Ecological Applications, 20(2), 2010, pp. 483–496

Tuning stochastic matrix models with hydrologic data to predict the population dynamics of a riverine fish

Peter C. Sakaris[1,3] and Elise R. Irwin[2]

[1]*Alabama Cooperative Fish and Wildlife Research Unit, 3301 Forestry and Wildlife Sciences Building, Auburn University, Auburn, Alabama 36849 USA*

[2]*U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, 3301 Forestry and Wildlife Sciences Building, Auburn University, Auburn, Alabama 36849 USA*

Abstract. We developed stochastic matrix models to evaluate the effects of hydrologic alteration and variable mortality on the population dynamics of a lotic fish in a regulated river system. Models were applied to a representative lotic fish species, the flathead catfish (*Pylodictis olivaris*), for which two populations were examined: a native population from a regulated reach of the Coosa River (Alabama, USA) and an introduced population from an unregulated section of the Ocmulgee River (Georgia, USA). Size-classified matrix models were constructed for both populations, and residuals from catch-curve regressions were used as indices of year class strength (i.e., recruitment). A multiple regression model indicated that recruitment of flathead catfish in the Coosa River was positively related to the frequency of spring pulses between 283 and 566 m^3/s. For the Ocmulgee River population, multiple regression models indicated that year class strength was negatively related to mean March discharge and positively related to June low flow. When the Coosa population was modeled to experience five consecutive years of favorable hydrologic conditions during a 50-year projection period, it exhibited a substantial spike in size and increased at an overall 0.2% annual rate. When modeled to experience five years of unfavorable hydrologic conditions, the Coosa population initially exhibited a decrease in size but later stabilized and increased at a 0.4% annual rate following the decline. When the Ocmulgee River population was modeled to experience five years of favorable conditions, it exhibited a substantial spike in size and increased at an overall 0.4% annual rate. After the Ocmulgee 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. In general, stochastic population growth in the Ocmulgee River was more erratic and variable than population growth in the Coosa River. We encourage ecologists to develop similar models for other lotic species, particularly in regulated river systems. Successful management of fish populations in regulated systems requires that we are able to predict how hydrology affects recruitment and will ultimately influence the population dynamics of fishes.

Key words: Coosa River, Alabama, USA; dams; fishes; flathead catfish; hydrology; lotic; matrix model; Ocmulgee River, Georgia, USA; population dynamics; Pylodictis olivaris; *riverine; river regulation.*

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 et al. 2000). In addition, dams cause major changes in fish assemblage structure following dam construction (Paragamian 2002, Quinn and Kwak 2003, Gillette et al. 2005) and can impede 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).

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). In a regulated reach of the Tallapoosa River (Alabama, USA; see Plate 1), variable flow conditions have reduced the stability and persistence of habitat, thereby reducing survival of young-of-the-year (YOY) fish (Freeman et al. 2001).

Manuscript received 12 February 2008; revised 9 April 2009; accepted 27 April 2009; final version received 22 June 2009. Corresponding Editor: K. B. Gido.

[3] Present address: Department of Biology, Chemistry, and Physics, Southern Polytechnic State University, Marietta, Georgia 30060 USA. E-mail: psakaris@spsu.edu

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 (New Mexico, USA), Propst and Gido (2004) demonstrated that manipulating spring discharges to mimic the natural flow regime would potentially enhance native fish recruitment.

Models that predict how fish populations respond to hydrologic variation have great utility in adaptive flow management programs. The main goal of adaptive flow management is to consistently improve management as uncertainty about a river system is reduced, which requires cooperation and commitment among natural resource agencies, private industry, landowners, and other stakeholders (Irwin and Freeman 2002). Adaptive flow management is an iterative process with a series of steps that include (1) prescription and implementation of a managed flow 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 (Irwin and Freeman 2002). When prescribing a flow regime in a regulated system, models can be used to predict how the fauna would potentially respond to the modified flow conditions. These models can be modified and improved as new information is collected and uncertainty about a system is reduced.

In this study, our main goal was to develop a stochastic model that could be used to demonstrate how managing for a more natural flow regime could increase productivity of catfish populations in regulated rivers. We also used the model to demonstrate the manner in which increased fishing mortality of specific length classes could be used to control population expansion and to simulate the implementation of a slot limit to protect the less abundant but reproductively valuable size classes. Specific objectives were to: (1) investigate the manner in which hydrology influences the recruitment of a representative lotic species, flathead catfish (*Pylodictis olivaris*), from a regulated reach of the Coosa River (Alabama, USA) and an unregulated section of the Ocmulgee River (Georgia, USA), (2) construct size-classified matrix models for these flathead catfish populations, (3) incorporate the effects of hydrologic variation on recruitment and variable mortality as stochastic factors influencing the dynamics and long-term growth of these populations, and (4) use these models to predict the manner in which the populations respond to prescribed flow and fisheries management regimes.

METHODS

Study species

The flathead catfish is primarily a riverine species, native to the Mobile (Alabama, USA), Mississippi–Missouri, and Rio Grande river drainages as well as portions of the lower Great Lakes region (Jackson 1999, Boschung and Mayden 2004). It also 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). Flathead catfish are generally dominant predators within river systems, becoming exclusively piscivorous as adults (Jackson 1999, Jolley and Irwin 2004). 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 typically differ between introduced and native flathead catfish. Native flathead catfish exhibit higher longevity than fish in introduced populations, whereas introduced fish grow more rapidly than native flathead catfish (Kwak et al. 2006, Sakaris et al. 2006). In this study, we examined a native population from a regulated reach of the Coosa River above the fall line in the Piedmont Upland (Alabama, USA) and an introduced population from the Ocmulgee River in the Atlantic Coastal Plain (Georgia, USA).

Developing matrix models for native and introduced flathead catfish populations

Flathead catfish were sampled using boat electrofishing (low-pulse frequency; 15 pulses/s) from a lower, 24-km section of the Ocmulgee River in 1997 and the lower Coosa River below Mitchell Dam in 2001 and 2002. Flathead catfish were weighed (in grams and kilograms for fish >6000 kg) and measured (in millimeters, total length [TL]). In a previous study, flathead catfish from each site were aged using otoliths, and von Bertalanffy growth models were derived for each population ($L_t = L_\infty[1 - e^{-k(t-t_0)}]$), where L_t is fish length at time t, L_∞ is the maximum theoretical length that can be obtained in the population, k is the growth coefficient, t is time or age in years, and t_0 is time in years when length would theoretically be equal to zero (Sakaris et al. 2006). 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*).

Size-classified matrix models were designed following the basic model:

$$\begin{pmatrix} (1-M_1)S_1 & m_2S_2/2 & m_3S_3/2 & m_4S_4/2 \\ M_1S_1 & (1-M_2)S_2 & 0 & 0 \\ 0 & M_2S_2 & (1-M_3)S_3 & 0 \\ 0 & 0 & M_3S_3 & S_4 \end{pmatrix} \quad (1)$$

where S_i was the probability of individuals in size class i surviving one year, M_i was the probability of an individual in size class i advancing to the next size class after one year, and m_i was the fecundity of an individual in size class i (Buckland et al. 2007). For both populations, size class 1 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. 2006). Therefore, size class 1 corresponded to age class 0, and the time spent in size class 1 equaled one year (i.e., $M_1 =$

1). 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 fish growth was much faster in the Ocmulgee River than in the Coosa River population. Because we 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. The number of size classes was constrained by the maximum fish length observed within each population. Studies have reported that flathead catfish typically reach maturity from 390 to 589 mm TL (Minckley and Deacon 1959, Perry and Carver 1977, Munger et al. 1994); therefore, we 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; Appendix A).

Survival estimation, S_{2+}.—Annual survival of flathead catfish (size classes 2+) for the Coosa and Ocmulgee river populations was determined using catch-curve analysis:

$$\ln(N_a) = \beta_0 + \beta_1 a \tag{2}$$

where N_a is the number of fish at age a and β_1 is an estimate of the instantaneous mortality rate (Z). Annual survival (S), assumed to be constant for all 2+ size classes, was calculated using the following equation:

$$S = e^Z. \tag{3}$$

Annual survival of fish in each size class included (1) a proportion of fish surviving and advancing to the next size class (M_i) and (2) a proportion of fish surviving but remaining in the size class ($1 - M_i$). The proportion of fish surviving and advancing to the next size class was estimated using the following equation:

$$M_i = 1/T_i \qquad T_i \geq 1 \text{ year} \tag{4}$$

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. We 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 size class, ~50% of the fish (i.e., in the upper half of the size class) would grow out of the size class after one year.

Fertility estimation.—In a birth pulse model with a post-breeding census, mature individuals within a population must survive through the year to successfully reproduce (Gotelli 2001). Therefore, fertilities (F_i, in the first row of the matrix) were estimated using

$$F_i = (m_i S_i) \times 0.50 \tag{5}$$

where m_i was the fecundity of an individual in size class i, S_i was the probability of individuals in size class i surviving one year, and 0.50 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. R. 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). Fecundity for each size class was predicted from a linear regression model between $\log_{10}$(fecundity) and $\log_{10}$(total length) ($N = 49$; $\log_{10}(F) = 2.897 \log_{10}(\text{TL}) - 4.0189$; $r^2 = 0.91$; $P < 0.01$; K. Hanson, *unpublished data*).

Survival of size class 1.—After fertilities and survival estimates of 2+ size classes were determined, we estimated survival of the first size class by assuming that both populations exhibited a stationary age distribution. This type of 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 survival of young-of-the-year English sole by assuming an intrinsic rate of population increase of 0. Therefore, population growth rates were initially set equal to one ($\lambda = 1$) before environmental stochasticity was incorporated into the models. After accounting for a stochastic factor, a decrease in λ (<1.0) would indicate a negative effect, whereas an increase in λ (>1.0) would indicate a positive effect on population growth.

Estimating recruitment and modeling effects of hydrology

We used residuals from catch-curve regressions as quantitative indices of relative year class strength for both flathead catfish populations (Maceina 1997, 2003, Maceina and Stimpert 1998, Bonvechio and Allen 2005). Catch-curve regressions were previously computed for both populations (Sakaris et al. 2006). In catch-curve analysis, we assume that survival (S) is constant for all age groups. If we let $N_{t,0}$ denote the recruitment in year t, then the abundance of age a fish from that cohort a years later is

$$N_{t+a,a} = N_{t,0} S^a. \tag{6}$$

Therefore,

$$\ln(N_{t+a,a}) = \ln(N_{t,0}) + a \ln(S) \tag{7}$$

$$\equiv (\beta_0 + \varepsilon_{t,0}) + \ln(S)a \equiv \beta_0 + \beta_1 a + \varepsilon_{t,0} \tag{8}$$

where $\beta_1 = \ln(S)$ and $\beta_0 + \varepsilon_{t,0} = \ln(N_{t,0})$. The survival probability and recruitment (i.e., deviations from mean recruitment) can be estimated if one has a sample of abundances by ages, $a = 1, \ldots, A$, in a single year, t, $N_{t-1,1}$, $N_{t-2,2}$, $\ldots$, $N_{t-A,A}$. The natural logarithm of abundances is regressed against age to estimate β_0 and β_1, from which survival can be estimated [$S = \exp(\beta_1)$] and the residuals, $\varepsilon_{t-a,0}$, are estimates of deviations from mean recruitment.

We evaluated the effects of hydrology on recruitment by fitting multiple regression models following the basic model:

$$\ln(N_{t+a,a}) = \beta_0 + \beta_1 a + \beta_2 h_t + \varepsilon_{t,0} \tag{9}$$

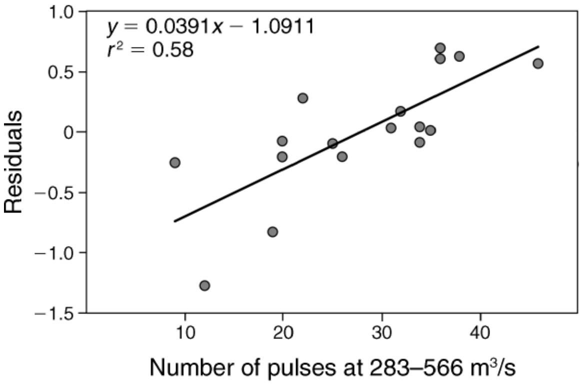

FIG. 1. Relation between residuals (i.e., indices of year class strength) and the number of spring pulses between 283 and 566 m^3/s in the Coosa River, Alabama, USA.

with a covariate, such as a hydrologic variable (h_t), explaining the formation of weak and strong year classes (i.e., residuals) after accounting for the effects of age (a) on abundance.

After significant models were fit, relations between residuals (i.e., year class strength) from the catch-curve and significant hydrologic variables were examined. Hydrologic data 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, Colorado), which included annual high and low pulse frequencies, mean monthly discharges, high and low pulse durations, maximum and minimum discharges, fall and rise rates, seasonal mean discharges, and number of reversals. Water years were started on 1 July of each year and ended on 30 June of the following year. We expected that most adult flathead catfish were spawning from late June into early July; therefore, this water year would best reflect the hydrologic conditions during a YOY fish's first year. Multicollinearity diagnostics were computed to determine whether independent variables covaried in multiple regression models (i.e., variance inflation factors [VIFs] and condition indices; Montgomery et al. 2001). All statistical analyses were conducted using Statistical Analysis System software (SAS 2003).

The AIC model selection.—For both populations, the models that best predicted abundance at age were selected and ranked using Akaike's Information Criterion (AIC) (Burnham and Anderson 1998). All multiple regression models that were ranked using AIC were highly significant ($P < 0.01$), with all individual model parameters (i.e., intercept, age, and hydrologic variables) significant at the $\alpha = 0.05$ level. A corrected AIC value (AIC_c) was calculated for each model as follows:

$$\text{AIC}_\text{c} = -2\log[L(\theta)] + 2K + [2K(K+1)]/(n-K-1) \tag{10}$$

where n is the sample size, K is the number of estimated parameters, $\log[L(\theta)] = -n/2\log(\hat{\sigma}^2)$, and $\hat{\sigma}^2 = \text{RSS}/n$ (i.e., RSS = residual sum of squares). The corrected AIC value should be calculated when $n/K < 40$. We calculated a Δ_i value for each candidate model using the following equation:

$$\Delta_i = \text{AIC}_{\text{c},i} - \min \text{AIC}_\text{c} \tag{11}$$

where $\text{AIC}_{\text{c},i}$ is the AIC_c value for model i and $\min\text{AIC}_\text{c}$ is the lowest AIC_c value observed among all of the candidate models. The Δ_i values rescale the AIC_c values as differences, allowing for easy interpretation, comparison, and ranking of candidate models. Top-ranked models (i.e., models receiving substantial support) were those models having Δ_i values within one to two of the "best" model (i.e., $\Delta_i < 2$; Burnham and Anderson 1998). An AIC weight (w_i) was also calculated for each model, which was considered the weight of evidence in favor of a given model (Burnham and Anderson 1998):

$$w_i = \exp(-1/2\Delta_i) \bigg/ \sum_{r=1}^{R} \exp(-1/2\Delta_i) \tag{12}$$

where the likelihood of model i equals $\exp(-1/2\Delta_i)$ divided by the sum of all of the likelihoods.

Linking hydrologic variation and population dynamics using stochastic matrix analyses

We 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 the second size class in the population each year. Therefore, recruitment was modeled in the first row of transition matrices by multiplying the fertilities of each size class ($m_iS_i/2$) by the survival estimate of the first size class (S_1). As a result, the second size class appeared as the first stage within the matrix (Appendix B). We let $R_i = (m_iS_i/2) \times S_1$, representing the contribution of each reproductive size class i to total recruitment (i.e., number of recruits per size class). Although these modified transition matrices were theoretically identical to the original models, our purpose was to compartmentalize recruitment so that it could be stochastically varied over time as a function of hydrologic variation. Specifically, we modeled recruitment (R_i) in the matrices to exhibit the same proportional and directional responses to hydrologic variables that were predicted by regression models. For example, a positive relation between residuals (i.e., year class strength) and the frequency of spring pulses between 283 and 566 m^3/s was apparent in the Coosa River (Fig. 1). Each recruitment value (R_i) in the matrix was then modeled to exhibit this same relation, with the respective R_i value representing average recruitment at the midpoint of the relation (Fig. 2A, B).

Effects of hydrologic variation on population dynamics

Three types of stochastic population projections were conducted over 50-year periods using these models. In the first stochastic projection, hydrologic variables that significantly influenced recruitment were varied annually. In the Ocmulgee River, hydrologic variables (mean March discharge and mean of low flows during June) conformed to normality, and thus hydrologic values were selected from a normal distribution at each yearly time step (Shapiro-Wilk statistic, $W = 0.945$, $P = 0.449$ for mean March discharge; $W = 0.968$, $P = 0.822$ for June low flow). Normal distributions were generated from hydrologic data that were acquired from the Ocmulgee River system; therefore, we modeled hydrologic conditions that flathead catfish would most likely experience in this river system. In the Coosa River, hydrologic values were randomly selected at each yearly time step from a specified range of values that were fully representative of hydrologic conditions in the system. Specifically, we used the frequency of spring pulses between 283 and 566 m^3/s as our hydrologic variable, which ranged annually from nine to 46 pulses in the Coosa River. All stochastic population projections were conducted in PopTools (Hood 2006), a program that was specifically designed to facilitate the analysis of matrix population models and simulation of stochastic processes. For all modeling routines, stochastic projections were simulated 1000 times using a Monte Carlo analysis to obtain mean stochastic growth rates (λ). All population projections were conducted with an initial population size of 100 000 individuals.

In the second stochastic projection, populations were exposed to five consecutive years of favorable hydrologic conditions during a 50-year projection. In the Coosa River, the frequency of spring pulses between 283 and 566 m^3/s was randomly selected from a range of 40–46 pulses during this five-year period. In the Ocmulgee River, mean March discharge and the mean of low flows during June were held at near-optimal conditions during this five-year period (i.e., mean March discharge held at 148 m^3/s and June low flow held at 112 m^3/s). Hydrologic conditions were varied during the rest of the projection period following the regime outlined in the first projection. We hypothesized that populations would respond to these favorable conditions by exhibiting spikes in population size, but then variably decline to previous levels.

In the third stochastic projection, populations were exposed to five consecutive years of "unfavorable" hydrologic conditions during a 50-year projection. In the Coosa River, the frequency of spring pulses between 283 and 566 m^3/s was randomly selected from a range of nine to 15 pulses during this five-year period. In the Ocmulgee River, mean March discharge and the mean of low flows during June were held at substandard levels during this five-year period (i.e., mean March discharge held at 453 m^3/s and June low flow held at 41 m^3/s). Hydrologic conditions were varied during the rest of the projection period following the regime outlined in the first projection. We hypothesized that populations would respond to unfavorable conditions by exhibiting substantial declines in population size, but variably recover to previous levels.

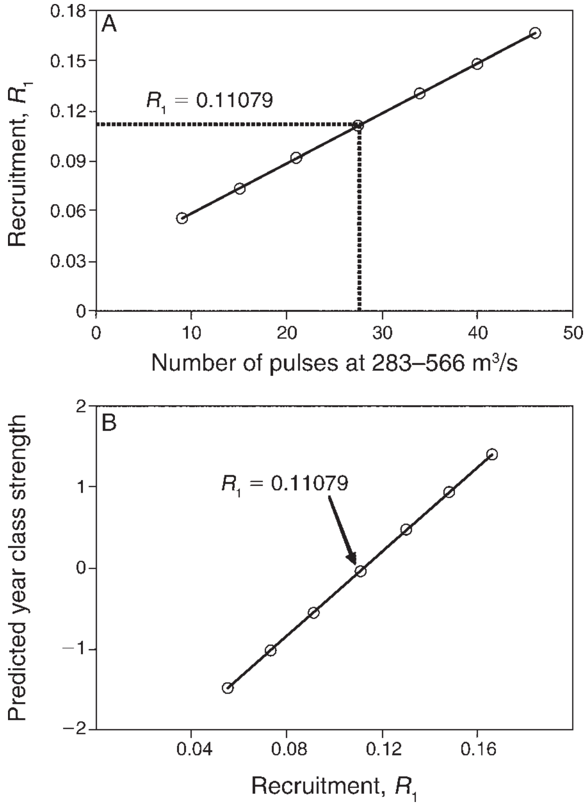

FIG. 2. (A) Recruitment values (R_i) in the transition matrices were modeled to exhibit the same relations observed between year class strength (i.e., residuals) and hydrologic variables. In this example, R_1 from the transition matrix for the Coosa River flathead catfish (*Pylodictis olivaris*) population was modeled over the number of spring pulses between 283 and 566 m^3/s, with the R_1 value (=0.11079) representing mean recruitment at the midpoint of the relation. (B) Relationship between the predicted estimates of year class strength and the modeled R_1 values.

Effects of variable harvest mortality on population dynamics

We also modeled fishing mortality as a stochastic process. Annual survival estimates of "harvestable-sized" fish were expressed 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. For both populations, stochastic projections were conducted by varying instantaneous mortality rates over a 50-year period. At

TABLE 1. Parameters used in the yield-per-recruit model in Fisheries Analyses and Simulation Tools (FAST; Slipke and Maceina 2001) to estimate the lifetime fecundity of a flathead catfish (*Pylodictis olivaris*) cohort in the Coosa (Alabama) and Ocmulgee (Georgia) rivers, USA.

Parameter	Coefficient
Coosa River	
Von Bertalanffy growth model	$L_\infty = 1137$ mm TL; $k = 0.0642$, $t_0 = -0.0255$
$\log_{10}$(Mass) : $\log_{10}$(TL) relation†	$b = 3.17$, $a = -5.409$
C_m	0.163
Maximum age	25
N_0	1000
Ocmulgee River	
Von Bertalanffy growth model	$L_\infty = 1113.5$ mm TL; $k = 0.195$, $t_0 = -0.4$
$\log_{10}$(Mass) : $\log_{10}$(TL) relation†	$b = 3.138$, $a = -5.316$
C_m	0.230
Maximum age	16
N_0	1000

Note: Abbreviations are: L_∞, theoretical maximum length in the population; k, growth coefficient; t_0, time in years when length would theoretically be equal to zero; C_m, conditional natural mortality; TL, total length; N_0, initial population size.

† Relation with mass in grams and TL in millimeters.

each yearly time step, survival estimates for harvestable-sized fish were varied within 10% (i.e., ±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, we 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 0–10% 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., ±10% of the original survival estimate). For the Ocmulgee River population, we 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 0–10% of the original survival estimate each year over a 50-year period.

Elasticity analyses.—We calculated the elasticity (e_{ij}) 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, $\mathbf{v}_i$ was the ith element of the reproductive vector, $\mathbf{w}_j$ was the jth element of the stable stage distribution, and $\langle w,v \rangle$ was the scalar cross-product of the right and left eigenvectors:

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\mathbf{v}_i \mathbf{w}_j}{\langle \mathbf{w}, \mathbf{v} \rangle} = \frac{\partial \log(\lambda)}{\partial \log(a_{ij})}. \tag{13}$$

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.—We 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, assuming that $Z = M$:

$$C_m = 1 - e^{-Z}. \tag{14}$$

Simulations were conducted with 1000 recruits (i.e., $N_0 = 1000$; Table 1).

RESULTS

In the Coosa River, total length and mass of flathead catfish ($N = 799$) ranged from 67 to 1054 mm and from 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 mass of flathead catfish ($N = 136$) ranged from 48 to 1074 mm and from 9 g 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 2023 to 23 208 and from 2386 to 24 105 offspring per female, respectively (Appendix C). Annual survival of 2+ size classes was 84.8% in the Coosa River population ($Z = -0.165$, $r^2 = 0.73$, $P < 0.01$) and 79.7% in the Ocmulgee River population ($Z = -0.227$, $r^2 = 0.88$, $P < 0.01$). In general, probabilities of surviving to the next size class ($M_i S_i$) decreased, while probabilities of remaining in a size class ($(1 - M_i)S_i$) increased from early to late stages (Appendix C). Survival of size class 1 in the Coosa River population ($S_1 = 0.0000548 = 0.00548\%$) was approximately two times higher than survival in the Ocmulgee River population ($S_1 = 0.00252\%$). In addition, 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, 21 871 650 eggs; Coosa River, 8 775 673 eggs).

TABLE 2. Stable stage distributions and reproductive values (proportions) from size-classified matrices constructed for native and introduced flathead catfish (*Pylodictis olivaris*) populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively.

	Stable stage distribution		Reproductive value	
Stage	Coosa River	Ocmulgee River	Coosa River	Ocmulgee River
1	0.999640	0.999876	0.000001	0.000002
2	0.000080	0.000025	0.025696	0.089627
3	0.000067	0.000024	0.033078	0.112455
4	0.000056	0.000022	0.043560	0.139643
5	0.000046	0.000020	0.059133	0.174056
6	0.000036	0.000018	0.075703	0.216503
7	0.000028	0.000015	0.096075	0.267715
8	0.000020		0.120580	
9	0.000014		0.149358	
10	0.000008		0.181926	
11	0.000005		0.214890	

Notes: The stable stage distribution is the proportion of individuals found in each size class (stage). The reproductive value measures the relative reproductive output (or contribution) of each size class.

The Coosa and Ocmulgee river flathead catfish populations exhibited similar patterns in their stable stage distributions and reproductive values from early to late stages (Table 2). In both populations, the final two stages had the highest reproductive values (i.e., fish >850 mm TL; Table 2). 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 (Appendix D).

Estimating recruitment and modeling effects of hydrology

Coosa River population.—A multiple regression model with age and the frequency of spring pulses between 283 and 566 m^3/s as independent variables explained the greatest amount of variation in abundance of flathead catfish in the Coosa River. After accounting for the effects of age on abundance ($r^2 = 0.73$, $P < 0.01$), the frequency of spring pulses between 283 and 566 m^3/s explained an additional 16% of the variation in the multiple regression model ($R^2 = 0.89$, $P < 0.01$; Table 3). This model received the most support in AIC model selection with the lowest ΔAIC_c value (=0) and the highest AIC weight (=0.81; Table 4). Year class strength of flathead catfish was positively related to the frequency of pulses between 283 and 566 m^3/s (Fig. 1), 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.

Ocmulgee River population.—A multiple regression model with age, mean of low flows during June (in cubic meters per second), and mean March discharge (in cubic meters per second) as independent variables explained the greatest amount of variation in abundance of flathead catfish in the Ocmulgee River. After accounting for the effects of age on abundance ($r^2 = 0.88$, $P < 0.01$), mean of low flows during June and mean March discharge explained an additional 9% of the variation in the regression model ($R^2 = 0.97$, $P < 0.01$; Table 5). This regression model received the most support in AIC model selection with the lowest ΔAIC_c value (=0) and the highest AIC weight (=0.76; Table 6). In general, the strongest year classes (1981 and 1988) were exposed to higher June low flows (≥ 72 m^3/s) and lower March discharges (≤ 187 m^3/s), whereas the weakest year classes (1983, 1986, 1991, and 1992) were exposed to very high March discharges (269–453 m^3/s).

In the Ocmulgee River, a pattern was also apparent between year class strength and frequency of pulses greater than 241 m^3/s during spring months (March–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 m^3/s). However, as the number of pulses increased from 11 to 73, we observed a substantial decline in year class strength ($r^2 = 0.56$, $P < 0.01$; Fig. 3). In general, spring discharges appeared to be the most important factor influencing year class strength of flathead catfish in both systems.

TABLE 3. Parameter estimates (mean ± SE) for all highly significant ($P < 0.01$) regression models that were derived to explain variation in abundance of flathead catfish (*Pylodictis olivaris*) in the Coosa River, Alabama.

	Parameter estimate					
Model parameter	β_0 (Intercept)	β_1 (Age)	β_2 (Hydro 1)	β_3 (Hydro 2)	R^2	P
Age	3.756 ± 0.290	−0.165 ± 0.026	···	···	0.729	<0.001
Age, Spring	2.944 ± 0.400	−0.149 ± 0.023	0.0022 ± 0.0008	···	0.817	<0.001
Age, Pulses_283_566	2.599 ± 0.327	−0.159 ± 0.017	0.0393 ± 0.0089	···	0.887	<0.001
Age, LP_N	4.243 ± 0.314	−0.130 ± 0.026	−0.0292 ± 0.0115	···	0.815	<0.001
Age, HP_N	2.958 ± 0.440	−0.153 ± 0.024	0.0626 ± 0.0280	···	0.800	<0.001
Age, 90_d_max	2.915 ± 0.391	−0.152 ± 0.022	0.00088 ± 0.00032	···	0.824	<0.001
Age, High_Rise	4.724 ± 0.383	−0.147 ± 0.021	−0.00823 ± 0.00261	···	0.842	<0.001
Age, LP_N, Nov_lowf	3.613 ± 0.379	−0.133 ± 0.023	−0.0279 ± 0.0100	0.0029 ± 0.0012	0.871	<0.001
Age, LP_N, Reversals	7.527 ± 1.438	−0.133 ± 0.023	−0.0303 ± 0.0100	−0.0180 ± 0.0078	0.869	<0.001

Note: Abbreviations are: Spring, mean spring discharge (m^3/s); Pulses_283_566, frequency of spring pulses between 283 and 566 m^3/s; LP_N, frequency of low pulses within each water year; HP_N, frequency of high pulses within each water year; 90_d_max, annual maxima, 90-day mean (m^3/s); High_Rise, maximum rise rate observed within the water year; Nov_lowf, mean of low flows during November (m^3/s); Reversals, number of times that flow switches between "rising" and "falling" periods.

TABLE 4. Ranking of candidate models, derived for the Coosa River population, Alabama, USA, using corrected Akaike's Information Criterion (AIC$_c$) model selection.

Model parameter	K	AIC$_c$	ΔAIC$_c$	AIC weight
Age, Pulses_283_566	3	−30.924	0.000	0.809
Age, High_Rise	3	−25.267	5.657	0.048
Age, LP_N, Nov_lowf	4	−25.240	5.684	0.047
Age, LP_N, Reversals	4	−25.003	5.921	0.042
Age, 90_d_max	3	−23.435	7.489	0.019
Age, Spring	3	−22.755	8.169	0.014
Age, LP_N	3	−22.577	8.347	0.012
Age, HP_N	3	−21.323	9.601	0.007
Age	2	−19.111	11.813	0.002

Note: See Table 3 for an explanation of model parameter abbreviations.

Effects of hydrologic variation on population dynamics

When the frequency of spring pulses between 283 and 566 m^3/s was incorporated as a stochastic factor influencing the population dynamics of flathead catfish in the Coosa River, population size remained relatively constant (i.e., $\lambda = 0.999$; Fig. 4, projection B). However, short periods of favorable hydrologic conditions occasionally resulted in brief spikes in population size. When the population was modeled to experience five years of favorable conditions, it exhibited a substantial spike in size and increased at an overall 0.2% annual rate ($\lambda = 1.002$; Fig. 4, projection A). When modeled to experience five years of unfavorable hydrologic conditions, the Coosa population initially exhibited a substantial decrease in size, but later stabilized and increased at a 0.4% annual rate following the decline (overall $\lambda = 0.997$; λ after decline = 1.004; Fig. 4, projection C).

When March discharges and June low flows were incorporated as stochastic factors influencing the population dynamics of flathead catfish in the Ocmulgee River, the stochastic growth rate of the population also remained relatively constant ($\lambda = 0.999$; Fig. 4, projection E). When the population was modeled to experience five years of favorable conditions, it exhibited a substantial spike in size and increased at an overall 0.4% annual rate ($\lambda = 1.004$; Fig. 4, projection D). After the population experienced five years of unfavorable conditions, a sharp decline in population size was predicted. However, the population quickly stabilized, after which population size increased at a 0.3% annual rate (overall $\lambda = 0.993$; λ after decline = 1.003; Fig. 4, projection F). In general, stochastic population growth in the Ocmulgee River was more erratic and variable than population growth in the Coosa River (see confidence limits; Fig. 4).

Effects of variable harvest mortality on population dynamics

In the Coosa River population, the incorporation of variable mortality as a stochastic factor resulted in a 0.3% decrease in population growth (stochastic growth rate, $\lambda = 0.997$; Fig. 5, projection B). The stochastic growth rate of the Ocmulgee River population remained constant ($\lambda = 1.000$; Fig. 5, projection C). 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 ($\lambda = 1.009$; Fig. 5, projection A). 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, $\lambda = 0.970$; Fig. 5, projection D).

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 and 566 m^3/s. This finding indicated that an optimal range of discharges enhanced the productivity of flathead catfish in the regulated reach of the Coosa River. Mechanisms underlying relations between discharge and year class strength of flathead catfish probably involved lateral interactions between the river channel and the riparian vegetation. Inundation of the riparian zone likely results 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). Jolley and Irwin (2004) reported that juvenile flathead catfish (<250 mm TL) from the Coosa River fed opportunistically on a wide variety of prey, including insects, crayfish, zooplankton, and fish. In

TABLE 5. Parameter estimates (mean ± SE) for all highly significant ($P < 0.01$) regression models that were derived to explain variation in abundance of flathead catfish (*Pylodictis olivaris*) in the Ocmulgee River, Georgia.

Model parameter	Parameter estimate				R^2	P
	β_0 (Intercept)	β_1 (Age)	β_2 (Hydro 1)	β_3 (Hydro 2)		
Age	3.620 ± 0.234	−0.227 ± 0.023	…	…	0.878	<0.001
Age, Dec	4.036 ± 0.258	−0.233 ± 0.020	−0.0026 ± 0.00102	…	0.920	<0.001
Age, Spring	4.275 ± 0.294	−0.222 ± 0.019	−0.0039 ± 0.0013	…	0.928	<0.001
Age, Dec, June	3.364 ± 0.351	−0.222 ± 0.017	−0.0026 ± 0.00086	0.00723 ± 0.00297	0.948	<0.001
Age, Mar, June	3.474 ± 0.359	−0.229 ± 0.017	−0.0025 ± 0.00078	0.01032 ± 0.00311	0.950	<0.001
Age, Mar, June_lowf	3.280 ± 0.311	−0.230 ± 0.014	−0.0031 ± 0.00070	0.01647 ± 0.00361	0.965	<0.001
Age, Spring, Dec	4.526 ± 0.260	−0.228 ± 0.016	−0.0033 ± 0.0011	−0.0021 ± 0.00081	0.956	<0.001

Note: Abbreviations are: Dec, mean December discharge (m^3/s); Spring, mean spring discharge (m^3/s); June, mean June discharge (m^3/s); Mar, mean March discharge (m^3/s); June_lowf, mean of low flows during June (m^3/s).

TABLE 6. Ranking of candidate models derived for the Ocmulgee River population, Georgia, USA, using corrected Akaike's Information Criterion (AIC_c) model selection.

Model parameter	K	AIC_c	ΔAIC_c	AIC weight
Age, Mar, June_lowf	4	−37.020	0.000	0.761
Age, Spring, Dec	4	−33.336	3.684	0.121
Age, Mar, June	4	−31.451	5.569	0.047
Age, Dec, June	4	−30.997	6.024	0.037
Age, Spring	3	−29.947	7.073	0.022
Age, Dec	3	−28.344	8.676	0.010
Age	2	−25.237	11.783	0.002

Note: See Table 5 for an explanation of model parameter abbreviations.

addition, studies have demonstrated that the channel catfish (*Ictalurus punctatus*), a closely related species, is an opportunistic feeder (with insects and plant material as the most common items; Jolley and Irwin 2004), consuming terrestrial plant foods and insects when they are available (Bailey and Harrison 1948). Therefore, we postulate that increased frequency of spring pulses between 283 and 566 m^3/s led to increased inundation of marginal habitats, which juvenile flathead catfish likely exploited for refuge from predators and alternative sources of prey. While moderately high discharges may enhance recruitment via riparian inundation, excessively high flows may have detrimental effects on catfish recruitment. For example, Holland-Bartels and Duval (1988) attributed a decrease in age 0 channel catfish abundance in the Mississippi River to a sharp increase in river discharge that likely disrupted spawning activity and flushed young from nests. Increased recruitment at intermediate discharges is a general pattern that has been demonstrated for species other than catfish (Rulifson and Manooch 1990, Lobon-Cervia and Rincon 2004, Grossman et al. 2006).

Based on this information, managers could prescribe a spring flow regime that would 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, we suspect that high spring pulses (283–566 m^3/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 (e.g., Propst and Gido 2004).

In the Ocmulgee River, the strongest year classes were exposed to higher June low flows (≥ 72 m^3/s) and lower March discharges (≤ 187 m^3/s), and the weakest year classes were exposed to very high March discharges (269–453 m^3/s). Therefore, optimal mean spring discharges for age 0 fish production probably range from ~72 to 187 m^3/s in this system. However, our results also indicated that ~11–21 high spring pulses >241 m^3/s were positively associated with 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).

When high pulses occurred too frequently in the Ocmulgee River, high flow variation and fall rates appeared to negatively affect recruitment. A comparison of spring hydrographs between low- and high-recruitment years revealed that moderate discharges with several smooth peaks in flow (>241 m^3/s) appeared to positively influence flathead catfish recruitment in the Ocmulgee River system (Fig. 6). Based on these findings, 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 (Fig. 6). Low and stable flows would theoretically result in minimal riparian and floodplain inundation, and extremely high fall rates would result in extensive changes in habitat availability and potentially strand age 0 flathead catfish in floodplains.

Survival of age 0 flathead catfish in the introduced population was lower than survival of age 0 fish in the native population. Because flathead catfish in the Ocmulgee River grew more rapidly than fish in the Coosa River (Sakaris et al. 2006), they probably matured earlier and produced more offspring than slow-growing fish in the Coosa River. In addition, simulations 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, we hypothesize that age 0 survival was influenced by density-dependent mecha-

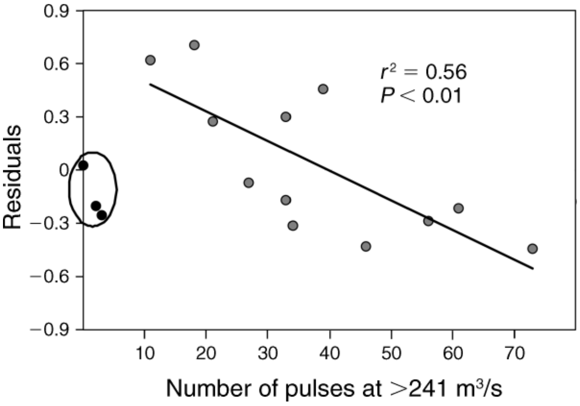

FIG. 3. Relation between residuals from catch-curve analysis (i.e., estimates of year class strength) and the number of spring pulses greater than 241 m^3/s in the Ocmulgee River, Georgia, USA. When less than four pulses greater than 241 m^3/s occurred, year class strength was relatively weak. However, a strong, negative relation was apparent between year class strength and the number of pulses >241 m^3/s (from 11 to 73 pulses).

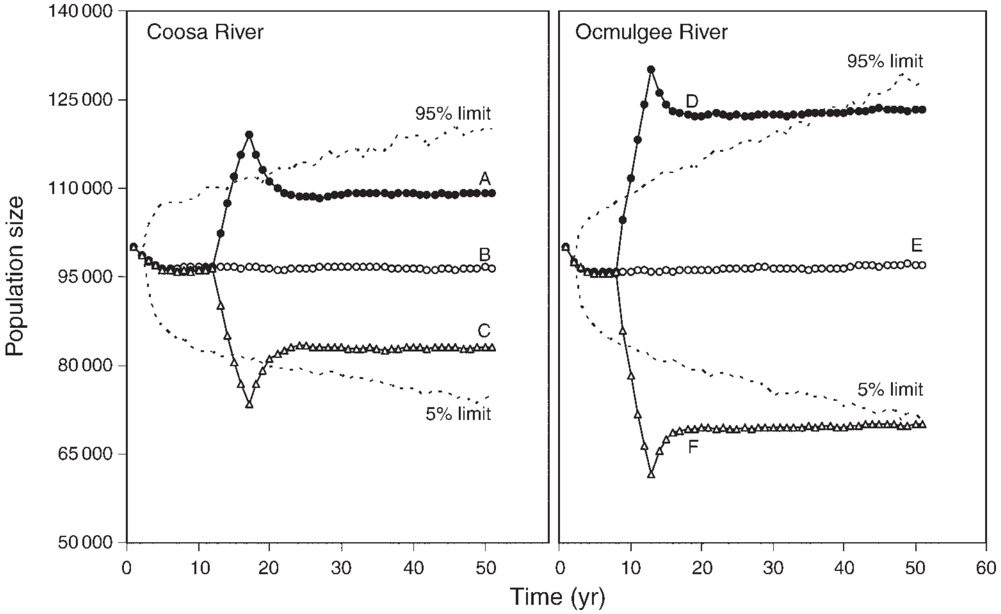

FIG. 4. Flathead catfish (*Pylodictis olivaris*) populations were projected 1000 times over 50-year periods with hydrologic variation modeled as a stochastic factor influencing recruitment in the Coosa (projections A–C) and Ocmulgee (projections D–F) rivers. Three scenarios were modeled: (1) five consecutive years of favorable hydrologic conditions (projections A and D); (2) annual variation in hydrology (projections B and E); and (3) five consecutive years of unfavorable hydrologic conditions (projections C and F). The number of spring pulses between 283 and 566 m^3/s was modeled as the stochastic factor in the Coosa River. June low flows and March discharges were modeled as stochastic factors in the Ocmulgee River. Upper (95%) and lower (5%) confidence limits were provided for projections B and E. In general, population projections were more variable for the Ocmulgee River population, as indicated by the wider confidence limits.

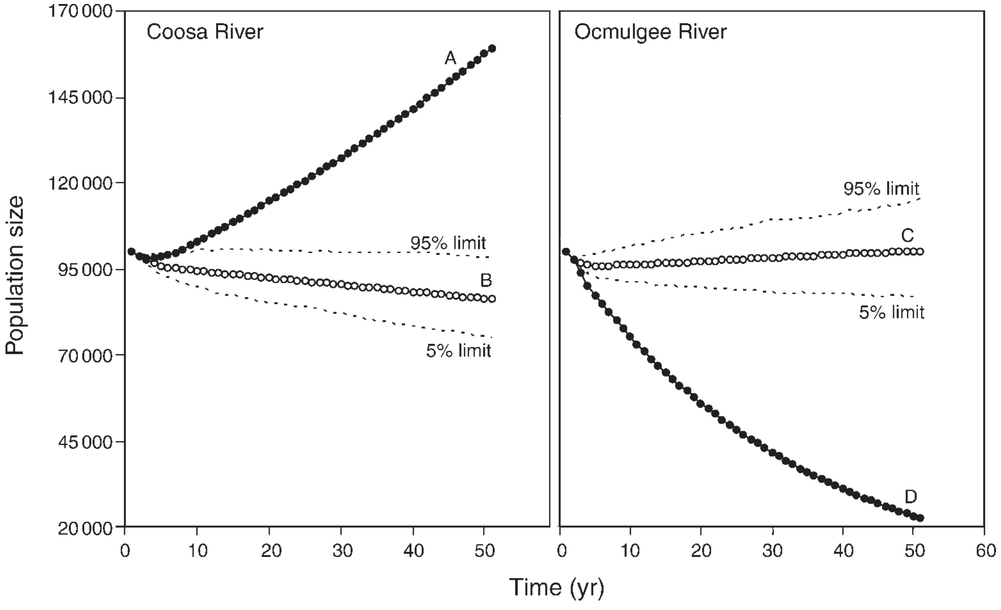

FIG. 5. Flathead catfish (*Pylodictis olivaris*) populations were projected 1000 times over 50-year periods with variable harvest mortality modeled as a stochastic factor influencing recruitment in the Coosa (projection B) and Ocmulgee (projection C) rivers. At each yearly time step, survival estimates for harvestable-sized fish were varied within 10% (i.e., ±10%) of the original survival estimates. For the Coosa River population, the implementation of a slot limit was simulated by protecting flathead catfish in size classes with the highest reproductive values (projection A). For the Ocmulgee River population, the effects of increased fishing mortality on the population across all harvestable-sized fish was simulated (projection D). Upper (95%) and lower (5%) confidence limits were provided for projections B and C.

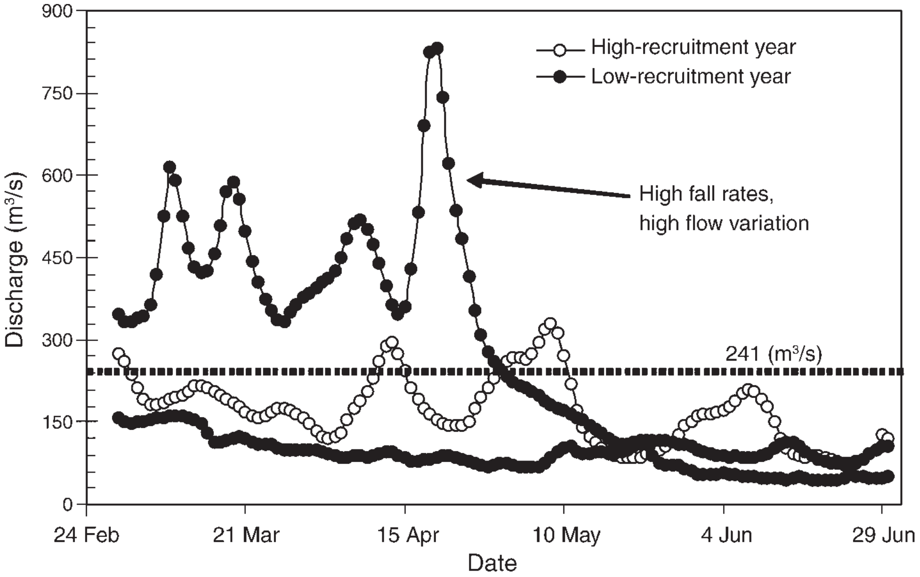

FIG. 6. Spring hydrographs during a high-recruitment year (open symbols) and two low-recruitment years (solid symbols) in the Ocmulgee River, Georgia.

nisms in the Ocmulgee River (i.e., increased mortality as a result of crowding). Jolley and Irwin (2004) reported that flathead catfish comprised ~22.5% (by mass) 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 models that incorporated five consecutive years of favorable hydrologic conditions indicated that the Coosa River population would positively respond to an increased frequency of spring pulses between 283 and 566 m^3/s. Prescription of these hydrologic conditions in spring could possibly improve flathead catfish productivity in the Coosa River system. Although these manipulated flow conditions may not naturally occur in unregulated systems, these conditions could be prescribed on a regular basis in a regulated system.

The Ocmulgee River population exhibited substantial spikes in size and grew at a faster rate than the Coosa population when 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 1970s (Thomas 1993). Both populations exhibited great resiliency when exposed to unfavorable hydrologic conditions. Although both populations decreased in size, they both stabilized and increased in size following their exposure to unfavorable hydrologic conditions.

In general, the Ocmulgee River population appeared to have a higher capacity for growth than the Coosa River population, which was reflected in their respective stochastic growth rates when exposed to favorable hydrologic conditions (Coosa, $\lambda = 1.002$; Ocmulgee, $\lambda = 1.004$). Differences in life history characteristics between the populations support this assertion. Flathead catfish in the Coosa River population had greater longevity (maximum age 25 yr), but grew more slowly (K, growth coefficient = 0.0642) than catfish in the Ocmulgee River (maximum age = 16 yr; $K = 0.195$; Sakaris et al. 2006). As a result, flathead catfish probably did not reach maturity until they were at least 7 yr old in the Coosa River. Munger et al. (1994) reported that 50% of flathead catfish reached sexual maturity at 390 mm TL. Consequently, at least 7 yr were required for stronger year classes to contribute reproductively to the Coosa River population. In contrast, Ocmulgee River fish would reach maturity and potentially contribute reproductively to the population only after 2 yr post-hatch.

Flathead catfish are highly sought after by anglers, especially in the Southeast and Midwest United States and have traditionally been an important commercial species (see review of flathead catfish fisheries and management; Jackson 1999). In general, flathead catfish angling has increased in overall popularity (Jackson 1999); thus, proper management of native flathead catfish populations should be implemented to maintain viable recreational fisheries. For example, management for improving survival of large flathead catfish could involve the implementation of slot and bag limits. The stationary stage distribution for the Coosa River population revealed that large flathead catfish (>804 mm TL) comprised a very low proportion of fish in the system, indicating that fish with the highest reproductive values were least abundant. When the implementation of

PLATE 1. Thurlow Dam (on the Tallapoosa River, Alabama, USA) when flows exceeded dam capacity. Photo credit: E. R. Irwin.

a slot limit was modeled to protect these fish in the Coosa River, the population responded by increasing in size at a 0.9% rate. Therefore, protection of reproductively valuable flathead catfish is predicted to enhance population status in the Coosa River.

In the Ocmulgee River, the introduction of flathead catfish 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 system, we predicted that a substantial reduction in population size would be observed over a 50-year period. Hypothetically, increased harvest of flathead catfish would reduce predation on other fishes (e.g., redbreast sunfish) and thereby increase their potential for reestablishment in the system.

In this paper, we presented an approach that incorporates hydrologic variation into size-classified matrix models to predict how fish populations respond to variable hydrologic conditions and other factors, such as variable mortality, in regulated river systems. These models are particularly valuable in prescribing flow regimes in adaptive flow management programs. Successful management of fish populations in regulated systems requires that we have an understanding and ability to predict how the manipulation of hydrology affects recruitment and ultimately influences the population dynamics of fishes. We encourage ecologists to develop similar models for other lotic species, particularly in regulated river systems.

Future studies should incorporate density dependence as a demographic factor influencing the dynamics of these populations. Little information exists regarding density-dependent survival of age 0 flathead catfish, which may be an important factor in population regulation. As more information is collected regarding these populations (e.g., population-specific fecundity estimates and evaluation of density dependence and size-specific survival), the models presented here can be improved and used to better predict population responses to hydrologic variation. Fine-tuning of models is inherent in the adaptive management process, as uncertainty about a system is reduced over time. For example, recruitment should be estimated on an annual basis during routine sampling surveys, providing more accurate estimates of year class strength than those provided by catch-curve analysis. Size-specific survival rates can also be estimated by mark–recapture techniques. Finally, habitat features other than hydrologic variables should be evaluated and their effects on recruitment and overall population dynamics should also be assessed. 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*. Persistence of these habitats may decrease in highly regulated systems (Bowen et al. 1998), thereby negatively influencing the recruitment of catfishes.

Acknowledgments

We thank Alabama Cooperative Fish and Wildlife Research Unit personnel for their assistance with fish collection and processing. We thank the Georgia Department of Natural Resources for collecting flathead catfish from the Ocmulgee River. F. S. Dobson, M. C. Freeman, and M. J. Maceina provided critical reviews of the manuscript. This research was partly funded by the Alabama Department of Conservation and Natural Resources. The cooperators of the Alabama Cooperative Fish and Wildlife Research Unit are: the U.S. Geological Survey; Alabama Agricultural Experiment Station, Auburn University; Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries; the Wildlife Management Institute; and the U.S. Fish and Wildlife Service.

Literature Cited

Bailey, R. M., and H. M. Harrison. 1948. Food habits of the southern channel catfish (*Ictalurus punctatus*) in the Des Moines River, Iowa. Transactions of the American Fisheries Society 75:110–138.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124:857–872.

Bonvechio, T. F., and M. S. Allen. 2005. Relations between hydrological variables and year-class strength of sportfish in eight Florida waterbodies. Hydrobiologia 532:193–207.

Boschung, H. T., and R. L. Mayden. 2004. Fishes of Alabama. Smithsonian Books, Washington, D.C., USA.

Bowen, Z. H., M. C. Freeman, and K. D. Bovee. 1998. Evaluation of generalized habitat criteria for assessing impacts of altered flow regimes on warmwater fishes. Transactions of the American Fisheries Society 127:455–468.

Buckland, S. T., K. B. Newman, C. Fernández, L. Thomas, and J. Harwood. 2007. Embedding population dynamics models in inference. Statistical Science 22:44–58.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer, Sunderland, Massachusetts, USA.

Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. North American Journal of Fisheries Management 5:330–339.

Dobbins, D. A., R. L. Cailteux, and J. J. Nordhaus. 1999. Flathead catfish abundance and movement in the Apalachicola River, Florida. American Fisheries Society Symposium 24:199–201.

Freeman, M. C., Z. H. Bowen, K. D. Bovee, and E. R. Irwin. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological Applications 11: 179–190.

Freeman, M. C., E. R. Irwin, N. M. Burkhead, B. J. Freeman, and H. L. Bart, Jr. 2004. Status and conservation of the fish fauna of the Alabama River system. American Fisheries Society Symposium 45:557–585.

Gillette, D. P., J. S. Tiemann, D. R. Edds, and M. L. Wildhaber. 2005. Spatiotemporal patterns of fish assemblage structure in a river impounded by low-head dams. Copeia 2005:539–549.

Gotelli, N. J. 2001. A primer of ecology. Third edition. Sinauer, Sunderland, Massachusetts, USA.

Grossman, G. D., R. E. Ratajczak, J. T. Petty, M. D. Hunter, J. T. Peterson, and G. Grenouillet. 2006. Population dynamics of mottled sculpin (Pisces) in a variable environment: information theoretic approaches. Ecological Monographs 76:217–234.

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

Holland-Bartels, L. E., and M. C. Duval. 1988. Variations in abundance of young-of-the-year channel catfish in a navigation pool of the Upper Mississippi River. Transactions of the American Fisheries Society 117:202–208.

Hood, G. M. 2006. PopTools. Version 2.7.5. ⟨http://www.cse.csiro.au/poptools⟩

Irwin, E. R., and M. C. Freeman. 2002. Proposal for adaptive management to conserve biotic integrity in a regulated segment of the Tallapoosa River, Alabama, U.S.A. Conservation Biology 16:1212–1222.

Irwin, E. R., M. C. Freeman, and K. M. Costley. 1999. Habitat use by juvenile channel catfish and flathead catfish in lotic systems in Alabama. Pages 223–230 *in* E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. Catfish 2000: proceedings of the International Ictalurid Symposium. Symposium 24. American Fisheries Society, Bethesda, Maryland, USA.

Jackson, D. C. 1999. Flathead catfish: biology, fisheries, and management. Pages 23–25 *in* E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. Catfish 2000: proceedings of the International Ictalurid Symposium. Symposium 24. American Fisheries Society, Bethesda, Maryland, USA.

Jolley, J. C., and E. R. Irwin. 2004. Food habits of catfishes in tailwater and reservoir habitats in a section of the Coosa River, Alabama. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 57:124–140.

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

Landahl, J. T., L. L. Johnson, J. E. Stein, T. C. Collier, and U. Varanasi. 1997. Approaches for determining the effects of pollution on fish populations in the Puget Sound. Transactions of the American Fisheries Society 126:519–535.

Lobon-Cervia, J., and P. A. Rincon. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. Oikos 105:641–646.

Maceina, M. J. 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. Fisheries Research 32:115–121.

Maceina, M. J. 2003. Verification of the influence of hydrologic factors on crappie recruitment in Alabama reservoirs. North American Fisheries Management 23:470–480.

Maceina, M. J., and M. C. Stimpert. 1998. Relations between reservoir hydrology and crappie recruitment in Alabama. North American Journal of Fisheries Management 18:104–113.

Minckley, W. L., and J. E. Deacon. 1959. Biology of the flathead catfish in Kansas. Transactions of the American Fisheries Society 88:344–355.

Montgomery, D. C., E. A. Peck, and G. G. Vining. 2001. Introduction to linear regression analysis. Third edition. John Wiley and Sons, New York, New York, USA.

Munger, C. R., G. R. Wilde, and B. J. Follis. 1994. Flathead catfish age and size at maturation in Texas. North American Journal of Fisheries Management 14:403–408.

Paragamian, V. L. 2002. Changes in the species composition of the fish community in a reach of the Kootenai River, Idaho, after construction of Libby Dam. Journal of Freshwater Ecology 17:375–383.

Perry, W. G., and D. C. Carver. 1977. Length at maturity, total-collarbone length, and dressout for flathead catfish and length at maturity of blue catfish, southwest Louisiana. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 31:529–537.

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

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical–temperate comparisons. BioScience 50:807–823.

Propst, D. L., and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society 133:922–931.

Quinn, J. W., and T. J. Kwak. 2003. Fish assemblage changes in an Ozark river after impoundment: a long-term perspective. Transactions of the American Fisheries Society 132:110–119.

Quinn, S. P. 1987. Stomach contents of flathead catfish in the Flint River, Georgia. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 41:85–92.

Quist, M. C., and C. S. Guy. 1998. Population characteristics of channel catfish from the Kansas River, Kansas. Journal of Freshwater Ecology 13:351–359.

Rulifson, R. A., and C. S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10:397–407.

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

SAS. 2003. SAS/STAT user's guide. Version 8. SAS Institute, Cary, North Carolina, USA.

Slipke, J. W., and M. J. Maceina. 2001. Fishery analyses and simulation tools (FAST 2.0). Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama, USA.

Thomas, M. E. 1993. Monitoring the effects of introduced flathead catfish on sport fish populations in the Altamaha River, Georgia. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 47:531–538.

Welcomme, R. L. 1979. Fisheries ecology in floodplain rivers. Longman, New York, New York, USA.

Weller, R. R., and C. Robbins. 1999. Food habits of flathead catfish in the Altamaha River System, Georgia. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 53:35–41.

Wunderlich, R. C., B. D. Winter, and J. H. Meyer. 1994. Restoration of the Elwha River ecosystem. Fisheries 19:11–19.

APPENDIX A

Structure of size-classified transition matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively (*Ecological Archives* A020-014-A1).

APPENDIX B

Modified structure of transition matrices constructed for stochastically varying recruitment as a function of variable hydrologic conditions (*Ecological Archives* A020-014-A2).

APPENDIX C

Transition matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively (*Ecological Archives* A020-014-A3).

APPENDIX D

Elasticities of matrix elements in matrices constructed for native and introduced flathead catfish populations from the Coosa (Alabama) and Ocmulgee (Georgia) rivers, respectively (*Ecological Archives* A020-014-A4).