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Associations between small dams and mollusk assemblages in Alabama streams

Michael M. Gangloff[1]
Biology Department, Appalachian State University, Boone, North Carolina 28608-2027 USA

Emily E. Hartfield[2]
Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA

David C. Werneke[3] AND **Jack W. Feminella**[4]
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849-5407 USA

Abstract. Small dams are ubiquitous yet poorly understood features in many streams. Dam removal is being used increasingly in stream restoration projects as a means to enhance habitat connectivity and ecosystem function. However, habitat- and assemblage-level effects of small dams on stream mollusk assemblages are poorly documented. We examined associations between stream physicochemical habitat variables and mollusk assemblages at 22 small (<10 m) dams in 3rd–5th order Alabama streams. We sampled 66 reaches (3 reaches/dam) associated with intact, breached, and relict small dams. For each dam, we designated 3 study reaches: 1) immediately downstream from the dam, 2) 500 to 5000 m downstream, and 3) 500 to 5000 m upstream from the impounded or formerly impounded zone. We used principal components analysis (PCA) to examine variation in physical-habitat conditions across all sites. Four principal components accounted for ~72% of the variation in physical-habitat conditions across sites. One PC score (PC_1, corresponding to increased substrate size) was negatively associated with several mollusk metrics including total mussel abundance, taxon richness, catch-per-unit-effort (CPUE), and density. We observed few significant differences between simple habitat variables at sites up- and downstream of dams. However, streams with intact dams had significantly higher mussel catch rates (CPUE) and taxon richness than did streams with breached or relict dams. We used forward-stepwise multiple regression to model the effects of habitat variables (as standardized PC scores) on mollusk assemblage metrics. PCs representing substrate composition were the strongest predictors of total mussel abundance and richness. Abundance of other mollusks including deposit-feeding snails, the exotic bivalve *Corbicula fluminea*, and fingernail clams was correlated with PC scores describing variability in substrate organic matter composition or stream gradient. We think these data indicate that some intact dams enhance mollusk habitat in downstream reaches. Streams with intact dams appear to be more geomorphically stable than streams with breached or relict dams and conditions in the mill reach may reflect preconstruction stream conditions. Breached dams warrant higher prioritization for removal than intact structures because habitat degradation may persist for decades and impede re-establishment of native mollusk populations.

Key words: Unionidae, Gastropoda, Mollusca, mill dam, physical habitat, substrate composition, water chemistry.

Impoundments are widely recognized as having dramatic negative effects on freshwater habitats. Dams transform upstream reaches to lentic habitats, restrict downstream sediment movement, and alter physicochemical characteristics of fluvial ecosystems. Large dams are numerous and widespread in many southeastern USA streams, e.g., currently >10,000 dams exist in the state of Alabama (Alabama Office of Water Resources; http://www.adeca.alabama.gov/). Large dams impound ~44% of the mainstem Alabama, Coosa, and Tallapoosa rivers in Alabama and Georgia and have transformed significant portions of many other large southeastern North American rivers

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[1] E-mail addresses: gangloffmm@appstate.edu

[2] hartfiee@science.oregonstate.edu

[3] wernedc@auburn.edu

[4] feminjw@auburn.edu

(Williams et al. 1992, 2008, Benke and Cushing 2005, Gangloff and Feminella 2007, Irwin et al. 2007).

Physical, chemical, and biological effects of large dams can include altered thermal and sediment regime, channel morphology, and fish dispersal (Fraser 1972, Baxter 1977, Cushman 1985, Irvine 1985, Travnichek et al. 1995, Blalock and Sickel 1996, Watters 1996, Dean et al. 2002, Gehrke et al. 2002, Poff and Hart 2002, McLaughlin et al. 2006). Hydropower peaking operations require large dams that often significantly alter the magnitude, frequency, and seasonality of minimum and maximum flow events (Poff et al. 1997, Magilligan and Nislow 2005, Graf 2006). In many tailwater systems, high-flow events are rare, sediment migration is reduced, and channels become incised and sediments armored. Geomorphic changes lead to decreased floodplain connectivity and reduce organic matter and nutrient exchange between lotic and riparian food webs (Welcomme 1975, Baxter 1977, Kingsford 2000, Junk and Wantzen 2004). Reaches downstream of large, hypolimnetic-release dams often are characterized by cold or O_2-poor waters and depauperate fish and mollusk and macroinvertebrate assemblages (Baxter 1977, Neves et al. 1997, Vaughn and Taylor 1999, Jansson et al. 2000, Hart et al. 2002).

The effects of large dams on aquatic organisms and lotic habitats have been well documented, but few studies have examined effects of more ubiquitous small, surface-release, or low-head dams (but see Watters 1996, Dean et al. 2002, Lessard and Hayes 2003). Low-head dams (dams with a hydraulic height <10 m) are typically overflow or spillway structures. According to census records, >65,000 low-head dams existed in the eastern US by 1840, most of which were built for water-powered milling (Walter and Merritts 2008). In contrast to large dams, most small dams are operated as run-of-the-river structures (i.e., most of the time, water levels and spill-over are proportional to natural hydrologic variation). Releases from mill dams usually are altered for only short durations when power is needed to operate machinery. Moreover, because most mill or low-head dams are overflow (top-release) structures, their tailwaters are typically warmer than up- or downstream reaches (Lessard and Hayes 2003). These more moderate changes to stream habitats associated with small dams produce relatively subtle and spatially-limited changes along stream continua. Intriguingly, effects of small dams appear to vary considerably across lotic taxa. Previous studies suggest that some invertebrates in reaches downstream from lake-outlets and low-head dams may benefit from lentic-derived food or temperature subsidies (Spence and Hynes 1971, Parker and Voshell 1983, Richardson 1984, Mackay and Waters 1986, Richardson and Mackay 1991, Singer and Gangloff 2011).

Alabama supports >65% of North America's native freshwater mussel and ~27% of its native snail taxa (Lydeard and Mayden 1995, Neves et al. 1997, Garner et al. 2004, Williams et al. 2008). Global freshwater mollusk imperilment is caused primarily by habitat alteration by dams and other water-control structures (Williams et al. 1992, Neves et al. 1997, Vaughn and Taylor 1999, Strayer et al. 2004, Haag 2009). Dams are thought to have contributed to the extinction or imperilment of >½ of Alabama's native freshwater mussel and snail taxa (Garner et al. 2004, Williams et al. 2008, Haag 2009).

In many parts of North America, private landowners, natural resource agencies, and nongovernment organizations (NGOs) advocate removing mill dams and other low-head structures to restore stream physicochemical and biotic connectivity. However, removal of these structures is often controversial (Stanley and Doyle 1993, Schuman 1995, Bednarek 2001, Grant 2001, Poff and Hart 2002). Dam removal can increase downstream sediment mobilization, and sediments previously stored in impoundments may contain elevated contaminant levels (Pejchar and Warner 2001, Hart et al. 2002, Ashley et al. 2006). Furthermore, dam removal may increase the spread of invasive aquatic species, and some authors have advocated using small dams to prevent these taxa from invading new habitats (Rahel and Olden 2008). Moreover, sediment movement and geomorphic adjustment associated with uncontrolled removals may have negative consequences for downstream mollusk populations (Sethi et al. 2004). Long-term implications of uncontrolled and controlled dam removals are poorly documented because few studies have followed post-dam-removal stream recovery for more than a few years (but see Vinson 2001). We studied associations between small dams and lotic mollusks in 22 Alabama streams. We examined how dam status (intact, breached, or relict) affects stream physicochemical habitat and the abundance, richness, and persistence of mollusk assemblages.

Methods

Study site

We sampled habitat conditions and mollusks at low-head dam sites in 22 streams across Alabama. We selected 10 intact, 6 breached, and 6 relict dams. Beached dams obstructed 25–95% of the channel, whereas relict dams obstructed <25% of the channel.

At 5 of 6 relict dam sites, only footers remained along the channel margin to indicate the former dam site. We attempted to select streams that were large enough (i.e., contained the necessary ions and productivity levels) to support freshwater mollusks. Sixteen dam sites were in the Mobile River Basin (MRB), 3 were in the Apalachicola-Chattahoochee-Flint (ACF) River Basin, 2 were in the Tennessee River Basin (TRB), and 1 was in the Choctawhatchee River Basin (CRB).

Physicochemical habitat

For each dam, we established three 150-m study reaches: 1) a mill reach extending from the dam to 150 m downstream, 2) a downstream reach >500 m (range 500–5000 m) downstream from the dam, and 3) an upstream reach in a free-flowing reach upstream from the impoundment. 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. We measured channel wetted width and substrate composition ($n = 320$ particles/site) for each transect. We quantified substrate composition with a modified Wolman pebble count (Wolman 1954) and measured the maximum diameter or characterized composition of 20 randomly selected substrate particles/transect. We computed the mean and median particle size and the proportion of the stream bed composed of unmeasured substrate particles (bedrock, organic matter, woody debris, sand, and silt) at each reach. We used US Geological Survey (USGS) topographic maps to compute link magnitude (the number of upstream 1st-order tributaries) for all reaches to serve as a proxy for stream catchment area/discharge (Gordon et al. 2004).

We collected grab samples for water-chemistry analyses from each study reach during low-water conditions in July and August 2007. Water samples were analyzed by the Auburn Fisheries and Allied Aquacultures Water Analysis Laboratory (AUFWAL). AUFWAL analyzed samples for NO_3-N and PO_4-P with mass spectrometry and persulfate digestion and ultraviolet (UV) analysis (APHA 1998), respectively. We measured specific conductance (Milwaukee Sharp C66; Milwaukee Instruments, Rocky Mount, North Carolina), pH (Milwaukee Sharp pH52), and dissolved O_2 (YSI 55; Yellow Springs Instruments, Yellow Springs, Ohio) on site concurrent with mollusk surveys and water-sample collection.

Mollusk assemblages

At each reach, we characterized mollusk assemblages with semiquantitative and quantitative techniques. We excavated five 0.25-m^2 quadrats along each transect ($n = 75$–80 quadrats/site, area $\approx$ 20 m^2). We spaced quadrats equidistantly across the channel and excavated them to a depth of $\sim$10 cm. We sieved excavated substrate through 8-mm mesh. Sieves effectively retained unionids and fingernail clams (Sphaeriidae) $>$6.5-mm total length (TL) and most adult snails (primarily Pleuroceridae and Viviparidae). The sieves generally did not retain young-of-year and smaller gastropods (e.g., *Physa*, Hydrobiidae).

We used semiquantitative (timed-search) surveys to characterize mussel assemblages at reaches with mussel densities below quadrat detection limits. Our sampling effort was sufficient to detect mussel populations at densities of 0.05 mussels/m^2 (i.e., 1 mussel from 20 m^2 or 80 0.25-m^2 quadrats). We also used replicate timed searches (RTSs) to assess mussel assemblage composition and relative abundance. We conducted 15 to 16 RTSs at each reach at 10-m intervals (between established transects). During each RTS, a team of 2 to 3 trained investigators used visual tactile searches to locate mussels. Typically, searchers used mask and snorkel or waded, but we also used SCUBA in deeper sections (mean depth $>$ 1.0 m).

We counted all mollusks encountered in quadrats and RTSs and identified them to the lowest practical taxonomic level (species for unionids, *Corbicula fluminea*, and snails in the family Viviparidae and Pleuroceridae; genus or family for all other taxa, e.g., *Physa* spp., Sphaeriidae). We pooled nonunionid mollusk data at the family level before analysis. We measured TL of all freshwater mussels. We deposited vouchers of all taxa encountered, including unionid shells, snails, and fingernail clams in the Auburn University Museum.

Last, we examined the effect of dam status on changes in freshwater mussel assemblages in 13 of our 22 focal streams that currently or historically supported species-rich ($>$6 species) assemblages. We used data from historical collections and distributional surveys (e.g., Jenkinson 1973, Hurd 1974, Brim-Box and Williams 2000, Gangloff and Feminella 2007, Williams et al. 2008) to recreate preimpoundment freshwater mussel assemblages. We then computed the percentage of the mussel assemblage in each stream that has been lost to date. For this analysis, we added a 4th dam classification (intact/breached) to better reflect either the dam's recent history (breached and repaired) or structural differences (some dams are intact but have an open sluiceway adjacent to the dam that permits movement of organisms). We then computed the mean % fauna lost for each dam category.

Statistical analyses

We computed reach-scale means for all habitat and mollusk data. We used total number of mussels as a qualitative measure of mussel abundance, but all other metrics were quantitative (mussel density, taxon richness) or semiquantitative (e.g., mussel CPUE). CPUE data were unavailable for some reaches. We transformed all data ($\sqrt{[n + 1]}$) prior to analysis to improve normality. We used analysis of variance (ANOVA) with Least Significant Difference (LSD) post hoc tests to examine differences in mollusk assemblage metrics across streams with intact, breached, or relict small dams. We used transect means to calculate reach-scale means that were treated as replicates within a stream.

Site did not significantly affect mollusk assemblage metrics in a 1-way ANOVA with site as a fixed factor. This result suggested that site position across all streams was not important. We also examined the data for evidence of reach × dam status interactions and found none. Use of complicated ANOVA designs can strongly decrease model degrees of freedom and, thus, power to detect patterns in the data. We think that the risks of overlooking important patterns outweigh the risks of reporting spurious patterns in our study. Therefore, we pooled reaches in analyses (we did not separate upstream, mill, and downstream reaches) to control for natural differences in mollusk assemblages and habitat conditions among streams. This approach is a conservative way to account for broad-scale differences between streams and to avoid Type II error (Toft and Shea 1983).

We used principal components analysis (PCA) to examine physical-habitat variability among study reaches. We were unable to compress water-chemistry data with PCA because they were incomplete. Physical habitat (depth, current velocity, channel width, substrate composition) data were rotated (varimax) and normalized (Kaiser) to maximize explained variance among components. We extracted principal components (PCs) with eigenvalues >1.0 and excluded reaches with missing habitat data. We then used forward-stepwise multiple regression (FSMR) analysis to examine relationships between habitat-based PC scores and mollusk assemblage metrics and to assess which PC scores were the best predictors of mollusk assemblage metrics.

Results

Mollusk assemblages

Mussel density, CPUE, and taxon richness differed significantly among dam statuses (ANOVA, $F > 3.5$, $p < 0.038$). Mussel CPUE was significantly greater in streams with intact dams than in streams with breached or relict dams (Fig. 1A). Mussel density and richness were not significantly different between streams with intact and relict dams (Fig. 1B, C). However both were significantly higher in streams with intact and relict dams compared to sites in streams with breached dams (Fig. 1B, C). Fingernail clam (Sphaeriidae) densities also differed significantly among streams with intact, relict, and breached dams. Fingernail clam densities were significantly lower in

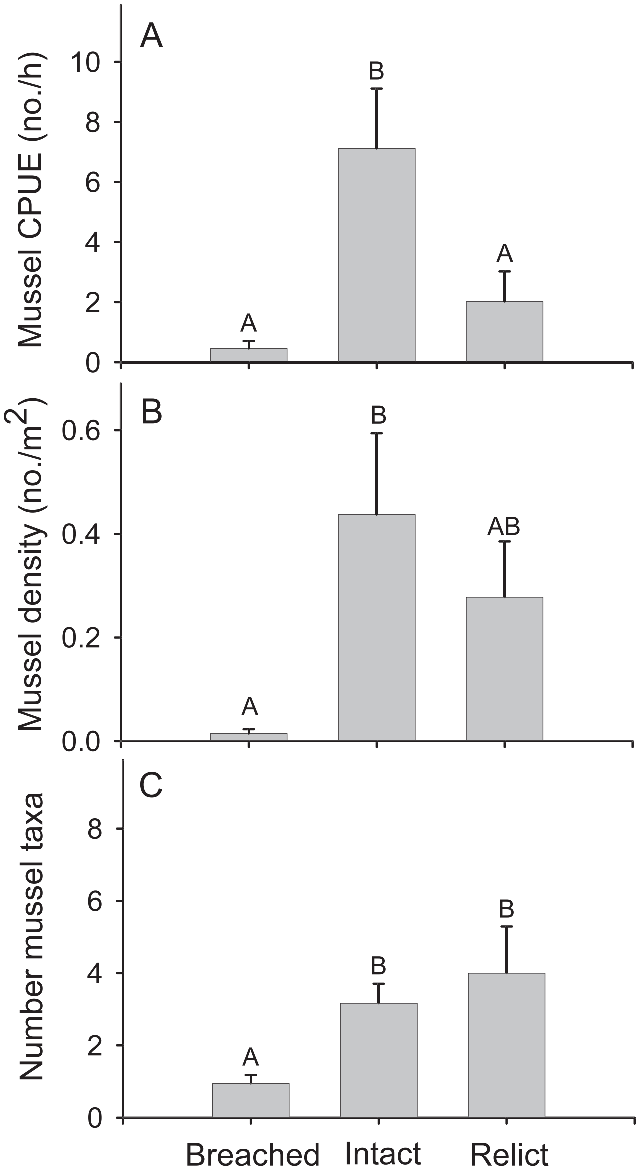

Fig. 1. Mean freshwater mussel catch-per-unit-effort (CPUE) (A), density (B), and number of taxa encountered alive (C) in streams with breached, intact, or relict small dams in Alabama. Bars sharing the same letter are not significantly different from one another.

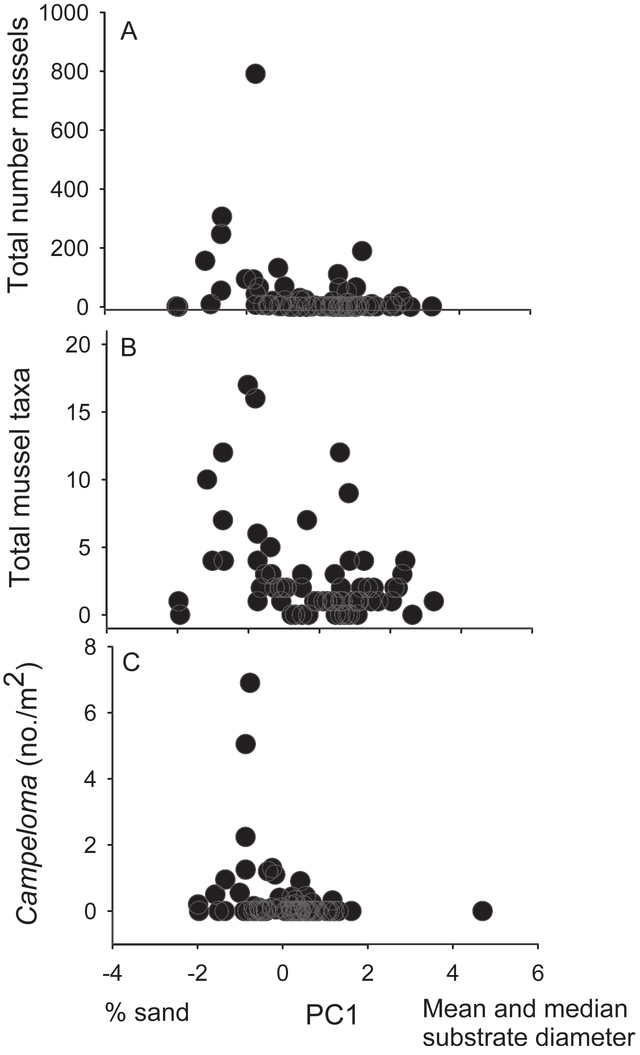

FIG. 2. Relationship between principal component (PC) 1 (substrate size) and total number of freshwater mussels (A), taxon richness (B) and *Campeloma* spp. (Gastropoda: Viviparidae) density (C) in streams with breached, intact, and relict small dams in 22 Alabama streams.

streams with relict dams but did not differ between streams with intact and breached dams.

FSMR models indicated that 1 synthetic variable, PC_1 (substrate size), was an important predictor of reach-scale mollusk assemblage metrics including total mussel abundance, taxon richness, and *Campeloma* density (Fig. 2A–C). Addition of PC_2 (substrate organic matter composition) to mollusk richness models marginally increased predictive ability of total mussel abundance and taxon richness models. When PC_2 was added, r^2 increased from 0.166 to 0.219 for CPUE mussel taxa and from 0.107 to 0.208 for total mussel taxa models (Table 1). Both pleurocerid and sphaeriid densities were related to stream size (as PC_4). Pleurocerid density was positively correlated with PC_4, and sphaeriid density was negatively associated with PC_4. Predictive abilities of all FSMR models were low (<22%; Table 1).

Examination of historical data revealed that streams with relict, breached, or intact/breached dams have all lost >80% of their historical freshwater mussel assemblages (Table 2). In contrast, streams with intact dams lost, on average, only 8.4% of their historical mussel assemblages. All sites had mill dams present when historical surveys were conducted.

Habitat variables

Link magnitude (LM) differed significantly between streams with intact, breached, and relict dams (ANOVA, $F = 25.8$, $p < 0.001$). Streams with intact dams were significantly smaller (i.e., had lower LM values) than streams with breached dams, and streams with relict dams were significantly larger than breached dams (all $p < 0.001$). We observed few statistically significant differences between habitat variables in streams with intact, breached, or relict dams. Channel widths were significantly lower in streams with intact dams than in streams with breached dams ($p = 0.01$). However, widths were not significantly different between streams with intact and relict dams. Stream current velocity differed significantly among streams (ANOVA, $F = 23.7$, $p < 0.001$) and was greatest in streams with breached dams.

Dissolved O_2 (DO) concentration also differed among streams (ANOVA, $F = 3.13$, $p = 0.48$) and was greatest in streams with breached dams. DO did not differ between streams with intact and relict dams. Total N concentration was significantly different among streams with intact, breached, or relict dam sites. Streams with intact dams had significantly lower total N concentrations than did streams with breached or relict dams (ANOVA, $F = 8.4$, $p < 0.001$). N concentrations did not differ between streams with breached and relict dams.

PCA of physical-habitat data revealed 4 PCs with eigenvalues >1.0 (Table 3). Together these PCs accounted for ~72% of the variation in among-reach physicochemical habitat conditions. PC_1 accounted for ~24.5% of the variation in habitat conditions at all reaches and was a proxy for substrate size. Mean and median substrate diameter and % bedrock loaded positively on PC_1 whereas % sand loaded negatively (Table 3). PC_2 was a proxy for stream organic matter content and included ~17% of the variability in habitat variables among reaches. Current velocity loaded positively and % silt loaded negatively on PC_3. PC_3 was a proxy of stream geomorphology and

TABLE 1. Results of forward-stepwise multiple regression model building process for freshwater mollusk assemblage metrics. df = 1,64 for all models except Pleuroceridae (df = 1,61). CPUE = catch-per-unit-effort.

Dependent variable	Independent variables	β	SE	*F*	*p*	r^2
Total mussels	PC_1 (Substrate)	−0.261	13.4	4.68	0.034	0.068
Total taxa	PC_1 (Substrate)	−0.327	0.410	8.3	0.001	0.208
	PC_2 (Organic wood)	0.319	0.410			
CPUE taxa	PC_1 (Substrate)	−0.340	0.393	8.8	<0.001	0.219
	PC_2 (Organic wood)	0.322	0.393			
Quadrat taxa	PC_2 (Organic wood)	0.281	0.297	5.49	0.022	0.079
Pleuroceridae	PC_4 (Stream size)	0.269	4.81	4.78	0.033	0.073
Sphaeriidae	PC_4 (Stream size)	−0.272	0.168	5.1	0.027	0.074

accounted for 16% of the variability in habitat variables among reaches. Channel width and depth loaded positively on PC_4, a proxy for stream size (Table 3).

Discussion

Our data suggest that streams with intact small dams are more likely to support intact freshwater mussel populations than streams with breached or relict dams. Furthermore, multiple regression models indicated that dam-mediated physical-habitat conditions may influence how mollusks respond to these structures. We observed elevated historical mussel extirpation rates in streams with breached, relict, and breached/intact dams. These patterns suggest a strong, yet counterintuitive link between dam condition and freshwater mussel diversity. At the present time, the extent to which these links are the result of the localized effects of dam breaching or much broader phenomena occurring within individual watersheds is not clear.

TABLE 2. Comparison of historical and present freshwater mussel species richness in the mill reach of 12 Alabama focal streams. Historical richness was determined from museum records, published studies, or data obtained during recent surveys of the up- and downstream reaches. Dams designated as intact/breached allow some flow to move through the old dam raceway (Little Cahaba) or through openings at the base of the dam (Hatchet). The Little Uchee dam was breached until ~2005 when it was repaired.

Dam status	Stream	Historical richness	Present richness	Mean % change
Breach	Big Canoe	6	1	90.7%
	Buttahatchee	17	1	
	Choctafaula	17	1	
Intact/ breached	Hatchet	16	1	84.5%
	Little Cahaba	13	2	
	Little Uchee	8	2	
Intact	Big Flat	14	14	8.4%
	Brushy	13	12	
	Halawakee	8	6	
	Sandy	7	7	
Relict	Paint Rock	47	12	82.8%
	Pea	18	3	
	Cahaba	21	2	

Geomorphic changes to Alabama's stream ecosystems may be a major factor contributing to freshwater mussel declines in many relatively low-human-impact catchments (Gangloff and Feminella 2007). We speculate that landuse-mediated changes in stream geomorphology and neglect of antiquated small dams may act synergistically and result in dramatic declines of freshwater mussels following uncontrolled dam breaches. We think that most of the breached and relict dam sites in our study were unmanaged and that dam failure occurred because of flooding or human intervention. Sethi et al. (2004) found that uncontrolled dam breaches were strongly detrimental to mussel populations in a low-gradient Wisconsin stream. We are aware of no other published studies documenting the response of mussels to either controlled or uncontrolled dam removal. However, because mussels are sedentary, slow-growing, and long-lived, full post-disturbance recovery probably takes decades.

Our analyses of links between physical-habitat variables and mollusk assemblages suggest a strong role of substrate in mediating localized effects of dams on mollusk assemblages. Substrate size (as PC_1) was selected by FSMR analysis as the best predictor of mussel numbers and richness. Including PC_2 (substrate wood and organic matter content) increased the ability of models to predict total and CPUE-derived mussel richness, although PC_2 was negatively correlated with mussel metrics (Table 1). These results suggest that modification (coarsening) of stream substrates downstream from small dams may be partly responsible for positive effects on downstream mollusk populations. Restoring mollusk habitats in these systems may necessitate either human interventions (including re-engineered channel geomorphology and substrate

TABLE 3. Principal components (PCs) extracted from the physical-habitat data set with eigenvalues >1.0 and component factor loadings. Data were subjected to varimax rotation with Kaiser normalization.

Variable	PC1	PC2	PC3	PC4
Width				0.796
Depth				0.747
Velocity			0.767	
Mean substrate	0.871			
Median substrate	0.727			
% bedrock	0.586			
% wood		0.750		
% organic		0.878		
% sand	−0.740			
% silt			−0.833	
% variance	24.5	16.6	16	14.9
Cumulative % variance	24.5	41.1	57.1	72.1

augmentation) or the patience to allow natural re-establishment of new geomorphic equilibria.

Comparisons between streams with intact and relict dams suggest that mussel assemblages in Alabama streams are very slow to recover following dam breaching (Table 2). Comparison of recent and historical data showed that mussel species richness downstream from breached, breached/intact, and relict dams have declined substantially (>80%) from historical conditions. In contrast, streams with intact dams appear to have retained a much higher proportion of their historical mussel fauna. Unfortunately, we are aware of no published studies that have attempted to quantify freshwater mussel stream recolonization rates or tracked population recovery following a dam removal. However, given the increasing popularity of dam removal as a stream restoration tool, this opportunity probably will present itself soon. We urge agencies and companies engaged in these activities to obtain extensive preremoval data sets and to implement rigorous long-term monitoring programs to improve understanding of how dam removals may affect sensitive mollusk populations.

An incomplete knowledge of the history of some focal dams probably impeded our ability to classify them accurately, hence our use of a 4th category (intact/breached dams) when examining differences between historical and recent mollusk assemblages. For example, the defunct Alabama Power Company dam on Hatchett Creek has openings near its base that allow water (and presumably biota) to move downstream but not upstream. Griffin Mill on Little Uchee Creek was breached for at least 10 y prior to our study (MG, personal observation) but was repaired immediately before the study began. The mill dam on the Little Cahaba River has an in-channel sluiceway that permits up-and-downstream organism movement. These 3 structures appeared to have very different effects on stream habitats and mollusk assemblages than did the other intact, epilimnetic-release dams in our study. Water moving through intact/breached dams probably is cooler, more acidic, and lower in suspended material than water moving over the top of a dam spillway. Overflow dams may increase suspended organic and inorganic matter export to downstream reaches and this export may supplement mussel food resources and enhance shell growth conditions in the mill reach (Singer and Gangloff 2011).

Dam status and physicochemical habitat appeared to have little or no effect on populations of other freshwater mollusks. In part, this result may be because freshwater gastropods, the exotic Asian clam *Corbicula fluminea* and native sphaeriids (both order Veneroida) are relatively resilient to environmental disturbance compared to freshwater mussels. We found few interesting correlations between PC scores and these groups. This lack of correlations probably is because freshwater snails and veneroid clams are relatively short-lived and highly fecund groups that can persist in a wide range of habitat types. In addition, both sphaeriids and *C. fluminea* brood larvae internally and release fully functioning juveniles into the environment. In contrast, freshwater mussel larvae are fish parasites and must encounter a suitable host to complete their life cycle (Williams et al. 2008). However, freshwater mussel recruitment rates are thought to be low because juvenile mussels are nearly microscopic when they excyst from the fish host. Few studies have successfully tracked recruitment in wild populations. It was initially hypothesized that high mussel densities downstream from some dams may result from fish aggregations. However, a complementary study addressed this question and found no evidence that dams aggregate fish hosts or otherwise alter downstream fish communities (Helms et al. 2011). Helms et al. (2011) found that dams primarily affect the composition of upstream fish communities via alteration of habitat conditions and that many excluded taxa were nonmigratory, widespread species.

Taken together, our findings suggest that small dams may have benefits for freshwater mussels, but the mechanisms responsible for these benefits remain unclear. Therefore, breaching or removing relatively benign smaller dams may ultimately prove detrimental to sensitive mussel taxa. Streams that still have intact, older dams also typically supported large mussel populations, probably because the channel is stable across broad temporal and spatial scales. Many mill dams have been in the same place for >100 y. Removing these structures can reinvigorate channel down-cutting and translate geomorphic disturbances over broad spatial scales. We recommend that subsequent stream restoration projects in these streams focus on breached dam sites. Breached dams are better removal targets than intact dams because reaches downstream from breached dams generally lack imperiled mussel populations. In addition, habitat degradation and destabilization (or substrate starvation) generally are greater in streams with breached dams, so restoration projects probably could benefit more severely affected habitats by targeting streams with breached dams. Controlled removal of breached and intact dams probably holds important benefits for future stream-restoration projects, but the appropriateness of dams for removal should be assessed on a case-by-case basis. Ideally, dam-removal projects should be linked to broader-scale efforts to restore and rehabilitate stream habitats.

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