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The influence of low-head dams on fish assemblages in streams across Alabama

Brian S. Helms[1] AND **David C. Werneke**[2]
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849 USA

Michael M. Gangloff[3]
Department of Biology, Appalachian State University, Boone, North Carolina 28607-2702 USA

Emily E. Hartfield[4] AND **Jack W. Feminella**[5]
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849 USA

Abstract. We quantified fish assemblages in 20 streams containing mill dams in various physical conditions (dams intact, partially breached, or relict with normal flows) in Alabama, USA, during the period from 2006 to 2008. We used a backpack electroshocker to sample three 150-m reaches per stream: 500 to 1000 m downstream of the dam, 0 to 100 m downstream of the dam, and 100 m upstream of the impoundment. Species- and trait-based analyses revealed slightly different, but often complementary, information about fish assemblages. Fish species richness and benthic conditions differed longitudinally among reaches in streams with dams. In streams with breached dams, species richness, but not trait richness, was lower in upstream reaches than in downstream reaches. Overall, species and trait richness were correlated with benthic-habitat variables in streams with relict dams and were significantly correlated with water physicochemical variables in streams with intact and breached dams. Nonmetric multidimensional scaling ordination failed to resolve any discernable site groupings based on species abundance data, and indicator species analysis revealed 1 indicator species, *Esox americanus*, upstream of relict dams. Fourth-corner trait analysis revealed more trait associations in reaches in streams with breached dams than in those with intact or relict dams. Generalist spawners (nest-guarding polyphils) increased and taxa with a preference for cobble substrates decreased upstream of breached dams. Few longitudinal differences were observed in streams with relict and intact dams. Taken together, dams, particularly those that are breached, appear to exert a strong upstream influence on fish species richness and functional composition and could alter the trophic structure of the entire stream through habitat modifications or limitation of fish movements.

Key words: serial discontinuity, trait analysis, stream fragmentation, low-head dams.

Physical, chemical, and biological effects of dams on aquatic systems can be dramatic. These effects may include alterations in hydrologic regime, water quality, sediment composition, and channel geomorphology. In addition, dams impede or prevent migration by fishes and other stream biota, thereby altering assemblage structure and potentially fragmenting and exacerbating extinction risks of imperiled aquatic populations (Baxter 1977, Blalock and Sickel 1996, Watters 1996, Poff and Hart 2002, McLaughlin et al. 2006).

Unnatural flow regimes from impoundments are a major source of habitat degradation that can alter stream communities (Cushman 1985, Irvine 1985, Travnichek et al. 1995, Gehrke et al. 2002, McLaughlin et al. 2006) and even riparian vegetation (Jansson et al. 2000). Coarsening of the stream bed or pooling downstream of many dams reduce habitat availability for benthic species by decreasing habitat heterogeneity, which, in turn, may reduce diversity and richness

[1] E-mail addresses: helmsbs@auburn.edu
[2] wernedc@auburn.edu
[3] gangloffmm@appstate.edu
[4] Present address: Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA. E-mail: hartfiee@science.oregonstate.edu
[5] feminjw@auburn.edu

(Hauer et al. 1989, Armitage and Blackburn 1990, Poff et al. 1997). Alteration of temperature regimes by impoundments can change fish distribution and behavior. Increased temperatures downstream of overflow dams can eliminate thermal cues vital to the life cycles of some invertebrate prey (Ward and Stanford 1982, Irvine 1985). In addition, increased water temperature can increase metabolic rates of fish and invertebrates and elevate demand for food to support growth and survival (Perry et al. 1987, Wotton 1995, Vinson 2001, Lessard and Hayes 2003). In reservoirs, deep, cold, anoxic water often lacks fish, and tailwaters of many hypolimnetic-release dams support depauperate or altered nonnative fish communities (Headrick and Carline 1993, Dean et al. 2002). These effects can lead to breaks in ecological connectivity.

Dams also impede longitudinal movements of stream organisms (Baxter 1977, Watters 1996, Dean et al. 2002). Upstream movement frequently is halted by dams, which can prevent individuals from reaching feeding or spawning habitat and can cause population declines (Raymond 1979). Decreased longitudinal connectivity across streams may cause population fragmentation and isolation of fish populations (Neraas and Spruell 2001, Olden et al. 2001), and 1-way (downstream) migration may reduce genetic diversity and population size, especially in upstream sections (Jager et al. 2001, Morita and Yamamoto 2002, Yamamoto et al. 2004).

Dams are numerous and widespread in eastern US streams. Large hydroelectric dams have radically altered large rivers of the eastern US, but low-head dams are much more prevalent (Walter and Merritts 2008). Low-head dams have a hydraulic height of <15 m and typically are overflow or spillway structures (Poff and Hart 2002). According to census records, >65,000 low-head dams, most of which were built for water-powered milling, existed in the eastern US by 1840 (Walter and Merritts 2008). More than 10,000 dams exist in Alabama alone (Alabama Office of Water Resources; http://www.adeca.alabama.gov/).

The effects of large dams on aquatic organisms are well documented, but fewer studies have assessed effects of mill and low-head dams on stream biota (Edwards 1967, Watters 1996, Dean et al. 2002, Lessard and Hayes 2003, Orr et al. 2008). Nevertheless, environmental agencies in many areas (particularly in the northeastern US) have begun aggressive programs to remove low-head dams and restore stream habitats, and the American Fisheries Society is developing protocols for these projects. Removal is often costly and can have negative consequences for downstream biota (Sethi et al. 2004). Therefore, a quantitative, statistically rigorous approach is needed to provide a better understanding of how low-head structures affect stream biota. The objective of our study was to assess the effect of small dams on fish assemblages across 20 focal streams in the southeastern US.

Methods

Physicochemical and fish sampling

We sampled fishes and their habitat at 20 mill-dam sites in Alabama (USA; Table 1). Nine of these 20 sites had intact dams, 6 had breached dams, and 5 had relict dams. Intact dams had a functional spillway, over-dam flow, and a reservoir with reduced current velocity. Breached dams were partially broken or had an open spillway with an absent or reduced (<50 m long at base flow) impoundment zone. Relict dams were mostly eroded, often had only bankside pilings, and allowed free water flow (Gangloff et al. 2011). We selected three 150-m reaches at each site: 500 to 1000 m downstream of the dam (D; below and removed from immediate dam effects), 0 to 100 m below the mill dam (M; immediately downstream of and affected by the dam), and upstream of observed or putative impoundment effects of the dam (U; free-flowing stream section above the immediate influence of the dam).

We established 16 transects at 10-m intervals in each reach. We measured current velocity and depth at 5 evenly spaced points along each transect and channel width and substrate composition (20 particles/transect, $n = 160$ per site) along each transect length. We computed mean particle size and the proportion of the stream bed composed of unmeasured particles (bedrock, organic matter, woody debris, sand, and silt). We measured water temperature continuously (3-h intervals) with iButton data loggers (Maxim, Inc., Sunnyvale, California) deployed in the U, D, and M reaches, and we measured conductivity (Milwaukee Sharp C66 meter; Milwaukee Instruments, Rocky Mount, North Carolina), pH (Milwaukee Sharp pH52 meter), and dissolved O_2 (YSI 55 meter; Yellow Springs Instruments, Yellow Springs, Ohio) at the time of fish capture. We determined link magnitude and stream order from US Geological Survey 7.5-min quadrangle topographic maps.

In each free-flowing reach, we sampled fish in 3 spatially segregated riffle–run–pool sequences (3 riffles, 3 runs, 3 pools) and the habitat near 1 stream bank (10 habitats total). We made an effort to sample representative available habitats in the reach. We sampled fishes in the selected habitats to depletion with a Smith-Root LR-24 electrofisher (Smith-Root,

TABLE 1. Dam and stream names, locations, order, and link magnitudes of study sites. B = breached mill dam, R = relict mill dam, I = intact mill dam.

Dam	Stream	Drainage	Latitude	Longitude	Sampling date	Dam condition	Order	Link magnitude
Goodwin's Mill	Big Canoe Creek	Coosa	33.818	−86.381	August 2007	B	4	18
Rikard's Mill	Big Flat Creek	Alabama	31.608	−87.414	June 2008	I	5	27
Chamblee's Mill	Blue Springs Creek	Black Warrior	34.061	−86.666	August 2007	R	3	24
Brushy	Brushy Creek	Black Warrior	34.287	−87.275	September 2007	I	4	25
Buttahatchee	Buttahatchee River	Tombigbee	34.126	−87.837	June 2008	B	4	35
Grant's Mill	Cahaba River	Alabama	33.511	−86.657	September 2007	R	5	24
Vaughn's Mill	Choctafaula Creek	Tallapoosa	32.508	−85.579	September 2009	B	3	13
Bean's Mill	Halawakee Creek	Chattahoochee	32.697	−85.267	June 2006	I	3	21
Hatchett	Hatchett Creek	Coosa	33.068	−86.096	August 2007	I	3	34
Cahaba	Little Cahaba River	Alabama	33.448	−86.697	September 2007	B	4	14
Carr's Mill	Little Hillabee Creek	Tallapoosa	33.204	−85.943	October 2008	R	4	53
Meadows' Mill	Little Uchee Creek	Chattahoochee	32.528	−85.253	September 2007	I	4	8
Macon's Mill	Loblockee Creek	Tallapoosa	32.662	−85.581	July 2006	I	4	10
Bushell's Mill	Lost Creek	Black Warrior	33.854	−87.445	June 2008	B	4	16
Kelly's Mill	New River	Tombigbee	33.923	−87.682	June 2008	I	3	14
Ferguson's Mill	Osanippa Creek	Chattahoochee	32.778	−85.193	July 2007	R	4	41
Shellgrove's Mill	Pea River	Choctawhatchee	31.518	−85.868	September 2007	R	5	81
Pearce's Mill	Pearces Mill Creek	Tombigbee	34.124	−87.839	June 2008	B	3	11
Jones' Mill	Sandy Creek	Tallapoosa	32.763	−85.588	September 2006	I	3	6
Shannon's Mill	Yellow Leaf Creek	Coosa	32.959	−86.603	September 2007	I	3	6

Inc., Vancouver, Washington). A team of 3 people (1 person used the electrofisher and 2 people collected stunned fishes with dip nets) worked habitats from downstream to upstream. Sampling effort was measured as time spent fishing per habitat(s) and as area of habitat sampled (m^2). However, sampling effort was not recorded consistently throughout the study (see *Data analysis*). After sampling was completed, we anesthetized fish in tricaine methanesulfonate (MS-222) and fixed them in a 10% formalin solution after they died. Seven days later, we transferred fish from formalin solution to water for 3 d then transferred them to 70% ethanol for permanent storage. We identified fishes in the laboratory and deposited them in the Auburn University Museum fish collection. We coded fish data from each site for dam condition and location relative to the dam (D, M, or U).

Assemblages and traits

We calculated species richness for each reach and assigned species to various ecological and life-history traits per the FishTraits database (Frimpong and Angermeier 2009) as potential indicators of disturbance associated with mill dams. This traits database includes information on: 1) trophic ecology; 2) body size, reproductive ecology, and life history; 3) habitat preferences; 4) temperature tolerances; and 5) geographic distribution. Species in the traits database are categorized at a finer resolution than we used, particularly for reproductive-ecology traits, so many traits were excluded or grouped a priori. In all, we assigned and analyzed 33 traits for each species (Table 2). We calculated trait richness (binary traits only) for each reach and site.

Data analysis

We sampled reaches exhaustively, but we used a conservative approach to data analysis because of inconsistencies in documenting sampling effort. We binary- or rank-transformed all fish-catch data. Binary and rank data are less sensitive than quantitative data but are more suitable when abundance estimates are unreliable (Kwak and Peterson 2007). We log(x)-transformed continuous and arcsine$\sqrt{(x)}$-transformed proportional physicochemical variables as needed to meet assumptions of normality (Zar 1998). We tested for potential seasonality with correlation analysis of species and trait richness and ordinal (Julian) sampling date, and for underlying habitat relationships with correlations of species and trait richness with physicochemical variables.

We used 1-way analysis of variance (ANOVA) to test whether stream-averaged physicochemical variables differed among dam states (intact, breached, relict). Next, we analyzed data from each dam state separately with General Linear Models (GLM) to assess longitudinal differences in species and trait richness among reach locations (D, M, U) with stream as a blocking variable. We used Tukey's test to make post hoc multiple pairwise comparisons among reach locations (Neter et al. 1990).

We used nonmetric multidimensional scaling (NMDS) of a species $\times$ reach matrix to describe taxonomic variation in fish assemblages among reaches (Sørenson distance). We based the NMDS on rank-transformed data with 40 runs with real data, 50 runs of randomized data, and 200 iterations using a random starting configuration (McCune and Grace 2002). We then related physicochemical variables to the resulting ordination. We followed the NMDS with indicator species analysis (ISA; Dufrêne and Legendre 1997) based on the same NMDS site $\times$ reach matrix to identify species that were most closely associated with each dam state and reach location. We used Monte Carlo randomization (1000 permutations) to test indicator values (Dufrêne and Legendre 1997, McCune and Grace 2002).

We used the improved 4^{th}-corner method to test relationships between species traits, site categories, and fish presence/absence as a means to determine functional associations with each dam state and reach location. We used a combination of permutation tests to reduce Type I errors and increase power of obtained links (Dray and Legendre 2008, Gallardo et al. 2009). First, we permuted site vectors to test the null hypothesis that species and reach categories are unrelated (permutation model 2). Then we permuted species vectors to test the null hypothesis that species and their traits are unrelated (permutation model 4). If both tests were significant, we rejected the null hypothesis that species traits are unrelated to reach categories and accepted the hypotheses that species traits, site categories, and fish presence/absence are linked. We used a Bonferroni correction for the 9 reach categories to determine statistical significance ($\alpha = 0.05/9 = 0.0056$).

We used Minitab (version 16; Minitab, State College, Pennsylvania) for ANOVA and GLM analyses and PC-ORD (version 4; MjM Software Design, Gleneden Beach, Oregon) for NMDS and ISA. For the 4^{th}-corner analysis, we used the *fourthcorner* function in the *ade4* (Dray and Dufour 2007) in R (version 2.12.0; R Foundation for Statistical Computing, Vienna, Austria).

Results

Physical conditions varied considerably across the sampling sites. Average depth ranged from 0.16 to 0.50 m, average width ranged from 6.55 to 28.91 m, and mean particle size ranged from 13.67 to

TABLE 2. Traits from FishTraits database used in data analysis.

Trait code	Data scale	Description
Trophic ecology		
BENTHIC	Binary	Benthic feeder
SURWCOL	Binary	Surface or water column feeder
ALGAE	Binary	Algae or phytoplankton
MACVASCU	Binary	Macrophytes or vascular plants
DETRITUS	Binary	Detritus feeder
INVLVFSH	Binary	Invertebrates and larval fish
FSHCRCRB	Binary	Larger fishes, crayfishes, crabs
Reproductive ecology		
A13	Binary	Nonguarders, open substratum spawners, lithophils
A15	Binary	Nonguarders, open substratum spawners, phytophils
A23	Binary	Nonguarders, brood hiders, lithophils
A24C	Binary	Nonguarders, brood hiders, speleophils
B13A	Binary	Guarders, substratum choosers, lithophils
B22	Binary	Guarders, nest spawners, polyphils
B23	Binary	Guarders, nest spawners, lithophils
B27	Binary	Guarders, nest spawners, speleophils
C	Binary	Substrate indifferent
Body size/physiology		
MAXTL	Continuous	Maximum total length (cm)
MATUAGE	Continuous	Mean, modal, or median age at maturity in years for females
LONGEVITY	Continuous	Longevity in years based on life in the wild
FECUNDITY	Continuous	Maximum reported fecundity
SEASON	Continuous	Length of spawning season
MAXTEMP	Continuous	30-y average maximum July temperature at range centroid
Habitat preference		
MUCK	Binary	Muck substrate
SAND	Binary	Sand substrate
GRAVEL	Binary	Gravel substrate
COBBLE	Binary	Cobble or pebble substrate
BOULDER	Binary	Boulder substrate
BEDROCK	Binary	Bedrock substrate
VEGETAT	Binary	Aquatic vegetation
DEBRDETR	Binary	Organic debris or detrital substrate
LWD	Binary	Large woody debris
Geographic distribution		
AREAKM2	Continuous	Range area (km^2)
PERIMETER	Continuous	Range perimeter (km)

221.67 mm (Table 3). Stream physicochemical variables differed considerably among dam states, but the only significant difference was that current velocities were higher in streams with intact than with relict dams (Table 3).

Over 17,000 fish representing 88 species from 12 families were sampled (Table 4). The most abundant fishes were minnows (Cyprinidae, 55%), darters (Percidae, 20%), and sunfishes (Centrarchidae, 14%). Species and trait richness were not significantly correlated with Julian date. Species richness was significantly lower in U reaches than in M reaches of streams with breached dams ($F_{2,17} = 10.28$, $p = 0.004$). A similar, but nonsignificant, trend was apparent in streams with I dams ($F_{2,17} = 2.77$, $p = 0.095$; Fig. 1A). Trait richness did not differ among U, M, and D reaches in streams with dams of any condition (Fig. 1B). Species richness was correlated with the % benthic wood ($r = 0.58$, $p = 0.025$) and % bedrock ($r = -0.59$, $p = 0.020$) in streams with relict dams, with conductivity ($r = -0.55$, $p = 0.019$) in streams with breached dams, and with mean water temperature ($r = 0.48$, $p = 0.017$) in streams with intact dams (Table 5). Trait richness was correlated with % bedrock ($r = 0.61$, $p = 0.016$) in streams with relict dams, with conductivity ($r = -0.47$, $p = 0.050$) and substrate size ($r = -0.49$, $p = 0.041$) in streams with breached dams, and with pH ($r = -0.53$, $p = 0.025$) and temperature ($r = 0.47$, $p = 0.018$) in streams with intact dams (Table 5).

TABLE 3. Ranges, overall means (SD), and means by dam condition of physicochemical conditions at time of sampling at study sites. *p*-values are associated with results of 1-way analyses of variance with dam condition (intact, breached, relict) as the independent variable. Italics indicate statistical significance.

Variable	Unit	Range	Mean	Intact	Breached	Relict	p
Depth	m	0.16–0.50	0.26	0.27 (0.08)	0.22 (0.05)	0.31 (0.14)	0.398
Velocity	m/s	0.01–0.24	0.11	0.066 (0.04)	0.15 (0.06)	0.09 (0.04)	*0.013*
Width	m	6.55–28.91	14.1	12.97 (4.92)	13.33 (6.42)	16.89 (9.35)	0.185
Substrate	mm	13.67–221.67	66.4	67.63 (42.67)	82.30 (62.94)	72.70 (70.68)	0.699
Bedrock	%	0–43.87	20.05	19.89 (16.01)	16.66 (14.59)	24.21 (19.84)	0.454
Wood	%	0.63–21.67	6.37	6.92 (7.29)	6.52 (4.88)	5.34 (4.17)	0.711
Organic	%	0–30.00	8.31	7.33 (5.70)	11.91 (10.95)	5.57 (2.59)	0.513
Sand	%	0.73–54.67	21.49	18.42 (9.84)	24.88 (21.49)	23.78 (14.98)	0.657
Silt	%	0–12.67	6.32	6.92 (3.65)	5.33 (3.85)	6.53 (3.67)	0.729
Conductivity	μS/cm	7.30–1219.30	189.9	107.8 (135.4)	325.2 (450.4)	171.4 (91.1)	0.339
pH		7.80–9.37	8.36	8.31 (0.57)	8.44 (0.49)	8.33 (0.19)	0.868
Dissolved O_2	mg/L	4.74–9.90	6.65	6.13 (0.95)	7.49 (1.73)	6.21 (1.70)	0.208
Temperature	°C	13.27–28	23.16	23.17 (4.94)	21.71 (3.89)	25.32 (3.03)	0.451

Together NMDS axes 1, 2, and 3 explained 82.6% of the variation in fish assemblages (30.1, 30.4, and 22.1% respectively, stress = 13.467, instability = 0.0072, iterations = 200; Fig. 2A–C). Grouping by dam condition was not discernable, and none of the physicochemical variables were correlated with the ordination axes. Only 1 taxon (*Esox americanus*) was a significant indicator species ($p = 0.009$). It was associated with U reaches of streams with relict dams (Table 6).

Fourth-corner analysis extracted 2 relationships that were significant at $\alpha = 0.0056$. Fishes with a preference for cobble substrates while guarding were negatively associated with U reaches of streams with breached dams, and nest-spawning polyphils were positively associated with U reaches of streams with breached dams (Table 6). Also, 4th-corner analysis revealed 10 more relationships at $\alpha < 0.05$. In streams with breached dams, benthic feeders were positively associated with D reaches and negatively associated with U reaches. Fishes with a preference for gravel were negatively associated with U reaches, whereas fishes with a preference for cobble were negatively associated with M reaches. Maximum temperatures were positively associated with U reaches, and guarder nest-spawning polyphils were positively associated with M reaches (Table 6). In streams with intact dams, algivores were positively associated with M reaches and substrate-choosing guarding lithophils were positively associated with U reaches (Table 6). In streams with relict dams, age at maturity was positively associated with U reaches and nonguarding lithophilic spawners were positively associated with D reaches (Table 6).

Discussion

Large dams probably affect fish populations in streams globally by blocking migrations and altering physicochemical habitat variables (Lessard and Hayes 2003). Our data suggest that small dams, particularly in the southeastern US, also may have significant effects on fish assemblages. Species richness was significantly lower in U reaches of streams with breached, and to a lesser extent, intact dams. More trait associations (negative and positive) were found in reaches of streams with breached dams than in reaches of streams with intact or relict dams, results suggesting that breached dams might influence the functional composition of fish assemblages. In contrast, species richness did not differ and traits differed minimally among reach locations in streams with relict dams, results suggesting that assemblages equilibrate once a dam structure has been removed.

In other regions, dams influence fish species richness by reducing fish passage and by altering physicochemical conditions (Cumming 2004, McLaughlin et al. 2006). Fish movement and assemblage structure are affected by low-head barrier dams implemented for sea lamprey (*Petromyzon marinus*) control (Porto et al. 1999, McLaughlin et al. 2006). Furthermore, breaches in dams allow previously entrained sediments to be displaced downstream, and unconsolidated material may persist for years in the stream (Stanley et al. 2002, Doyle et al. 2003). Sediments released from low-head dams can smother downstream habitats and can contain heavy metals, polychlorinated biphenyls (PCBs), and other contaminants that can adversely affect fishes, other aquatic biota, and humans (Gray and Ward 1982, Shuman 1995). Stream-channel scouring and pooling downstream of dams can be equally destructive and can destroy natural stream habitats. In our study, many stream beds in M reaches were scoured down to bedrock, and these reaches had significantly greater current velocities in streams with

TABLE 4. List of families, species, and common names of fishes captured during the study.

Family	Species	Common name	Family	Species	Common name
Aphredoderidae	*Aphredoderus sayanus*	Pirate perch	Esocidae	*Esox americanus*	Redfin pickerel
Atherinopsidae	*Labidesthes sicculus*	Brook silverside		*Esox niger*	Chain pickerel
Catostomidae	*Erimyzon oblongus*	Creek chubsucker	Fundulidae	*Fundulus olivaceus*	Blackspotted topminnow
	Hypentelium etowanum	Alabama hog sucker		*Fundulus stellifer*	Southern studfish
	Minytrema melanops	Spotted sucker	Ictaluridae	*Ameiurus brunneus*	Snail bullhead
	Moxostoma duquesnii	Black redhorse		*Ameiurus natalis*	Yellow bullhead
	Moxostoma erythrurum	Golden redhorse		*Ictalurus punctatus*	Channel catfish
	Moxostoma poecilurum	Blacktail redhorse		*Noturus funebris*	Black madtom
	Scartomyzon lachneri	Greater jumprock		*Noturus gyrinus*	Tadpole madtom
Centrachidae	*Ambloplites ariommus*	Shadow bass		*Noturus leptacanthus*	Speckled madtom
	Lepomis auritus	Redbreast sunfish		*Noturus nocturnus*	Freckled madtom
	Lepomis cyanellus	Green sunfish		*Pylodictis olivaris*	Flathead catfish
	Lepomis gulosus	Warmouth	Percidae	*Etheostoma artesiae*	Redfin darter
	Lepomis macrochirus	Bluegill		*Etheostoma chuckwachatte*	Greenbreast darter
	Lepomis marginatus	Dollar sunfish		*Etheostoma coosae*	Coosa darter
	Lepomis megalotis	Longear sunfish		*Etheostoma fusiforme*	Swamp darter
	Lepomis microlophus	Redear sunfish		*Etheostoma jordani*	Greenbreast darter
	Lepomis miniatus	Redspotted sunfish		*Etheostoma lachneri*	Snubnose darter
	Micropterus coosae	Redeye bass		*Etheostoma nigrum*	Johnny darter
	Micropterus henshalli	Alabama bass		*Etheostoma ramseyi*	Alabama darter
	Micropterus salmoides	Largemouth bass		*Etheostoma rupestre*	Rock darter
	Pomoxis nigromaculatus	Black crappie		*Etheostoma stigmaeum*	Speckled darter
Cottidae	*Cottus carolinae*	Banded sculpin		*Etheostoma swaini*	Gulf darter
Cyprinidae	*Campostoma oligolepis*	Largescale stoneroller		*Etheostoma tallapoosae*	Snubnose darter
	Campostoma pauciradii	Bluefin stoneroller		*Percina brevicauda*	Coal darter
	Cyprinella callistia	Alabama shiner		*Percina kathae*	Mobile logperch
	Cyprinella gibbsi	Tallapoosa shiner		*Percina smithvanizi*	Longhead darter
	Cyprinella trichroistia	Tricolor shiner		*Percina maculata*	Blackside darter
	Cyprinella venusta	Blacktail shiner		*Percina nigrofasciata*	Blackbanded darter
	Hybopsis lineopunctata	Lined chub		*Percina palmaris*	Bronze darter
	Hybopsis winchelli	Clear chub		*Percina sciera*	Dusky darter
	Luxilus chrysocephalus	Striped shiner	Petromyzontidae	*Ichthyomyzon castaneus*	Chestnut lamprey
	Luxilus zonistius	Bandfin shiner		*Ichthyomyzon gagei*	Southern brook lamprey
	Lythrurus alegnotus	Pretty shiner	Poeciliidae	*Gambusia affinis*	Western mosquitofish
	Lythrurus atrapiculus	Blacktip shiner		*Gambusia holbrooki*	Eastern mosquitofish
	Lythrurus bellus	Pretty shiner			
	Macrhybopsis storeriana	Silver chub			
	Nocomis leptocephalus	Bluehead chub			
	Notemigonus crysoleucas	Golden shiner			
	Notropis ammophilus	Orangefin shiner			
	Notropis amplamala	Silverjaw minnow			
	Notropis baileyi	Rough shiner			
	Notropis hypsilepis	Highscale shiner			
	Notropis longirostris	Longnose shiner			
	Notropis stilbius	Silverstripe shiner			
	Notropis texanus	Weed shiner			
	Notropis xaenocephalus	Coosa shiner			
	Phenacobius catostomus	Riffle minnow			
	Pimephales notatus	Bluntnose minnow			
	Pimephales vigilax	Bullhead minnow			
	Pteronotropis merlini	Flagfin shiner			
	Semotilus atromaculatus	Creek chub			
	Semotilus thoreauianus	Dixie chub			

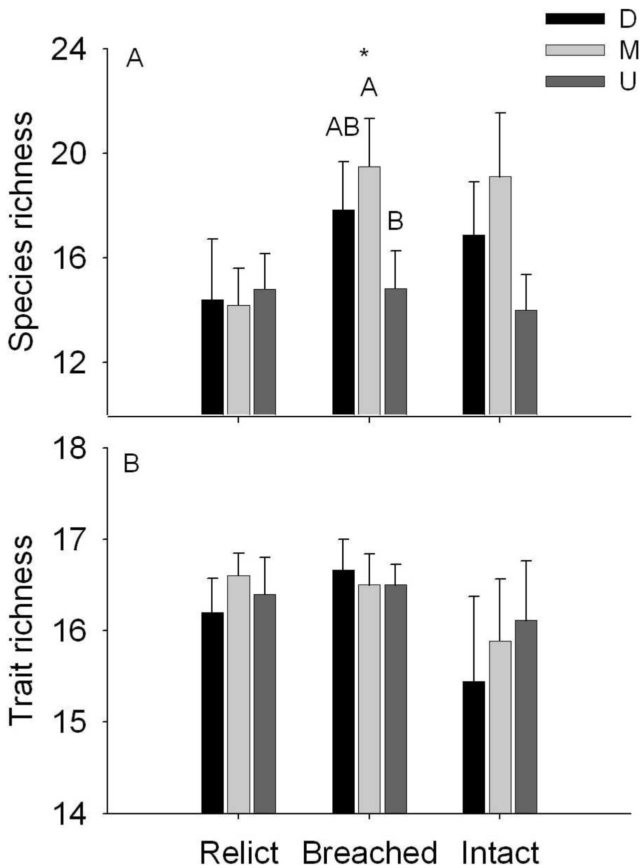

FIG. 1. Species (A) and trait (B) richness in reaches far downstream (D), immediately downstream (M), and upstream (U) of intact, breached, or relict mill dams in streams in Alabama, USA. * indicates a significant difference among reach locations within a particular dam condition. Bars with different letters within groups are significantly different (general linear model, $p < 0.05$).

breached than in streams with intact or relict dams. Also, reaches below intact dams often had large plunge pools, high algal cover, and harbored vast numbers of algivores (e.g., *Campostoma* spp., among others) (4th-corner analysis). Most physicochemical conditions we measured did not differ in relation to dam condition, but we observed intense sedimentation and altered geomorphology in several U and M reaches, a trend that has been documented in other systems with mill dams (Walter and Merritts 2008). Such conditions probably would be tolerable to many generalist spawners (polyphils) and less-conducive to nonguarding lithophilic spawners and could partially explain patterns revealed in the 4th-corner analysis.

We used a combination of taxonomic and functional measures to evaluate fish assemblage structure in these streams. These measures conveyed somewhat different (often complementary) information regarding fish responses. For example, species richness was lower in U than in M reaches, but trait richness did not differ between reach locations. Functional associations, especially of trophic, reproductive, and habitat traits, with reach location were observed in streams with breached dams. Ordination of species data generally was not informative because no discernable groupings or correlations with physicochemical conditions could be determined. However, ISA showed that *E. americanus* was an indicator for U reaches in streams with relict dams. This result was supported by 4th-corner analysis, which identified a tendency for fishes with increased age at maturity to occur in U reaches of streams with relict dams. *Esox americanus* is often found in vegetated stream margins and slow backwater areas (Boschung and Mayden 2004). We did not sample impoundments, but many of our U reaches in streams with relict dams probably were closer to the former impoundment than were our U reaches in streams with intact or breached dams. Thus, the association of *E. americanus* with reaches upstream of relict dams may be a result of dispersal of fauna associated with the former impoundment.

Seasonal movements of some species (e.g., certain catastomids and cyprinids) are well documented, but most of the species we found would not be considered migratory (Boschung and Mayden 2004). Nevertheless, these dams could be a barrier to recruitment/dispersal even to nonmigratory fishes (Ward and Stanford 1995). Trait analysis identified an increase in nonguarding, open-substrate lithophilic spawners in D reaches of streams with relict dams, but no associations in reaches of streams with breached and intact dams. This group included 9 cyprinid species and all of the 7 catastomid species we collected. The evidence is indirect, but it suggests a higher prevalence of fishes that require seasonal movement for spawning in streams with relict dams than in streams with intact or breached dams. This assemblage pattern indicates that the dam structure might be an impediment to the movement of certain species or that upstream habitat conditions are being influenced by the dam. However, our data should be interpreted cautiously because constraints on fish assemblages vary spatially and temporally (Schlosser 1991), and our sampling regime might not have captured the critical habitat conditions or timing dictating these assemblage patterns, particularly in regard to reproductive biology.

Other authors have suggested that low-head dams can influence water volume and temperature and pose considerable threats to fish assemblages (Cumming 2004). We did not detect physicochemical and hydrologic-connectivity changes associated with mill dams, but our data support the contention that water

TABLE 5. Correlation coefficients (r) from correlation analyses of physicochemical variables and species and trait richness. Only significant relationships are shown. * = $p < 0.05$.

	Intact		Breached		Relict	
Species richness	Temperature	0.48*	Conductivity	−0.55*	% bedrock	−0.59*
					% wood	0.58*
Trait richness	pH	−0.53*	Conductivity	−0.47*	% bedrock	−0.61*
	Temperature	0.47*	Substrate	−0.49*		

physicochemical conditions associated with mill dams may influence fish assemblages. Measures of benthic habitat were strong correlates of species and trait richness in streams with relict dams, but physicochemical measures (e.g., water temperature, pH, conductivity) were strong correlates in streams with intact and breached dams. This result suggests that the factors influencing fish assemblages in streams recovering from dams might differ from the factors influencing fishes in streams that currently possess dams. Furthermore, our knowledge of the timing of many of the dam breaches and removals in this study is incomplete (Gangloff et al. 2011). Not all dates of dam removal or damage were available in our study area, but streams with relict dams probably have been in their current condition for >50 y, whereas breached dams have been in their current condition for <20 y (Gangloff et al. 2011). Therefore, the apparent recovery of fish assemblages associated with relict dams may simply be a function of differences in system stability associated with the length of time since dam removal compared to relatively recent and ongoing disturbance associated with dam breaching.

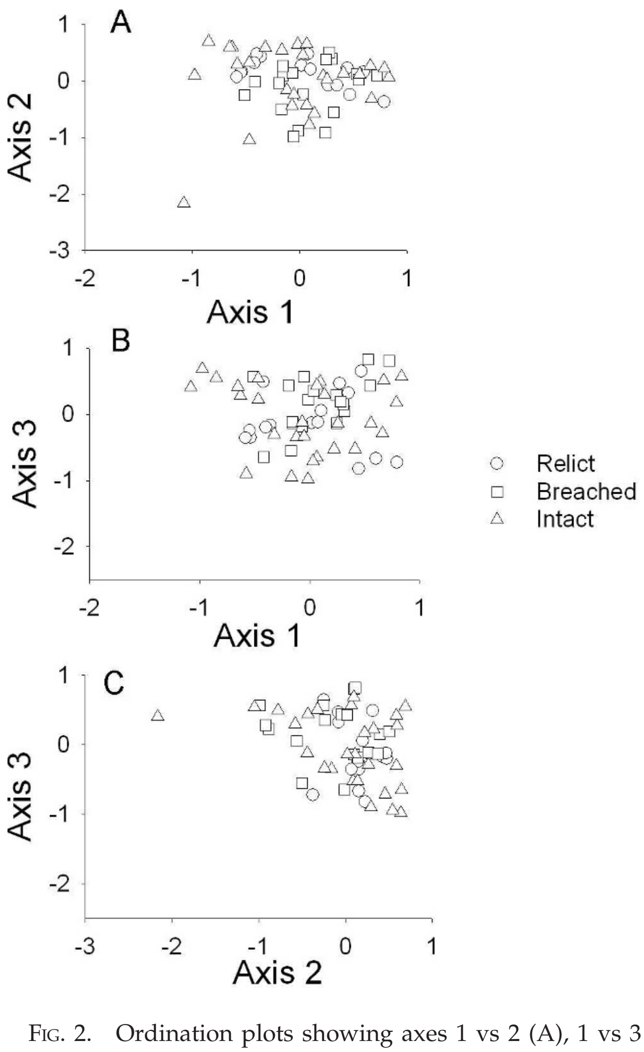

FIG. 2. Ordination plots showing axes 1 vs 2 (A), 1 vs 3 (B), and 2 vs 3 (C) of a nonmetric multidimensional scaling ordination of sites in species space based on fish rank abundance. Axis 1 explained 30.1%, axis 2 explained 30.4%, and axis 3 explained 22.1% of the variation in fish assemblages across the sites.

Breached dams had stronger effects than intact or relict dams on fish assemblages. This pattern was echoed by the results of studies of freshwater mussels (Gangloff et al. 2011) and crayfish (Hartfield et al. 2011) in these streams. Gangloff et al. (2011) found that breached dams had greater negative effects than intact or relict dams on mussel abundance and diversity. Hartfield et al. (2011) found larger among-reach differences in crayfish assemblages in streams with breached dams than in streams with intact or relict dams. However, the effects of intact dams on fish assemblages were relatively weak. This lack of strong effect may be partially attributable to the conservative analysis used in our study, but it also suggests the importance of structural stability to fish assemblages, particularly in the case of breached dams.

Recovery times seemed to differ among fish, mussel, and crayfish assemblages. Fish traits differed less among reach locations in streams with relict dams than in streams with breached dams, a result that suggests recovery (or at least homogenization) following dam removal/failure. A similar trend was observed with crayfishes, but mussel assemblages appeared to be influenced by relict dams, a result suggesting they have a longer recovery time. Thus, the magnitude of ongoing effects of and time needed for recovery from dams probably depend on the

Table 6. Significant species and trait relationships to dam condition and reach location based on indicator species analysis and 4th-corner analysis. B = breached mill dam, R = relict mill dam, I = intact mill dam, + = positive relationship, − = negative relationship, * = $p < 0.05$, ** = $p < 0.005$.

	Intact			Breached			Relict		
Indicator	D	M	U	D	M	U	D	M	U
Species									
Esox americanus									+ *
Trophic									
Benthic				+ *		− *			
Algae		+ *							
Physiology									
Age at maturity									+ *
Maximum temperature						+ *			
Reproductive									
Nonguarder, open substrate, lithophil							+ *		
Guarder, substrate chooser, lithophil			+ *						
Guarder, nest spawner, polyphil					+ *	+ **			
Habitat									
Gravel						− *			
Cobble					− *	− **			

natural histories of the assemblages of interest (e.g., mobility, colonization, habitat specificity).

Our results show that fish assemblages are influenced by small, low-head mill dams in southeastern US streams and that these structures continue to influence fish after they have been breached. Fish recovery from the effects of dams was evidenced by longitudinal similarity of reaches in streams with relict dams. This evidence suggests fish assemblages above an existing structure probably would not benefit from its breaching but might benefit from its removal. In contrast, removal of breached structures could pose significant risks to other sensitive species downstream (Gangloff et al. 2011). Thus, dam breaching and removal projects should include extensive, case-specific cost/benefit evaluations of stream biota and associated habitats and subsequent monitoring that allows sufficient recovery time for measurable effects.

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