Ecological Applications, 11(1), 2001, pp. 179–190
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FLOW AND HABITAT EFFECTS ON JUVENILE FISH ABUNDANCE IN NATURAL AND ALTERED FLOW REGIMES

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Abstract. Conserving biological resources native to large river systems increasingly depends on how flow-regulated segments of these rivers are managed. Improving management will require a better understanding of linkages between river biota and temporal variability of flow and instream habitat. However, few studies have quantified responses of native fish populations to multiyear (>2 yr) patterns of hydrologic or habitat variability in flow-regulated systems. To provide these data, we quantified young-of-year (YOY) fish abundance during four years in relation to hydrologic and habitat variability in two segments of the Tallapoosa River in the southeastern United States. One segment had an unregulated flow regime, whereas the other was flow-regulated by a peak-load generating hydropower dam. We sampled fishes annually and explored how continuously recorded flow data and physical habitat simulation models (PHABSIM) for spring (April–June) and summer (July–August) preceding each sample explained fish abundances. Patterns of YOY abundance in relation to habitat availability (median area) and habitat persistence (longest period with habitat area continuously above the long-term median area) differed between unregulated and flow-regulated sites. At the unregulated site, YOY abundances were most frequently correlated with availability of shallow-slow habitat in summer (10 species) and persistence of shallow-slow and shallow-fast habitat in spring (nine species). Additionally, abundances were negatively correlated with 1-h maximum flow in summer (five species). At the flow-regulated site, YOY abundances were more frequently correlated with persistence of shallow-water habitats (four species in spring; six species in summer) than with habitat availability or magnitude of flow extremes. The associations of YOY with habitat persistence at the flow-regulated site corresponded to the effects of flow regulation on habitat patterns. Flow regulation reduced median flows during spring and summer, which resulted in median availability of shallow-water habitats comparable to the unregulated site. However, habitat persistence was severely reduced by flow fluctuations resulting from pulsed water releases for peak-load power generation. Habitat persistence, comparable to levels in the unregulated site, only occurred during summer when low rainfall or other factors occasionally curtailed power generation. As a consequence, summer-spawning species numerically dominated the fish assemblage at the flow-regulated site; five of six spring-spawning species occurring at both study sites were significantly less abundant at the flow-regulated site. Persistence of native fishes in flow-regulated systems depends, in part, on the seasonal occurrence of stable habitat conditions that facilitate reproduction and YOY survival.

Key words: flow regulation; habitat stability; hydrologic alteration; instream habitat; juvenile fish; PHABSIM; riverine fishes; southeastern U.S. river; Tallapoosa River.

INTRODUCTION

Conserving biological resources native to large river systems increasingly depends on how flow-regulated segments of these rivers are managed. Extensive damming worldwide continues to fragment river systems (Benke 1990, Dudgeon 1992, Dynesius and Nilsson 1994, McCully 1996), often leaving flow-regulated segments as the only available habitat for large-river faunal communities incapable of persisting in impounded waters. Managing streamflows in these segments can become a critical element in conserving or restoring riverine fisheries (e.g., *Morone saxatilis* in the Roanoke River; Rulifson and Manooch [1990]), endangered species (e.g., endemic fishes in the upper Colorado River Basin; Tyus [1992], Stanford [1994]), or more generally, the ecological integrity of flow-regulated reaches (Orth 1987, Petts 1989, Hesse and Mestl 1993, Poff et al. 1997). Contention over flow regime management arises, not only from competition among water uses (Stalnaker et al. 1995), but also from the difficulty of specifying flow requirements that will pro-

Manuscript received 4 May 1999; revised 7 January 2000; accepted 10 January 2000.

tect ecological integrity in these variable and complex systems (Orth 1987, Stanford 1994, Richter et al. 1997).

Hydropower dams affect flow regimes in rivers worldwide (McCully 1996) and pose major challenges relative to conservation of native riverine biota. These dams not only fragment river systems, but also alter downstream flow regimes and extant river fauna (Cushman 1985, Bain et al. 1988, Kinsolving and Bain 1993, Travnichek et al. 1995, Schmidt et al. 1998). Hydropower dams operated for peak-load power generation impose frequent (often daily) flow fluctuations equivalent to storm-runoff events in natural systems, as well as altering seasonal flows. Ecologists have argued that flow-regulated rivers should be managed to mimic as closely as possible the pre-impact patterns of flow (Hesse and Mestl 1993, Stanford et al. 1996, Poff et al. 1997, Richter et al. 1997) or instream habitat (Nestler et al. 1993). However, approximating all aspects of natural flow or habitat patterns in rivers regulated by peak-load hydropower dams clearly is confounded by the short-term fluctuations inherent in peak-load operations.

In this study we analyzed annual variation in juvenile fish abundances in relation to habitat availability and flow extremes in flow-regulated and unregulated segments of a southeast U.S. river system. Several studies have examined population responses by lotic fishes to natural levels of environmental variability (Nehring and Anderson 1993, Bovee et al. 1994, Grossman et al. 1998, Mion et al. 1998). However, fewer studies (e.g., Rulifson and Manooch 1990) have quantified fish population responses to multiyear (>2 yr) patterns of hydrologic or habitat variability in flow-regulated systems and particularly not in species-rich rivers of the southeastern United States. Hydropower has been extensively developed in the southeastern United States, a global center of temperate freshwater fish and invertebrate diversity (Lydeard and Mayden 1995). We sought to identify flow or habitat features that affect the persistence of native fishes in a river segment that was strongly hydrologically altered by operations of a hydropower dam. We focused on juvenile abundance because hydrologic and habitat variation can strongly affect reproductive success or juvenile survival in lotic fish populations (Starrett 1951, Schlosser 1985, Rulifson and Manooch 1990, Nehring and Anderson 1993, Mion et al. 1998). Consequently, increased early mortality represents a major potential limitation to fish populations in flow-altered rivers.

Our study tested a hypothesis that extended periods of stable instream habitat conditions can facilitate reproduction by native fishes in a strongly flow-regulated river (Bowen et al. 1998). We sampled fishes at two sites, one strongly flow-regulated by an upstream hydropower dam and one with an unregulated flow regime, in the Tallapoosa River, Alabama. Our samples lengthened data collection begun by Bowen et al. (1998) to four years of site-specific fish abundance estimates. We used continuously recorded discharge data and physical habitat simulation (PHABSIM; Milhous et al.1989) models to quantify temporal availability of habitat types of known importance to the fish fauna (Bain 1995, Freeman et al. 1997, Bowen et al. 1998). We then tested for correlations between young-of-year (YOY) fish abundances and antecedent habitat conditions in years that differed in hydrologic regime. We predicted that YOY abundances would be positively correlated with the occurrence of extended periods of stable instream habitat conditions. We also used PHABSIM models together with hydrologic records to compare habitat conditions between the flow-regulated and unregulated sites. Finally, we tested whether common fishes differed in abundances between sites. We specifically examined whether fishes that spawned in spring or summer were more abundant in the flow-regulated site, which would link seasonal differences in hydrologic alteration to effects on fish assemblage structure. We end by suggesting management options that would benefit native fishes in flow-regulated systems.

Methods

Study sites

The Piedmont portion of the mainstem Tallapoosa River includes a 143-km unregulated segment and a 78-km flow-regulated segment downstream from Harris Dam, a hydropeaking facility completed in 1983 (Fig. 1). During power generation at Harris Dam, water passes through one or two turbines each capable of discharging 226 m^3/s. During nongeneration, the facility is required to maintain a discharge of at least 1.27 m^3/s (lowest recorded pre-dam daily flow) as measured at a gage 22 km downstream from the dam. The dam normally releases water for power generation once or twice a day, Monday through Friday. At least 60 native fish species may inhabit this portion of the Tallapoosa River (Mettee et al. 1996).

We sampled fishes and monitored flows and habitat in one regulated and one unregulated reach of the mainstem Tallapoosa River. Within these two areas, study sites were chosen to allow for (1) accessibility, (2) proximity to flow gages, and (3) continuation of long-term data collection (Travnichek and Maceina 1994, Bowen et al. 1998). The flow-regulated site was ~20 km downstream from Harris Dam, at river km 199.7 to 203.8 (U.S. Army Corp of Engineers, Mobile District, Alabama–Mississippi stream mileage tables) in Randolph County, Alabama. Drainage area above the site was ~4,336 km^2; riparian areas typically were forested, although occasionally riparian zones were narrow, bordered by agricultural fields. The channel averaged 108 m wide, with an average gradient of 0.5 m/km. Instream habitat was diverse, composed of extensive riffles with gravel- to boulder-sized substrata and

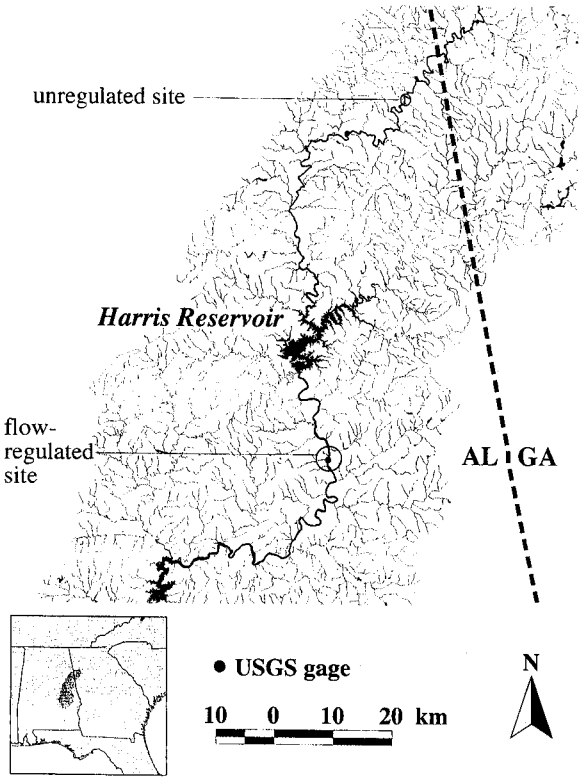

FIG. 1. Map of the study area in the Tallapoosa River, Alabama, USA, showing locations of study sites (open circles) and USGS gages (filled circles) in relation to Harris Reservoir. The dashed line represents the state boundary between Alabama (AL) and Georgia (GA). Data for the upstream gage (station 02412000) were scaled to drainage area for the unregulated site; data for the downstream gage (station 02414500) were used directly to quantify flows at the flow-regulated site.

fringing patches of emergent macrophytes (*Justicia* spp.), woody debris along channel margins, and deep mid-channel pools with sand to bedrock substrata.

The unregulated study site was ~53 km upstream from Harris Reservoir, at river km 324.6 to 327.4 in Cleburne County, Alabama. No mainstem impoundments were upstream of the unregulated site. Drainage area upstream from the site was ~997 km^2; riparian areas typically were forested, although logging in the upper half of the site reduced forest cover to a narrow fringe of trees on one side of the stream. The river channel averaged ~36 m in width, and was characterized by alternating riffle, run, and pool habitats with an average gradient of 0.3 m/km. Woody debris commonly occurred along stream margins; emergent macrophytes (*Justicia* spp.) occurred in patches near riffles.

Fish sampling

We sampled fishes during the summers of 1994 through 1997 (see also Bowen et al. 1998). Sampling dates were 23–24 June and 21–22 July 1994, 15–16 August 1995, 10–11 September 1996 and 2–3 September 1997 at the unregulated site, and 3–8 August 1994, 29–30 August 1995 and 18–19 September 1996, and 14–15 September 1997 at the flow-regulated site. We sampled using prepositioned area electrofishers (PAEs; Bain et al. 1985, Travnichek and Maceina 1994, Bowen et al. 1998). PAEs were constructed of two 6-m long electrodes, separated by 1.5 m, and remotely powered with alternating current by a 3500 W generator and pulsator unit (Smith-Root 3.5 GPP; Smith-Root, Vancouver, Washington, USA). The generated electrical field was concentrated between the electrodes; consistently low (<55 μS/cm) water conductivity at our study sites minimized variability in sampling efficiency (Bowen et al. 1998). To collect a sample, a PAE was placed on the streambed, left undisturbed for at least 15 min, and then energized for 20 s while two persons netted fish with dip nets (in low-velocity areas) or held a seine downstream from the PAE to collect floating fishes. A 20-s pulse was sufficient to stun fishes within the sampled area. A person kicking downstream through the sampled area toward the seine also dislodged fishes from the substrata. At each site we collected 100 PAE samples every year, except in 1997 at the flow-regulated site, where we collected only 91 samples. Previous analysis revealed that increasing effort beyond 90–100 samples was unlikely to increase species richness values; ~60 PAE samples typically collected at least 90% of the observed species richness (Bowen and Freeman 1998). We sampled within similar areas (riffles and accessible runs and pools) each year, where we haphazardly deployed PAEs throughout available habitats up to ~1.5 m in depth. Fishes collected were identified, counted, and measured (total length [TL] in millimeters) in the laboratory.

Hydrologic and habitat analyses

We used hourly streamflow data recorded at two gages by the U. S. Geological Survey (Pearman et al. 1998; Fig. 1) to describe hydrologic regimes at both sites for 1994–1997. We used hourly flow data in order to include flow variations caused by hydropeaking at Harris Dam and storms at the unregulated site. To place flow regimes during this study in the context of naturally occurring variation, we computed seasonal median and 1-d maximum flows from historical daily mean discharge data (long-term hourly data were not available). Daily mean flow data for the unregulated site spanned 1952 through 1997; for the flow-regulated site we used data for 1924 through 1967, the years preceding initial construction activities for Harris Reservoir (i.e., predam).

To quantify relative instream habitat availability for fishes, we used the PHABSIM programs (Milhous et al. 1989) to compute habitat availability in relation to stream discharge (Bowen et al. 1998). PHABSIM and similar models have been used widely to examine physical habitat-flow relations and are built on field measurements of channel shape, substrate characteristics,

and stage–discharge relations. We used standard survey procedures to describe channel cross-section profiles for use in hydraulic simulation (Bovee and Milhous 1978). At each site, we measured streambed elevation (or depth) and average water column velocity, and visually estimated dominant substratum type and the presence of cover (e.g., woody debris, boulders) at intervals of 1.5 m (unregulated site) or 3.0 m (flow-regulated site) along channel cross-sections. We surveyed habitat at 31 cross-sections placed every 91 m in the unregulated site and at 22 cross-sections placed every 183 m in the regulated site. PHABSIM models are sensitive to cross-section number and placement (Williams 1996). Preliminary habitat mapping revealed that these cross-section spacings would adequately represent riffles, runs, and pools in the study sections (Bowen et al. 1998). We also surveyed streambed cross-sections at all hydraulic controls and measured water surface elevations at two or more discharges as input to the hydraulic simulation programs. We calibrated the hydraulic models by using one or more of the procedures available in PHABSIM (WSP, MANSQ, and IFG4) to establish stage–discharge relations, and IFG4 to calibrate for water velocities (Bowen et al. 1998). Using calibrated PHABSIM models for each site, we simulated water depths and average velocities at 1.5 or 3 m intervals along cross-sections over a range of discharges. For each discharge, hydraulic simulations were used to compute the area coverage of three of the five key fish habitats originally modeled by Bowen et al. (1998). These three key habitats, (1) shallow-fast, ≤35 cm deep and velocity ≥55 cm/s; (2) deep-fast, >35 cm deep and velocity >45 cm/s; and (3) shallow-slow, <35 cm deep and velocity <35 cm/s, represented habitats correlated with fish abundances in the Tallapoosa system (Bowen et al. 1998).

We used the habitat-flow relations estimated from PHABSIM models at each site to translate stream discharge through time into habitat conditions through time. We computed habitat patterns during spring (1 April–30 June) and summer (1 July–31 August, or through the day before we sampled fishes if before 31 August) of each year, 1994–1997, to estimate habitat conditions potentially affecting YOY fish abundances. Seasons thus defined represented the typical reproductive period for spring-spawning fishes (April–June) and the period additionally available for reproduction by fishes with more prolonged spawning periods (July–August), as well as for juvenile growth of all fishes.

We quantified two aspects of habitat, availability, and persistence. We defined availability as the median area (expressed as square meters per 305 m of stream length) of a key habitat present during a season. We computed habitat persistence as the maximum time that the area of a key habitat type continuously exceeded the seasonal (either spring or summer) long-term median area (Bowen et al. 1998). We used daily flows for the entire period of record for the unregulated site and the pre-dam period for the flow-regulated site to compute long-term habitat medians. Using the PHABSIM models to describe pre-dam habitat availability required the assumption that channel morphology measured during the post-dam period accurately reflected pre-dam conditions. The nature of the Tallapoosa River channel, with extensive bedrock substrata resistant to degradation, and the placement of the study site ≥20 km downstream from the dam supported the assumption of relative channel stability at the study site between pre- and post-dam periods. Additionally, the stage-discharge rating for a U.S. Geological Survey (USGS) gage located at the study site had remained stable for almost 75 yr, including the post-dam period (J. L. Pearman, *personal communication*), providing further evidence of channel stability.

Data analysis

Young-of-year were defined as individuals smaller than length thresholds derived from published length-at-age data or by inspection of length-frequency distributions in our samples and those collected in 1990 through 1992 (V. Travnichek, *unpublished data*). Length-frequency data for most species were distinctly multimodal when YOY were present, with one peak clearly corresponding to YOY. Although some individuals near the length thresholds could be incorrectly designated either YOY or older, this error was small relative to total numbers. Numbers of YOY for each species in each sample were ln-transformed to improve normality and homoscedasticity before analyses. For species with ≥10 YOY in at least 1 yr, we used ANOVA and Tukey-Kramer multiple comparisons (experiment-wise alpha = 0.05; SAS 1989) to test for among-year differences in YOY abundances. We did not analyze YOY abundances for *Ictalurus punctatus* because diel movements to shallow-water habitats by juveniles (Costley 1998) may have biased our estimates for *Ictalurus* YOY. Juveniles of most other Tallapoosa fishes do not shift among habitats between day and night (Costley 1998; E. Irwin, *unpublished data*).

For species with significant among-year YOY differences, we tested for significant correlations between YOY abundances (expressed as geometric mean number per sample in each year) and (1) 1-h maximum and minimum flows, (2) median availability of each key habitat, and (3) persistence of each key habitat, during spring and summer. We tested correlations for spring and summer separately to evaluate effects of differential timing of flow and habitat conditions on subsequent YOY abundances. For the unregulated site, we additionally tested YOY correlations with the lowest 7-d flow in each season, to reflect chronic habitat limitation. For the flow-regulated site, we only examined 1-h maximum and minimum flows because flows averaged for ≥1 d masked much larger hourly flow fluctuations imposed by hydropeaking at the dam. Finally, to examine patterns of covariation among influential

habitat and flow variables, and their joint relation to YOY, we applied principal component analysis (PCA) to the correlation matrix of the three variables exhibiting the most correlations with YOY abundances. We then tested for significant correlations between YOY abundance for each species and the PCA component explaining the maximum amount of habitat variation during 1994–1997.

To compare assemblages between sites, we ranked species at each site by total abundance in samples for all years combined to identify common species (i.e., the highest ranked species that together composed ≥90% of all captured individuals at each site). We then tested for between-site differences in abundance of each common species using two-way ANOVA (of ln-transformed sample abundance data) which included site, year, and a site x–year interaction. If the interaction term was significant, we tested for significant between-site differences in each year 1994–1997, and designated a species as more abundant at a site if that site had significantly (t test, $P \leq 0.05$) higher abundances in at least three of four years. We also compared assemblage composition between sites in terms of reproductive season, based on published life-history accounts, to examine whether species that spawned during spring or summer were differentially less abundant in the flow-regulated site.

Results

Hydrologic and habitat patterns

Unregulated site.—Spring median and peak flows were low to average during 1994 through 1997, ranging 10.8–14.7 m^3/s (median flows) and 39.2–111 m^3/s (1-d maximum), compared to long-term spring medians (1953–1997) of 13.9 and 109.0 m^3/s, respectively. Summer flows varied more widely among years. Intense summer rains in 1994 and 1997 produced elevated median (12.3 and 7.90 m^3/s) and peak (54.0 and 75.1 m^3/s) flows, compared to long-term summer medians of 5.74 and 26.1 m^3/s, respectively. Summer flows were substantially lower in 1995 (median = 3.11 m^3/s, peak = 9.11 m^3/s). Habitat availability reflected the median flow patterns (Fig. 2). Low-flow summers produced high availability of shallow-water habitats (i.e., 1995–1996), whereas high-flow summers of 1994 and 1997 produced greater availability of fast-water habitats (Fig. 2). Habitat persistence also varied most greatly during summer, e.g., from 11 h in 1994 to 640 h in 1995 for shallow-slow habitat (Fig. 3). During spring, persistence was generally high for all habitat types, with deep-fast having the lowest value of 210 h in 1995 (Fig. 3).

Flow-regulated site.—Operation of Harris Dam, specifically the limited water release at the dam between hydropower generation events, resulted in low median flows relative to pre-dam conditions. During spring1994–1997, median hourly flows ranged 9.25–15.2 m^3/s, falling substantially below all median spring flows recorded during 44 yr of pre-dam flow (median = 55.2 m^3/s). Summer median hourly flows ranged 5.18–11.4 m^3/s during 1995–1997 and were <97% of the pre-dam median summer flows (44-yr median = 30.6 m^3/s). Only during summer 1994, when intense rains fueled extended water release in July, was the median flow comparable to pre-dam values. The 1994 summer median, 46.1 m^3/s, exceeded 90% of pre-dam median summer flows.

Lower median flows produced by operation of the dam resulted in relatively high availability of shallow-water habitats and low availability of deep-fast habitat (Fig. 2). The only exception occurred in summer 1994, when higher flows enhanced the availability of deep-fast habitat (Fig. 2). In contrast to habitat availability, habitat persistence generally was low for all key-habitat types at the regulated site (Fig. 3), as a result of the hydropeaking operation and consequent daily flow fluctuations (often ≥300 m^3/s within 24 h). When pulsed water releases from the dam reached the study site, shallow-water habitats were eliminated except at the channel edges. Conversely, deep-fast habitat was sharply reduced during low-flow periods between pulses. As a result, persistence of all habitat types was <120 h in spring, substantially lower than any values observed at the unregulated site (Fig. 3). We observed greater annual variation in persistence during summer (Fig. 3) resulting from prolonged periods without hydropower production during the drier summers of 1995 and 1996. In 1995, persistence of shallow-fast and shallow-slow habitats (225 and 240 h, respectively) exceeded estimates for some years at the unregulated site.

YOY abundances in relation to hydrologic and habitat patterns

Fish assemblages included 16 and 10 species with ≥10 YOY in at least 1 yr at the unregulated and flow-regulated sites, respectively, including eight species in common between sites (Table 1). Most of these species displayed significant among-year variation in YOY abundance (Table 1), primarily with significantly more YOY in 1995 or 1995 and 1996 (i.e., 62.5% of tested species at the unregulated site and 70% at the flow-regulated site). Two species, *Campostoma oligolepis* and *Etheostoma chuckwachatte,* had highest YOY abundances in different years at the two sites (Table 1).

Variation in YOY abundances was significantly (product-moment correlation coefficient, $P \leq 0.10$) correlated with flow or habitat variables for 10 fishes at the unregulated site. These species all had greatest YOY abundances in 1995 (and in some cases 1996; Table 1) and were all positively correlated with availability of shallow-slow habitat in summer (Table 2). Three other variables were significantly correlated with YOY abundances of eight or more species: summer availability of shallow-fast habitat (negative correla-

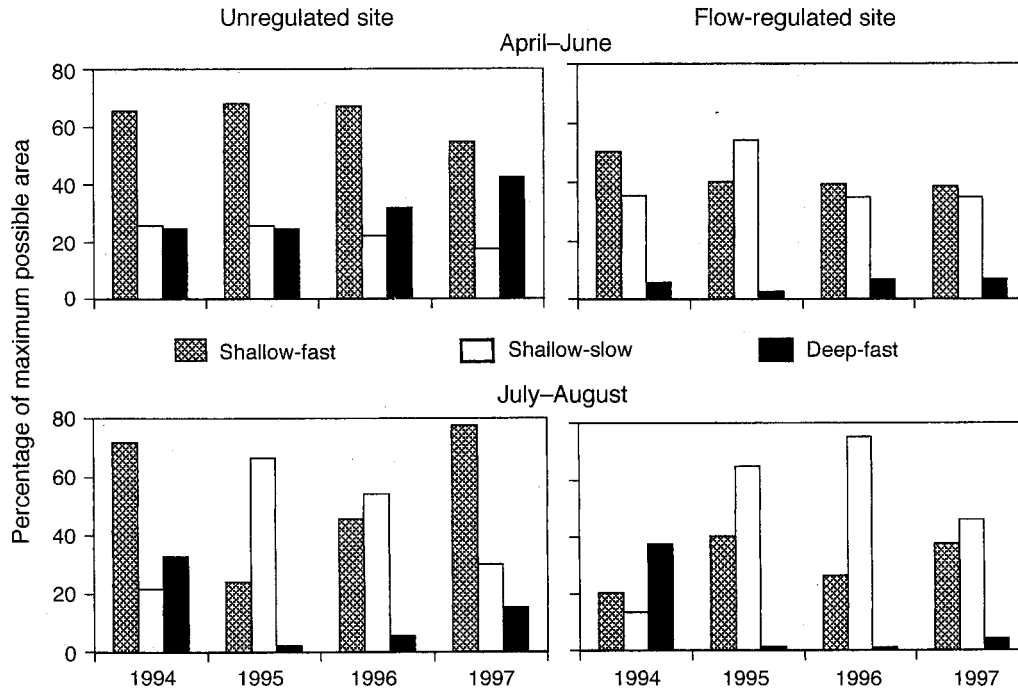

FIG. 2. Median habitat availability in spring (April–June) and summer (July–August) at the unregulated and flow-regulated study sites, 1994–1997, in the Tallapoosa River, Alabama. Medians for each habitat type are plotted as the percentage of the maximum area attainable at the study site, as estimated by habitat simulation models.

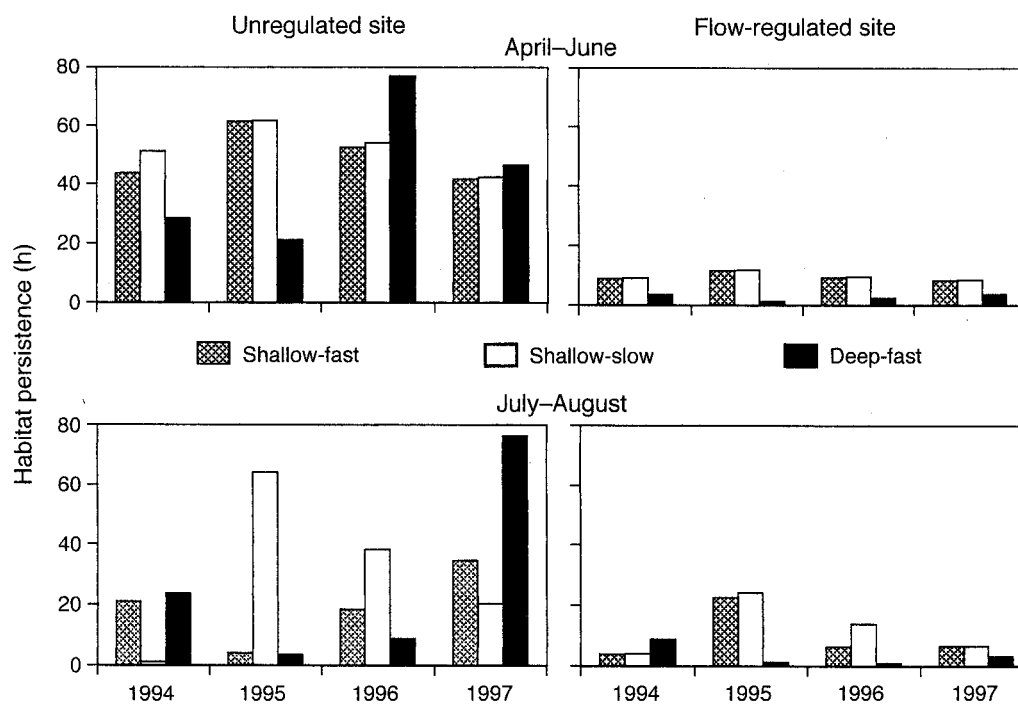

FIG. 3. Habitat persistence in spring (April–June) and summer (July–August) at the unregulated and flow-regulated study sites, 1994–1997, in the Tallapoosa River, Alabama. Persistence is computed as the longest period in a season with habitat area exceeding the long-term median area.

TABLE 1. Among-year differences in young-of-year abundances at the Tallapoosa River study sites, 1994–1997.

Species	Unregulated site			Flow-regulated site		
	ANOVA		Among-year differences (Tukey-Kramer test, $P < 0.05$)	ANOVA		Among-year differences (Tukey-Kramer test, $P < 0.05$)
	F	P		F	P	
Campostoma oligolepis	7.60	0.0001	1996, 1995 > 1994, 1997	6.62	0.0002	1994 > 1995, 1996, 1997
Cyprinella callistia	20.12	0.0001	1995 > 1996, 1997 > 1994	13.98	0.0001	1995, 1996 > 1994; 1995 > 1997
Cyprinella gibbsi	2.17	0.09		2.14	0.09	
Cyprinella venusta	6.72	0.0002	1995 > 1997, 1994	11.09	0.0001	1995 > 1996, 1994, 1997
Hypentelium etowanum	9.98	0.0001	1996, 1995 > 1994, 1997	2.72	0.04	1995 > 1997
Percina palmaris	23.93	0.0001	1995 > 1996 > 1994, 1997	32.73	0.0001	1995 > 1996 > 1994, 1997
Percina sp. cf. *P. macrocephala*	38.57	0.0001	1995, 1996 > 1997, 1994	31.75	0.0001	1995 > 1997, 1996, 1994
Etheostoma chuckwachatte	9.70	0.0001	1994 > 1996, 1995, 1997	7.90	0.0001	1995, 1996 > 1994, 1997

Notes: Additional species with significant among-year differences were as follows (with years of highest abundances in parentheses): *Luxilus chrysocephalus* (1995, 1996), *Pimephales vigilax* (1995), *Noturus leptacanthus* (1994), *Noturus funebris* (1995), and *Etheostoma stigmaeum* (1995) at the unregulated site; and *Lepomis auritus* (1995) at the flow-regulated site. Sample sizes for the four-year period were 400 (unregulated site) and 391 (flow-regulated site). For ANOVA results, df = 3, 396 (unregulated site) and 3, 387 (flow-regulated site).

tion with YOY); summer persistence of shallow-slow habitat; and spring persistence of shallow-fast habitat (Table 2). Two darter species, *Percina palmaris* and *Etheostoma stigmaeum,* also were positively correlated (0.94, 0.93) with spring persistence of shallow-slow habitat, and negatively correlated (−0.94,−0.92) with summer persistence of shallow-fast habitat. YOY abundance was not correlated with spring habitat availability (correlation coefficients: 0.28–0.76, shallow-fast; 0.26–0.62, shallow-slow; −0.25 to −0.61, deep fast), which was less variable among years (Fig. 2). YOY abundances of five species were negatively correlated with maximum 1-h flow, primarily during summer (Table 2). Correlations with low flow extremes mostly were not significant; *Cyprinella callistia, Luxilus chrysocephalus, Pimephales vigilax,* and *Percina* sp. were negatively correlated with 1-h minimum flows in summer (coefficients = −0.90 to −0.92). No species displayed significant correlations with 7-d minimum flow in either season; coefficients were negative (range −0.36 to −0.83) except for *Etheostoma chuckwachatte* and *Noturus leptacanthus,* which increased with higher 7-d minimum flows in summer (coefficients = 0.89, P = 0.11). The latter two species had highest YOY abundances in 1994 and were not significantly correlated with any other flow or habitat measures.

YOY abundances at the flow-regulated site were primarily correlated with habitat persistence rather than availability. Six species were strongly positively correlated with summer persistence of shallow-water habitats (Table 3). In contrast to the unregulated site, YOY abundances were not strongly associated with median habitat availability. The single species (*Campostoma oligolepis*) with highest YOY abundances in 1994 was positively associated with fast-habitat availability in spring (shallow-fast, 0.99) and summer (deep-fast, 0.99) and with maximum (0.93, summer and spring) and minimum (0.95, summer) flows. The only other significant correlations between YOY abundance and habitat availability were for three species during spring

TABLE 2. Correlations between young-of-year abundances and habitat availability, persistence, and maximum flow, 1994–1997 in the unregulated site, Tallapoosa River.

Species	Habitat availability		Habitat persistence		1-h Maximum flow	
	Summer: SS	Summer: SF	Summer: SS	Spring: SF	Summer	Spring
Campostoma oligolepis	0.90†	NS	NS	NS	−0.95**	−0.99***
Cyprinella callistia	0.92†	NS	0.98*	0.91†	NS	NS
Cyprinella venusta	0.96*	−0.97*	0.97*	0.98*	NS	NS
Luxilus chrysocephalus	0.99*	−0.99*	0.97*	0.99*	NS	NS
Pimephales vigilax	0.99**	−0.98*	0.97*	0.98*	NS	NS
Noturus funebris	0.95†	−0.97*	0.96*	0.98*	NS	NS
Hypentelium etowanum	0.94†	−0.93†	NS	0.91†	−0.95†	−0.98*
Percina palmaris	0.94†	−0.99**	0.92†	0.99**	−0.90†	NS
Percina sp. cf. *P. macrocephala*	0.99**	−0.98*	0.95†	0.97*	−0.91†	−0.91†
Etheostoma stigmaeum	0.96*	−0.99**	0.93†	0.99**	−0.90†	NS

Notes: Habitat types are shallow-slow (SS) and shallow-fast (SF). Values are product-moment correlation coefficients between geometric mean YOY abundances and habitat variables for four years, df = 2; NS indicates not significant.
† $P \leq 0.10$; *$P \leq 0.05$; ** $P \leq 0.01$.

TABLE 3. Correlations between young-of-year abundances and habitat persistence and availability, 1994–1997, in the flow-regulated site, Tallapoosa River.

Species	Habitat persistence, summer		Habitat availability, spring		Habitat persistence, spring		
	SS	SF	SS	DF	SF	SS	DF
Cyprinella callistia	0.99**	0.91†	NS	NS	NS	NS	−0.96*
Cyprinella venusta	0.97*	0.97*	0.96*	−0.92†	0.99**	0.99**	−0.96*
Hypentelium etowanum	NS	NS	NS	NS	NS	NS	−0.91†
Lepomis auritus	NS	0.99*	0.99**	−0.98*	0.97*	0.97*	NS
Percina palmaris	0.99*	NS	NS	NS	0.94†	0.95†	−0.99**
Percina sp. cf. *P. macrocephala*	0.92†	0.99**	0.98*	−0.92†	0.94†	0.94†	NS
Etheostoma chuckwachatte	0.93†	NS	NS	NS	NS	NS	−0.97*

Notes: Habitat types are shallow-fast (SF), shallow-slow (SS), and deep-fast (DF). Values are product-moment correlation coefficients between geometric mean YOY abundances and habitat variables for four years, df = 2; NS indicates not significant.
† $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$.

(Table 3). Seven fishes also were significantly correlated with spring habitat persistence (Table 3). All of the significant correlations with spring variables reflected positive associations with shallow habitats and negative associations with deep-fast (Table 3), excepting *C. oligolepis* as reported above. The actual influence of habitat persistence during spring on YOY abundances likely was less than during summer because spring persistence only differed by ≤33 h among years (Fig. 3). In contrast, summer persistence of shallow-water habitats varied by >200 h among years (Fig. 3).

Analyzing covariation among the habitat variables, having the most associations with YOY abundances, produced a multivariate axis for each site that was strongly correlated with the original variables and with YOY abundances for most tested species. The first extracted component explained 98.1% and 95.0% of the total variance in the correlation matrices analyzed for the unregulated and flow-regulated sites, respectively. At the unregulated site, 10 species were positively correlated (0.90–0.99, $P \leq 0.10$) with scores on the first component, excepting only *E. chuckwachatte* and *N. leptacanthus*. High YOY abundances were associated with high shallow-slow habitat availability in summer, high shallow-fast persistence in spring and low summer availability of shallow-fast habitat (correlations with component 1 = 0.98, 0.99, −0.99 respectively). At the flow-regulated site, the first component described increasing persistence of shallow-fast and shallow-slow habitats in summer (correlations with component 1 = 0.96 and 0.99, respectively). Persistence of deep-fast habitat in the spring was negatively correlated (−0.98) with this component, but only varied 13–37 h, whereas persistence of shallow-water habitats in summer varied more substantially, as noted above. Six species, excepting *C. oligolepis* and *Hypentelium etowanum*, were significantly correlated (0.90–0.99) with scores on this component, reflecting increased YOY abundances with increasing persistence of shallow-fast and shallow-slow habitats in summer.

Fish assemblage comparisons

Species composition of fish assemblages overlapped extensively between the unregulated and flow-regulated study sites, reflecting a common species pool. We collected 39 species at each site, with 30 species occurring at both sites. Only one common native species (*Notropis baileyi*) had a geographic range that did not include both sites. Eight of the 10 most abundant fishes at the flow-regulated site also ranked among the 10 most abundant species at the unregulated site (Table 4).

Differences between sites were most evident in species abundances and in representation of spring-spawning fishes. Nine fishes had significantly greater abundances at the unregulated site, four species showed inconsistent between-site differences, and only one species was significantly more abundant in the flow-regulated site (Table 4). Four of the five species that were not less abundant at the flow-regulated site had reproductive seasons that potentially extended into July or later (Table 4). Conversely, five of six spring-spawning species (i.e., reproductive season extending not later than June) had significantly greater abundances at the unregulated site (Table 4). Overall, spring-spawning species comprised 44% of individuals of common species at the unregulated site, compared to 27% at the flow-regulated site.

DISCUSSION

Juvenile fish abundances were strongly associated with flow and instream habitat variables. Juvenile abundances at the unregulated site were strongly correlated with average habitat availability and persistence, as well as peak flow. In contrast, the temporal sequence of flows appeared more important than habitat availability or flow extremes to YOY abundances in the hydropeaking regime. Flow regulation dramatically reduced temporal habitat stability in comparison to the unregulated site. Persistence of shallow-water habitats was only comparable to unregulated site conditions during summer (in two of four sample years). Habitat

TABLE 4. Rank abundances and reproductive timing of the most common fishes at the unregulated and flow-regulated sites, Tallapoosa River.

Species	Rank abundance†		Reproductive timing‡		References§
	Regulated	Unregulated	Months	Season	
Percina palmaris	1	2	Mar–Jul	SUM	1
Percina sp. cf. *P. macrocephala*	2[b]	7	Mar–Jul	SUM	2
Cyprinella callistia	3	1[a]	May–Nov	SUM	3
Etheostoma chuckwachatte	4	3	Apr–Jun	SPR	4
Cyprinella venusta	5	9	May–Aug	SUM	3
Notropis baileyi	6	...	May–Sep	SUM	5
Campostoma oligolepis	7	4[a]	Apr–Jun	SPR	3
Hypentelium etowanum	8	8[a]	Mar–Apr	SPR	3
Lepomis auritus	9	14	May–Aug	SUM	6
Etheostoma stigmaeum	10	5[b]	Mar–May	SPR	6, 7
Luxilus chrysocephalus	16	6[b]	May–Jun	SPR	3, 6
Noturus leptacanthus	15	10[b]	May–Aug	SUM	3, 8
Notropis stilbius	11	11[a]	May–Jun	SPR	3
Pimephales vigilax	17	12[a]	May–Jul	SUM	3–6
Cyprinella gibbsi	14	13[b]	...	...	...

Note: Species ranked 1–11 and 1–14 comprised ≥90% of all fish captured at the regulated and unregulated sites, respectively.

† An underlined rank indicates the site where a species was significantly more abundant (more abundant in three or more of four single-year comparisons, t test, $P \leq 0.05$). ANOVA results: superscript letter "a" indicates that site effects were significant in a two-way model, $P < 0.001$; superscript letter "b" indicates that the site × year interaction term was significant in a two-way model.

‡ Reproductive season is spring (SPR) or spring through (SUM), depending on the range of months with documented spawning activity.

§ References; 1, Wieland 1984; 2, Wieland and Ramsey 1987; 3, Etnier and Starnes 1993; 4, Orr and Ramsey 1990; 5, Mathur and Ramsey 1974; 6, Jenkins and Burkhead 1994; 7, Hubbs 1985; 8, Clark 1978 (as cited in Etnier and Starnes [1993]).

persistence was uniformly low across all years during the spring. Correspondingly, the fish assemblage at the flow-regulated site was dominated numerically by species capable of spawning during summer. All common spring-spawning species, except one, were less abundant at the flow-regulated site than at the unregulated site. Fishes could persist in the flow-regulated regime, but successful juvenile production largely depended upon periods of habitat stability created when low rainfall or other factors limited hydropeaking operations at the dam.

Our results for the unregulated Tallapoosa River site are concordant with previous work. Year-to-year flow variability likely influences biotic assemblages in many lotic systems by facilitating recruitment by different species in different years (Grossman et al. 1982, 1998, Walker and Thoms 1993, Sparks 1995). Increased abundances of some Tallapoosa species in drier years appear strongly associated with greater availability or persistence of shallow-water habitats. Similarly, facets of YOY habitat availability have been correlated with subsequent year class strength of stream centrarchid (Bovee et al. 1994) and salmonid (Nehring and Anderson 1993) populations. Negative correlation between juvenile abundances and shallow-fast habitat availability, as well as peak flows in summer, suggests that stable low-flows are critical for juveniles of some Tallapoosa species. Floods may cause substantial mortality to small YOY fish (Harvey 1987), and stable low-flow conditions subsequent to spawning have been correlated with increased juvenile abundances of subsets of species within assemblages (Starrett 1951, Schlosser 1985, Freeman et al. 1988). Conversely, at least two common Tallapoosa fishes may thrive under higher flow conditions, as shown by highest abundances in the wettest year and weak positive associations with higher 7-d minimum flows in summer. These contrasts indicate that even similar species (i.e., congeners of *Etheostoma* and *Noturus*) differ in responses to environmental variability.

Results for the flow-regulated site demonstrate the importance of temporal habitat stability independently of habitat availability. Hydropeaking can substantially dampen seasonal and interannual variation (Poff et al. 1997, Bowen et al. 1998), while imposing artificially high, short-term variation detrimental to biota unable to adapt to rapid fluctuations (Cushman 1985). Abundances of many small-bodied riverine fishes that use shallow-water habitats (Bain 1995, Freeman et al. 1997) are reduced in the flow-regulated Tallapoosa River site as in other hydropeaking-regulated systems (Bain et al. 1988, Kinsolving and Bain 1993), even though average availability of shallow-water habitats is comparable to the unregulated site. However, a suite of small-bodied fishes persists at the flow-regulated site in densities similar to the unregulated site. Most of these species may spawn at least into July; YOY abundances of these dominant fishes were correlated positively with persistence of shallow-water habitats in summer, suggesting that stable-flow periods during summer facilitates their survival in the flow-regulated regime. Only one species, *C. oligolepis,* had YOY

abundances positively correlated with fast-habitat availability, suggesting that suitable spawning habitat (flowing water over gravel) is limited in the reduced median flows of the hydropeaking regime. *C. oligolepis,* in addition to nearly all other spring-spawning species (excepting *E. chuckwachatte*), were less abundant in the flow-regulated regime than at the unregulated site. Electrofishing data from deep-water habitats also reveal lower abundances of spring-spawning redhorse suckers (*Moxostoma* spp.) in flow-regulated compared to unregulated segments of the Tallapoosa River (Travnichek and Maceina 1994). Reduced habitat persistence, which is most severe in spring, likely is the primary cause of lower fish abundances in the flow-regulated site and is not compensated by high average habitat availability.

Increased hydrologic variability should select for more generalist taxa (Horwitz 1978, Townsend and Hildrew 1994, Poff and Allan 1995). At hydrologically variable sites, Poff and Allan (1995) demonstrate a shift to more generalized feeding strategies and greater tolerance for low velocity habitats. Because numerically dominant fishes in our study mostly feed opportunistically on macroinvertebrates, we had little opportunity to quantify such diet shifts. Similarly, the dominant species at both study sites are fluvial specialists (excepting only *Cyprinella venusta*; Travnichek and Maceina 1994) that generally use a similar array of shallow-water microhabitats (Bain 1995, Freeman et al. 1997) and spawn in similar substrata, either gravel (i.e., *Percina* and *Etheostoma* species) or crevices (i.e., *Cyprinella* species; Etnier and Starnes 1993, Jenkins and Burkhead 1994). At present, the trait most clearly associated with species dominance in the flow-regulated site is a prolonged reproductive season (i.e., extending into July or later).

Variables other than flow and habitat patterns may influence fish populations and species persistence in the flow-regulated regime; these warrant further investigation. For example, we have collected small YOY *E. chuckwachatte* in late summer at the flow-regulated site (M. C. Freeman, Z. H. Bowen, K. D. Bovee, and E. R. Irwin, *unpublished data*), suggesting that it may spawn later there than in unregulated streams (Orr and Ramsey 1990). Because thermal regimes are altered by hydropeaking and may influence reproductive timing, we are currently collecting data to quantify thermal patterns in relation to flow in the regulated site. Flow regulation also may influence assemblages by altering intensity of biotic variables, such as predation; we have no data on effects of flow-alteration on interspecific interactions. Additionally, tributary populations could influence mainstem fish abundances, especially rarer species. Possibly, the YOY increases quantified in 1995 and 1996 in the flow-regulated site resulted from increased reproductive success in tributary streams rather than locally. We believe this is unlikely because none of the dominant species is known to exhibit large-scale larval drift or juvenile migrations. Clearly, we have a long way to go in understanding all mechanisms responsible for native species survival in flow-altered systems, however the strong influences of flow and habitat patterns justify examining management strategies to address these effects.

Management implications

Just as rivers have been incrementally modified, they can be incrementally restored.

—Poff et al. (1997)

Management strategies of flow-altered rivers often have focused on provision of minimum flows, intended to prevent deleterious biological impacts of frequent or extreme water depletion (Stalnaker et al. 1995, Poff et al. 1997). Preventing prolonged and excessive low flows is important to protecting managed river ecosystems. Travnichek et al. (1995) document substantial recovery of the fish fauna in a hydropeaking-regulated reach following implementation of a minimum continuous flow. Importantly, our flow-regulated reach maintains extensive shallow-slow and shallow-fast habitat during low-flow periods, primarily because channel storage and tributary inflows augment flows between Harris Dam and our study site. If extended low-flow periods desiccated shallow-water habitats at our study site (as presently occurs in the channel nearer the dam), we would not expect a positive YOY response to stable, low-flow episodes. Maintaining adequate instream habitat during low-flows obviously is critical, but not sufficient, to protect river assemblages in strongly regulated river systems (Stalnaker et al. 1995, Poff et al. 1997).

The natural flow paradigm (Richter et al. 1997, Poff et al. 1997) incorporates a holistic approach to management that explicitly recognizes the complex relationships between flow regimes and river ecosystem function. This approach advocates incorporating flow magnitude, frequency, duration, timing, and the rate of change of naturally occurring hydrologic conditions into strategies for managing regulated rivers. Clearly, all aspects of a pre-impact flow regime can not be restored while accommodating hydropeaking. However, restoring critically important features of the natural flow regime (Poff et al. 1997), or managing so as to avoid habitat bottlenecks (Orth 1987, Stalnaker et al. 1995) could alleviate negative effects. Flow management for hydropeaking alters seasonal occurrence of stable habitat, an aspect of the natural flow regime critical to persistence of riverine fishes. Our data support the hypothesis that providing periods of stable flow conditions below hydropower facilities during appropriate seasons should facilitate reproduction by native riverine fishes. Stable flow should be sufficiently large and long to allow spawning, larval development, and juvenile residence.

An adaptive management approach that included

flow manipulations (e.g., provision of stable flows for varying periods) and population monitoring could determine necessary modifications to the regulated flow regime. Because our hypotheses are based on a data set limited to four years, we believe fish populations should continue to be monitored to further elucidate how hydrologic variation influences species persistence. Understanding how other taxa (e.g., macroinvertebrates) and processes (e.g., primary and secondary production) respond to flow variability could enhance our ability to modify flow so as to increase the ecological integrity of regulated systems. Cooperation among water resource developers and natural resource managers to implement and monitor experimental flow modifications in managed systems could significantly contribute to conservation of native riverine fauna.

Acknowledgments

We appreciate logistical support and guidance by Johnie Crance and Clair Stalnaker, and field assistance by Lane Hill, Amy Strong, Keith Walker, David Watson, Holly Weyers, Greg Lein, Kristin Costley, Glenn Kowalski, Rob Andress, Ben Dowling, Dave Buckmeier, Richard Weyers, Scott Peyton, Kurt Knowles, Scott Spearman, Dan Catchings, Carl Couret, Tom Meronic, and Vince Travnichek. Dr. Travnichek also generously shared length data for his 1990–1992 collections. Brian Toth drafted Fig. 1. J. L. Pearman, USGS, provided hourly and daily flow data for Tallapoosa River gages. Andy Shepard, Alabama Power Company, responded to numerous inquiries concerning water release schedules. We especially appreciate comments on various versions of the manuscript by anonymous reviewers, Roy Stein, Catherine Pringle, and the Pringle lab group.

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