of 34 m³/s was established below Thurlow Dam (i.e., the terminal dam). As a result, fish diversity increased at a site three km below the dam, which suggested that modification of the flow regime could enhance diversity of fish assemblages in the regulated system (Travnichek et al. 1995). However, Thurlow Dam has still exhibited high annual variability in discharge that often exceeds dam capacity, resulting in prolonged periods of high flow (> 283 m³/s). No studies have been conducted to assess relations between hydrologic variation and growth and recruitment of fishes in the lower Tallapoosa River.

In this study, my objectives were to: 1) assess and compare early growth histories and hatch frequencies of age-0 channel catfish from regulated and unregulated sites located in the Piedmont Upland and East Gulf Coastal Plain within the Tallapoosa River Basin, Alabama; 2) determine how hydrology influenced the early growth and hatching success of age-0 channel catfish in regulated and unregulated river reaches within the

Tallapoosa River Basin; 3) recommended a flow regime that would potentially enhance growth of age-0 channel catfish and spawning success in regulated reaches of the Tallapoosa River below Harris and Thurlow dams.

Methods

Fish collection

Age-0 channel catfish were collected using Prepositioned Area Electrofishers (PAEs) and backpack electrofishing from three sites in the Coastal Plain in fall 2003 and four sites in the Piedmont in fall 2005 within the Tallapoosa River Basin, Alabama (Figure 1). Sites were: 1) Uphapee Creek, 2) Cubahatchee Creek, 3) Dozier's bar, on the main stem of the lower Tallapoosa River downstream of Thurlow Dam, 4) Hillabee Creek, 5) Upper Tallapoosa River, 6) Malone and Wadley sites, on the main stem of the middle Tallapoosa River downstream of Harris Dam, and 7) Peter's Island, downstream of the Malone and Wadley sites below Harris Dam. Uphapee and Cubahatchee creeks were unregulated and were located in the East Gulf Coastal Plain below the fall line. Dozier's Bar was a regulated site, also located in the Coastal Plain. Hillabee Creek and Upper Tallapoosa River sites were unregulated and were located in the Piedmont Upland above the fall line. The Malone, Wadley and Peter's Island sites were regulated, also located in the Piedmont (Figure 1). In this study, Malone and Wadley sites were combined (i.e., Malone-Wadley), due to lower sample sizes at both sites. These sites were in close proximity to each other and were much closer to Harris Dam than the Peter's Island site.

Laboratory methods

Age-0 channel catfish were measured to the nearest 0.1 mm TL and weighed to the nearest 0.01 g. Otoliths were extracted from fish using fine-tipped forceps with a dissecting microscope and stored dry prior to preparation. All fish were aged following methods described by Sakaris (Chapter II). Otoliths were embedded in a clear epoxy resin and ground to the core on both sides with fine sandpaper (600 grit) until a thin, transverse section was obtained. Otolith rings were counted from the outer edge to the core at 400X magnification using an image analysis system (Image-Pro® Plus, Media Cybernetics, Inc., Silver Spring, Maryland). Otolith radii were measured from the center of the core to the outer edge (to the nearest μm ; Image-Pro® Plus, Media Cybernetics, Inc., Silver Spring, Maryland). Radii were also measured from the core towards the edge of each otolith at 20 d increments to estimate incremental growth (i.e., 0-20, 20-40, 40-60, 60-80, 80-100, and 100-120 d post-hatch; Image-Pro® Plus). Sakaris (Chapter II) reported that strong relations existed between total length of age-0 channel catfish and otolith radius ($r^2 = 0.92 - 0.96$), indicating that otolith growth was a robust predictor of fish growth.

Statistical Analyses

Linear regression analyses were used to assess relations between the following variables: 1) Growth rate (= TL/age, mm/d) and age, 2) Total length and otolith radius (μm), and 3) Age and otolith radius. Hatch dates were calculated by subtracting specimen age from collection date. Hatch frequency histograms were constructed for fish that were collected in 2003 and 2005.

Growth comparisons.—Two-factor analysis of variance (ANOVA) was used to determine if growth differed among sites and age groups. Incremental growth data from 0-20, 20-40, and 40-60 d post-hatch were used in this analysis, because data were limited beyond 60 d post-hatch for the Uphapee Creek site (i.e., only two fish were older than 70 d in the sample). If a site*age interaction existed, ANOVA was used to compare growth among sites within each age group. Duncan's Multiple Range Test was used for post-hoc comparisons of means ($\alpha = 0.05$). The Dozier's Bar site was excluded from this analysis, because only one age-0 channel catfish was collected from this location.

Hydrologic relations with growth.—Multiple regression models were derived to assess relations between fish growth and hydrology at five locations (i.e., Uphapee Creek, Upper Tallapoosa River, Malone-Wadley, Peter's Island, and Hillabee Creek).

Hydrologic data were obtained from USGS gage stations that were in close proximity to the five locations: 1) USGS 02419000, Uphapee Creek near Tuskegee, Alabama, 2) USGS 02412000, Upper Tallapoosa River near Heflin, Alabama, 3) USGS 02414500, Middle Tallapoosa River at Wadley, Alabama (for Malone-Wadley and Peter's Island sites), and 4) USGS 02415000, Hillabee Creek near Hackneyville, Alabama. Various hydrologic variables were derived for each site (e.g., mean discharge, fall rate, rise rate, high and low pulse frequencies) and were used as independent variables in multiple regression models (see hydrologic variables listed and defined in Table 1). Hydrologic variables were similar to variables that are generated in the Indicators of Hydrologic Alteration program (IHA, Sustainable Waters Program, The Nature Conservancy, Boulder, CO). Multiple regression models were developed similar to the model presented by Maceina (1992), with age (AGE) as the main, independent factor explaining

variability in growth and hydrologic variables (ENV) explaining some of the remaining variation:

$$1) \text{ GROWTH} = b_0 + b_1(\text{AGE}) \pm b_2(\text{ENV}),$$

where b_0 , b_1 , and b_2 were the regression coefficients for intercept and slope, respectively (Maccina 1992). Incremental growth data (GROWTH in μm) from otoliths were used in these analyses as estimates of fish growth, and age was defined as the midpoint of each growth interval (e.g., 20 – 40 d post-hatch, age = 30 d). Single or multiple variable models with only age or hydrologic variable(s) as independent factors were also considered when hydrologic variables explained more of the growth variation than age. Growth of age-0 fish during the first 20 d of life was not included in this analysis, because I assumed most of this period was spent transitioning from a yolk-sac larva (i.e., endogenous feeding) to a free-swimming larva (i.e., exogenous feeding). Growth of age-0 channel catfish during these early stages was likely influenced by other physiological factors that were not influential at later stages. Multicollinearity diagnostics were computed to determine if independent variables co-varied in multiple regression models (i.e., variance inflation factors, VIF's, and condition indices; Montgomery et al. 2001). I expected that parameters (i.e., x and x^2) in second-degree polynomial regressions ($y = \alpha + b_0*x + b_1*x^2$) would be highly correlated and exhibit multicollinearity in models. Significance was set at $\alpha=0.05$, and all statistics were conducted using Statistical Analysis System software (SAS 2003).

AIC model selection.—For each site, the best predictive models (i.e., highly significant models with the highest R^2 values) were selected and ranked using Akaike’s Information Criterion (AIC) (Burnham and Anderson 1998):

- 2) $AIC_c = -2 \log(L(\theta)) + 2K + \frac{2K(K+1)}{n-K-1}$
(n = sample size, K = number of estimable parameters)
- 3) $\log(L(\theta)) = -n/2 * \log(\sigma^2)$
- 4) $\sigma^2 = RSS/n$, where RSS = residual sum of squares
- 5) $\Delta AIC_c = AIC_i - \min AIC$

Akaike’s Information Criterion balances the minimization of residual error (RSS) with problems associated with over-parameterization (or data “over-fitting”); therefore, AIC can be used to identify the most “parsimonious” model(s) with the least amount of bias from a set of candidate models (Burnham and Anderson 1998).

I calculated ΔAIC_c values for models that were considered for model selection (equations 2-5; Burnham and Anderson 1998). Top-ranked models (i.e., models receiving substantial support) were those models having ΔAIC_c values within 1-2 of the “best” model (i.e., $\Delta AIC_c < 2$; Burnham and Anderson 1998). An AIC weight (AIC wt) was also calculated for each model, which was considered as the “weight of evidence in favor of a given model (Burnham and Anderson 1998).”

Results

A total of 91 age-0 channel catfish were collected and aged in this study. In the Coastal Plain (2003), total length and weight of age-0 channel catfish ($N = 52$) ranged from 26 to 87 mm and 0.11 to 4.89 g, respectively. In the Piedmont (2005), total length and weight of age-0 channel catfish ($N = 39$) ranged from 29 to 110 mm and 0.18 to 9.19

g, respectively. In the Coastal Plain (2003), ages and growth of age-0 fish ranged from 20 to 90 d and 0.83 to 1.50 mm/d, respectively. In the Piedmont (2005), ages and growth of age-0 fish ranged from 34 to 126 d and 0.60 to 1.07 mm/d, respectively. Growth was negatively related to age ($r^2 = 0.57$, $P < 0.01$; Figure 2). Otolith radius (μm) was positively related to total length ($r^2 = 0.87$, $P < 0.01$) and age ($r^2 = 0.83$, $P < 0.01$) of age-0 channel catfish (Figure 3a-b).

Age-0 channel catfish from the Coastal Plain hatched from 7 June to 27 August 2003 (Figure 4a). Channel catfish from the Piedmont hatched from 8 June to 15 Sept 2005 (Figure 4b). All age-0 fish that hatched in September ($N=4$) originated from the regulated site at Peter's Island (Figure 4c). In 2005, the majority of age-0 fish from unregulated sites hatched in June and July (89%, 17/19), whereas most of the hatches at regulated sites occurred later in the season over three months (July – Sept: 95%, 19/20; Figure 5).

Growth comparisons

Otolith growth of age-0 channel catfish differed among age groups; growth was highest during the first 20 d of life (mean = 189.3 μm), intermediate from 20 to 40 d post-hatch (mean = 111.9 μm), and lowest from 40 to 60 d post-hatch (mean = 93.4 μm ; ANOVA: $F = 699.5$, $P < 0.01$). A site*age interaction (ANOVA: $F = 2.24$, $P = 0.017$) indicated that growth differences among sites varied across age groups (Figure 6). During the first 20 d of life, growth of age-0 channel catfish was similar among most sites, with the exception of higher growth at the Uphapee Creek site than at the Peter's Island, Hillabee Creek, and Upper Tallapoosa River sites (ANOVA: $F = 5.46$, $P < 0.01$; Figure 6). Growth from 20 to 40 d post-hatch was different among several groups; in

general, growth was highest among channel catfish from the Uphapee and Cubahatchee creeks in the Coastal Plain, intermediate among fish from the Malone-Wadley and Peter's Island sites in the regulated reach, and lowest among fish from Hillabee Creek and the Upper Tallapoosa River (ANOVA: $F = 20.87$, $P < 0.01$; Figure 6). Growth from 40 to 60 d post-hatch was highest among fish from the Uphapee Creek, Cubahatchee Creek, and Malone-Wadley sites and lowest among fish from the Hillabee Creek and Upper Tallapoosa River sites (ANOVA: $F = 8.46$, $P < 0.01$; Figure 6).

Hydrologic relations with growth

Uphapee Creek.—Thirteen multiple and linear regression models were considered in AIC model selection for predicting daily growth of age-0 channel catfish from Uphapee Creek (Table 2). The model with PULSES_2.8_11.3 and $\text{LOG}_e(\text{AGE})$ as independent variables received the most support with the lowest ΔAIC_c value ($= 0$) and the highest AIC weight ($= 0.63$; Table 2). PULSES_2.8_11.3 and $\text{LOG}_e(\text{AGE})$ explained approximately 44% of the variability in channel catfish growth in the regression model ($R^2 = 0.44$, $P < 0.01$; Table 3). $\text{LOG}_e(\text{AGE})$ was a slightly stronger variable ($\text{spr}^2 = 0.18$, $t = -3.36$, $P < 0.01$) that explained channel catfish growth followed by PULSES_2.8_11.3 ($\text{spr}^2 = 0.17$, $t = 3.23$, $P < 0.01$). $\text{LOG}_e(\text{AGE})$ and PULSES_2.8_11.3 did not covary in the model. PULSES_2.8_11.3 was positively related to growth of age-0 channel catfish ($r^2 = 0.31$, $P < 0.01$; Figure 7a).

The multiple regression model with MEAN, MEANSQ, and $\text{LOG}_e(\text{AGE})$ as independent variables received considerably less support in AIC model selection ($\Delta\text{AIC}_c = 4.34$, AIC weight = 0.07; Table 2). However, MEAN, MEANSQ, and $\text{LOG}_e(\text{AGE})$ explained approximately 42% of the variability in channel catfish growth in the

regression model ($R^2 = 0.42$, $P < 0.01$; Table 3). MEAN and MEANSQ accounted for an additional 10% of the variation in growth after accounting for the effects of $\text{LOG}_e(\text{AGE})$ (Table 2). Although this model received less support in AIC model selection, a dome-shaped relation was predicted between growth of age-0 channel catfish and mean discharge in Uphapee Creek (Figure 7b). Multicollinearity diagnostics indicated that MEAN and MEANSQ covaried in this model.

Upper Tallapoosa River.—Ten multiple and linear regression models were considered in AIC model selection for predicting daily growth of age-0 channel catfish from the Upper Tallapoosa River (Table 4). A single variable model with MIN as the independent variable received the most support with the lowest ΔAIC_c value (= 0) and the highest AIC weight (= 0.25; Table 4). MIN explained approximately 69% of the variability in channel catfish growth in the regression model ($r^2 = 0.69$, $P < 0.01$; Table 3); growth of age-0 channel catfish and minimum discharge were positively related (Figure 8A). The addition of $\text{LOG}_e(\text{AGE})$ as an independent variable did not substantially improve this model ($R^2 = 0.72$, $P < 0.01$; Table 4). In addition, the single variable model with $\text{LOG}_e(\text{AGE})$ ranked very low in AIC model selection (Table 4), indicating that a hydrologic variable was a better predictor of growth than age.

The multiple regression model with $\text{LOG}_e(\text{AGE})$ and HP_17 as independent variables also received considerable support in AIC model selection ($\Delta\text{AIC}_c < 2$, AIC weight = 0.10; Table 4). $\text{LOG}_e(\text{AGE})$ and HP_17 explained approximately 70% of the variability in channel catfish growth in the regression model ($R^2 = 0.70$, $P < 0.01$; Table 3). $\text{LOG}_e(\text{AGE})$ was a slightly stronger variable ($\text{spr}^2 = 0.18$, $t = -2.11$, $P = 0.05$) that explained channel catfish growth followed by HP_17 ($\text{spr}^2 = 0.16$, $t = 2.01$, $P = 0.06$).

$\text{LOG}_e(\text{AGE})$ and HP_{17} did not covary in this model. HP_{17} was positively related to growth of age-0 channel catfish in the Upper Tallapoosa River ($r^2 = 0.64$, $P < 0.01$; Figure 8b).

Malone_Wadley.—Eight multiple and linear regression models were considered in AIC model selection for predicting daily growth of age-0 channel catfish from the Malone_Wadley site in the regulated reach of the Tallapoosa River (Table 5). The model with SPIKES_14.2, SPSQ, and $\text{LOG}_e(\text{AGE})$ as independent variables received the most support with the lowest ΔAIC_c value ($= 0$) and the highest AIC weight ($= 0.23$; Table 5). SPIKES_14.2, SPSQ, and $\text{LOG}_e(\text{AGE})$ explained approximately 40% of the variability in channel catfish growth in the regression model ($R^2 = 0.40$, $P < 0.01$; Table 3). SPIKES_14.2 and SPSQ accounted for an additional 13% of the variation in growth of age-0 channel catfish after accounting for the effects of $\text{LOG}_e(\text{AGE})$ (Table 5). This model predicted that a dome-shaped relation existed between growth of age-0 channel catfish and the frequency of spikes ($> 14.2 \text{ m}^3/\text{s}$) in the regulated reach of the Tallapoosa River. Multicollinearity diagnostics indicated that SPIKES_14.2 and SPSQ covaried in this model.

The second-degree polynomial model with SPIKES_14.2 and SPSQ as independent variables received substantial support in AIC model selection ($\Delta\text{AIC}_c = 0.43$, AIC weight = 0.19; Table 5), explaining approximately 34% of the variability in channel catfish growth in the regression model ($R^2 = 0.34$, $P < 0.01$; Figure 9a). In addition, this model ranked much higher in AIC model selection than the model with $\text{LOG}_e(\text{AGE})$ as the only independent variable, also indicating that hydrologic variables were

better predictors of growth of channel catfish than age alone. Multicollinearity diagnostics indicated that SPIKES_14.2 and SPSQ covaried in this model.

The linear regression model with RISE as an independent variable also received considerable support in AIC model selection ($\Delta AIC_c = 0.34$, AIC weight = 0.19; Table 5). RISE was positively related to growth of age-0 channel catfish ($r^2 = 0.29$, $P < 0.01$; Figure 9b; Table 3).

Peter's Island.—Nine multiple and linear regression models were considered in AIC model selection for predicting daily growth of age-0 channel catfish from the Peter's Island site in the regulated reach of the Tallapoosa River (Table 6). The model with $\text{LOG}_e(\text{AGE})$, FALL, and SPIKES_28.3 as independent variables received the most support with the lowest ΔAIC_c value (= 0) and the highest AIC weight (= 0.44; Table 6). $\text{LOG}_e(\text{AGE})$, FALL, and SPIKES_28.3 explained approximately 63% of the variability in channel catfish growth in the regression model ($R^2 = 0.63$, $P < 0.01$; Table 2). All variables were equally strong in explaining daily growth of channel catfish ($\text{spr}^2 = 30.2 - 30.7$, P 's < 0.01). Independent variables did not covary in this model.

The multiple regression model with $\text{LOG}_e(\text{AGE})$, FALL_28.3, and SPIKES_28.3 as independent variables also received substantial support in AIC model selection ($\Delta AIC_c = 0.48$, AIC weight = 0.34; Table 6). $\text{LOG}_e(\text{AGE})$, FALL_28.3, and SPIKES_28.3 explained approximately 63% of the variability in channel catfish growth in the regression model ($R^2 = 0.63$, $P < 0.01$; Table 2). $\text{LOG}_e(\text{AGE})$ was a slightly stronger variable ($\text{spr}^2 = 0.33$, $t = -3.19$, $P < 0.01$) that explained channel catfish growth followed by FALL_28.3 ($\text{spr}^2 = 0.29$, $t = -2.95$, $P < 0.01$) and SPIKES_28.3 ($\text{spr}^2 = 0.15$, $t = 1.96$, $P = 0.06$). Independent variables did not covary in this model. Growth of age-0 channel

catfish was negatively related to FALL_28.3 (i.e., the number of falling discharges > 28.3 m³/s; $r^2 = 0.33$, $P < 0.01$; Figure 10). Growth of age-0 channel catfish was positively related to SPIKES_28.3 ($r^2 = 0.23$, $P = 0.02$).

Hillabee Creek.—Eleven multiple and linear regression models were considered in AIC model selection for predicting daily growth of age-0 channel catfish from Hillabee Creek (Table 7). The model with LOG_e(AGE) as an independent variable received the most support with the lowest ΔAIC_c value (= 0) and the highest AIC weight (= 0.51; Table 7). LOG_e(AGE) explained approximately 59% of the variability in channel catfish growth in the regression model ($r^2 = 0.59$, $P < 0.01$). However, the model with LOG_e(AGE), SPIKES_1.4 and SPSQ also received substantial support ($\Delta AIC_c = 0.10$, AIC weight = 0.49; Table 7), explaining approximately 64% of the variability in growth of age-0 channel catfish ($R^2 = 0.64$, $P < 0.01$; Table 3). SPIKES_1.4 and SPSQ only accounted for an additional 5% of the variation in growth of age-0 channel catfish after accounting for the effects of LOG_e(AGE). This model predicted that a dome-shaped relation existed between growth of age-0 channel catfish and the frequency of spikes (> 1.4 m³/s) in Hillabee Creek. Multicollinearity diagnostics indicated that SPIKES_1.4 and SPSQ covaried in this model.

Hydrologic relations with hatching success

In Uphapee Creek, age-0 channel catfish hatched on days when discharges ranged from 3.4 to 22.6 m³/s (mean = 9.6 m³/s, S. D. = 4.7). The majority of hatches (76%, N = 34) occurred when discharges were less than 10.6 m³/s. When hatching was not observed during the spawning period (7 June – 27 August), discharges ranged from 3.6 to 164.0 m³/s (mean = 17.9 m³/s, S. D. = 28.7). Examination of hatch frequency indicated that

age-0 channel catfish typically hatched during periods with relatively low and stable flows (Figure 13). No clear patterns were observed between hatch frequency and hydrology at other sites, presumably due to lower sample sizes.

Discussion

This study has demonstrated that growth rates of age-0 channel catfish were highly variable within the Tallapoosa River Basin. Fish growth was highest in the Coastal Plain compared to the Piedmont, potentially due to lateral interactions that may occur between the river and floodplain in coastal plain systems. In the Kansas River, Quist and Guy (1998) attributed an increase in growth among channel catfish (ages 1-4) to high discharges that exceeded banks and inundated the floodplain, presumably increasing stream production and prey availability. In June-August 2003, discharges in Uphapee Creek were substantially higher than discharges in most previous years (Figure 12), including a high pulse event ($= 164 \text{ m}^3/\text{s}$; Figure 11) in early July that likely resulted in significant bank and possibly floodplain inundation. In the Piedmont, growth of age-0 channel catfish at unregulated sites was unexpectedly lower than fish growth in the regulated section of the Tallapoosa River below Harris Dam. Irwin and Freeman (2002) reported that water temperatures dramatically fluctuated (up to $10 \text{ }^\circ\text{C}$) with flow variation below Harris Dam; however, these unstable thermal conditions did not appear to depress growth rates of age-0 channel catfish.

In 2003, most of the age-0 channel catfish (51/52; 98%) were collected from tributaries (i.e., Uphapee and Cubahatchee creeks) of the lower Tallapoosa River in the Coastal Plain. Only one age-0 fish was collected from Dozier's Bar in the main stem of the Tallapoosa River below Thurlow Dam. I hypothesize that altered hydrologic

conditions due to hydropower operations below Thurlow Dam prohibited successful spawning and recruitment of channel catfish in the regulated section. I suspect that tributaries of the regulated main stem were used as spawning and nursery habitats by channel catfish. These tributaries have probably served as sources for re-colonization of the main stem by channel catfish within the lower Tallapoosa River system. Although more age-0 channel catfish were collected from the regulated reach below Harris Dam in 2005 (N = 19), sampling efforts were very intensive (i.e., 100 PAE and 50 backpack electrofishing samples) indicating that abundance of age-0 channel catfish was also low in this regulated river section. Furthermore, Irwin et al. (1999) reported that juvenile channel catfish (mean total length = 30.6 mm) utilized shallow habitats with fast velocities and coarse substrata; this habitat type is more commonly found in Piedmont-level systems than in coastal plain systems. The habitat in the lower Tallapoosa River near Dozier's Bar was characterized by deep and slowly moving water over fine substrata (sand and silt), which is not conducive for channel catfish recruitment.

Age-0 channel catfish primarily hatched from early June to late August in unregulated reaches of the Tallapoosa River Basin, which was relatively consistent with the findings of Holland-Bartels and Duval (1988). In a review of channel catfish biology, Hubert (1999) reported that most spawning occurred in June and July throughout their range. However, age-0 fish in the regulated reach of the Tallapoosa River also hatched in September (20%; 4/20), indicating that channel catfish had a protracted spawning period in the regulated river section below Harris Dam. This protracted spawning season exhibited by fish in the regulated reach may be part of a bet-hedging strategy, which will sometimes be an alternative life history strategy in variable or unpredictable

environments (Einum and Fleming 2004). In a variable environment, fishes exhibiting a bet-hedging strategy will have a longer spawning period, delayed sexual maturity, and longer reproductive lifespan, and they will also produce larger eggs and larvae at hatching (e.g., Atlantic Menhaden, *Brevoortia tyrannus*; Powell 1994). In addition to a longer spawning season, adult channel catfish below Harris Dam had greater longevity, which further supports this “bet-hedging” hypothesis. Nash (1999) aged adult channel catfish from two regulated sites (including Wadley below Harris Dam) and two unregulated sites in the Tallapoosa River Watershed. Channel catfish at the Wadley site had a maximum age of 16 years and were older than fish at the unregulated sites (Nash 1999). Hubert (1999) reported that the most frequently observed maximum age for channel catfish across their range was eight years. In addition, faster growth among recently hatched larvae (0-60 d post-hatch) in the regulated section suggested that larvae in the regulated reach may have received more of a parental investment than larvae at unregulated sites. The channel catfish population below Harris Dam should to be fully examined to test this “bet- hedging” hypothesis.

Hydrologic relations with growth

This study demonstrated that an increase in discharge, in some capacity, would enhance the growth of age-0 channel catfish (after 20 d post-hatch). Typically, growth was positively related to mean discharge, minimum discharge, number of high pulses, rise rates, and number of spikes in flow. However, in several cases, growth of age-0 channel catfish exhibited a non-linear response, reaching a maximum value at some “ideal” hydrologic condition and subsequently declining at what appeared to be a slow rate. For example, growth of age-0 fish at the Malone-Wadley site increased with the

number of spikes ($> 14.2 \text{ m}^3/\text{s}$) reaching a maximum at four or five spikes during a 20 d period (i.e., growth was measured every 20 d). Thereafter, growth appeared to decline when spikes occurred too frequently. These second-degree polynomial relations were analogous to habitat suitability curves (HSC's), which have been developed for fishes to identify optimal habitat conditions in freshwater systems (Orth and Maughan 1982; Glova and Duncan 1985; Pajak and Neves; Heggenes J. and S. J. Saltveit 1990).

Mechanisms underlying relations between discharge and growth of age-0 channel catfish probably involved lateral interactions between the river channel and the riparian (in the Piedmont) and floodplain (in the Coastal Plain). Inundation of the floodplain will result in increased nutrient input, availability of habitat (i.e., refuge from predators) and prey resources for age-0 fish (e.g., terrestrial insects; Welcomme 1979). In addition, studies have indicated that juvenile channel catfish are opportunistic feeders (with insects and plant material as the most common items; Jolley and Irwin 2004), and they will consume terrestrial plant foods and insects when they are available (Bailey and Harrison 1948). Therefore, an increase in high pulse frequency or mean discharge may lead to increased inundation of marginal habitats, which age-0 channel catfish may exploit for refuge from predators and alternative sources of prey.

This study also indicated that too many fluctuations in discharge (i.e., spikes in flow) within a 20-d period would have a negative effect on growth. Frequent fluctuations in discharge would produce a highly variable and energetically demanding environment (i.e., variable water levels, temperature and habitat availability) for age-0 fish. In addition, growth of age-0 channel catfish was negatively influenced by the frequency of high fall rates (e.g., Peter's Island; Figure 10). High fall rates would shorten the duration

of riparian or floodplain inundation and drastically change water levels, temperature and habitat availability over a short time interval.

Hydrologic relations with hatching success

In Uphapee Creek, channel catfish spawning typically occurred during periods of low and stable flow conditions. Spawning and hatching were interrupted when creek discharges exceeded 160 m³/s in early July. During the reproductive season, channel catfish prepare nests and exhibit considerable parental care including fanning and manipulating fertilized eggs (Hubert 1999); therefore, any substantial spikes in discharge would probably disrupt spawning activity and potentially flush young from nests. A similar pattern between spawning success and discharge was observed in the Upper Mississippi River (Holland-Bartels and Duval 1988). I observed no successful hatches from 20 June to 30 June 2003, an 11-d period before discharges increased to 164 m³/s. If hatches occurred during this 11-d period, channel catfish larvae may have been flushed from nests when high discharges occurred.

Management Recommendations

Researchers have recently implemented an adaptive approach for managing regulated river systems. The main goal of adaptive-flow management is to continually improve management as more is learned about a system (Irwin and Freeman 2002). Therefore, adaptive flow management is an iterative process with a series of steps that include 1) prescription of a flow/management regime, 2) monitoring and evaluation of the flow regime's effect on habitat and biota, and 3) the recommendation of a new and improved management regime. For example, a flow regime below Harris Dam could be prescribed that would potentially enhance growth of age-0 channel catfish and spawning

success. During the summer months, several periods of relatively low and stable flow conditions should be provided so that channel catfish will have opportunities to successfully spawn in the system. Secondly, a moderate number of high pulses (or spikes) with slow and steady fall rates (e.g., $-2.8 \text{ m}^3/\text{s}/\text{day}$) should be provided to enhance early growth of age-0 channel catfish (see prescribed flow regime; Figure 13). Finally, the release and maintenance of a higher base/minimum flow may also improve growth of age-0 channel catfish (based on findings in the Upper Tallapoosa River).

Conclusions

Relations between hydrology and growth of age-0 channel catfish are complex and may not be fully described by linear regression. In several cases, fish growth responded non-linearly to hydrologic changes. In addition, hydrologic variables appeared to be almost as important as age in predicting growth of age-0 fish in most of the multiple regression models. In the Upper Tallapoosa River, growth was actually more dependent on minimum discharge than age. I recommend that researchers investigate relations between growth (or recruitment) and hydrologic variables other than mean discharges. Although relations between growth and mean discharge may be significant, relations with other variables, such as high and low pulse frequencies, rise and fall rates, maximum and minimum flows, and low and high pulse duration, have more value and can be more easily applied and controlled in adaptive flow management programs. Finally, Akaike's Information Criterion was a valuable tool in determining which models were most appropriate for our data.

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Table 1. List of hydrologic variables that were generated to explain growth of age-0 channel catfish from five sites within the Tallapoosa River Watershed. Only those variables that were found significant in multiple regression models are listed.

Site	Hydrologic Variable	Definition
<i>Hillabee</i>	SPIKES_1.4	Number of spikes (or rises) in daily discharges $\geq 1.4 \text{ m}^3/\text{s}$
	MIN	Minimum discharge (m^3/s)
	HP_7.8	Number of daily discharges greater than $7.8 \text{ m}^3/\text{s}$; similar to a high pulse frequency
	MED	Median discharge (m^3/s)
	MEAN	Mean discharge (m^3/s)
	LP_3.5	Number of daily discharges less than $3.5 \text{ m}^3/\text{s}$; similar to a low pulse frequency
<i>Malone-Wadley</i>	SPIKES_14.2	Number of spikes (or rises) in daily discharges $\geq 14.2 \text{ m}^3/\text{s}$
	RISE	Rise rate = mean of all positive differences between consecutive daily values ($\text{m}^3/\text{s}/\text{d}$)
	MED	Median discharge (m^3/s)
	LP_28.3	Number of daily discharges less than $28.3 \text{ m}^3/\text{s}$; similar to a low pulse frequency
	MEAN	Mean discharge (m^3/s)
<i>Peter's_Island</i>	SPIKES_28.3	Number of spikes (or rises) in daily discharges $\geq 28.3 \text{ m}^3/\text{s}$
	FALL	Fall rate = mean of all negative differences between consecutive daily values ($-\text{m}^3/\text{s}/\text{d}$)
	FALL_28.3	Number of daily fall rates that exceeded $-28.3 \text{ m}^3/\text{s}/\text{d}$ (i.e., number of high falling discharges)

Table 1. Continued.

Site	Hydrologic Variable	Definition
<i>Uphapee Creek</i>	PULSES_2.8_11.3	Number of discharges between 2.8 and 11.3 m ³ /s
	PULSES_L2.8_G14.2	Number of discharges less than 2.8 m ³ /s and greater than 14.2 m ³ /s
	MEAN	Mean discharge (m ³ /s)
	PULSE_5.7	Number of spikes (or rises) in daily discharges ≥ 5.7 m ³ /s
	MED	Median discharge (m ³ /s)
	PULSE_4.2	Number of spikes (or rises) in daily discharges ≥ 4.2 m ³ /s
<i>Upper Tallapoosa River</i>	MIN	Minimum discharge (m ³ /s)
	MED	Median discharge (m ³ /s)
	HP_17	Number of daily discharges greater than 17 m ³ /s; similar to a high pulse frequency
	MEAN	Mean discharge (m ³ /s)
	FALL_2.8	Number of daily fall rates that exceeded -2.8 m ³ /s/d (i.e., number of high falling discharges)
	LP_9.2	Number of daily discharges less than 9.2 m ³ /s; similar to a low pulse frequency

Table 2. Parameters from multiple and linear regression models describing growth of age-0 channel catfish in Uphapee Creek, Alabama. Models having ΔAICc within 1-2 of the best model have substantial support.

Parameters	K	AICc	ΔAICc	AIC Wt	R ²	Model p-value
PULSES_2.8_11.3 LOG_eAGE	3	288.84	0.00	0.630	0.44	< 0.01
PULSES_L2.8_G14.2 LOG_eAGE	3	291.41	2.57	0.174	0.41	< 0.01
MEAN MEANSQ LOG _e AGE	4	293.18	4.34	0.072	0.42	< 0.01
PULSE_5.7 PULSE_5.7SQ LOG _e AGE	4	294.95	6.11	0.030	0.40	< 0.01
MED MEDSQ LOG _e AGE	4	294.97	6.13	0.029	0.40	< 0.01
PULSE_4.2 PULSE_4.2SQ LOG _e AGE	4	295.45	6.61	0.023	0.39	< 0.01
PULSES_L2.8_G14.2	2	296.31	7.48	0.015	0.33	< 0.01
LOG _e AGE	2	296.63	7.79	0.013	0.32	< 0.01
PULSES_2.8_11.3	2	297.37	8.53	0.009	0.31	< 0.01
MEAN MEANSQ	3	299.47	10.64	0.003	0.31	< 0.01
MED MEDSQ	3	301.86	13.02	0.001	0.28	< 0.01
PULSE_4.2 PULSE_4.2SQ	3	302.11	13.27	0.001	0.28	< 0.01
PULSE_5.7 PULSE_5.7SQ	3	302.63	13.79	0.001	0.27	< 0.01

Table 3. Multiple regression models that were derived to explain growth of age-0 channel catfish from five sites within the Tallapoosa River Watershed.

Site	Model	R²	P-value
<i>Uphapee Creek</i>	GROWTH = 198.86 - 30.43 (LOG_e (AGE)) + 2.07 (PULSES_2.8_11.3)	0.44	< 0.01
<i>Upper Tallapoosa River</i>	GROWTH = 201.35 - 33.71 (LOG_e (AGE)) + 13.57 (MEAN) - 0.966 (MEAN)²	0.42	< 0.01
	GROWTH = 46.57 + 3.29 (MIN)	0.69	< 0.01
<i>Malone_Wadley</i>	GROWTH = 127.02 - 15.036 (LOG_e (AGE)) + 1.042 (HP_17)	0.70	< 0.01
	GROWTH = 109.98 - 12.33 (LOG_e (AGE)) + 18.57 (SPIKES_14.2) - 2.14 (SPIKES_14.2)²	0.40	< 0.01
<i>Peter's Island</i>	GROWTH = 80.72 + 0.821 (RISE)	0.29	< 0.01
	GROWTH = 171.51 - 17.289 (LOG_e (AGE)) + 1.894 (FALL) + 10.349 (SPIKES_28.3)	0.63	< 0.01
<i>Hillabee Creek</i>	GROWTH = 168.57 - 18.27 (LOG_e (AGE)) - 7.436 (FALL_28.3) + 6.96 (SPIKES_28.3)	0.63	< 0.01
	GROWTH = 145.89 - 18.34 (LOG_e (AGE)) + 5.52 (SPIKES_1.4) - 0.742 (SPIKES_1.4)²	0.64	< 0.01

Table 4. Parameters from multiple and linear regression models describing growth of age-0 channel catfish in the Upper Tallapoosa River, Alabama.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
MIN	2	96.22	0.00	0.247	0.69	< 0.01
LOG_e(AGE) MED	3	96.88	0.66	0.177	0.72	< 0.01
LOG_e(AGE) MIN	3	97.57	1.35	0.126	0.71	< 0.01
LOG_e(AGE) HP_17	3	98.10	1.88	0.096	0.70	< 0.01
LOG_e(AGE) MEAN	3	98.14	1.92	0.095	0.70	< 0.01
LOG _e (AGE) FALL_2.8	3	98.92	2.70	0.064	0.69	< 0.01
MED	2	99.03	2.81	0.061	0.65	< 0.01
LOG _e (AGE) LP_9.2	3	99.17	2.95	0.057	0.69	< 0.01
LOG _e (AGE)	2	99.72	3.50	0.043	0.64	< 0.01
HP_17	2	100.11	3.89	0.035	0.64	< 0.01

Table 5. Parameters from multiple and linear regression models describing growth of age-0 channel catfish at the Malone_Wadley site in a regulated reach of the Tallapoosa River, Alabama.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
SPIKES_14.2 SPSQ LOG_eAGE	4	162.05	0.00	0.231	0.40	< 0.01
RISE	2	162.39	0.34	0.195	0.29	< 0.01
SPIKES_14.2 SPSQ	3	162.49	0.43	0.186	0.34	< 0.01
RISE LOG_eAGE	3	163.07	1.02	0.139	0.33	< 0.01
LOG_eAGE	2	163.54	1.48	0.110	0.27	< 0.01
MED	2	164.16	2.11	0.081	0.25	< 0.01
LP_28.3	2	166.03	3.98	0.032	0.21	< 0.01
MEAN	2	166.37	4.32	0.027	0.20	< 0.01

Table 6. Parameters from multiple and linear regression models describing growth of age-0 channel catfish at the Peter's Island site in a regulated reach of the Tallapoosa River, Alabama.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
LOG_eAGE FALL SPIKES_28.3	4	121.97	0.00	0.435	0.63	< 0.01
LOG_eAGE FALL_28.3 SPIKES_28.3	4	122.45	0.48	0.342	0.63	< 0.01
LOG_eAGE FALL_28.3	3	123.79	1.82	0.175	0.56	< 0.01
LOG _e AGE FALL	3	128.09	6.12	0.020	0.47	< 0.01
LOG _e AGE SPIKES_28.3	3	128.28	6.31	0.019	0.47	< 0.01
LOG _e AGE	2	131.26	9.29	0.004	0.34	< 0.01
FALL_28.3	2	131.43	9.46	0.004	0.33	< 0.01
FALL	2	135.16	13.19	0.001	0.23	0.02
SPIKES_28.3	2	135.18	13.21	0.001	0.23	0.02

Table 7. Parameters from multiple and linear regression models describing growth of age-0 channel catfish in Hillabee Creek of the Tallapoosa River, Alabama.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
LOG_eAGE	2	160.36	0.00	0.512	0.59	< 0.01
LOG_eAGE SPIKES_1.4 SPSQ	4	160.46	0.10	0.487	0.64	< 0.01
MED	2	174.40	14.04	0.000	0.41	< 0.01
HP_7.8	2	175.17	14.81	0.000	0.40	< 0.01
MEAN	2	177.07	16.71	0.000	0.37	< 0.01
LP_3.5	2	179.27	18.92	0.000	0.34	< 0.01
LP_3.5 SPIKES_1.4 SPSQ	4	179.95	19.59	0.000	0.40	< 0.01
MIN MINSQ	3	181.92	21.56	0.000	0.33	< 0.01
MIN SPIKES_1.4 SPSQ	4	183.75	23.39	0.000	0.34	< 0.01
MIN	2	184.17	23.82	0.000	0.25	< 0.01
SPIKES_1.4 SPSQ	3	186.72	26.36	0.000	0.24	< 0.01

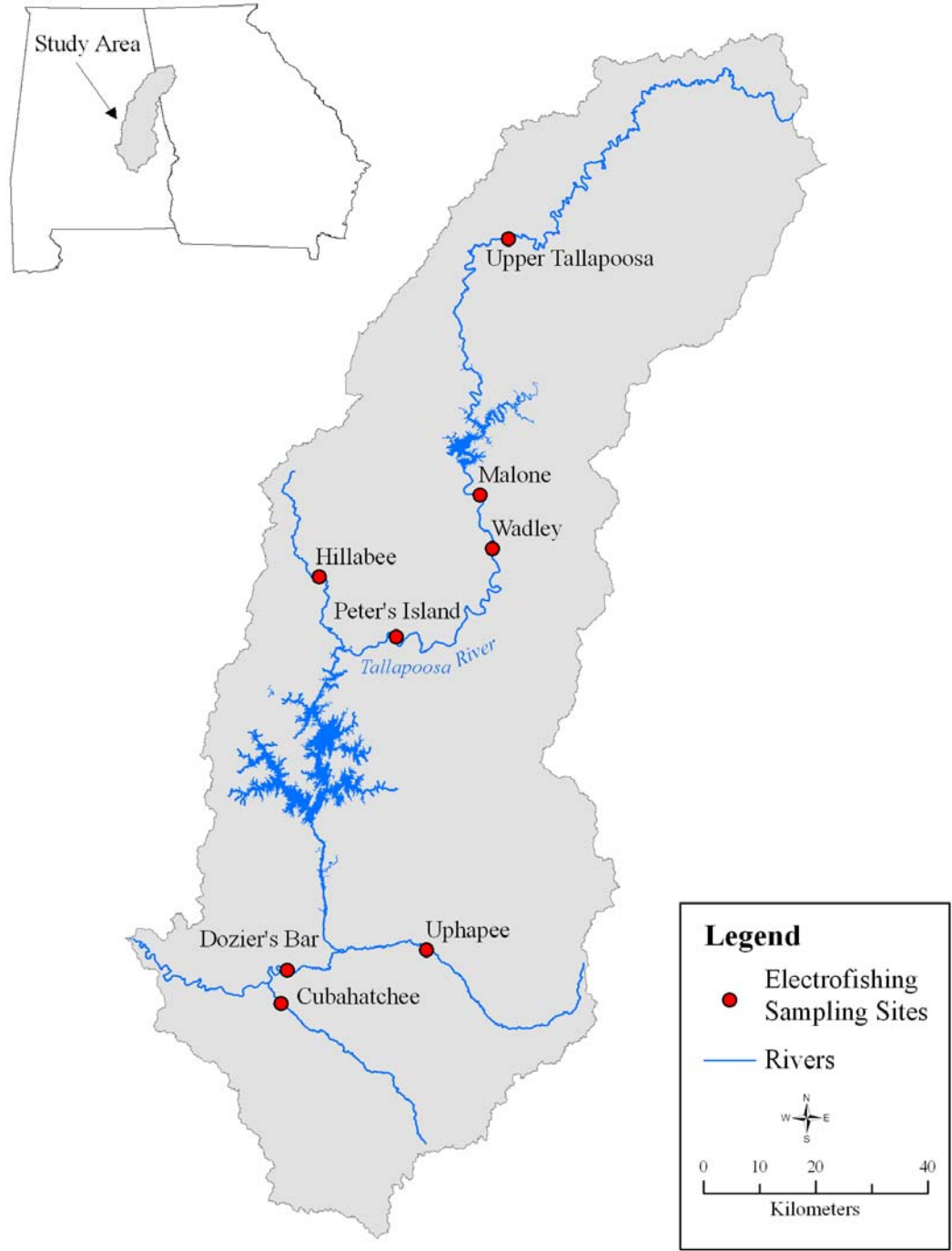


Figure 1. Backpack electrofishing and Pre-positioned Area Electrofisher sampling locations in the Tallapoosa River Watershed.

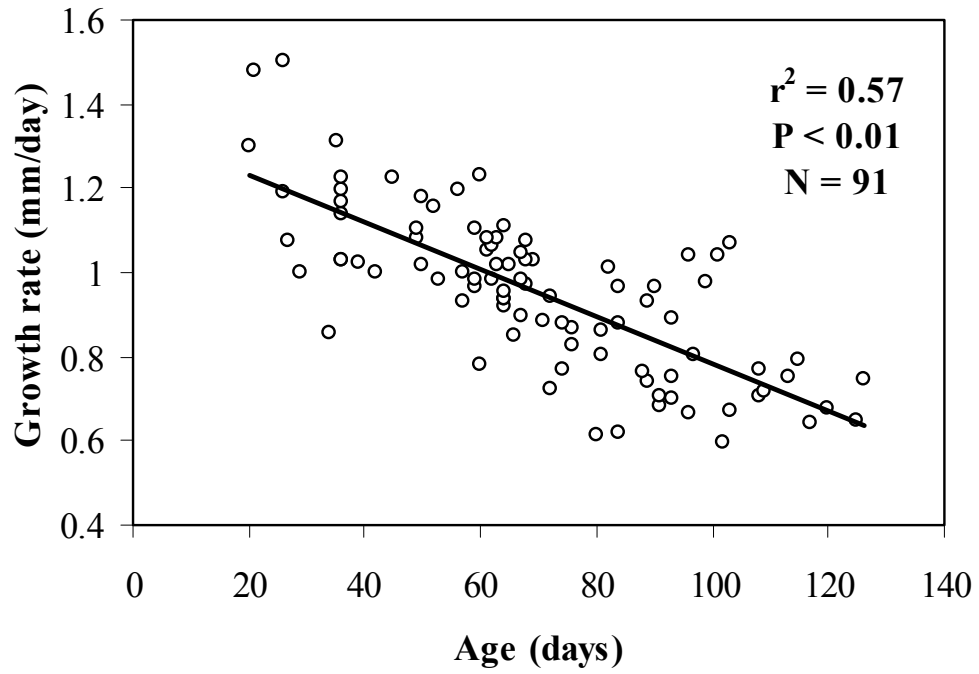


Figure 2. Negative relation between growth rate and age for age-0 channel catfish from the Tallapoosa River Basin, Alabama.

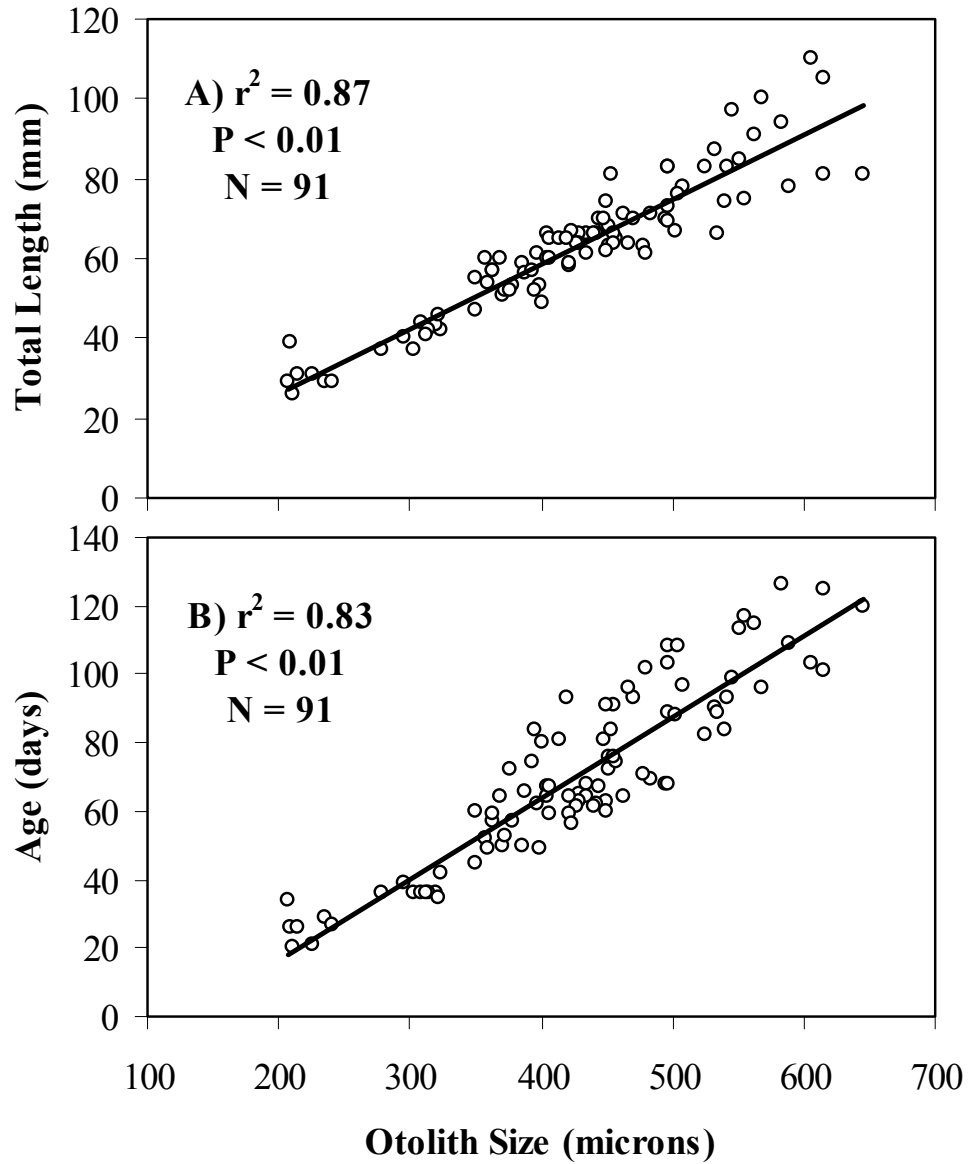


Figure 3. Positive relations between A) total length and otolith size and B) age and otolith size for age-0 channel catfish from the Tallapoosa River Basin, Alabama.

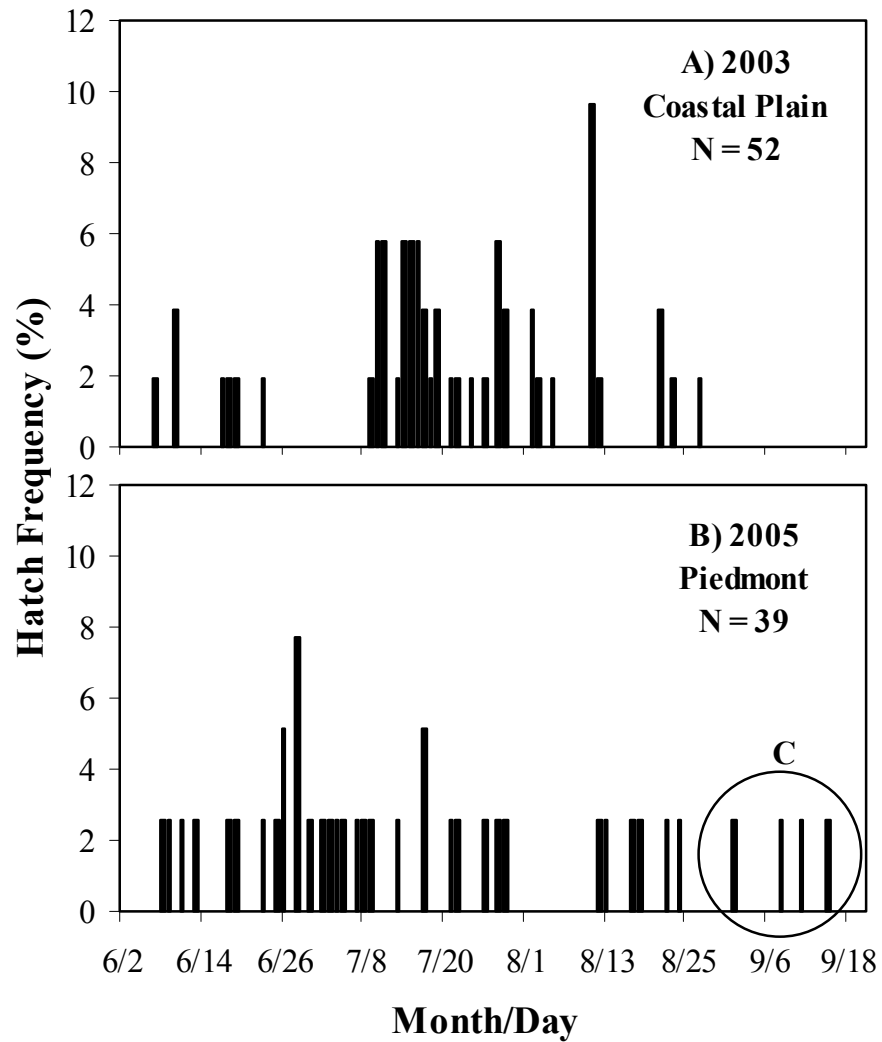


Figure 4. Hatch frequencies for age-0 channel catfish from the Tallapoosa River Basin in 2003 and 2005. All of the September hatches (c) occurred in the regulated reach.

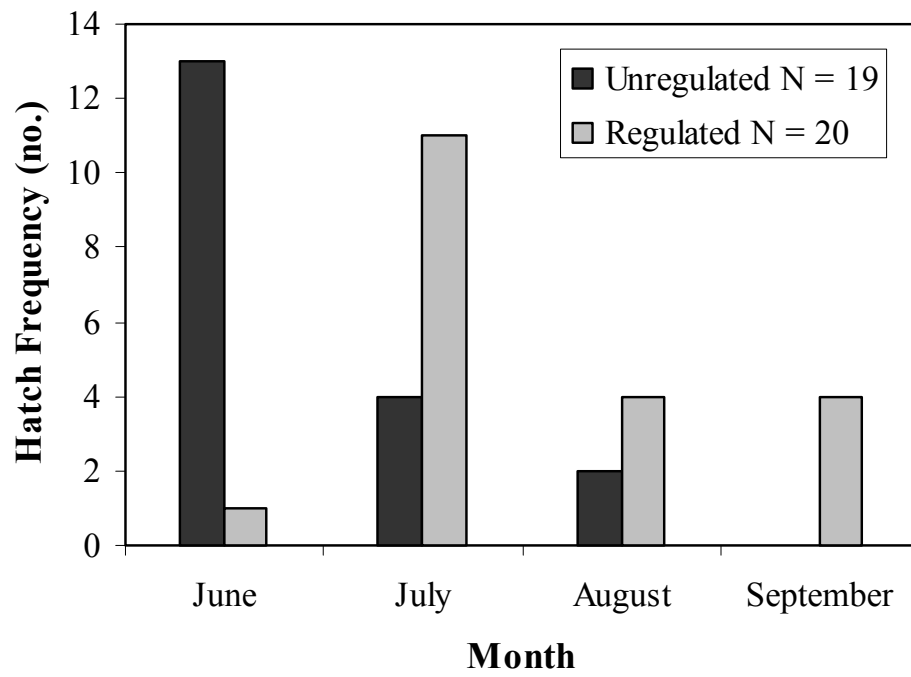


Figure 5. Hatch frequencies on a monthly basis for age-0 channel catfish from unregulated and regulated sites in Tallapoosa River Basin in 2005.

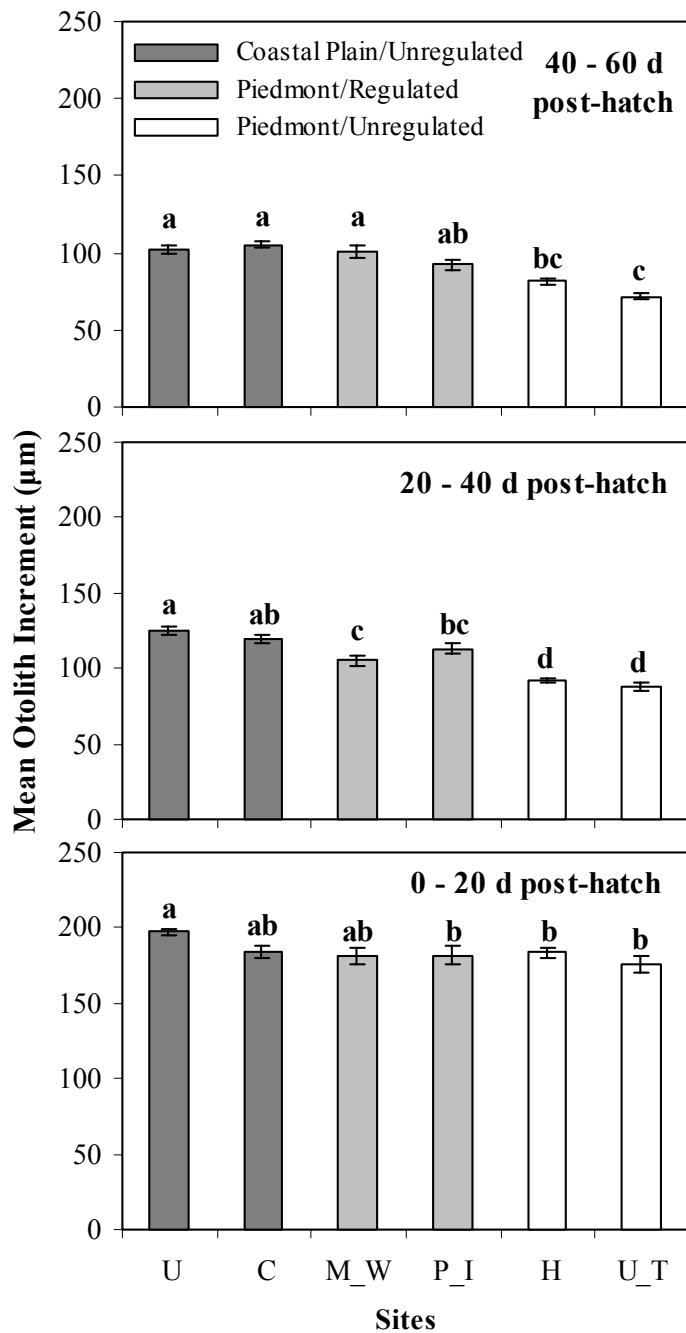


Figure 6. Growth of age-0 channel catfish during 0-20, 20-40, and 40-60 d post-hatch among sites within the Tallapoosa River Basin, Alabama (U = Uphabee Creek, C = Cubahatchee Creek, M_W = Malone_Wadley, P_I = Peter's Island, H = Hillabee Creek, and U_T = Upper Tallapoosa; significant differences are indicated by letter, $\alpha = 0.05$).

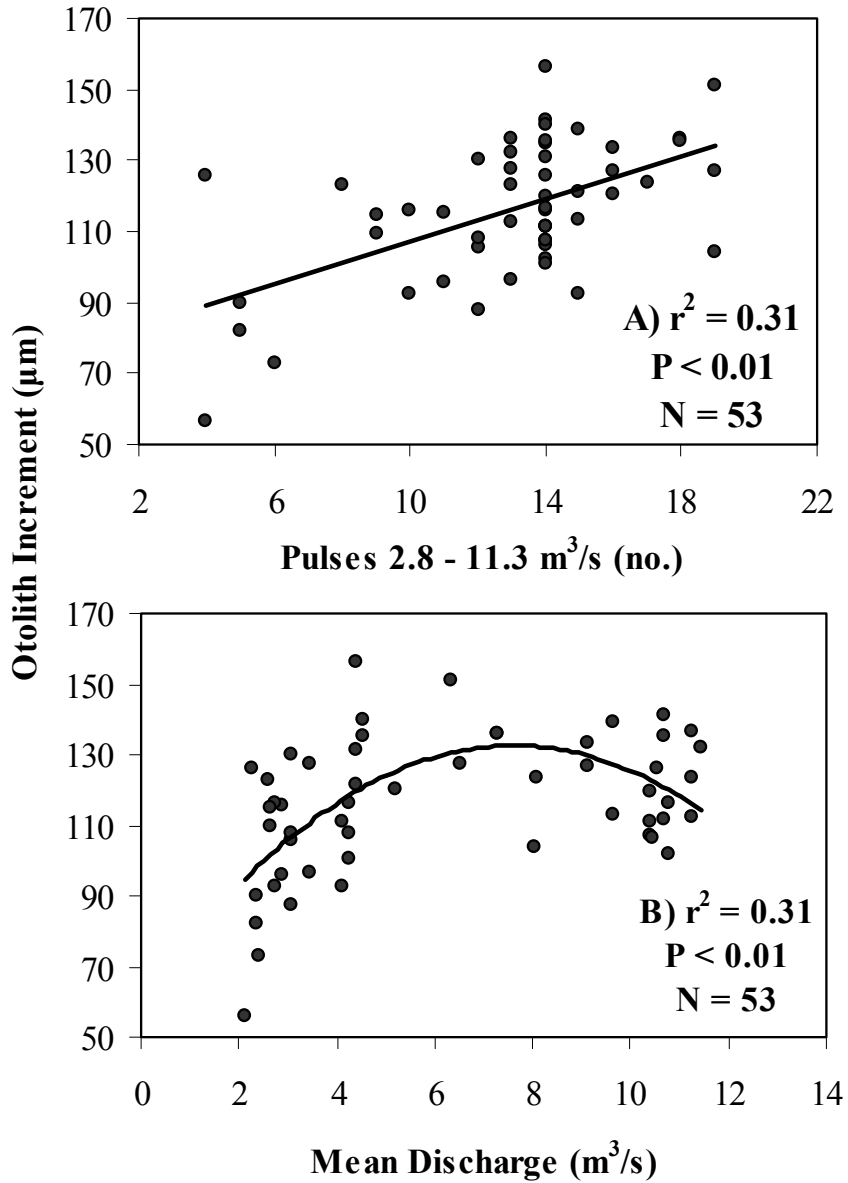


Figure 7. A) Relation between growth of age-0 channel catfish and the number of daily discharges between 2.8 and 11.3 m³/s in Uphapee Creek. B) Second degree polynomial relation between channel catfish growth and mean discharge in Uphapee Creek.

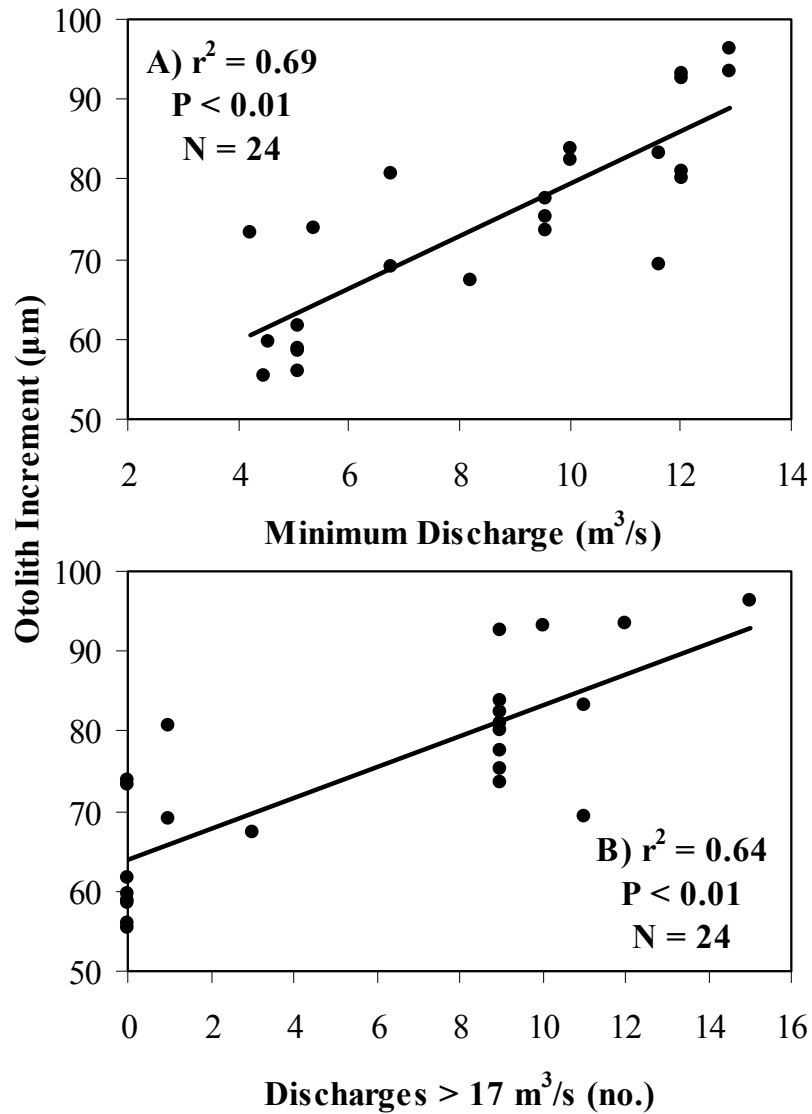


Figure 8. A) Relation between growth of age-0 channel catfish and minimum discharge in the Upper Tallapoosa River. B) Relation between growth of age-0 channel catfish and the number of daily discharges $> 17 \text{ m}^3/\text{s}$ in the Upper Tallapoosa River.

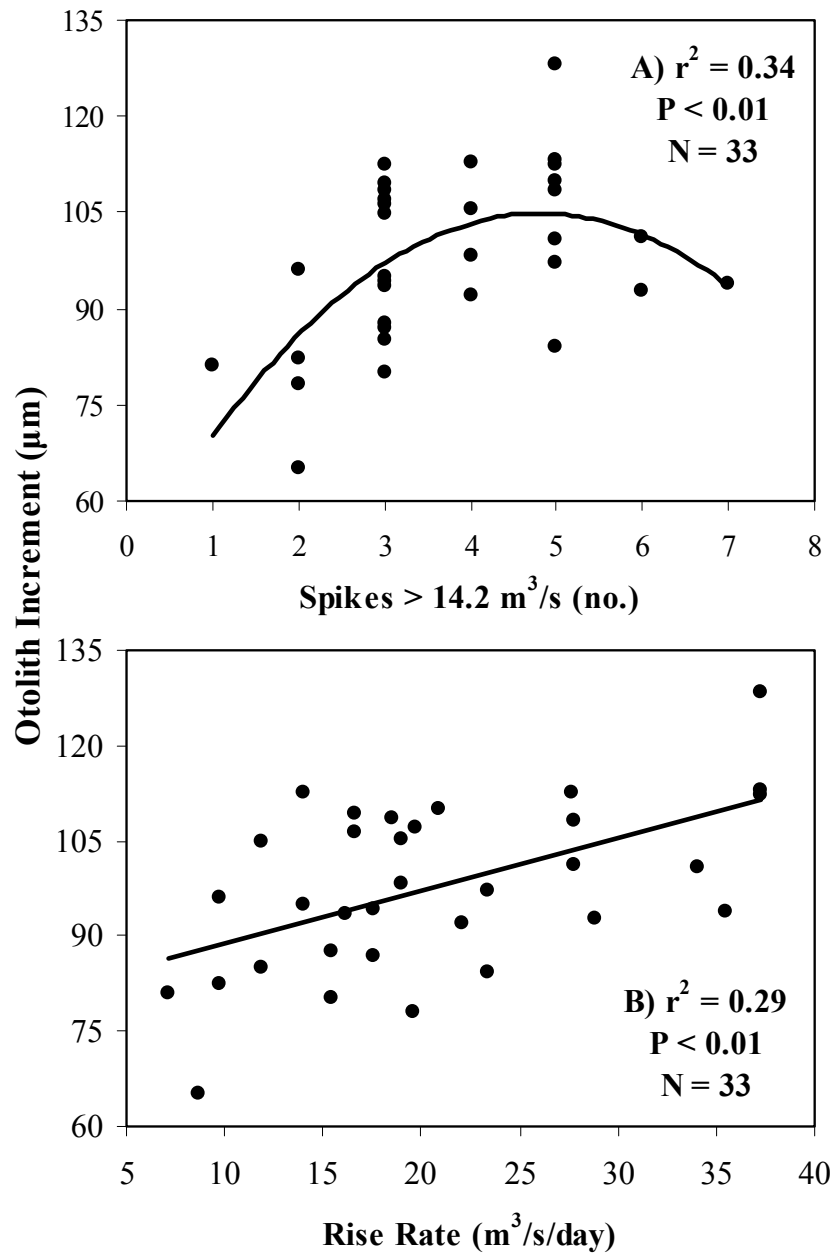


Figure 9. A) Second degree polynomial relation between growth of age-0 channel catfish and the number of spikes > 14.2 m³/s at the Malone_Wadley site in a regulated section of the Tallapoosa River. B) Relation between growth of age-0 channel catfish and rise rate at the Malone_Wadley site in a regulated section of the Tallapoosa River.

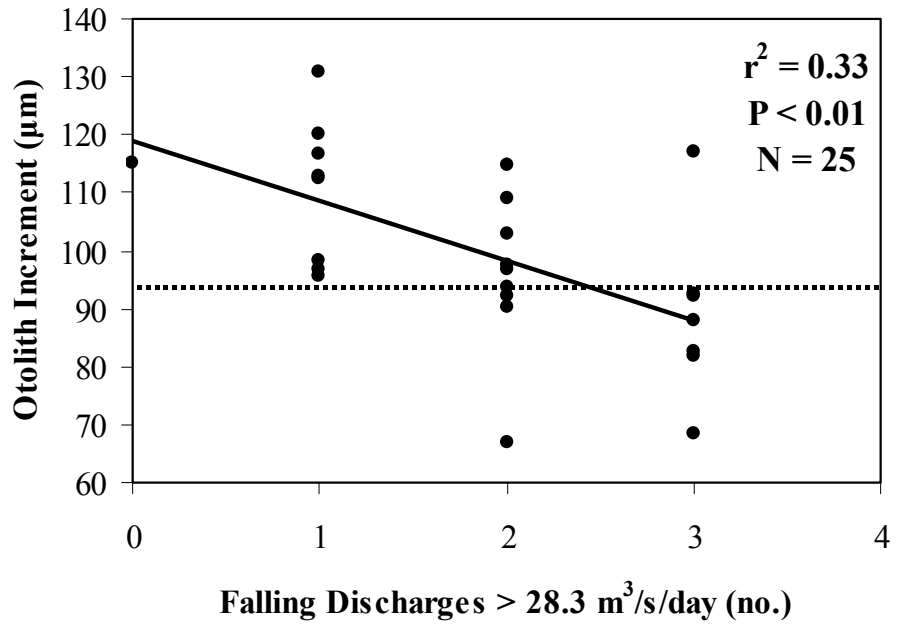


Figure 10. Relation between growth of age-0 channel catfish and the number of falling discharges (> 28.3 m³/s/day) at the Peter's_Island site in a regulated section of the Tallapoosa River.

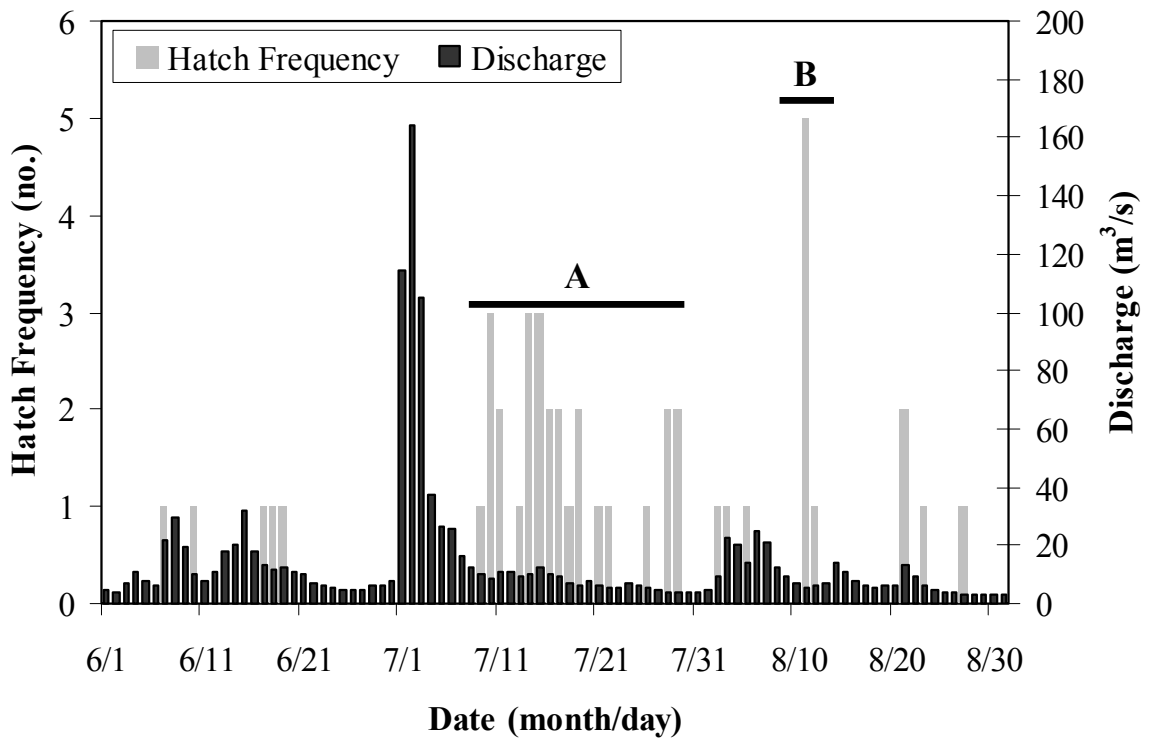


Figure 11. Hatch frequency and discharge in Uphapee Creek in 2003. The majority of hatches typically occurred during periods with low and stable discharges (A-B).

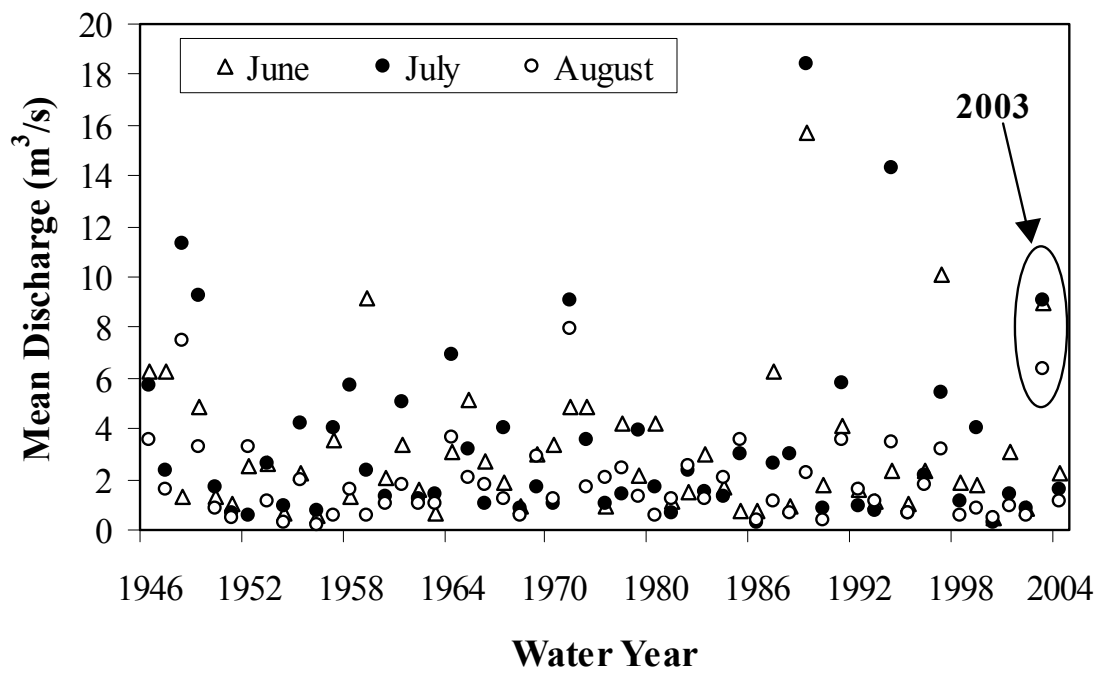


Figure 12. Mean discharges in June, July, and August in Uphapee Creek (AL) from 1946 to 2004.

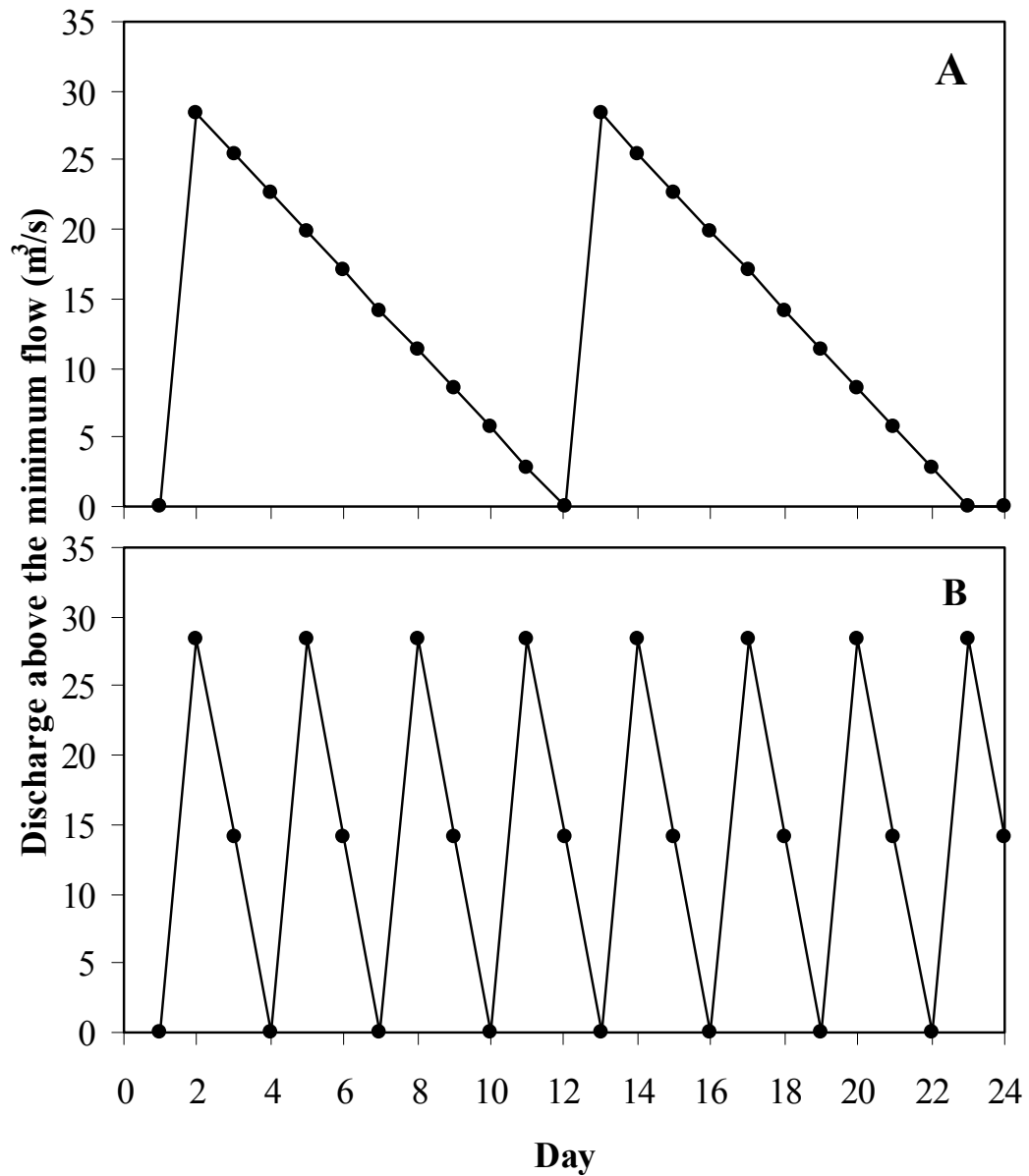


Figure 13. A) Prescribed flow regime (on a 24-d basis) that would potentially enhance the growth of age-0 channel catfish. Discharges would spike approximately 28.3 m³/s above a specified minimum/base flow and gradually decline over a 10-d period (i.e., -2.8 m³/s/d fall rate). B) Scenario that would most likely depress the growth of age-0 channel catfish (i.e., high frequency of spikes with a very high fall rate, -14.2 m³/s/d).

IV. INCORPORATION OF HYDROLOGIC VARIATION AND MORTALITY AS
STOCHASTIC FACTORS INFLUENCING THE GROWTH OF FLATHEAD
CATFISH POPULATIONS: IMPLICATIONS FOR ECOLOGY AND MANAGEMENT

Abstract.—I incorporated variable hydrology and mortality as stochastic factors influencing the population growth of native and introduced flathead catfish populations from the Coosa (Alabama, USA) and Ocmulgee (Georgia, USA) rivers, respectively. Size classified matrix models were constructed for both populations, and student residuals from catch-curve regressions were used as indices of year-class strength. A multiple regression model indicated that recruitment of flathead catfish in the Coosa River was positively related to mean spring discharge and November low flow. In addition, flathead catfish recruitment was positively related to the number of pulses between 283 – 566 m³/s, indicating that an optimal range of spring discharges were required for enhanced recruitment in the regulated reach of the Coosa River. For the Ocmulgee River population, a multiple regression model indicated that year-class strength was negatively related to mean March discharge and positively related to June low flow. In general, a negative relation between mean spring discharge and year-class strength was apparent, with strongest year classes recruiting when spring discharges ranged from 79 to 161 CFS in the Ocmulgee River. Incorporation of variable hydrology

as a stochastic factor resulted in a slowly declining population in the Coosa River. This stochastic population response indicated that the current flow regime in the regulated reach would have a negative, long-term impact on population growth in the system. In contrast, incorporation of hydrologic variation resulted in a slowly growing population in the Ocmulgee River. By modeling a reduction in mortality of flathead catfish (> 804 mm TL) with the highest reproductive values, population growth increased over a 50-year period in the Coosa River. Simulation of increased mortality of harvestable sized flathead catfish in the Ocmulgee River resulted in a substantial decline in population size. I encourage managers to use this approach for managing native and introduced flathead catfish populations in regulated and unregulated river systems.

Introduction

Recruitment of sport fishes has been related to hydrology in freshwater ecosystems in the southeast USA (Rulifson and Manooch 1990; Sammons and Bettoli 2000; Maceina 2003; Bonvechio and Allen 2005). Rulifson and Manooch (1990) determined that striped bass recruitment was positively influenced by low to moderate discharges (142-311 m³/s) in the Roanoke River, North Carolina. In Florida rivers, recruitment of sunfish species *Lepomis* spp. appeared to be positively related to pre-spawn fall median flow rates and negatively related to fall median flow rates; whereas, black basses *Micropterus* spp. were positively influenced by winter median flow rates and negatively related to spring median flow rates (Bonvechio and Allen 2005). In southeastern reservoirs, crappie *Pomoxis* spp. recruitment was positively influenced by shorter winter retention and longer post-winter retention rates (Maceina 2003). Few

studies, however, have investigated how hydrology has influenced the recruitment and population dynamics of catfishes.

In regulated river systems, fish recruitment was negatively affected by hydrologic alteration (Wildhaber et al. 2000; Freeman et al. 2001; Irwin and Freeman 2002; Propst and Gido 2004). Hydrologic alteration and river fragmentation resulting from dam construction has adversely impacted the reproductive success of diadromous and migratory fish species in the Alabama River system (Freeman et al. 2004). In a regulated reach of the Tallapoosa River (Alabama), variable flow conditions have reduced the stability and persistence of habitat and, as a result, negatively influenced young-of-the-year (YOY) fish survival (Freeman et al. 2001). Other studies have indicated that year classes of fish were strongest when flow regimes were similar to pre-impoundment conditions (Rulifson and Manooch 1990). In the San Juan River system, Propst and Gido (2004) demonstrated that manipulating spring discharges to mimic the natural flow regime would potentially enhance native fish recruitment.

Few studies have investigated the recruitment of catfishes in regulated river systems. Wildhaber et al. (2000) reported that increased minimum flows could be used to enhance populations of the threatened Neosho madtom (*Noturus placidus*) and potentially benefit other catfish species in the regulated Neosho River (Kansas). In addition, Holland-Bartels and Duval (1988) postulated that variation in year-class strength of channel catfish (*Ictalurus punctatus*) was related to discharges in the Mississippi River. No studies have investigated relations between hydrology and recruitment of flathead catfish (*Pylodictis olivaris*) in regulated or unregulated river systems.

The flathead catfish is a riverine species that has been introduced in numerous river systems outside of its native range (Guier et al. 1981; Quinn 1987; Thomas 1993; Dobbins et al. 1999; Jackson 1999). In Atlantic slope drainages, introduced populations have rapidly expanded throughout several river systems, reducing the abundances of native fishes through predation (Guier et al. 1981; Thomas 1993; Weller and Robbins 1999; Pine et al. 2005). In addition, life history characteristics have differed between introduced and native flathead catfish. Native flathead catfish exhibit higher longevity than fish in introduced populations; whereas, introduced fish have grown more rapidly than native flathead catfish (Kwak et al. 2006; Sakaris et al. *in press*).

I hypothesize that hydrology in Atlantic slope drainages has provided more favorable conditions for recruitment of flathead catfish than hydrology in their native range. For example, inundation of the relatively large floodplain of the lower Ocmulgee River (Georgia) has undoubtedly provided prey-rich, nursery habitat for age-0 and juvenile flathead catfish, thereby potentially enhancing the status of the introduced population. In contrast, unnatural flow regimes in regulated reaches of the Alabama River system have probably reduced the productivity of native flathead catfish populations. Rapidly varying flows in regulated systems have reduced fish productivity by interfering with fish reproduction, reducing the densities of benthic invertebrates (i.e., potential prey items for YOY or juvenile fishes), and rapidly fluctuating water quality and temperature (Cushman 1985). Holland Bartels and Duval (1988) suspected that year-class strength of a closely related species (i.e., channel catfish) was lowest when sharp increases in river discharge either disrupted spawning activity or flushed fish larvae from their nests. Successful management of native and introduced flathead catfish populations

will require that we have a better understanding and ability to predict how hydrology influences recruitment and will ultimately influence population dynamics of the species.

Models have been developed to assess the recruitment of fishes in relation to environmental variables (Maceina 1997). In addition, Leslie matrix models have been developed for various fishes for predicting population responses to changing (or degraded) environmental conditions (e.g., English sole, *Pleuronectes vetulus*, Atlantic croaker, *Micropogonias undulatus*, largemouth bass, *Micropterus salmoides*, and walleye, *Stizostedion vitreum*, Hayes et al. 1995; Landahl et al. 1997; Diamond et al. 2000). Environmental stochasticity can be incorporated into matrix population models to evaluate the impacts of environmental variation (e.g., hydrologic variation) on population growth over time. In environmentally stochastic matrix models, vital rates are varied randomly over time as a function of environment variation (Caswell 2001). Caswell (2001) explained that there are three, major characteristics of a stochastic matrix model: 1) the model must produce a sequence of environmental states, 2) a function must exist that links the matrix to each environmental state, and 3) a sequence of population vectors must result from applying the matrix to an initial population vector.

In this study, my objectives were to: 1) determine how hydrology influences the recruitment of native and introduced flathead catfish from the Coosa and Ocmulgee rivers respectively, 2) develop size-classified matrix models for the native and introduced populations, and 3) incorporate effects of variable hydrology on recruitment and variable fishing mortality as stochastic factors influencing the population growth of these populations.

Methods

Data Collection

Flathead catfish were sampled using boat electrofishing (low-pulse frequency; 15 pps) from a lower, 24-km section of the Ocmulgee River (Georgia, USA) in the Atlantic Coastal Plain in 1997 and a regulated reach of the Coosa River above the fall line in the Piedmont Upland in 2001 and 2002 (Alabama, USA; Fig. 1). Flathead catfish were weighed (g and kg for fish > 6000 g) and measured (mm TL). In a previous study, flathead catfish from each site were aged using otoliths, and von Bertalanffy growth models ($L_t=L_\infty(1-e^{-k(t-t_0)})$) were derived for each population (Sakaris et al. *in press*). The von Bertalanffy growth model for the Coosa River population was slightly modified to increase the predicted lengths of older fish (> 20 years old). I included length-at-age data from four memorable-sized fish (> 850 mm TL) that were collected by Jolley (2003) within the Coosa River system. Predicted length at age 25 increased from 874 to 909 mm TL in the modified model, which was a more accurate representation of fish growth in the population. For modeling purposes, fecundity data for flathead catfish from a Mississippi River population were provided by the Iowa Department of Natural Resources (K. Hanson, unpublished data).

Model Development

Model structure.—Size-classified matrix models were designed following the basic model presented by Caswell (2001):

$$A = \begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

where P was the probability of remaining in the size class, G was the probability of survival to the next size class, and F was the fertility of each size class. For my basic models, I assumed birth-pulse models with post-breeding censuses (Caswell 2001). For both populations, the first size class was set from 0 mm to the length at age-1, which was predicted from von Bertalanffy growth models (Coosa River population: $L_{\infty} = 1137$ mm TL, $k = 0.0642$, $t_0 = -0.0255$; Ocmulgee River population: $L_{\infty} = 1113.5$ mm TL, $k = 0.195$, $t_0 = -0.4$; Sakaris et al. *in press*). Therefore, survival of the first size class was modeled to reflect survival during the first year, which included survival of eggs, larvae, and age-0 fish. The remaining size classes were set at 100-mm intervals for the Coosa River population and 150-mm intervals for the Ocmulgee River population. Because I intended to project population growth over yearly time steps, models were designed so that a minimum of one year was required for fish to grow through a respective size class. Fish growth was much faster in the Ocmulgee River than in the Coosa River population, so a wider size class interval (150-mm) was used for the Ocmulgee River population. The number of size classes was constrained by the maximum fish length observed within each population. Studies have reported that flathead catfish typically become mature from 390 to 589 mm TL (Minckley and Deacon 1959; Perry and Carver 1977; Munger et al. 1994); therefore, I assumed that fish became mature at size classes that were within the 390 – 589 mm range (i.e., the 404 – 504 mm size class for the Coosa River population and the 416 – 566 mm size class for the Ocmulgee River population, Table 1).

Fertility estimation.— In a birth pulse model with a post-breeding census, mature individuals within a population must survive through the age class to successfully reproduce (Gotelli 2001). Therefore, fertilities in a basic model are calculated by:

1) $F_i = P_i m_i$, where P_i is the probability of survival of an individual in size class i , and m_i is reproductive output of an individual in size class i . Because my models were size classified, fertilities were estimated using a slightly modified equation:

2) $F_i = (P_i + G_i) m_i (0.5)$, where P_i was the probability of remaining in size class i , G_i was the probability of surviving to the next size class, m_i was the fecundity of an individual in size class i , and 0.5 was the proportion of females in the population. The sex ratio was approximately 1:1 in the Coosa River population below Mitchell Dam (49.2% females, 50.8 % males, E. Irwin, unpublished data). Minckley and Deacon (1959) also reported that flathead catfish exhibited a 1:1 sex ratio in the Big Blue and Neosho rivers (Kansas). In models developed for cutthroat trout, *Oncorhynchus clarki*, and English sole, *Pleuronectes vetulus*, populations were assumed to have a 1:1 sex ratio (Landahl et al 1997, Hilderbrand 2002). Fecundity for each size class was predicted from a linear regression model between \log_{10} (fecundity) and \log_{10} (total length) ($N = 49$; $\log_{10}(F) = 2.897\log_{10}(TL) - 4.0189$, $r^2 = 0.91$; $P < 0.01$; K. Hanson, Iowa DNR, unpublished data).

Survival estimation.— Survival of flathead catfish in size classes 2 – 11 and 2 – 7 for the Coosa and Ocmulgee river populations was determined using Pauly's (1984) length converted catch-curve:

3) $\ln(N_i) = a - b \cdot \ln(t_i)$, where N_i was the number of fish in the length interval (or size class i) and t_i was the relative age. Relative age was calculated using the equation:

4) $t_i = 1 - L_{\text{mid}}/L_{\infty}$, where L_{mid} was the midpoint of each size class and L_{∞} was the theoretical maximum length from the von Bertalanffy growth model. The instantaneous mortality rate (Z) was calculated from the slope of the catch-curve:

5) $Z = K(1 - b)$, where K was the von Bertalanffy growth coefficient. Annual survival (S) was calculated using the equation:

$$6) S = e^{-Z}.$$

Annual survival of fish in each size class included a proportion of fish remaining in the size class (P_i) and a proportion of fish surviving to the next size class (G_i):

$$7) S = P_i + G_i.$$

These proportions were estimated using the following equations:

8) $P_i = S (1 - 1/T_i)$ and 9) $G_i = S (1/T_i)$, $T_i \geq 1$ year, where T_i was the amount of time required for a fish to grow through the entire size class i , which was predicted from von Bertalanffy growth models (i.e., $1/T_i$ = probability of growing out of the size class in one year, $1 - 1/T_i$ = probability of remaining in the size class in one year). I assumed that fish lengths were evenly distributed within each size class. For example, if two years were required for fish to grow through an entire length class, approximately 50% of the fish (i.e., in the upper half of the size class) would grow out of the class after one year.

After fertilities and survival estimates of 2+ size classes were determined, I estimated survival of the first size class by assuming that both populations exhibited a stationary age distribution. This type of age distribution is characterized by constant relative and absolute numbers of individuals within each size class over time (Gotelli 2001). Landahl et al. (1997) also used this method to estimate age-0 survival of English sole by assuming an intrinsic rate of population increase (r) of 0.

Elasticity analyses.— I calculated the elasticity of population growth rate (λ) to proportional changes in matrix elements (Caswell 2001), where a_{ij} was the matrix element in row i , column j , v_i was the i th element of the reproductive vector, w_j was the

jth element of the stable stage distribution, and $\langle \mathbf{w}, \mathbf{v} \rangle$ was the scalar cross-product of the right and left eigenvectors:

$$10) e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} \frac{V_i W_j}{\langle \mathbf{w}, \mathbf{v} \rangle} = \frac{\partial \log \lambda}{\partial \log a_{ij}}$$

Reproductive values (elements in the right eigenvector) and the stable stage distribution (elements in the left eigenvector) were also computed and interpreted for each model.

Lifetime Reproductive Potential

I used the Yield-Per-Recruit model in Fisheries Analyses and Simulation Tools (FAST, Slipke and Maceina 2001) to estimate the number of eggs produced by a cohort over its lifetime in the Coosa and Ocmulgee River populations. Conditional natural mortality estimates (C_m) in FAST were calculated from instantaneous mortality rates (Z) derived from length-converted catch-curves. Because estimates of exploitation were not available for the Coosa and Ocmulgee river fisheries, I modeled all of the mortality as naturally caused (i.e., $Z = M$):

$$11) C_m = 1 - e^{-M}$$

Simulations were conducted with 1000 recruits (i.e., $N_0 = 1000$; Table 2).

Hydrologic effects on recruitment

I used student residuals from catch-curve regressions as quantitative indices of relative year-class strength for both flathead catfish populations (Maceina 1997; Maceina and Stimpert 1998; Maceina 2003; Bonvechio and Allen 2005). Catch-curve regressions were previously computed for both populations (Sakaris et al. *in press*). Hydrologic data (i.e., mean daily discharges) for the Coosa River below Mitchell Dam were provided by the Alabama Power Company. Hydrologic data for the Ocmulgee River were obtained

from a USGS gage station that was in close proximity to the study site (USGS 02215500, Lumber City, Georgia). Various hydrologic variables were generated in the Indicators of Hydrologic Alteration Program (IHA, Sustainable Waters Program, The Nature Conservancy, Boulder, CO), which included annual high and low pulse frequencies, average monthly discharges, high and low pulse durations, maximum and minimum discharges, fall and rise rates, seasonal mean discharges and number of reversals (Table 3). Because flathead catfish spawn during the summer months (Jackson 1999), water years were started on July 1 of each year and ended on June 30 of the following year. Initially, multiple regression models were derived following the model described by Maceina (1997):

11) $\text{Log}_e(\text{NUMBER}) = b_0 - b_1(\text{AGE}) \pm (\text{HYDRO})$, where a hydrologic variable explained the formation of weak and strong year classes (i.e., residual variation) after accounting for the effects of age on abundance. After potentially important hydrologic variables were identified, multiple regression models were then derived to relate student residuals (i.e., year-class strength) from catch-curves to hydrologic variables:

$$12) \text{STURESID} = b_0 \pm b_1(\text{HYDRO}_1) \dots \pm b_n(\text{HYDRO}_n)$$

Multicollinearity diagnostics were computed to determine if independent variables co-varied in multiple regression models (i.e., variance inflation factors, VIF's, and condition indices; Montgomery et al. 2001).

AIC model selection.—For both populations, the models that best predicted year-class strength were selected and ranked using Akaike’s Information Criterion (AIC) (Burnham and Anderson 1998):

$$13) AIC_c = -2 \log(L(\theta)) + 2K + \frac{2K(K+1)}{n-K-1}$$

(n = sample size, K = number of estimable parameters)

$$14) \log(L(\theta)) = -n/2 * \log(\sigma^2)$$

$$15) \sigma^2 = RSS/n, \text{ where } RSS = \text{residual sum of squares}$$

$$16) \Delta AIC_c = AIC_i - \min AIC$$

I calculated ΔAIC_c values for models that were considered for model selection (equations 13-16; Burnham and Anderson 1998). Top-ranked models (i.e., models receiving substantial support) were those models having ΔAIC_c values within 1-2 of the “best” model (i.e., $\Delta AIC_c < 2$; Burnham and Anderson 1998). An AIC weight (AIC wt) was also calculated for each model, which was considered as the “weight of evidence in favor of a given model (Burnham and Anderson 1998).”

Stochastic Matrix Analyses

Stochastic matrix model.—I assumed that recruitment (or year-class strength) was dependent on the number of eggs that were produced and the proportion of those eggs that survived to age-1 in the population each year. Therefore, recruitment was modeled in the first row of transition matrices by multiplying the number of eggs produced by each size class (F_i) by the survival estimate of the first year class (G_1). As a result, the second size class appeared as the first stage within the matrix (Table 4). Although these modified transition matrices were theoretically identical to the original models, recruitment was compartmentalized to stochastically vary it over time as a function of hydrologic variation (Table 4). Specifically, I modeled recruitment values in the matrices

to exhibit the same proportional and directional responses to hydrologic variables that were predicted by multiple regression models.

Case 1: Hydrologic Variation

Three types of stochastic population projections were conducted over 50-year periods using these models: 1) Hydrologic variables that influenced recruitment were varied annually. In most cases, hydrologic variables conformed to normality and were selected from a normal distribution at each yearly time step. However, if hydrologic variables conformed to normality after a \log_{10} -transformation, variables were selected from a \log_{10} -normal distribution at each yearly time step. Normal and \log_{10} -normal distributions were generated from hydrologic data that were acquired for each site; therefore, I modeled hydrologic conditions that flathead catfish would most likely experience in their particular river system. If hydrologic data did not conform to normality after \log_{10} -transformation, values were randomly selected at each yearly time step from a specified range of hydrologic values that were characteristic of conditions in the system. 2) Populations were exposed to a five, consecutive years of “favorable” hydrologic conditions during a 50-year projection. Hydrologic conditions were varied during the rest of the projection period. I hypothesized that populations would respond to these favorable conditions by exhibiting spikes in population size, but then variably decline to previous levels. 3) Populations were exposed to a five, consecutive years of “unfavorable” hydrologic conditions during a 50-year projection. Hydrologic conditions were varied during the rest of the projection period. I hypothesized that populations would respond to unfavorable conditions by exhibiting substantial declines in population size, but variably recover to previous levels.

Case 2: Variable Mortality

I also modeled environmental stochasticity as a result of variable fishing mortality. I expressed annual survival estimates (i.e., elements P_i and G_i) of “harvestable-sized” fish as, $S = e^{-Z}$, where Z was the instantaneous mortality rate. Flathead catfish were considered harvestable at the 404-504 mm TL and 416-566 mm TL size ranges in the Coosa and Ocmulgee River populations, respectively. That is, I assumed that flathead catfish would be harvested from a fishery at 16 in. For both populations, stochastic projections were conducted by varying instantaneous mortality rates over a 50-year period. At each yearly time step, an instantaneous mortality rate was randomly selected from a specified range of values for each matrix element. Specifically, survival estimates for harvestable-sized fish were varied within 10% (i.e., $\pm 10\%$) of the original survival estimates. Fertilities were also varied as a function of changing survival rates, given that fish had to survive through the year to reproduce. For the Coosa River population, I also simulated the implementation of a slot limit by protecting flathead catfish in size classes with the highest reproductive values. In this modeling exercise, survival estimates for these fish were variably increased by 0 to 10% of the original survival estimate each year over a 50-year period. Survival estimates for harvestable-sized fish were simply varied within ranges specified in the previous model (i.e. $\pm 10\%$ of the original survival estimate). For the Ocmulgee River population, I simulated the effects of increased fishing mortality on the population across all harvestable sized fish. In this modeling exercise, survival estimates were variably decreased by 0 to 10% of the original survival estimate each year over a 50-year period. For all modeling routines, stochastic projections were simulated 1000 times using a Monte Carlo analysis to obtain average

stochastic growth rates with upper (97.5%) and lower (2.5%) confidence limits. All statistical analyses were conducted in Statistical Analysis System software (SAS 2003). All population modeling was conducted in PopTools (Hood 2005).

Results

In the Coosa River, total length and weight of flathead catfish ($N = 799$) ranged from 67 – 1054 mm and 2 g to 16.5 kg. However, only one flathead catfish was longer than 1000 mm TL (0.1%), and only 18 fish were longer than 900 mm TL (2.3%). In the Ocmulgee River, total length and weight of flathead catfish ($N = 136$) ranged from 48 – 1074 mm and 9g to 18.8 kg. Nine flathead catfish were longer than 1000 mm TL (6.6%), and 20 fish were longer than 900 mm TL (14.7%). Fertilities of flathead catfish from the Coosa and Ocmulgee rivers ranged from 1997 – 22907 and 2305 – 23288 offspring per female, respectively (Table 5). Annual survival of 2+ size classes was 83.7 % in the Coosa River population ($Z = - 0.178$, $r^2 = 0.94$, $P < 0.01$) and 77.0 % in the Ocmulgee River population ($Z = - 0.262$, $r^2 = 0.81$, $P = 0.014$). In general, probabilities of surviving to the next size class (G_i) decreased, while probabilities of remaining in a size class increased from early to late stages (Table 5). Survival from egg stage to age-1 in the Coosa River population ($G_1 = 0.0000668$) was two times higher than survival in the Ocmulgee River population ($G_1 = 0.0000333$). Flathead catfish in the Ocmulgee River population were predicted to produce 2.5 times more eggs than flathead catfish in the Coosa River population over the lifetime of a cohort ($N_0 = 1000$ individuals; Ocmulgee River: 21871650 eggs, Coosa River: 8775673 eggs).

The Coosa and Ocmulgee river populations exhibited similar patterns in their stable stage distributions and reproductive values from early to late stages (Table 6). In

both populations, the final two stages had the highest reproductive values (i.e., fish > 850 mm TL, Table 6). Elasticities were typically higher among survival probabilities than fertilities in both matrix models, indicating that population growth rate (λ) was more influenced by proportional changes in survival than fertility of flathead catfish (Table 7).

Hydrologic effects on recruitment

Coosa River Population.— A multiple regression model was derived with AGE and PULSES_283_566 as independent variables explaining variation in abundance of flathead catfish in the Coosa River below Mitchell Dam. After accounting for the effects of AGE on abundance ($r^2 = 0.73$, $P < 0.01$), PULSES_283_566 explained an additional 16% of the variation in the regression model ($R^2 = 0.89$, $P < 0.01$):

$$\text{Log}_e(\text{NUMBER}) = 2.59866 - 0.15940(\text{AGE}) + 0.03929(\text{PULSES}_{283_566}).$$

AGE and PULSES_283_566 did not exhibit multicollinearity in the model.

In addition, PULSES_283_566 explained approximately 58% of the variability in student residuals (i.e., year-class strength; $r^2 = 0.58$, $P < 0.01$). This regression model received the most support in AIC model selection with the lowest ΔAIC_c value (= 0) and the highest AIC weight (= 0.83; Table 8):

$$\text{STURESID} = -2.19877 + 0.07840(\text{PULSES}_{283_566})$$

Year-class strength of flathead catfish was positively related to the frequency of pulses between 283 and 566 m^3/s (Figure 2a), indicating that an optimal range of discharges in spring may be required for enhanced recruitment of flathead catfish in the regulated reach of the Coosa River below Mitchell Dam.

A multiple regression model was also derived with AGE, SPRING_MEAN, SPRSQ, and NOV_LOWF as independent variables explaining variation in abundance.

After accounting for the effects of AGE on abundance, SPRING_MEAN, SPRSQ, and NOV_LOWF explained an additional 17% of the variation in the regression model ($R^2 = 0.90$, $P < 0.01$):

$$\text{Log}_e(\text{NUMBER}) = 0.7471 - 0.1378(\text{AGE}) + 0.0138(\text{SPRING_MEAN}) - 0.00001884(\text{SPRING_MEAN})^2 + 0.0029(\text{NOV_LOWF}).$$

SPRING_MEAN and SPRSQ exhibited multicollinearity in the model.

A multiple regression model with SPRING_MEAN, SPRSQ, and NOV_LOWF explaining year-class strength received less support in AIC model selection ($\Delta\text{AIC}_c = 6.91$, AIC weight = 0.03; Table 8). However, SPRING_MEAN, SPRSQ, and NOV_LOWF explained approximately 57% of the variability in student residuals in the regression model ($r^2 = 0.57$, $P = 0.01$):

$$\text{STURESID} = -4.86612 + 0.02346(\text{SPRING_MEAN}) - 0.00003208(\text{SPRING_MEAN})^2 + 0.00604(\text{NOV_LOWF}).$$

NOV_LOWF explained an additional 17% of the variation in student residuals after accounting for the effects of SPRING_MEAN and SPRSQ (Table 8). This model predicted that a non-linear relation existed between year-class strength of flathead catfish and spring discharge ($R^2 = 0.40$, $P = 0.03$, Fig. 2b), with year-class strength reaching a maximum value at approximately 425 m³/s and declining at high discharges (> 510 m³/s). Year-class strength was positively related to November low flows ($r = 0.49$, $P < 0.05$).

Ocmulgee River Population.— A multiple regression model was derived with AGE, JUN_LOWF, and MAR as independent variables explaining variation in abundance of flathead catfish in the Ocmulgee River. After accounting for the effects of AGE on

abundance ($r^2 = 0.88$, $P < 0.01$), JUN_LOWF and MAR explained an additional 9% of the variation in the regression model ($R^2 = 0.97$, $P < 0.01$):

$$\text{Log}_e(\text{NUMBER}) = 3.2805 - 0.2296(\text{AGE}) + 0.01647(\text{JUN_LOWF}) - 0.00313(\text{MAR}).$$

AGE, JUN_LOWF, and MAR did not exhibit multicollinearity in the model.

In addition, JUN_LOWF and MAR explained approximately 71% of the variability in student residuals ($r^2 = 0.71$, $P < 0.01$). This regression model received the most support in AIC model selection with the lowest ΔAIC_c value (= 0) and the highest AIC weight (= 0.74; Table 9). JUN_LOWF and MAR were equally strong in explaining year-class strength ($\text{spr}^2 = 0.66 - 0.67$, P 's < 0.01) and did not covary in the regression model:

$$\text{STURESID} = -1.02025 + 0.04556(\text{JUN_LOWF}) - 0.00856(\text{MAR}).$$

Individually, JUN_LOWF and MAR were weakly correlated with year-class strength in the Ocmulgee River (June low flow: $r = 0.42$, $P = 0.12$, March discharge: $r = -0.40$, $P = 0.14$). However, the strongest year classes (1981 and 1988) were exposed to higher June low flows ($\geq 72 \text{ m}^3/\text{s}$) and lower March discharges ($\leq 187 \text{ m}^3/\text{s}$); whereas, the weakest year classes (1983, 1986, 1991, and 1992) were exposed to very high March discharges (269 – 453 m^3/s).

A multiple regression model was also derived with AGE, DEC, and SPRING_MEAN as independent variables explaining variation in abundance. After accounting for the effects of AGE on abundance, DEC and SPRING_MEAN explained an additional 8% of the variation in the regression model ($R^2 = 0.96$, $P < 0.01$):

$$\text{Log}_e(\text{NUMBER}) = 4.526 - 0.228(\text{AGE}) - 0.00212(\text{DEC}) - 0.0033(\text{SPRING_MEAN}).$$

AGE, DEC, and SPRING_MEAN did not exhibit multicollinearity in the model.

In addition, DEC and SPRING_MEAN explained approximately 63% of the variability in student residuals ($r^2 = 0.63$, $P < 0.01$). This regression model received less support in AIC model selection ($\Delta AIC_c = 3.54$, AIC weight = 0.13; Table 9).

SPRING_MEAN was a slightly stronger variable explaining year-class strength ($spr^2 = 0.44$, $t = -3.09$, $P < 0.01$) followed by DEC ($spr^2 = 0.39$, $t = -2.78$, $P = 0.02$). DEC and SPRING_MEAN did not covary in the regression model:

$$STURESID = 2.48474 - 0.00591 (\text{DEC}) - 0.00904 (\text{SPRING_MEAN}).$$

Year-class strength was negatively related to mean spring discharge ($r^2 = 0.40$, $P = 0.01$, Fig. 3a), with the strongest year classes recruiting when spring discharges ranged from 79 to 161 m^3/s . Year-class strength was also negatively related to mean December discharge ($r^2 = 0.34$, $P = 0.02$, Fig. 3b)

In the Ocmulgee River, a pattern was also apparent between year-class strength and number of pulses greater than 241 m^3/s during spring months (Mar – June). Year-class strength was relatively low when very few pulses occurred (≤ 3 pulses); whereas, year-class strength was highest when there were 11-21 spring pulses ($> 241 \text{ m}^3/\text{s}$). However, as the number of pulses increased from 11 to 73, I observed a substantial decline in year-class strength ($r^2 = 0.56$, $P < 0.01$, Fig. 4). In general, spring discharges appeared to be the most important factor influencing year-class strength of flathead catfish in both systems.

Stochastic Population Models: Hydrology

Spring discharges and November low flows were incorporated as stochastic factors influencing the year-class strength and population growth of flathead catfish in the Coosa River. The stochastic growth rate (λ) of the population was 0.982, which indicated

a 1.3% decrease in population growth rate after accounting for hydrologic variation in the system (Fig. 5a). Because I modeled from a range of hydrologic conditions that flathead catfish have experienced in the regulated reach, these findings indicated that the current flow regime would have a negative, long-term impact on population growth in the system. However, stochastic projections were highly variable, and short periods of favorable hydrologic conditions occasionally resulted in brief spikes in population size (Fig. 5a). This potential for exhibiting spikes in population size was demonstrated when the Coosa River population was modeled to experience five years of favorable hydrologic conditions. As expected, the population exhibited a brief spike in abundance, but continued to decline shortly afterwards at a 1.0% annual rate (stochastic growth rate, $\lambda = 0.990$, Fig. 5b). When the population was modeled to experience five years of unfavorable hydrologic conditions, it exhibited little resiliency by briefly increasing and then decreasing at a 1.9% annual rate (stochastic growth rate, $\lambda = 0.981$, Fig. 5c)

March discharges and June low flows were incorporated as stochastic factors influencing the year-class strength and population growth of flathead catfish in the Ocmulgee River. The stochastic growth rate (λ) of the population was 1.0, which indicated no changes in population growth rate after accounting for hydrologic variation in the system (Fig. 6a). When the population was modeled to experience five years of favorable conditions, it exhibited a substantial spike in size and continued to increase at a 0.6% annual rate (stochastic growth rate, $\lambda = 1.006$, Fig. 6b). After the population experienced five years of unfavorable conditions, a sharp decline in population size was predicted. However, the population quickly recovered, with population size increasing at a 0.3% annual rate following the decline (stochastic growth rate after the decline, $\lambda =$

1.003, Fig. 6c). In general, stochastic population growth in the Ocmulgee River was more erratic and variable than population growth in the Coosa River.

Stochastic Population Models: Mortality

In the Coosa River population, the incorporation of mortality as a stochastic factor resulted in a minimal (0.2 %) decrease in population growth (stochastic growth rate, $\lambda = 0.998$, Fig. 7a). A similar response was observed in the Ocmulgee River population (0.3% decrease, stochastic growth rate, $\lambda = 0.997$, Fig. 8a). By protecting flathead catfish with the highest reproductive value (i.e., with a slot limit), population growth was improved by 0.9% in the Coosa River (stochastic growth rate, $\lambda = 1.009$, Fig. 7b). Simulation of increased mortality of harvestable-sized fish in the Ocmulgee River indicated that population size could theoretically be reduced over a 50-yr period with substantial exploitation rates (stochastic growth rate, $\lambda = 0.957$, Fig. 8b). In these modeling routines, stochastic population growth in the Ocmulgee River was also more erratic and variable than population growth in the Coosa River.

Discussion

Recruitment of flathead catfish in the Ocmulgee and Coosa rivers was closely linked to spring discharges. In the Coosa River, year-class strength was positively related to increased frequency of spring pulses between 283 to 566 m³/s. This finding indicated that an optimal range of discharges enhanced the productivity of flathead catfish in the regulated reach of the Coosa River. Based on this information, managers could prescribe a spring flow regime that will potentially improve flathead catfish productivity in the system, preferably within an adaptive management framework (Irwin and Freeman 2002). Dams have altered the timing and reduced the frequency of high pulses (or flood

events) that would normally result in floodplain or riparian inundation and ultimately promote fish productivity (Pringle et al 2000). Although pre-dam discharge data were not available for the Coosa River, I suspect that high spring pulses (283 - 566 m³/s) occurred more frequently within the system and were dampened after dams were constructed. When used correctly, mimicry of natural flow regimes can have a positive effect on the status of native fish fauna in regulated river systems (Propst and Gido 2004). Although analyses indicated that a second-degree polynomial relation existed between recruitment of flathead catfish and spring discharge in the Coosa River, no data was available to assess the effects of higher pulses (> 566 m³/s) on flathead catfish recruitment in the system. Therefore, I was unable to determine if extremely high pulses would have detrimental effects on recruitment.

In the Ocmulgee River, we observed a negative trend between year-class strength and mean spring discharge. Optimal mean spring discharges for YOY fish production appeared to range from 85 to 170 m³/s. However, results also indicated that approximately 11-21 high spring pulses (> 241 m³/s) enhanced flathead catfish recruitment within the system. These high pulses may have inundated the floodplain, which presumably enhanced the survival of age-0 flathead catfish by increasing the availability of refuge habitat and terrestrial sources of prey (Welcomme 1979). Quist and Guy (1998) suggested that recruitment and growth of a closely related species (channel catfish) was positively related to over-bank discharges that resulted in floodplain inundation. When high pulses occurred too frequently in the Ocmulgee River, I suspect that high flow variation and fall rates may have negatively affected recruitment. When comparing spring hydrographs between low and high recruitment years, it is apparent that

moderate discharges with several smooth peaks in flow ($> 241 \text{ m}^3/\text{s}$) positively influenced flathead catfish recruitment in the Ocmulgee River system (Figure 9). In contrast, two scenarios appeared to have negative effects on recruitment: 1) very low and stable flows (i.e., no peaks or spikes in flow) and 2) extreme spikes in flow with high flow variation and fall rates (Figure 9). Low and stable flows would result in minimal riparian and floodplain inundation, and extremely high fall rates would result in dramatic changes in habitat availability and conditions and potentially strand age-0 flathead catfish in floodplains.

Mortality of age-0 flathead catfish in the introduced population was higher than mortality of age-0 fish in the native population. Because flathead catfish in the Ocmulgee River grew more rapidly than fish in the Coosa River (Sakarlis et al. *in press*), they probably matured earlier and produced more offspring than slow-growing fish in the Coosa River. Simulations in FAST predicted that flathead catfish in the Ocmulgee River population would produce 2.5 times more eggs than fish in the Coosa River population over the lifetime of a cohort. As a result, I postulate that age-0 survival was influenced by density-dependent mechanisms in the Ocmulgee River (i.e., increased deaths due to crowding). Jolley (2004) reported that flathead catfish comprised approximately 22.5% (by weight) of the diet of mid-sized flathead catfish (250-500 mm TL) in tailwaters. Therefore, higher densities of age-0 flathead catfish may have resulted in higher cannibalism rates in the Ocmulgee River. Studies should further examine the potential for density-dependent, age-0 survival in introduced populations.

Stochastic Projections

Coosa River.—Incorporation of hydrologic variation as a stochastic factor resulted in a slowly declining population in the Coosa River. I modeled hydrologic conditions that flathead catfish typically experienced in the regulated reach below Mitchell Dam; therefore, this stochastic population response indicated that the current flow regime would have a negative, long-term impact on population growth in the system. However, prescription of “favorable” hydrologic conditions in spring could maintain or possibly improve flathead catfish productivity in the system. Models incorporating five, consecutive years of “favorable” conditions in spring indicated that the population would positively respond to increased spring discharges. Although these manipulated flow conditions may not naturally occur in unregulated systems, these conditions could be prescribed annually (or on some regular basis) in a regulated system.

The Coosa River population was not resilient when it was exposed to several years of “unfavorable” flow conditions. Life history characteristics of flathead catfish in this population were not conducive for a quick recovery after exposure to harsh conditions. Flathead catfish in the Coosa River population had great longevity (max age = 25, but grew very slowly (Sakaris et al. *in press*). Maximum age in the Ocmulgee River was 16 years (Sakaris et al. *in press*). Munger et al (1994) reported that 50% of flathead catfish reached sexual maturity at 390 mm TL, which was relatively low compared to other lengths at maturity reported for flathead catfish in the literature. Therefore, flathead catfish probably did not reach maturity until they were, at least, seven years old in the Coosa River. Consequently, at least seven years were required for

stronger year classes to contribute reproductively to the population. Studies are needed to determine the precise age and length at maturity of flathead catfish in the Coosa River.

The stationary stage distribution indicated that large flathead catfish (> 804 mm TL) comprised a very low proportion of fish in the Coosa River population, indicating that fish with the highest reproductive values were least abundant. When the implementation of a slot limit was modeled to protect these fish in the Coosa River, the population responded by slowly increasing in size at a 0.9% rate. Therefore, protection of reproductively valuable flathead catfish would enhance population status in the Coosa River. Management for improving survival of large flathead catfish could involve the implementation of slot and/or bag limits.

Ocmulgee River.— Incorporation of hydrologic variation as a stochastic factor resulted in stationary population growth ($\lambda = 1.00$) in the Ocmulgee River. In addition, the Ocmulgee River population exhibited substantial spikes in size when it was exposed to favorable hydrologic conditions. In some projections, spikes in population size briefly appeared exponential. This response to favorable hydrologic conditions and the potential to briefly exhibit exponential growth may partly explain why this population rapidly expanded throughout the system following introduction in the early 1970's (Thomas 1993). In addition, the Ocmulgee River population was more resilient than the Coosa River population when it was exposed to several years of “unfavorable” flow conditions. Based on the findings of Munger et al. (1994), flathead catfish would reach maturity after two years post-hatch in the Ocmulgee River. Therefore, flathead catfish in the Ocmulgee River could contribute reproductively to the population in only two to 3 years post-hatch.

The introduction of flathead catfish in the Ocmulgee River has resulted in substantial declines in abundances of native sunfish and ictalurid species (Thomas 1993). Centrarchids and ictalurids were the dominant prey items consumed by flathead catfish in the Altamaha River System, which included the Ocmulgee River (Weller and Robbins 1999). By using our stochastic models to simulate increased mortality of harvestable sized flathead catfish in the Ocmulgee River, I predicted that a substantial decline in population size would be observed over a 50-year period. Therefore, I recommend that flathead catfish be minimally protected in the Ocmulgee River system. Because anglers will be able to harvest more flathead catfish from this introduced population, reduced predation may provide other fishes (e.g., redbreast sunfish) with an opportunity to become reestablished in the system.

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Table 1. Structure of size-classified transition matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

Size Class	0-104	104-204	204-304	304-404	404-504	504-604	604-704	704-804	804-904	904-1004	1004-1104
<i>Coosa River</i>	0	0	0	0	F ₅	F ₆	F ₇	F ₈	F ₉	F ₁₀	F ₁₁
	G ₁	P ₂	0	0	0	0	0	0	0	0	0
	0	G ₂	P ₃	0	0	0	0	0	0	0	0
	0	0	G ₃	P ₄	0	0	0	0	0	0	0
	0	0	0	G ₄	P ₅	0	0	0	0	0	0
	0	0	0	0	G ₅	P ₆	0	0	0	0	0
	0	0	0	0	0	G ₆	P ₇	0	0	0	0
	0	0	0	0	0	0	G ₇	P ₈	0	0	0
	0	0	0	0	0	0	0	G ₈	P ₉	0	0
	0	0	0	0	0	0	0	0	G ₉	P ₁₀	0
	0	0	0	0	0	0	0	0	0	G ₁₀	P ₁₁
Size Class	0-266	266-416	416-566	566-716	716-866	866-1016	1016-1166				
<i>Ocmulgee River</i>	0	0	F ₃	F ₄	F ₅	F ₆	F ₇				
	G ₁	P ₂	0	0	0	0	0				
	0	G ₂	P ₃	0	0	0	0				
	0	0	G ₃	P ₄	0	0	0				
	0	0	0	G ₄	P ₅	0	0				
	0	0	0	0	G ₅	P ₆	0				
	0	0	0	0	0	G ₆	P ₇				

Table 2. Parameters used in the Yield-Per-Recruit model in FAST to estimate the lifetime fecundity of a flathead catfish cohort in the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

Population	Parameters	Coefficients
<i>Coosa</i>	Von Bertalanffy growth model	$L_{\infty} = 1137$ mm TL, $k = 0.0642$, $t_0 = - 0.0255$
	Log ₁₀ (WT): Log ₁₀ (TL) relation	$b = 3.17$, $a = - 5.409$
	Conditional Natural Mortality (C_m)	0.163
	Maximum Age	25
	N_0	1000
<i>Ocmulgee</i>	Von Bertalanffy growth model	$L_{\infty} = 1113.5$ mm TL, $k = 0.195$, $t_0 = - 0.4$
	Log ₁₀ (WT): Log ₁₀ (TL) relation	$b = 3.138$, $a = -5.316$
	Conditional Natural Mortality (C_m)	0.230
	Maximum Age	16
	N_0	1000

Table 3. List of hydrologic variables that were generated to explain recruitment of flathead catfish in the Coosa and Ocmulgee rivers, respectively. Only those variables that were found significant in multiple regression models are listed.

Site	Hydrologic Variable	Definition
<i>Coosa River</i>	LP_N	Number of low pulses within each water year
	HP_N	Number of high pulses within each water year
	NOV_LOWF	Mean of low flows during November (m ³ /s)
	REV	Number of times that flow switches between "rising" and "falling" periods
	PULSES_283_566	Number of spring pulses between 283 and 566 m ³ /s
	SPRING_MEAN	Mean spring discharge (m ³ /s)
	90_D_MAX	Annual maxima, 90-d mean
<i>Ocmulgee River</i>	DEC	Mean December discharge (m ³ /s)
	JUN	Mean June discharge (m ³ /s)
	JUN_LOWF	Mean of low flows during June (m ³ /s)
	MAR	Mean March discharge (m ³ /s)
	SPRING_MEAN	Mean spring discharge (m ³ /s)

Table 4. Modified structure of transition matrices constructed for stochastically varying recruitment as a function ($f(x)$) of variable hydrologic conditions. Recruitment was modeled in the first row of transition matrices by multiplying the fertility of each size class (F_i) by the survival estimate of the first year class (G_1).

Size Class	104-204	204-304	304-404	404-504	504-604	604-704	704-804	804-904	904-1004	1004-1104
<i>Coosa River</i>	P_2	0	0	$f(F_5G_1)$	$f(F_6G_1)$	$f(F_7G_1)$	$f(F_8G_1)$	$f(F_9G_1)$	$f(F_{10}G_1)$	$f(F_{11}G_1)$
	G_2	P_3	0	0	0	0	0	0	0	0
	0	G_3	P_4	0	0	0	0	0	0	0
	0	0	G_4	P_5	0	0	0	0	0	0
	0	0	0	G_5	P_6	0	0	0	0	0
	0	0	0	0	G_6	P_7	0	0	0	0
	0	0	0	0	0	G_7	P_8	0	0	0
	0	0	0	0	0	0	G_8	P_9	0	0
	0	0	0	0	0	0	0	G_9	P_{10}	0
	0	0	0	0	0	0	0	0	G_{10}	P_{11}
<hr/>										
Size Class	266-416	416-566	566-716	716-866	866-1016	1016-1166				
<i>Ocmulgee River</i>	P_2	$f(F_3G_1)$	$f(F_4G_1)$	$f(F_5G_1)$	$f(F_6G_1)$	$f(F_7G_1)$				
	G_2	P_3	0	0	0	0				
	0	G_3	P_4	0	0	0				
	0	0	G_4	P_5	0	0				
	0	0	0	G_5	P_6	0				
	0	0	0	0	G_6	P_7				

Table 5. Transition matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

Size Class	0-104	104-204	204-304	304-404	404-504	504-604	604-704	704-804	804-904	904-1004	1004-1104
<i>Coosa River</i>	0	0	0	0	1996.6	3554.2	5748.1	8680.4	12451.7	17161.2	22906.8
	0.0000668	0.315	0	0	0	0	0	0	0	0	0
	0	0.522	0.364	0	0	0	0	0	0	0	0
	0	0	0.473	0.417	0	0	0	0	0	0	0
	0	0	0	0.420	0.471	0	0	0	0	0	0
	0	0	0	0	0.366	0.525	0	0	0	0	0
	0	0	0	0	0	0.312	0.579	0	0	0	0
	0	0	0	0	0	0	0.258	0.633	0	0	0
	0	0	0	0	0	0	0	0.204	0.687	0	0
	0	0	0	0	0	0	0	0	0.150	0.742	0
	0	0	0	0	0	0	0	0	0	0.095	0.837
Size Class	0-266	266-416	416-566	566-716	716-866	866-1016	1016-1166				
<i>Ocmulgee River</i>	0	0	2304.7	4989.2	9174.4	15172.2	23288.4				
	0.0000333	0	0	0	0	0	0				
	0	0.770	0.150	0	0	0	0				
	0	0	0.620	0.301	0	0	0				
	0	0	0	0.469	0.453	0	0				
	0	0	0	0	0.317	0.609	0				
	0	0	0	0	0	0.161	0.770				

Table 6. Stable stage distributions and reproductive values from size-classified matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

Stage	Stable Stage Distribution		Reproductive Value	
	Coosa River	Ocmulgee River	Coosa River	Ocmulgee River
1	0.999591	0.999855	0.000002	0.000003
2	0.000097	0.000033	0.023441	0.082450
3	0.000080	0.000030	0.030758	0.107079
4	0.000065	0.000027	0.041347	0.136580
5	0.000052	0.000023	0.057407	0.174323
6	0.000040	0.000019	0.074444	0.221270
7	0.000029	0.000013	0.095506	0.278295
8	0.000021		0.120964	
9	0.000013		0.150997	
10	0.000008		0.185157	
11	0.000005		0.219978	

Table 7. Elasticities of matrix elements in matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

Size Class	0-104	104-204	204-304	304-404	404-504	504-604	604-704	704-804	804-904	904-1004	1004-1104	
<i>Coosa River</i>	0	0	0	0	0.0065	0.0089	0.0107	0.0114	0.0106	0.0085	0.0066	
	0.0633	0.0291	0	0	0	0	0	0	0	0	0	
	0	0.0633	0.0362	0	0	0	0	0	0	0	0	
	0	0	0.0633	0.0454	0	0	0	0	0	0	0	
	0	0	0	0.0633	0.0564	0	0	0	0	0	0	
	0	0	0	0	0.0568	0.0628	0	0	0	0	0	
	0	0	0	0	0	0.0479	0.0658	0	0	0	0	
	0	0	0	0	0	0	0.0372	0.0641	0	0	0	
	0	0	0	0	0	0	0	0.0258	0.0566	0	0	
	0	0	0	0	0	0	0	0	0.0152	0.0435	0	
	0	0	0	0	0	0	0	0	0	0.0066	0.0341	
Size Class	0-266	266-416	416-566	566-716	716-866	866-1016	1016-1166					
<i>Ocmulgee River</i>	0	0	0.0079	0.0152	0.0240	0.0321	0.0346					
	0.1139	0	0	0	0	0	0					
	0	0.1139	0.0201	0	0	0	0					
	0	0	0.1059	0.0456	0	0	0					
	0	0	0	0.0907	0.0752	0	0					
	0	0	0	0	0.0667	0.1038	0					
	0	0	0	0	0	0.0346	0.1158					

Table 8. Parameters from multiple and linear regression models describing recruitment of flathead catfish in the Coosa River below Mitchell Dam, Alabama.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
PULSES_283_566	2	-10.282	0.000	0.834	0.58	< 0.01
90_D_MAX NOV_LOWF	3	-3.995	6.287	0.036	0.49	< 0.01
SPRING_MEAN SPRSQ NOV_LOWF	4	-3.376	6.906	0.026	0.57	0.01
LP_N NOV_LOWF	3	-2.815	7.468	0.020	0.45	0.01
LP_N REV	3	-2.566	7.717	0.018	0.45	0.02
HP_N NOV_LOWF	3	-2.156	8.126	0.014	0.43	0.02
SPRING_MEAN SPRSQ REV	4	-1.998	8.285	0.013	0.53	0.02
SPRING_MEAN	2	-1.577	8.706	0.011	0.30	0.02
SPRING_MEAN SPRSQ	3	-1.219	9.064	0.009	0.40	0.03
SPRING_MEAN NOV_LOWF	3	-0.806	9.477	0.007	0.39	0.03
HP_N	2	-0.537	9.746	0.006	0.26	0.04
LP_N	2	0.017	10.299	0.005	0.23	0.05

Table 9. Parameters from multiple and linear regression models describing recruitment of flathead catfish in Ocmulgee River, Georgia.

Parameters	K	AICc	ΔAICc	AIC Wt	R²	Model p-value
JUN_LOWF MAR	3	-10.237	0.000	0.742	0.71	< 0.01
DEC SPRING_MEAN	3	-6.697	3.540	0.126	0.63	< 0.01
JUN MAR	3	-4.722	5.515	0.047	0.58	< 0.01
DEC JUN	3	-4.408	5.829	0.040	0.57	< 0.01
DEC JUN_LOWF	3	-3.201	7.036	0.022	0.54	< 0.01
SPRING_MEAN	2	-2.422	7.815	0.015	0.40	0.01
DEC	2	-1.108	9.129	0.008	0.34	0.02

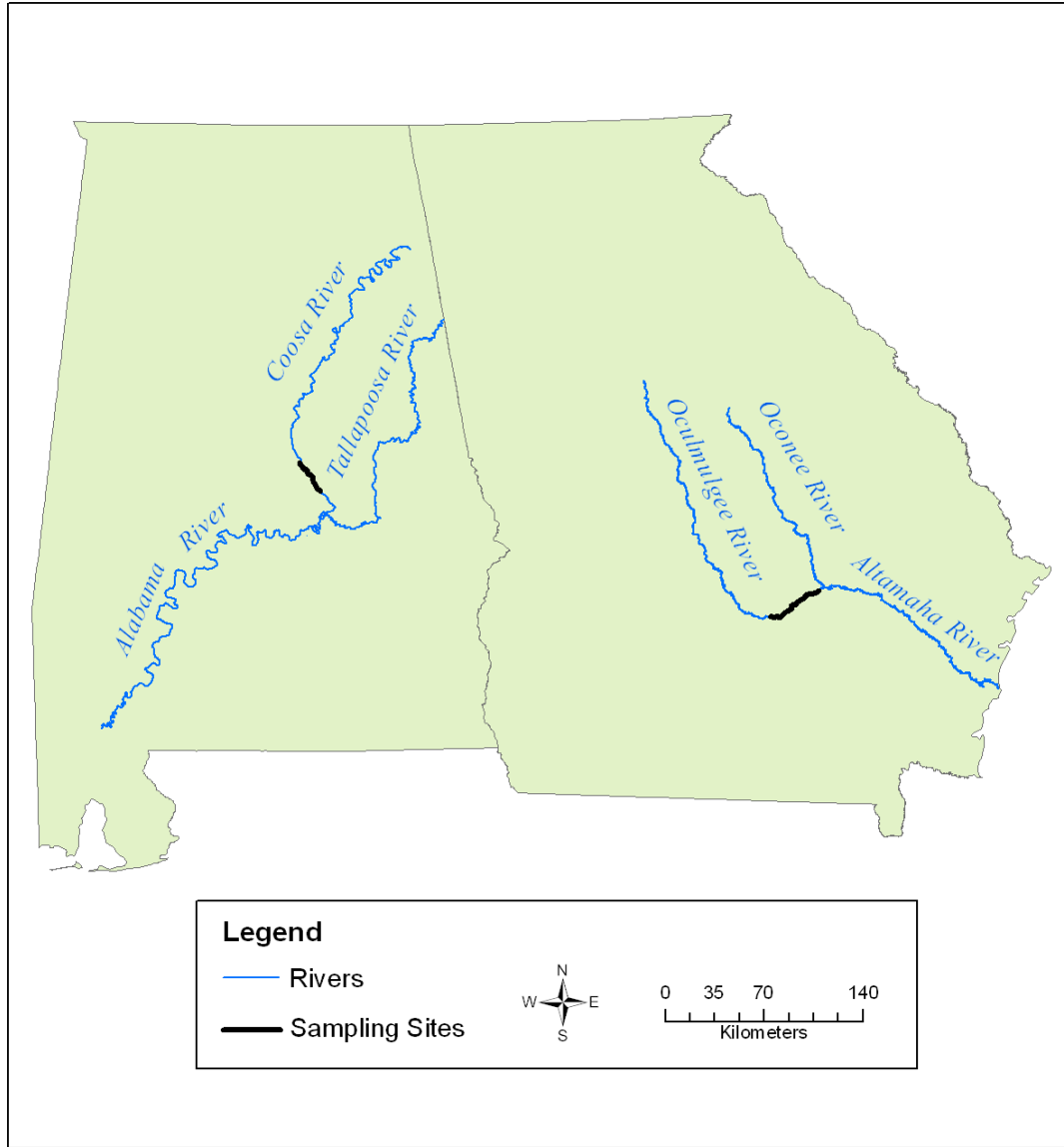


Figure. 1. Locations of sampling sites in the Coosa River (Alabama, USA) and the Ocmulgee River (Georgia, USA)

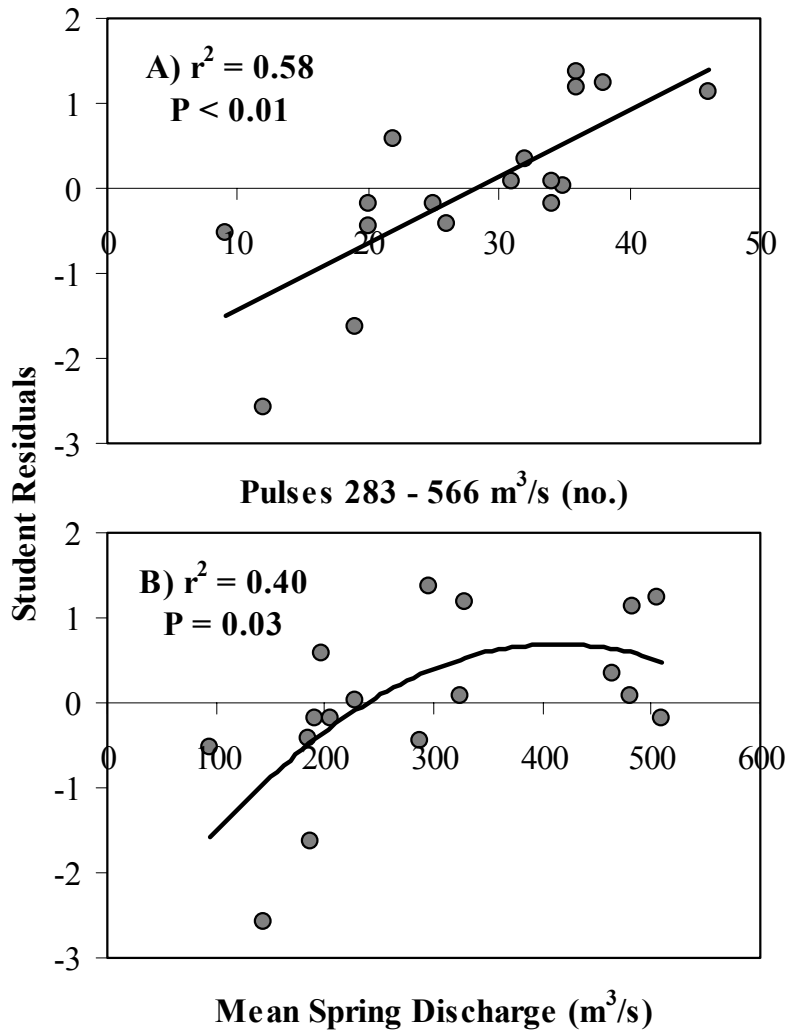


Figure. 2. Relations between student residuals (i.e., year-class strength of flathead catfish) and a) number of spring pulses between 283 and 566 m³/s and b) mean spring discharge in the Coosa River (Alabama, USA).

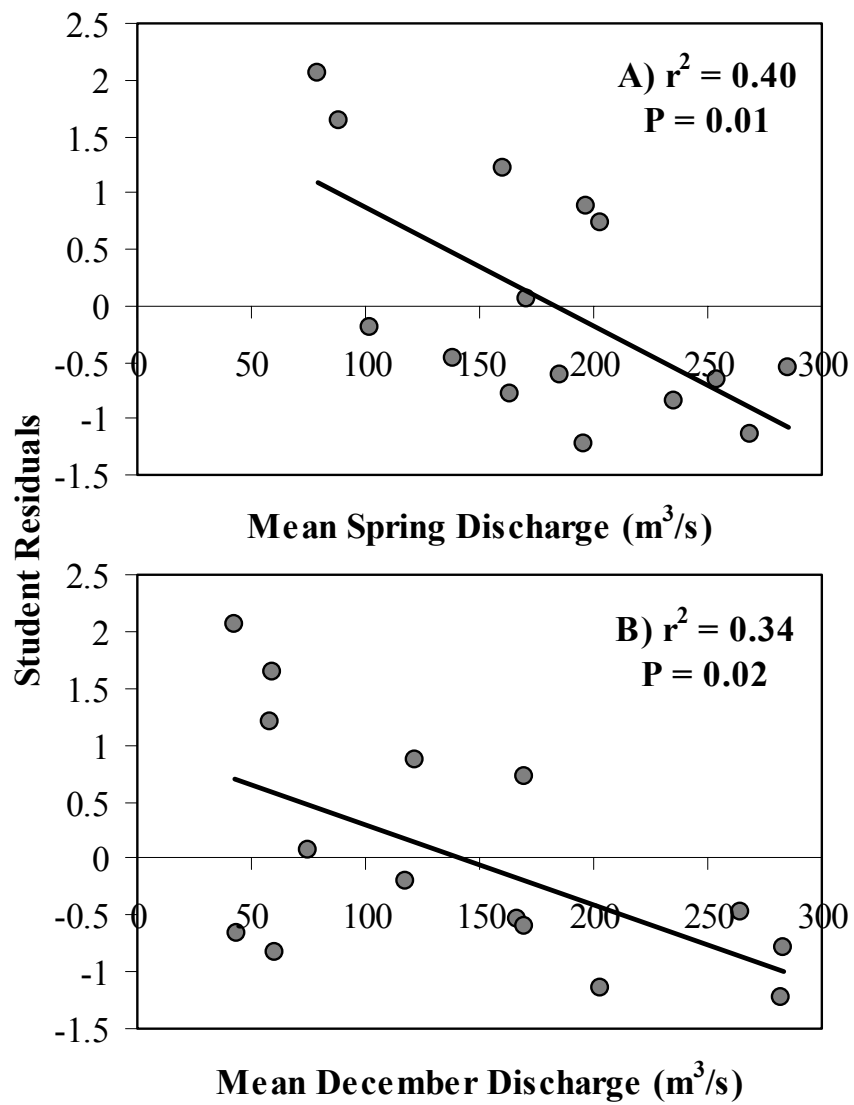


Figure. 3. Relations between student residuals (i.e., year-class strength of flathead catfish) and a) mean spring discharge and b) mean December discharge.

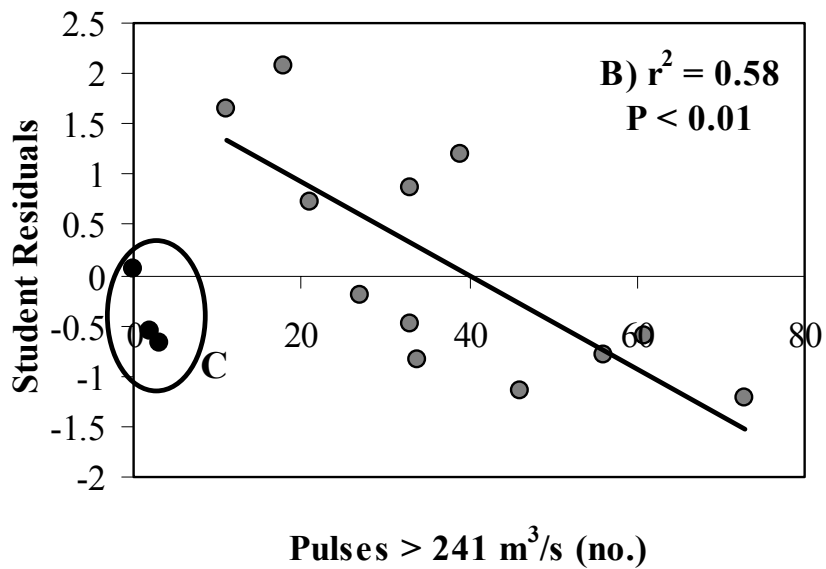


Figure 4. Relation between student residuals (i.e., year-class strength of flathead catfish) and number of spring pulses greater than 241 m³/s in the Ocmulgee River (Georgia, USA). When less than four pulses greater than 241 m³/s occurred, year-class strength was relatively weak. However, a strong, negative relation was apparent between year-class strength and the number of pulses > 241 m³/s (from 11 to 73 pulses).

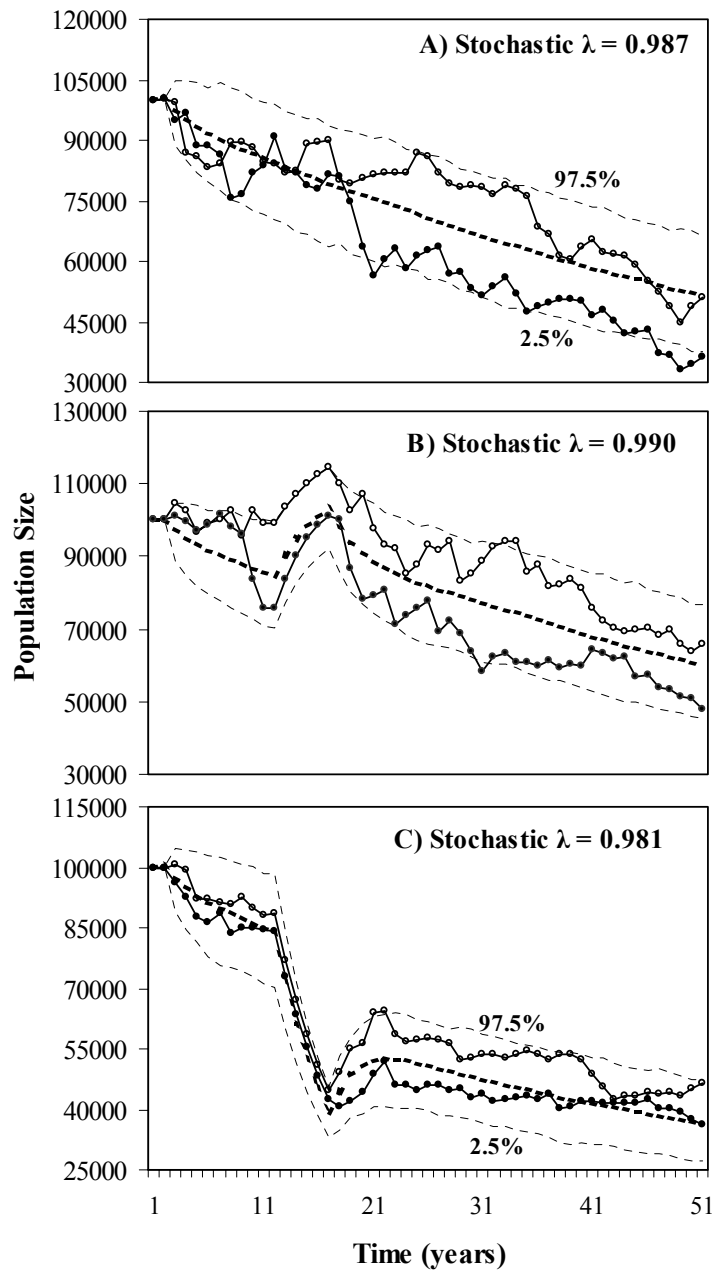


Figure 5. Flathead catfish populations were projected 1000 times with hydrologic variation modeled as a stochastic factor influencing recruitment in the Coosa River (Alabama). Three scenarios were modeled: A) Annual variation in hydrology, B) Five years of favorable hydrologic conditions, and C) Five years of unfavorable hydrologic conditions. Two examples of stochastic projections are illustrated for each scenario. Spring discharges and November low flows were modeled as stochastic factors. Upper and lower 95% and 2.5% confidence limits are labeled.

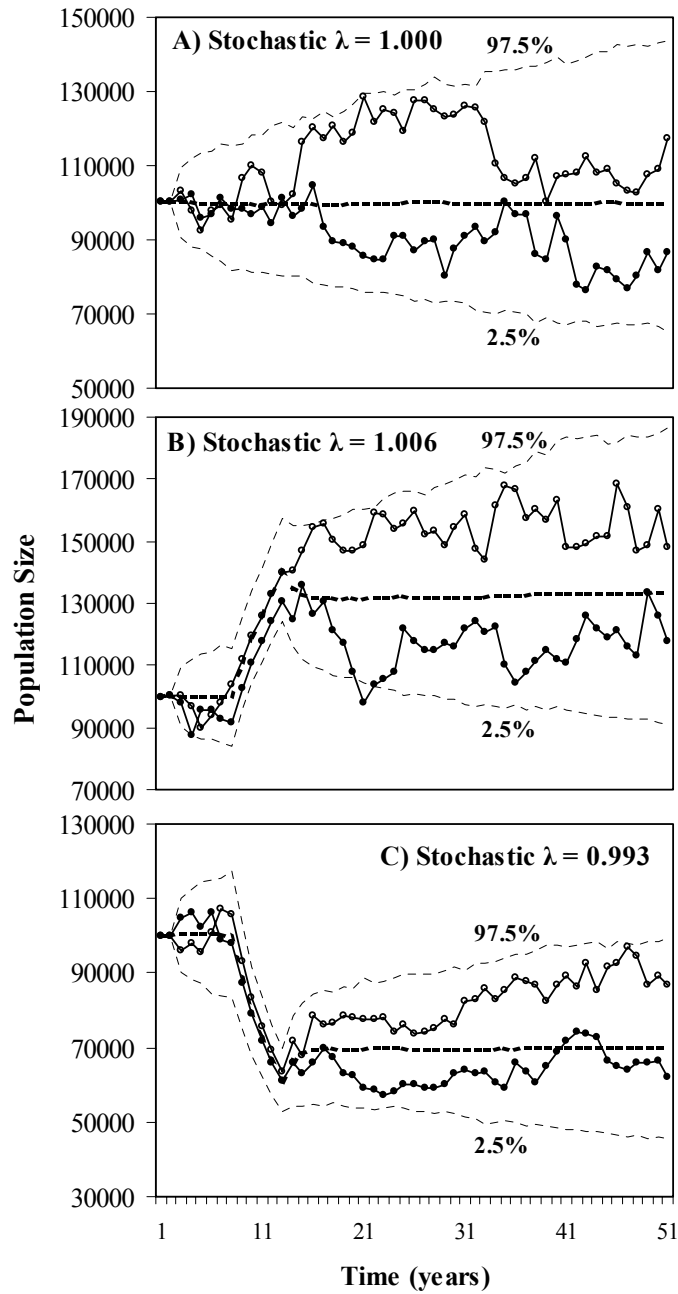


Figure 6. Flathead catfish populations were projected 1000 times with hydrologic variation modeled as a stochastic factor influencing recruitment in the Ocmulgee River (Georgia). Three scenarios were modeled: A) Annual variation in hydrology, B) Five years of favorable hydrologic conditions, and C) Five years of unfavorable hydrologic conditions. Two examples of stochastic projections are illustrated for each scenario. June low flows and March discharges were modeled as stochastic factors. Upper and lower 95% and 2.5% confidence limits are labeled.

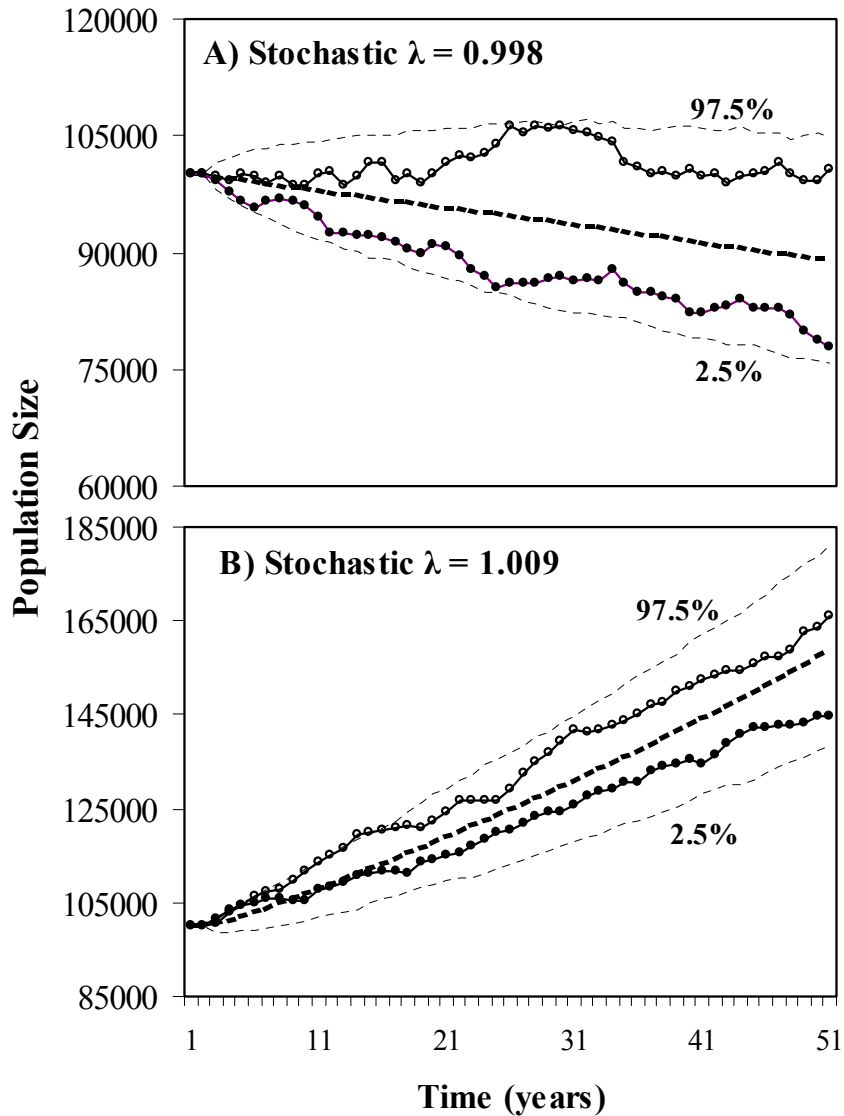


Figure. 7. Flathead catfish populations were projected 1000 times with mortality of harvestable sized fish modeled as a stochastic factor influencing population growth in the Coosa River (Alabama). Two scenarios were modeled: A) Annual variation in mortality and B) Simulation of an implemented slot limit to protect fish with the highest reproductive values. Two examples of stochastic projections are illustrated for each scenario. Upper and lower 95% and 2.5% confidence limits are labeled.

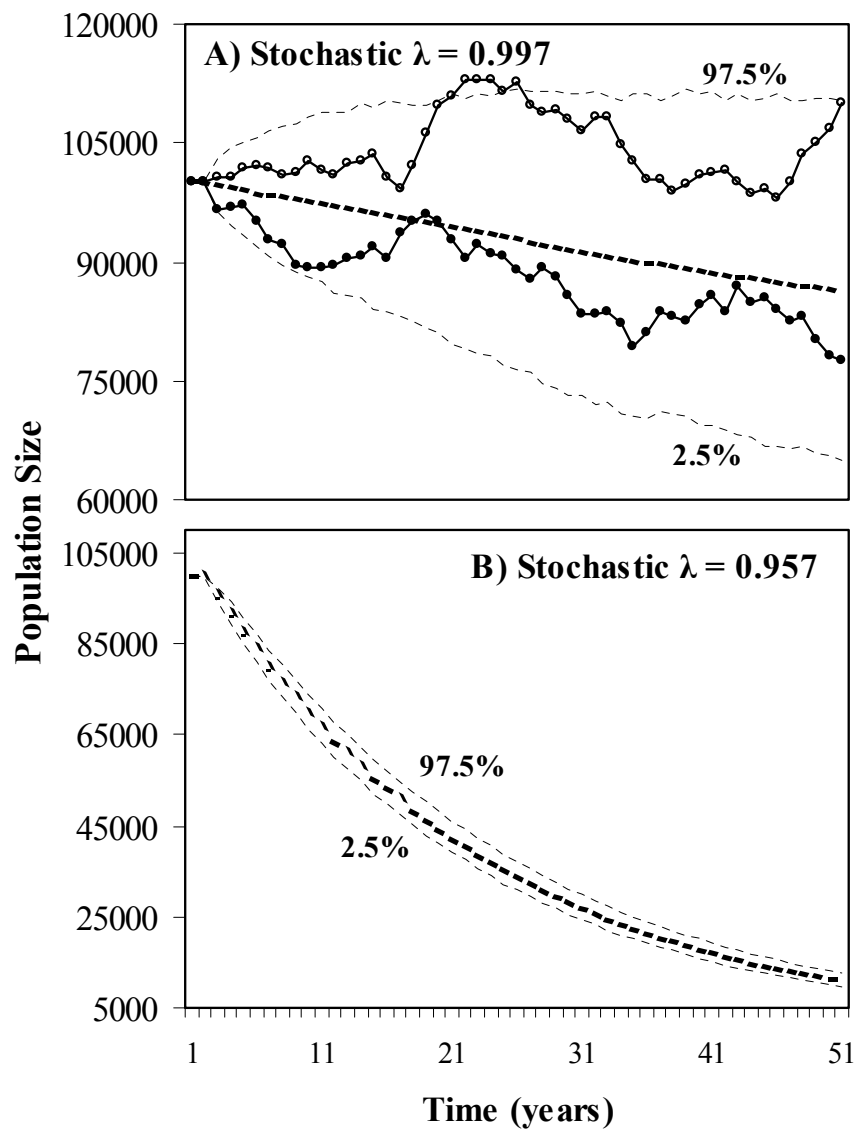


Figure. 8. Flathead catfish populations were projected 1000 times with mortality of harvestable sized fish modeled as a stochastic factor influencing population growth in the Ocmulgee River (Georgia). Two scenarios were modeled: A) Annual variation in mortality and B) Simulation of an increased mortality of harvestable sized fish. Two examples of stochastic projections are illustrated for the first (A) scenario. Upper and lower 95% and 2.5% confidence limits are labeled.

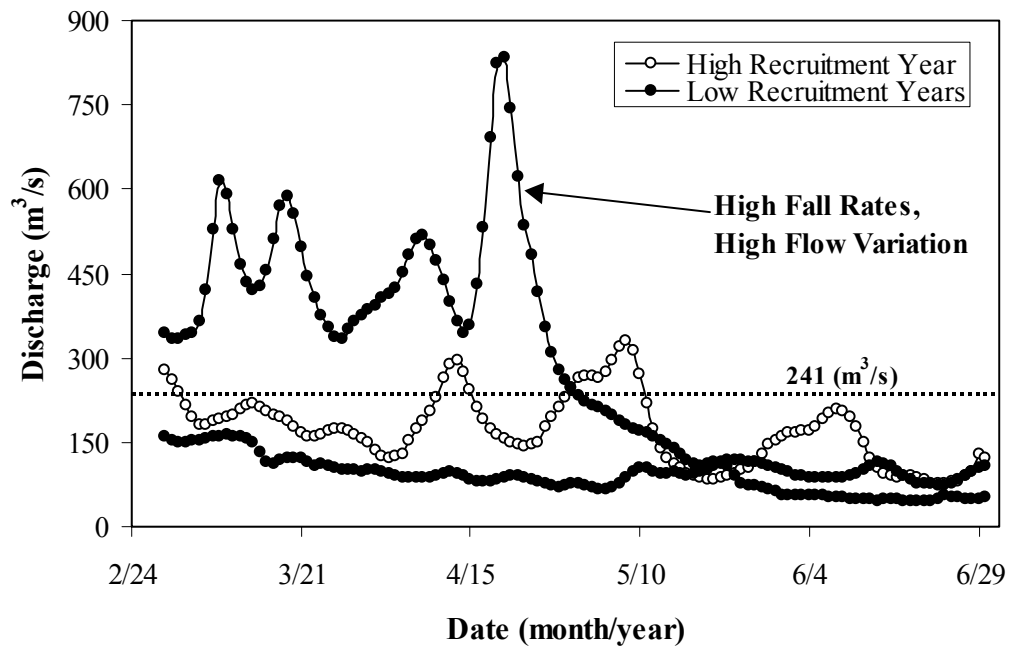


Figure. 9. Spring hydrographs during a high recruitment year (open symbol) and two low recruitment years (solid symbol).

V. CONCLUSIONS

Daily aging of age-0 channel catfish

Daily aging of age-0 channel catfish was a successful technique using transverse sections of sagittal otoliths. This method should be used for estimating growth and hatching success of channel catfish up to 120 d post-hatch. Validation studies for aging fishes allow us to evaluate the accuracy and precision of our techniques and increase our confidence in data that are derived from aging wild fish. These studies should also be performed to compare accuracy and precision among different structures for aging fishes (e.g., otoliths and spines, Buckmeier et al. 2002).

Age-0 channel catfish: Growth Vs. Hydrology

Early growth of age-0 channel catfish was related to hydrologic conditions in unregulated and regulated river sections of the Tallapoosa River System. Growth of age-0 fish generally increased with increasing discharges, and, in several cases, relations between growth and hydrology were non-linear. In the Upper Tallapoosa River, elevated minimum flows appeared to have a strong, positive effect on growth of age-0 channel catfish. These findings indicated that higher minimum flows should be prescribed below dams for improving productivity of channel catfish, and possibly other catfishes, in regulated rivers. Higher minimum flows may provide fish with more riffle habitats, which were utilized by juvenile channel catfish in the Tallapoosa River System (Irwin et al. 1999). In addition, other studies have reported that higher minimum flows would

have a positive effect on fish assemblages in regulated river systems. Neosho madtom densities were positively correlated with increased minimum flows below John Redmond dam in the Neosho River Basin (Wildhaber et al. 2000). Travnicek et al. (1995) demonstrated that increased, continuous minimum flows positively influenced the diversity of fishes below Thurlow Dam on the lower Tallapoosa River.

Elevated fall rates (above some critical value) appeared to have a negative effect on growth of age-0 channel catfish. Substantial declines in discharge over short time intervals likely resulted in significant changes in water temperature and habitat availability. Therefore, habitat instability resulting from high fall rates probably hindered the growth of age-0 channel catfish. Managers prescribing flow regimes below dams should consider reducing fall rates during hydropeaking operations.

In general, age-0 channel catfish in the Coastal Plain grew faster than fish in the Piedmont. I attributed this difference in growth to lateral interactions that may occur between the main channel and floodplain in Coastal Plain systems. However, growth of age-0 fish (0 – 60 d post-hatch) was unexpectedly higher at regulated sites than at unregulated locations in the Piedmont. I hypothesized that adult channel catfish in the highly variable, flow-regulated river section exhibited a bet hedging strategy. This “bet hedging hypothesis” was supported by the following observations: 1) Channel catfish had higher longevity in the regulated section compared to the unregulated sections (Nash 1999). 2) Channel catfish appeared to have a protracted spawning period in the regulated reach. 3) In the regulated reach, faster growth among recently hatched larvae implied that parents potentially produced larger eggs and larvae at hatch.

Hatching Success Vs. Hydrology

In Uphapee Creek, age-0 channel catfish typically hatched during periods with relatively low and stable flows. Similar findings were reported for channel catfish in the Mississippi River (Holland-Bartels and Duval 1988). High river discharges likely disrupted spawning activity and flushed larvae from nests (Holland-Bartels and Duval 1988). Therefore, periods of low and stable flows should be prescribed during the spawning period to allow for successful spawning and hatching of age-0 channel catfish below dams.

Flathead Catfish Recruitment Vs. Hydrology

Recruitment of native flathead catfish appeared to be positively related to spring discharges in a regulated reach of the Coosa River below Mitchell Dam. However, this relation was non-linear, and an “optimal” range (10,000 – 20,000 CFS) of spring discharges was identified for enhancing recruitment of flathead catfish in the regulated river section. When the effect of hydrologic variability on recruitment was incorporated as a stochastic factor in a matrix model constructed for this population, population size was projected to slowly decline over a 50-year period (stochastic growth rate (λ) = 0.988). Because I modeled hydrologic conditions that flathead catfish have typically experienced in the regulated river section, these results indicated that the current flow regime would ultimately reduce the growth of the Coosa River population. However, models also predicted that protection of flathead catfish with the highest reproductive values would enhance population growth within the system.

In general, recruitment of introduced flathead catfish appeared to be negatively related to spring discharges in the lower Ocmulgee River. However, a moderate number of high pulses (11-21 pulses > 8500 CFS) positively influenced recruitment of flathead catfish in the system. A strong decline in year-class strength was observed when these high pulses occurred too frequently. When the effect of hydrologic variability on recruitment was incorporated as a stochastic factor in a matrix model constructed for this population, population size was projected to remain stable over a 50-year period (stochastic growth rate (λ) = 1.000). In addition, stochastic models indicated that the introduced population was more resilient than the native population when they were exposed to several, consecutive years of unfavorable flow conditions. Finally, models also predicted that increased mortality among harvestable sized fish would considerably reduce the Ocmulgee River population.

Future Directions

Validation studies should be conducted for using otoliths to daily age other age-0 catfishes (i.e., flathead catfish and blue catfish, *Ictalurus furcatus*). Information was not reported regarding daily growth and hatching success of age-0 flathead catfish in relation to hydrologic variables. Age-0 flathead catfish were not successfully collected using PAE's and backpack electrofishers from unregulated and regulated sites within the Tallapoosa River system, which indicated the following: 1) sampling efficiency and abundance was potentially low for this species resulting in low detection and/or 2) age-0 flathead catfish may have been utilizing different habitats than channel catfish. Future studies should examine relations between hydrology and growth and hatching success of age-0 flathead catfish in the Alabama River System.

More studies are needed to fully examine the dynamics of channel catfish populations throughout the Tallapoosa River System. The following issues/hypotheses should be addressed: 1) Channel catfish may be using unregulated tributaries instead of regulated main stem sections as their primary spawning and nursery sites. Variable flow conditions are probably not conducive for spawning in regulated river sections below dams. 2) Fish in regulated river sections may be exhibiting a bet hedging strategy. Specifically, channel catfish in these regulated sections may have a longer spawning period, delayed sexual maturity, and longer reproductive lifespan. In addition, fish may be exerting smaller reproductive effort per spawning episode and producing fewer, but larger, eggs and larvae at hatching (Stearns 1976). Studies should examine if other fishes (e.g., centrarchids and cyprinids) are exhibiting this life history strategy in regulated river systems. 3) Finally, mechanisms underlying relations between hydrology and growth and hatching success of age-0 channel catfish should be more intensively explored.

Models derived in this dissertation should be used as tools in adaptive-flow management programs in the Alabama River System. Specifically, these models can be used to help prescribe flow regimes in regulated river systems. For example, the prescription of minimum, continuous flows below dams may increase growth rates of age-0 channel catfish in regulated sections of the Tallapoosa River. Furthermore, stochastic models that link hydrologic variation to population growth can be used to predict how flathead catfish populations would respond to a prescribed flow regime. These stochastic models can be developed for other sport fishes and non-game fishes if 1) the appropriate life history information is collected and 2) quantitative analyses are conducted relating recruitment or reproductive success to hydrologic variation in a

regulated system. In addition, qualitative observations reported in this dissertation may be useful in prescribing flow regimes in regulated systems. For example, by providing periods of relatively low and stable flows during the spawning period, spawning success and ultimately recruitment of channel catfish may improve in regulated systems. Finally, models developed in this dissertation need to be continually improved by collecting more data and closely monitoring population responses to variable flow conditions in regulated river systems.

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