

**Consequences of Low-head Dams on Crayfish Distribution and Gene Flow in  
Alabama Streams**

by

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## Abstract

Dams are numerous in many eastern US streams, and instream physicochemical and biotic impacts of dams can alter flow and sediment regimes and channel geomorphology as well as reducing longitudinal movement by fishes and other mobile organisms. In addition, dams can fragment populations, thus decreasing genetic diversity while increasing extinction vulnerability. I quantified freshwater crayfish abundance and their habitats at reaches upstream (1000–5000 m), immediately downstream (mill reaches), and  $\geq 500$  m downstream of 22 low-head milldams within 9 Alabama drainages in 2006–2008. Eleven dams were intact, 5 were partially breached, and 6 were considered relict with more natural flow regimes. On streams with intact dams, crayfish abundance was lower at mill reaches than at reaches upstream of impoundments or further downstream, whereas on streams with breached dams abundance was higher at upstream reaches than at mill or downstream reaches. In contrast, longitudinal patterns in crayfish abundance were similar among sites on streams with relict dams. Predatory fish abundance was higher at mill reaches on streams with intact dams than at sites upstream or further downstream, suggesting that predatory fish aggregations at dam reaches were responsible for low crayfish abundance. Genetic diversity and population connectivity of 2 crayfish species (*Cambarus striatus* and *C. coosae*) also was quantified from upstream, mill, and downstream

reaches of 2 focal, intact dam sites by sequencing a fragment of the mitochondrial cytochrome oxidase I (COI) gene. *Cambarus striatus* in Sandy Creek showed evidence of upstream population isolation with movement limited to downstream migration across the dam, whereas *C. coosae* in Hatchett Creek showed no evidence of population structure. Our results suggest that small low-head dams and their reservoirs can alter abundance and impede longitudinal migration of some freshwater crayfishes.

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## Chapter One: Introduction and Literature Review

Dams are numerous and widespread throughout the state of Alabama and elsewhere in the US, with >10,000 dams occurring in Alabama alone (AL Office of Water Resources <http://www.adeca.alabama.gov/>) and up to 44% of the mainstem Alabama, Coosa, and Tallapoosa rivers being impounded (Irwin et al. 2007). These structures were built for flood control, hydroelectricity, water storage, recreation, and irrigation. However, most dams within the state are not large hydroelectric structures. Of the >2200 Alabama dams included in the US Army Corps of Engineers National Inventory of Dams (NID) 2009 data set, 69% were <7.5 m in height and 29% were between 7.5 and 15.25 m tall. It is important to note that the NID includes only dams of  $\geq$  2 m height and 50 acre-ft (61700 m<sup>3</sup>) of storage or  $\geq$  7.5 m height and 15 acre-ft (18510 m<sup>3</sup>) of water storage (<http://crunch.tec.army.mil/>).

The effects of large dams on aquatic organisms and their habitats in large rivers have been well documented, whereas little research has been done to assess effects of small, surface-release, or low-head dams on low-order streams (Watters 1996, Dean et al. 2002, Lessard and Hayes 2003). Low-head dams are those with a hydraulic height of <15m and are typically overflow or spill-way structures

(Poff and Hart 2002). 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).

### *Physicochemical Impacts*

Physicochemical impacts of dams can be dramatic. Perhaps the most obvious effects of dams on streams are changes in the hydrologic regime, channel geomorphology, water temperature, and chemistry, both within the impounded footprint and downstream of dams. Dams and dam alteration may alter the magnitude of minimum flow events typically increases and number of maximum flow events decreases (Poff et al. 1997); in addition, the rate of change in flow (flashiness) increases, although the duration and magnitude of these events often decrease (Poff et al. 1997). Timing of seasonal high and low flow events is altered, resulting in more predictable and less variable flow regimes (Magilligan and Nislow 2005, Graf 2006). In turn, lower magnitude of high-flow events downstream reduces nutrient uptake by flood plains through the deposition of silt during floods, thereby reducing flood plain–stream nutrient exchange (Welcomme 1975, Baxter 1977, Kingsford 2000, Junk and Wantzen 2004).

Decreased current velocity in the impounded section increases sediment deposition upstream of the dam, which usually causes tailwaters to become sediment-starved and downstream sections to exhibit increased scour, streambed lowering, and bed coarsening (Baxter 1977, Chien 1985, Graf 2005). Moreover, reduced magnitude of high-flow events and decreased deposition often cause

tailwaters to become less geomorphically complex, with fewer bars and islands and reduced shallow-water habitat (Poff et al. 1997, Graf 2006). At the watershed level, such dramatic changes may transform slow-flowing marshy streams into fast-flowing gravel-bottomed systems (Walter and Merritts 2008).

In addition to streambed alterations, dams also alter natural thermal regimes (Baxter 1977). Reduced current velocity and increased solar inputs within reservoirs can increase surface water temperatures and plankton growth rates (Baxter 1977). Reduction in current velocity in impounded sections also may cause depth stratification, resulting in a colder but oxygen-poor hypolimnetic zone relative to surface waters (Hart et al. 2002). Increased surface water temperature in impounded waters can result in higher densities of primary producers (e.g., algae and cyanobacteria), which, by increased respiration rates, may result in anoxia or hypoxia (Carmago et al. 2005). In addition, most low-head dams are overflow dams and often result in a significant increase in temperature of dam tailwaters (Lessard and Hayes 2003). The resulting low dissolved oxygen levels can, in turn, cause fish kills and release of macronutrients normally bound to bottom sediments (Correll 1998). Such releases may cause reservoirs to act as nutrient sources, thereby creating downstream eutrophication (Wright 1967).

Dams may also affect the stream nitrogen cycle. Nitrification has been shown to increase in impounded streams, especially in surface waters, where decreased current velocity and increased temperature may accelerate transformation of  $\text{NH}_4^+$  to  $\text{NO}_3^-$  (Polak 2004, Straus et al. 2004). In contrast, in

deeper anoxic sections ammonium denitrification and increases in N concentrations also can occur (Allen 1995). In addition, the physical force of water flowing over dams may cause tailwaters to become supersaturated with oxygen and atmospheric N<sub>2</sub> in downstream sections (Morris et al. 1968). Following dam construction, increases in N<sub>2</sub> concentrations in downstream reaches of >20% have been documented to cause gas bubble disease and mortality in fish (Beiningen and Ebel 1968, Rucker 1972, Baxter 1977).

### *Biological Impacts*

Altered flow regimes from impoundments have been shown to affect stream animal assemblages (Fraser 1972, Cushman 1985, Irvine 1985, Travinchek et al. 1995, Gerhke et al. 2002, McLaughlin et al. 2006) and even riparian vegetation (Janson et al. 2000). Coarsening of the streambed by erosion of sediment-poor tailwaters reduces habitat availability for benthic species by decreasing habitat heterogeneity, which, in turn, may reduce species diversity and richness (Armitage and Blackburn 1990, Hauer et al. 1989, Poff et al. 1997). Alterations in temperature regimes from impoundments also may alter organism distribution and behavior. Increased temperatures downstream of overflow dams can eliminate thermal cues vital to some invertebrate life cycles (Lehmkuhl 1974, Ward and Stanford 1982, Irvine 1985). In addition, increased water temperature affects metabolic rates for fish and invertebrates, which, in turn, increase demands for food to maintain growth and survival (Gibbons 1976, Wotton 1995, Perry et al. 1987, Vinson 2001, Lessard and Hayes 2003). Within reservoirs the deep,

cold, anoxic water often is a fish- and mollusc-free zone (Headrick and Carline 1993, Dean et al. 2002).

The few studies that were designed to examine effects of small dams have reported similar alterations but smaller in magnitude than those resulting from large dams (Graf 2006). In particular, Cumming (2004) found that low-head dams increase summer maximum temperatures and decrease fish richness at reaches upstream of impoundments. Taylor et al. (2001) documented shifts in fish composition, from a cyprinid- to a centrarchid-dominated assemblage after impoundment of a stream by a low-head earthen dam.

#### *Habitat fragmentation and population isolation*

Physical barriers presented by dam structures (including the dam itself, the impounded zone, and the affected tailwaters) impede longitudinal movements of stream organisms (Baxter 1977, Watters 1996, Dean et al. 2002). Genetic drift can result after such separations as rare alleles become common or fixed in a population while other alleles become less frequent or disappear (Lande 1976). Natural selection may expedite the divergence between reproductively isolated populations occurring in different habitats (Felsenstein 1976), but isolation has a greater influence on genetic divergence between populations than selection (Dillon 1984, Finlay et al. 2006). The degree of divergence between separated populations can be quantified by analyzing the accumulation of fixed mutations in the genome of each population (Nei 1977).

Impeded migration of fishes and other mobile organisms by small dams has been observed, preventing individuals from reaching feeding and/or spawning habitat. Among fish, decreased longitudinal connectivity across streams exacerbates population isolation (Neraas and Spruell 2001, Olden et al. 2001). One-way (downstream) migration of fish, commonly observed in impounded systems, reduces genetic diversity and population size in upstream reaches (Jager et al. 2001, Morita and Yamamoto 2002, Yamamoto et al. 2004).

Dams have similar effects on freshwater mussels by restricting migration and distribution of their host fish through impounded sections (Watters 1996, Kelner and Sietman 2000). Similar consequences on other invertebrates also have been observed. Watanabe and Omura (2007) demonstrated greater genetic differentiation among sub-populations of caddisflies separated by large reservoirs than among sub-populations on unimpounded reference streams. It is unknown how low-head dams affect habitat conditions or longitudinal movements of stream crayfishes, although it is likely that migration of some species is impeded (Miya and Hamano 1988).

Habitat fragmentation is of great conservation concern because ecological theory predicts that isolated populations can decrease in size and genetic diversity, making them more vulnerable to extinction (MacArthur and Wilson 1967, Lande 1988, Lande 1999). Without sufficient immigration from neighboring populations, natural stochastic events or anthropogenic impacts that reduce population size can lead to loss of genetic diversity and inbreeding depression (Charlesworth and Charlesworth 1987, Crnokrak and Roff 1999), thus reducing

population fitness and ultimately causing local extinction (Hansson and Westerberg 2002, Reed and Frankham 2003, Watanabe and Omura 2007). Further, by reducing the likelihood of interaction among populations, fragmentation also reduces the chance of successful recolonization after local extinctions, thus threatening metapopulation persistence (Saunders et al. 1991, Young et al. 1996, Fagan 2002).

### *Crayfish diversity in Alabama*

Alabama is a freshwater biodiversity “hotspot,” as it supports 60% of North America’s native mussel species, 43% of native freshwater snails, 38% of native fishes, and 24% of native crayfishes, many of which are endemic to the southeastern US(Lydeard and Mayden 1995, Crandall et al. 2000, Schuster and Taylor 2004). In addition, Alabama’s streams are considered its most imperiled ecosystems due, in part, to flow modification from impoundments (Dudgeon et al. 2005).

Freshwater crayfishes are highly diverse within Alabama, with at least 83 species in 6 genera and 25 subgenera occurring in the state (Schuster and Taylor 2004). Diverse life history strategies are represented, including cave and spring dwellers, and primary, secondary, and tertiary burrowers. Primary burrowers dig elaborate burrows in flood plains and moist low-lands where they spend most of their lives. Secondary burrowers dig more simplistic borrows, usually opening to a permanent body of water such as streams, lakes, and sloughs, and may forage in the open water. In contrast, tertiary burrowers live primarily in permanent

flowing water and dig burrows only during drought or when females tend eggs (Taylor and Schuster 2004). In addition, some species can facultatively use multiple burrowing strategies (Schuster and Taylor 2004, Finlay et al. 2006).

Crayfish are polyphagous, consuming primarily macroalgae, but also feed on detritus and animal prey (Creed 1994, Momot 1995). Predators of crayfish include fish, wading birds, mammals, and larger crayfish (Stein and Magnuson 1976, Englund and Krupa 2000). Male crayfish show cyclical reproduction, molting into the form I (reproductively active) stage at the onset of breeding, and back to form II (reproductively inactive) stage after reproduction (Crandall and Fitzpatrick 1996). Form I and form II males are distinguished by the sclerotized condition of the gonopods, which are used to transfer sperm to females. Females of some species also may exhibit form alteration (Wetzel 2002), and typically carry fertilized eggs and newly hatched young on the venter of the abdomen until their second or third juvenile molt. Breeding for most species occurs in autumn, winter, and early spring (Taylor and Schuster 2004); however, life history and reproductive strategies of many of freshwater crayfish species, including those in Alabama, are unknown.

Most of Alabama's stream crayfish occur in the genera *Cambarus*, *Procambarus*, and *Orconectes*. The genera are readily distinguished by the gonopods of form I males, and most form II males. The form I male gonopods are important in identification of most crayfish species (Hobbs 1981, Crandall and Fitzpatrick 1996, Taylor and Schuster 2004); however, distinguishing species within a genus is considerably more difficult, if only form II or female specimens

are available. It is likely that there are undescribed crayfish species in Alabama, and several museum specimens at the Auburn University Museum and the University of Alabama Museum are listed as undescribed (Schuster and Taylor 2004, E. Hartfield, personal observations).

Unlike many aquatic animals, crayfish may migrate both through water and, over land. Long-distance dispersal occurs primarily during floods (Lodge et al. 2000). Overland migration is limited by tolerance to desiccation, which varies among species (Larson and Magoulick 2008) and is usually limited to rain events, when relative humidity is high. For this reason, migration mostly occurs within a single drainage, although inter-drainage movements do occur (Fetzner and Crandall 2003). In addition, introduction of some species may occur via bait-bucket transfer by humans (Lodge et al. 2000).

Population genetics studies have revealed extensive gene flow and large effective population sizes in several species of subterranean- and surface-dwelling crayfish; however, molecular data also have suggested recent declines in genetic variability and effective population size in some widespread non-burrowing taxa (Buhay and Crandall 2005, Finlay et al. 2006). Such declines are of special concern because species with restricted ranges are highly vulnerable to genetic isolation resulting from habitat fragmentation (Lande 1999).

### *Objectives*

Currently, there is little information available on historic distribution and population sizes, or ecology of Alabama's crayfishes, especially endemic species

(Butler et al. 2003). Only 5 species of crayfish in Alabama have been listed as High Conservation Concern (Schuster and Taylor 2004). In the southeastern US, including Alabama, the high prevalence of small dams along streams and rivers has the potential to affect many imperiled aquatic species primarily through habitat fragmentation and population isolation (Travnicheck et al. 1995, Jager et al. 2001, Dean et al. 2002, Lessard and Hayes 2003, Irwin et al. 2007). Thus, the general paucity of knowledge of crayfish population size, life history, and ecology in Alabama, coupled with the high prevalence of impoundments, requires elucidation of the effects of impoundments on crayfish species assemblages, and increased ecological data on crayfish population dynamics within the state and elsewhere in the southeastern US.

The objectives of my research were to examine if presence and condition of low-head dams affect crayfish assemblages, and whether small low-head dams impede gene flow among crayfish populations. These objectives are important to crayfish conservation because 1) Alabama is a species-rich region with many endemic and undescribed taxa, 2) range, lifehistory, and ecology of many Alabama crayfish are unknown, and 3)patchy and fragmented habitats increase reproductive isolation and may increase likelihood of extinction/extirpation (Taylor et al. 2007). Finally, low-head dams are widespread globally and increasing in abundance (Wu et al. 2003), so an increased understanding of how these structures contribute to population fragmentation may enhance management of imperiled aquatic species across regional and global scales.

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## Chapter Two: Consequences of Low-head Dams on Crayfish Distributions and Gene Flow in Alabama Streams

### Introduction

Fragmented populations are more vulnerable to local extinction than contiguous populations (MacArthur and Wilson 1967, Lande 1988, Frankham 1997, Lande 1999). Without sufficient immigration from neighboring populations, natural stochastic events and/or anthropogenic impacts that reduce population size can lead to loss of genetic diversity and inbreeding depression (Charlesworth and Charlesworth 1987, Crnokrak and Roff 1999), thus reducing population fitness and ultimately causing local extinction (Hansson and Westerberg 2002, Reed and Frankham 2003, Watanabe and Omura 2007). Following extirpation, fragmentation reduces the likelihood of successful recolonization of patches, which may reduce the size of and exchange within metapopulations and further threatening persistence (Saunders et al. 1991, Young et al. 1996, Fagan 2002).

Streams are special cases when considering habitat fragmentation because of their linear structure. Many lotic organisms are restricted to the wetted channel, so migration can only occur bidirectionally (i.e., upstream or downstream; Fagan 2002, Hughes et al. 2009). Moreover, stream habitats often are naturally patchy (Townsend 1989). Terrestrial dispersal may alleviate instream constraints for some aquatic species, but even these organisms are

restricted to or near stream corridors (Finn et al. 2007). Thus, a single barrier bisecting a stream corridor may have dire consequences by restricting or eliminating connectivity for populations on either side.

Dams are extreme examples of anthropogenic barriers that can fragment stream populations, and effects of large dams on lotic biota and their habitats in large rivers can be profound. Environmental consequences of these structures include severe alteration of assemblage structure of both animals (Fraser 1972, Cushman 1985, Irvine 1985, Travinchek et al. 1995, Gerhke et al. 2002, McLaughlin et al. 2006) and vegetation (Janson et al. 2000). In addition, increased temperatures in tailwaters of overflow dams can increase energetic demands and physiological stresses for downstream fauna (Gibbons 1976, Wotton 1995, Perry et al. 1987, Vinson 2001, Lessard and Hayes 2003).

Interruptions in longitudinal dispersal by large dams have been well-documented for several species. Dams may halt upstream migration of fishes and other mobile animals, preventing individuals from reaching feeding and/or spawning habitat, which, in turn, drive population declines (Raymond 1979, Larinier 2001, Neraas and Spruell 2001, Olden et al. 2001). The one-way (downstream) migration of fish, commonly observed in impounded systems, reduces genetic diversity and population size, particularly in upstream reaches (Jager et al. 2001, Morita and Yamamoto 2002, Yamamoto et al. 2004). Dams can have similar impacts on freshwater mussels by restricting migration and distribution of their host fish through impounded sections and thus breaking mussel life cycles (Watters 1996, Kelner and Sietman 2000).

Longitudinal movement by crayfishes is common within streams (Fetzner and Crandall 2003, Lodge et al. 2000; however, unlike many lotic species, crayfishes are not restricted to the wetted channel. Overland dispersal is possible for some species (Viosca 1953, Penn 1956, Cappelli and Magnuson 1983), particularly those that are desiccation-tolerant (Larson et al. 2009). Given that crayfish dispersal ability varies among species, it is difficult to predict the degree to which instream barriers, such as dams, affect population connectivity. Furthermore, the systematics, life history and ecology are poorly known for most crayfish species in North America, and a number of species remain undescribed (Taylor et al. 2007). Understanding impacts of dams on crayfishes is critical for their conservation.

Consequences of dams on aquatic organisms and their habitats in large rivers have been well-documented, whereas comparatively little work has been done to assess effects of small, surface-release, and/or low-head dams on smaller streams (Watters 1996, Dean et al. 2002, Lessard and Hayes 2003). Low-head dams are those with a hydraulic height of  $\leq 8$  m that typically have over-dam flow or lateral spillways (IFC Consulting Report 2005). Such structures are pervasive across the Eastern US; according to census records,  $>65,000$  low-head dams existed in the region by 1840, most of which were built for water-powered milling (Walter and Merritts 2008). The few studies designed to examine effects of small dams have reported similar types of alterations as with large dams, although effects are considerably smaller in magnitude (Graf 2006). Low-head dams are increasing in abundance globally (Wu et al. 2003), so it is essential to understand

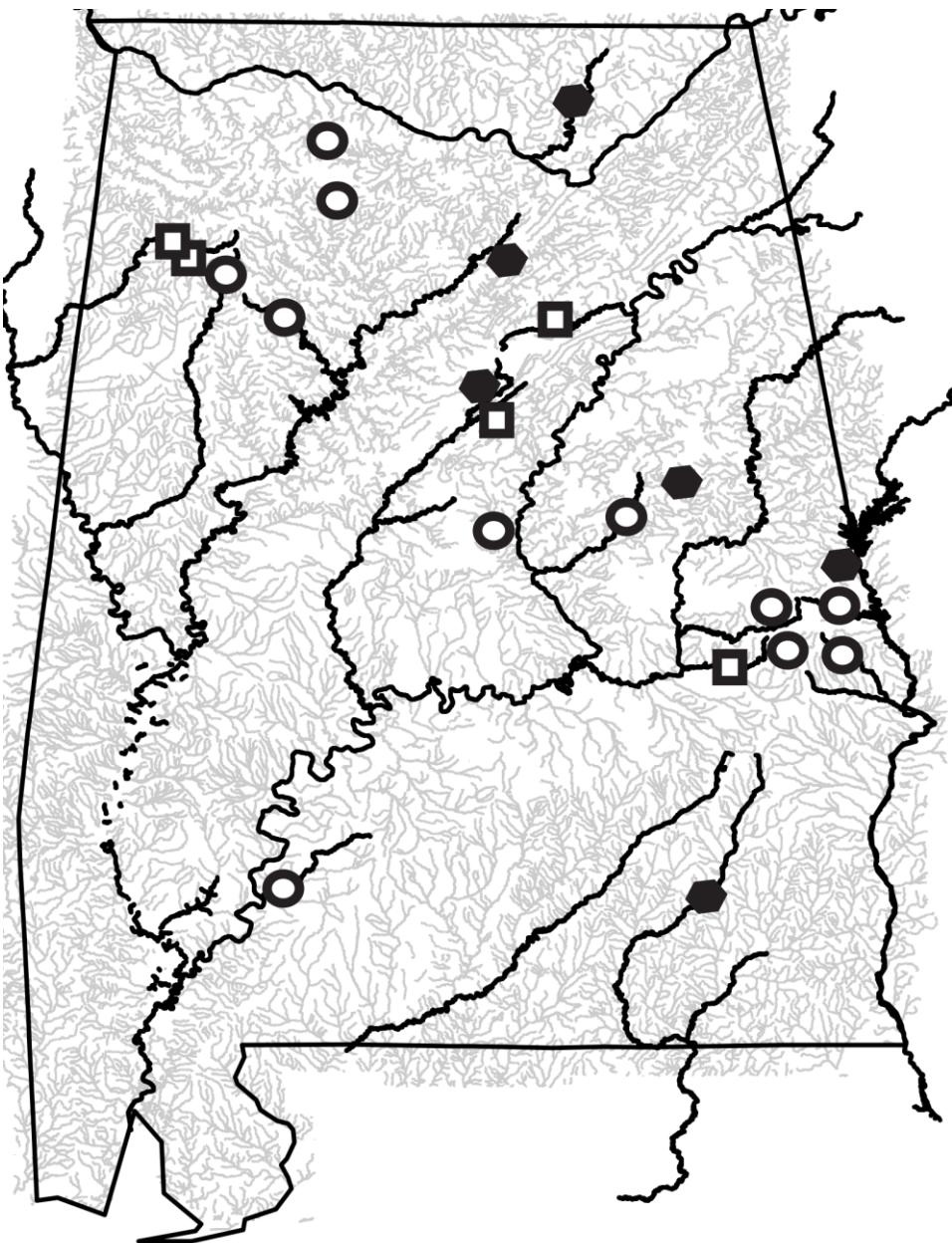
the degree to which these structures contribute to population fragmentation and reproductive isolation of aquatic species. This study was designed to examine the degree to which variation in environmental conditions associated with low-head dams affected the abundance, distribution, and gene flow of crayfish populations across a range of dam conditions within impounded or historically impounded streams in Alabama.

## Materials and Methods

### *Study sites*

I studied 22 low-head dams in 9 of the major drainages within Alabama (Fig. 1). Study sites spanned the full range of physiographic provinces with the state, including Highland Rim, Cumberland Plateau, Alabama Ridge and Valley, and Eastern Gulf Coastal Plain (Hackney et al. 1993). Study streams ranged from 3<sup>rd</sup> to 5<sup>th</sup>-order, and sites drained predominantly forested watersheds, although a mosaic of agricultural, suburban and urban land uses also was present. Because of the high variability across provinces and drainages, habitat types and conditions and associated animal assemblages greatly varied among sites.

Dams are abundant throughout Alabama, and many were discovered during previous surveys and from discussions with local residents (Gangloff and Feminella 2007). Sites were selected based on the 3 dam condition categories (below), landowner approval, and accessibility of the dam and upstream and further downstream reaches. Also, sites were selected due to presence of endangered or threatened aquatic taxa (i.e., mussels, snails, fish, or crayfish)



**Figure 1.** Map of study sites across Alabama. Open circles represent intact dams, open squares represent breached dams, and black hexagons represent relict dams.

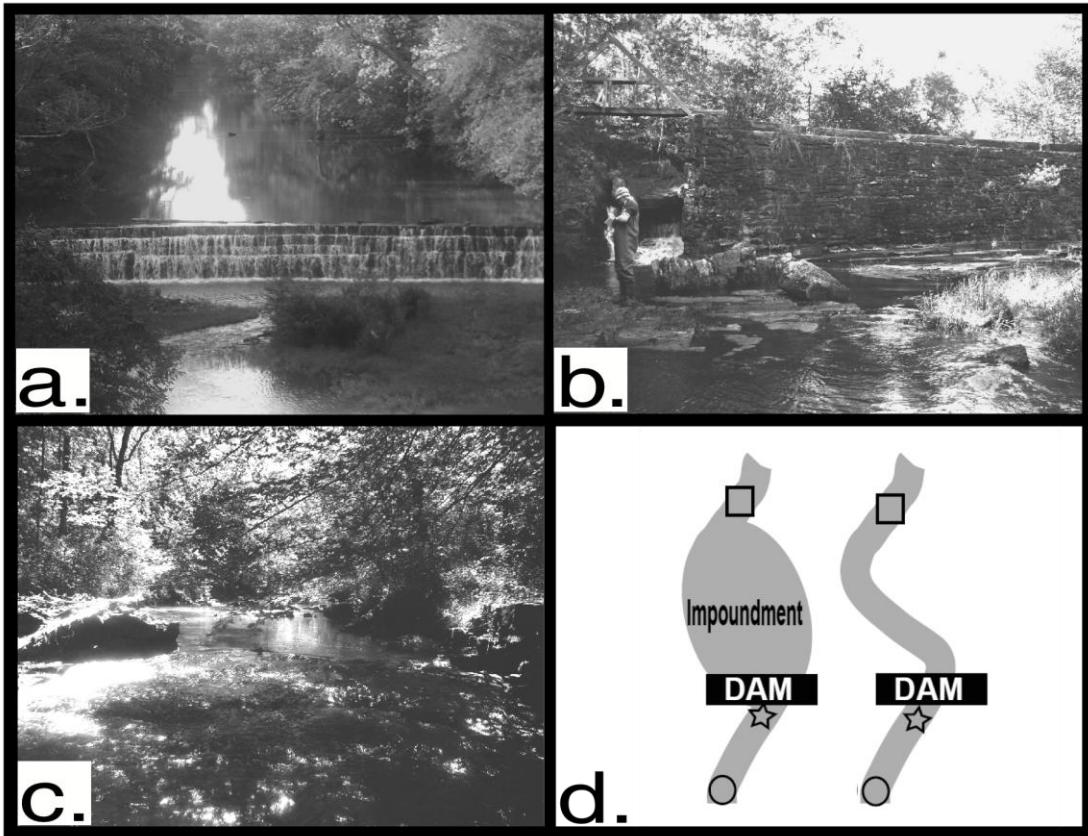
nearby. Of the selected sites, 11 dams were intact, 5 were breached, and 6 were considered relict. *Intact dams* were those where the impoundment structure had a functional spillway, over-dam flow, and a reservoir with slow current velocity relative to nearby free-flowing reaches (Fig. 2A). *Breached dams* were those where the impoundment structure was either partially broken or the spillway was open and the impoundment zone was absent or <50m long at base flow (Fig. 2B). Last, *relict dams* were those where impoundment structures were almost entirely eroded (e.g., often showing only pilings on the bank to indicate original dam location, Fig. 2C), usually from advanced age and the action of hydrologic forces during flood events, thus allowing the return of more typical free-flowing conditions.

#### *Study design*

I established three 150-m study reaches at each study dam: 1) upstream of impounded reaches (= *upstream*, 1500-5000 m), 2) immediately downstream of the dam (= *mill*; 0-150 m), and 3) 500 to 3000 m downstream of the dam (= *downstream*; usually <1000 m) (Fig. 2D). I estimated longitudinal length of pre-breached impoundment for breached and relict dams using information from local landowners or long-term residents. Thus, I established this reach an equivalent distance upstream of dams in all conditions (Fig. 2D).

**Table 1.** Study streams, drainages, milldam names and their condition (see text), geographic location, and key dates of construction and/or breach, where known.

Stream	Drainage	Mill	Cond- ition	Lat. (N)	Long. (W)	Dates
Big Flat	Alabama	Rikard's Mill	Intact	31.782	-87.223	Built 1868
Cahaba	Alabama	Grant's Mill	Relict	33.509	-86.644	
Little Cahaba	Cahaba	Unnamed Mill	Breached	33.451	-86.694	
Lost	Black Warrior	Boshell Mill	Intact	33.855	-87.414	Built 1885
Brushy	Black Warrior	Unnamed Mill	Intact	34.292	-87.273	Built 1966
Blue Springs	Black Warrior	Chamblee Mill	Relict	34.060	-86.662	
Halawakee	Chatahoochee	Bean's Mill	Intact	32.697	-85.267	Built 1834
Osanippa	Chatahoochee	Ferguson Mill	Relict	32.778	-85.193	
Little Uchee	Chatahoochee	Meadow Mill	Intact	32.528	-85.253	
Pea	Choctawhatchee	Shellgrove Mill	Relict	31.521	-85.869	Built 1890's
Big Canoe	Coosa	Goodwin Mill	Breached	33.819	-86.384	Breached 1990's
Yellow Leaf	Coosa	Shannon Mill	Intact	32.935	-86.611	
Hatchett	Coosa	Old AL Power Mill	Intact	33.068	-86.096	Built 1920's
Choctafaula	Tallapoosa	Vaughn's Mill	Breached	32.513	-85.578	Built 1940 Breached 1990's
Loblockee	Tallapoosa	Macon's Mill	Intact	33.653	-85.584	
Sandy	Tallapoosa	Jones' Mill	Intact	32.751	-85.560	Built 1830's
Little Hilabee	Tallapoosa	Carr's Mill	Relict	33.204	-85.943	Breached 1940's
Paint Rock	Tennessee	Butler's Mill	Relict	34.579	-86.301	Built 1820's
Turkey	Tennessee	Masterson Mill	Intact	34.538	-87.283	Built 1870's
Buttahatchee	Tombigbee	Unnamed Mill	Breached	34.126	-87.837	Built 1920's Breached 1980's
New	Tombigbee	Kelly's Mill	Intact	33.930	-87.680	
Pearce's Mill	Tombigbee	Pearce's Mill	Breached	34.122	-87.836	Built 1920's Breached 1980's



**Figure 2.** Examples of dams showing intact (a), breached (b), and relict (c) conditions, and layout of study reaches (d) for streams with intact (left) and breached or relict (right). Square symbols represent upstream sites, stars represent mill sites, and circles represent downstream sites.

I measured a full range of physicochemical variables (mean current velocity, stream depth, substrate size, and channel width) thought to vary among sites concurrently with biotic sampling over Spring-Summer and Fall 2007 and 2008. I established cross-stream transects every 10 m in each reach and measured wetted width, and current velocity (measured at 0.6x the channel depth, Gore 2006), depth (n=5/transect), substrate size (pebble counts method [Wolman 1954], n=20/transect at random intervals), and proportion of unmeasured substrate in the channel (wood, bedrock, organic matter, sand/silt). Streamwater chemistry data included conductivity (Sharp C66 meter), pH (Sharp pH52), and dissolved oxygen (YSI 55), measured from grab samples from each reach and in the impoundment zone or its equivalent during summer base flow (July 2008). Conditions at all reaches on a stream were measured within 1 or 2 d of each other to ensure similar physical conditions among reaches. I measured water temperature continuously (3-h intervals) using iButton data loggers deployed at downstream, mill, and upstream reaches; I deployed a 4<sup>th</sup> logger in the impoundment zone of intact dams, or in a reach of equivalent distance upstream from the dam for breached and relict sites.

#### *Crayfish and fish sampling*

I quantified crayfishes in each reach using a combination of trapping, seining, and electrofishing, thus minimizing sampling bias of any single method (Rabeni et al. 1997, Ratcliffe and DeVries 2004). I set 8 crayfish traps, baited with perforated cans of cat food, over night once in each reach during May-

September. All reaches on a stream were typically sampled the same night or within a day of each other to ensure similar conditions upstream to downstream.

I used kick-seining (mesh size=0.25mm) and a backpack electrofishing unit (Smith-Root LR-24 electrofishing unit) to quantify fishes, potential biotic controls on crayfishes, in the full range of habitat unit types available in study reaches (i.e., riffles, runs, pools, backwaters).

Crayfish specimens were kept alive on ice and later preserved in 95% ethanol in the laboratory where they were identified to species using keys in Hobbs (1981, 1989) and Taylor and Schuster (2004). I anesthetized fishes in tricane methanesulfonate (MS-222), fixed them in a 10% formalin solution, and then transferred them to 70% ethanol for permanent storage. In the laboratory, I identified fishes to species and classified them according to feeding guilds (Berkman and Rabeni 1987, Boschung and Mayden 2004, B. Helms unpublished data). All specimens were deposited in the Auburn University Learning Center.

### *Statistical analysis*

I used a General Linear Model (PROC GLM, SAS 9.1) with reach (upstream, mill, downstream) as a fixed factor and site (intact, breached, relict dam condition) as a random factor with an interaction term to test for differences in substrate size and percentages of bedrock, wood, organic matter, and fine sediments (i.e., silt and sand).

For each reach I calculated reach- and stream-specific catch per unit effort (CPUE) using mean trap success (mean number crayfishes per trap) as a measure

of abundance. Traps are an efficient way to sample crayfishes in vegetated or highly structured environments (Feminella and Resh 1989). Moreover, our streams were spread throughout a range of physiographic provinces with a large array of habitat conditions (turbidity, substrate particle size, macrophyte and woody debris abundance, etc.) so traps were the most replicable method of sampling crayfish abundance (Hubert 1996). In contrast, to guard against potential trap bias against trap-shy species, for crayfish richness I used electrofishing and kick-seining to obtain more accurate estimates (Jordan et al. 2000).

Crayfish abundance and richness data were non-normal and could not be normalized using transformations; thus, I used non-parametric Kruskal-Wallace tests (Zar 1999) to test the null hypothesis that crayfish abundance and richness did not differ among streams of contrasting dam conditions (i.e., intact vs. breached vs. relict sites). I used Friedman's test (Zar 1999) to test the null hypothesis that crayfish abundance and richness did not differ among reaches for streams of similar dam conditions (i.e., upstream vs. mill vs. downstream reaches of relict, breached, and intact dams). Multiple comparisons were made using the Friedman's Test on each pair of treatments ( $\alpha=0.05$ ).

In addition, I used a General Linear Model (PROC GLM, SAS 9.1) with reach (upstream, mill, downstream) as a fixed factor, site as a random factor, and mean water depth as a covariate was used for each dam condition (intact, breached, relict) to test the null hypothesis that predatory fish abundance did not differ among reaches. Predatory fishes were defined as those individuals in the families Centrarchidae, Cottidae, Esocidae, and Ictaluridae, all of which are

known to consume crayfishes (Berkman and Rabeni 1987, Boschung and Mayden 2004). I did not use a minimum size threshold for counting predatory fish and instead assumed that fish large enough to be caught in seines were potential predators of juvenile and/or adult crayfishes.

### *Crayfish population genetics*

For 2 sites with intact dams, Sandy Creek (Tallapoosa Drainage) and Hatchett Creek (Coosa Drainage), I quantified gene flow among crayfish subpopulations of impounded streams. Genetic analyses focused on *Cambarus striatus* (the ambiguous crayfish) from Sandy Creek, and *Cambarus coosae* (the Coosa crayfish) from Hatchett Creek. I chose these species because they were locally common (i.e., had no conservation concerns) and were easily collected and identified in their respective streams. In addition, the strongly disparate distributions of the 2 species promoted a contrast in their degree of endemism. *Cambarus striatus* is widespread throughout the Southeastern US; in contrast, *C. coosae* is restricted to the Coosa and Cahaba River Drainages (Hobbs 1981). Tissue samples used for genetic analysis were taken from the abdominal muscle of crayfishes from each reach and stored in 95% ethanol before animals were preserved (Fetzner and Crandall 2003).

I extracted genomic DNA using a 2X CTAB extraction protocol as detailed in Coffroth et al. (1992) and amplified a portion of the mitochondrial cytochrome oxidase subunit I (COI) gene using the polymerase chain reaction (PCR) for all individuals using the primers HCO2198 and LCO1490 (Folmer et

al. 1994). The COI gene has been used widely in decapod phylogenetic and phylogeography studies because of its relatively high rate of substitution (Tontelj et al. 2005).

Reactions were conducted in 25 µL using the following reagent concentrations: 2.5 µL 10 x buffer (1.5 µM), 0.5 µL dNTPs (10 µM), 0.1 µL Taq polymerase, 0.5 µL magnesium chloride (25 µM), 1 µL of each primer (10 µM), and 1 µL DNA template (~10-50 ng). Thermocycling was performed with a PTC-100<sup>TM</sup> thermocycler (MJ Reactions) using the following program: an initial denaturing step of 96°C for 3 min, followed by 40 cycles of 94°C for 1 min, annealing at 50°C for 1 min, and 72°C for 1 min, with a final elongation of 72°C for 5 min. I purified amplified products with Montage<sup>TM</sup> PCR Filter Units (Millipore) according to the supplier's recommendations and sequenced using an ABI 3100 Genetic Analyzer (Applied Biosystems) in both directions. I then edited sequences by comparing each read to its compliment strand using Sequencher v4.6 (Gene Codes Corporation) and aligned manually with Se-Al v2.0a11 (available at <http://evolve.zoo.ox.ac.uk/>).

#### *Genetic data analysis*

I assessed levels of genetic polymorphism and structure among subpopulations (e.g., upstream, mill, and downstream) of each species with DnaSP v4.06 (Rozas et al. 2003). Specifically, I calculated nucleotide ( $\pi$ ) and haplotype ( $H_d$ ) diversity estimates (Nei 1987) within each subpopulation and overall (i.e., across all 3 subpopulations). In these cases,  $\pi$  represents the mean

number of nucleotide differences per locus between any 2 sequences whereas  $H_d$  reflects the haplotype richness within a subpopulation. I estimated genetic differentiation of subpopulations using the nearest neighbor statistic,  $S_{nn}$  (Hudson et al. 1992), which quantifies the frequency of the most similar sequence of a given haplotype being recovered from the same locality. I also quantified population structure and gene flow using  $F_{st}$  and  $Nm$  (Hudson et al. 1992), where  $F_{st}$  measures the proportion of genetic variation found among subpopulations within a larger population,  $Nm$  is the effective number of migrants exchanged between subpopulations per generation,  $N$  = the number of individuals in each subpopulation, and  $m$  is the fraction of migrants in each subpopulation per generation.

To separate population history from population structure, I constructed networks for the COI haplotypes within each species using TCS v1.21 (Clement et al. 2000) and used in a nested clade analysis (NCA, Templeton et al. 1987). I tested the null hypothesis of no geographic association among haplotypes by calculating clade distance ( $D_c$ ) and nested clade distance ( $D_n$ ) by 5000 permutations in the GeoDis v2.5 software package (Posada et al. 2000).  $D_c$  measures the geographical range of a haplotype at each nested level whereas  $D_n$  measures the evolutionary distance between haplotypes in different levels of the nesting. I assessed the output of GeoDis in the context of the most recent (i.e., April 2009) NCA inference key. This approach can help explain what evolutionary events (e.g., restricted gene flow) led to current levels of genetic

diversity and geographic distribution of haplotypes within a species (Templeton 2005).

## Results

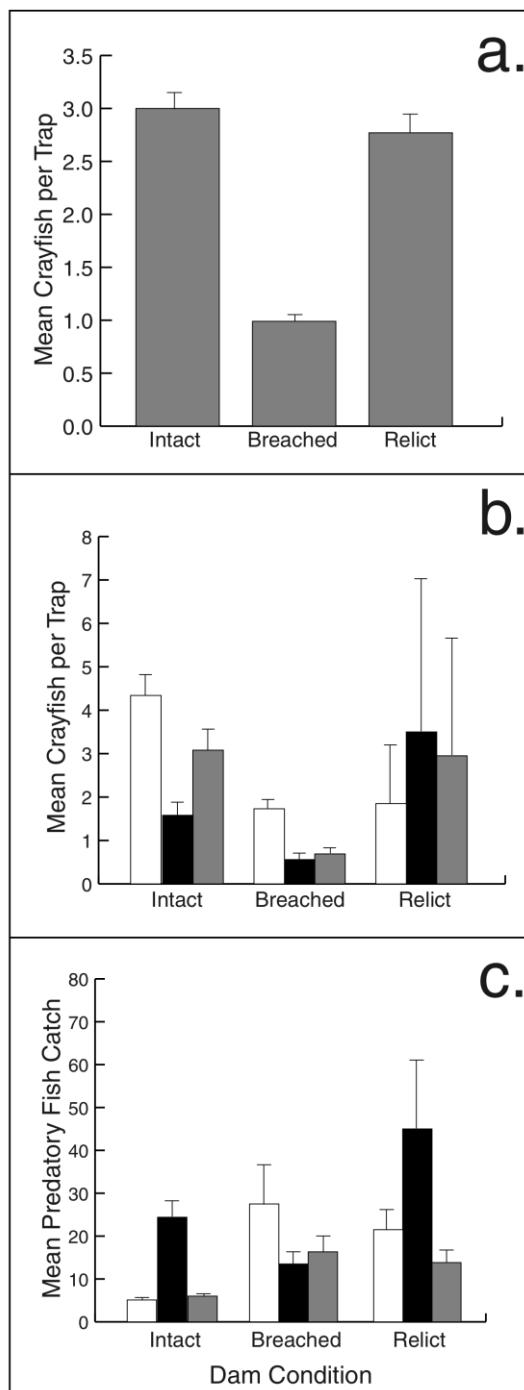
### *Instream habitat, and crayfish and predatory fish assemblage variation*

*Instream Habitat.*—There was high variation in substrate characteristics across reaches, with mean particle width ranging from 0.6 to 272.2 mm, mean bedrock cover from 0 to 65%, and mean sand and silt cover from 1 to 78% (Table 2). Only substrate composition differed significantly among reaches, and only for intact dam sites. There, percentage of fine particles (as sand and silt) in the stream bed was significantly lower at mill than at upstream reaches (22.1 vs. 35.6%, respectively,  $p=0.015$ ); % sand and silt at downstream reaches (28.8%) was not significantly different from upstream or mill reaches ( $p>0.05$ ).

*Crayfish.*—A total of 20 crayfish taxa was collected from the 22 study sites (Appendix A). Richness and total catch did not differ among streams with different dam conditions ( $H=0.244$ ,  $p=0.885$  and  $H=0.033$ ,  $p=0.984$ , respectively). However, when expressed as CPUE there were significant differences among dam conditions ( $H=7.923$ ,  $p=0.019$ ). Mean CPUE for streams with breached dams was significantly lower than that of relict and intact dams (Fig. 3A).

**Table 2.** Summary of physicochemical and crayfish data from the study streams. Up= site 1500-5000 m upstream of the dam, Mill= site immediately downstream of the dam, Down= site 500-3000 m downstream of the dam. Cond. = specific conductance, DO = dissolved oxygen, Temp = water temperature, CPUE=crayfish catch per trap and crayfish species found at each reach type. Mean  $\pm$  SD.

Dam condition	Study reach	Current velocity (m/s)	Stream Depth (m)	Wetted width (m)	Mean substrate (mm)	% Bedrock	% Woody debris	% Organic matter	% Sand / silt	Cond. (uS/cm)	pH	DO (mg/L)	Temp (C)	CPUE
Intact	Overall	0.05 $\pm$ 0.04	0.26 $\pm$ 0.12	11.97 $\pm$ 5.03	116.91 $\pm$ 59.59	18.50 $\pm$ 16.56	9.41 $\pm$ 9.24	8.44 $\pm$ 7.42	28.85 $\pm$ 13.63	111.92 $\pm$ 134.69	8.33 $\pm$ 0.58	6.18 $\pm$ 1.20	22.93 $\pm$ 5.29	3.00 $\pm$ 0.15
	Up	0.04 $\pm$ 0.03	0.26 $\pm$ 0.15	10.46 $\pm$ 5.26	113.10 $\pm$ 63.99	16.18 $\pm$ 15.87	11.57 $\pm$ 10.68	8.29 $\pm$ 5.37	35.64 $\pm$ 14.94	114.63 $\pm$ 134.49	8.52 $\pm$ 0.69	5.88 $\pm$ 0.99	21.29 $\pm$ 5.67	4.34 $\pm$ 0.48
	Mill	0.07 $\pm$ 0.05	0.26 $\pm$ 0.11	13.09 $\pm$ 4.75	133.47 $\pm$ 53.42	18.02 $\pm$ 13.41	6.22 $\pm$ 6.26	8.68 $\pm$ 8.66	22.09 $\pm$ 11.45	116.88 $\pm$ 149.93	8.12 $\pm$ 0.53	5.94 $\pm$ 1.47	24.24 $\pm$ 4.90	1.58 $\pm$ 0.31
	Down	0.05 $\pm$ 0.05	0.26 $\pm$ 0.10	12.35 $\pm$ 5.22	103.78 $\pm$ 63.60	21.31 $\pm$ 20.91	10.44 $\pm$ 10.20	8.35 $\pm$ 8.58	28.81 $\pm$ 11.92	105.11 $\pm$ 137.28	8.38 $\pm$ 0.56	6.71 $\pm$ 1.08	23.28 $\pm$ 5.54	3.08 $\pm$ 0.049
Breached	Overall	0.16 $\pm$ 0.07	0.28 $\pm$ 0.11	13.08 $\pm$ 6.12	138.88 $\pm$ 77.83	20.50 $\pm$ 17.19	5.98 $\pm$ 4.35	7.91 $\pm$ 7.11	29.21 $\pm$ 19.04	313.71 $\pm$ 420.00	8.47 $\pm$ 0.50	7.62 $\pm$ 2.00	21.09 $\pm$ 4.00	0.99 $\pm$ 0.06
	Up	0.16 $\pm$ 0.07	0.30 $\pm$ 0.30	14.04 $\pm$ 8.18	124.36 $\pm$ 101.94	24.14 $\pm$ 17.43	8.03 $\pm$ 3.89	7.79 $\pm$ 6.32	35.70 $\pm$ 29.03	326.71 $\pm$ 446.05	8.40 $\pm$ 0.61	6.28 $\pm$ 2.32	20.27 $\pm$ 4.61	1.73 $\pm$ 0.21
	Mill	0.15 $\pm$ 0.09	0.30 $\pm$ 0.11	13.96 $\pm$ 3.89	143.22 $\pm$ 55.38	18.17 $\pm$ 14.53	5.94 $\pm$ 4.61	7.36 $\pm$ 8.87	27.37 $\pm$ 9.73	240.14 $\pm$ 225.43	8.40 $\pm$ 0.57	7.55 $\pm$ 1.54	21.85 $\pm$ 3.31	0.56 $\pm$ 0.11
	Down	0.18 $\pm$ 0.05	0.25 $\pm$ 0.06	11.23 $\pm$ 6.06	149.08 $\pm$ 79.66	19.20 $\pm$ 21.14	3.96 $\pm$ 4.13	8.59 $\pm$ 7.01	24.57 $\pm$ 13.88	374.29 $\pm$ 572.21	8.60 $\pm$ 0.32	8.76 $\pm$ 1.64	21.17 $\pm$ 4.56	0.69 $\pm$ 0.15
Relict	Overall	0.11 $\pm$ 0.06	0.32 $\pm$ 0.17	19.28 $\pm$ 0.73	109.98 $\pm$ 127.81	18.96 $\pm$ 21.08	7.25 $\pm$ 5.05	7.11 $\pm$ 5.43	31.41 $\pm$ 16.11	146.89 $\pm$ 81.43	8.23 $\pm$ 0.15	5.99 $\pm$ 1.91	26.76 $\pm$ 1.52	2.77 $\pm$ 0.17
	Up	0.08 $\pm$ 0.05	0.30 $\pm$ 0.15	19.85 $\pm$ 12.04	65.61 $\pm$ 75.06	11.18 $\pm$ 13.29	9.52 $\pm$ 2.98	10.26 $\pm$ 5.55	33.58 $\pm$ 22.26	147.00 $\pm$ 91.33	8.20 $\pm$ 0.10	3.82 $\pm$ 0.10	26.60 $\pm$ 1.65	1.85 $\pm$ 1.36
	Mill	0.14 $\pm$ 0.09	0.28 $\pm$ 0.12	19.83 $\pm$ 9.66	163.57 $\pm$ 165.24	23.58 $\pm$ 21.61	4.60 $\pm$ 4.36	6.42 $\pm$ 4.99	24.86 $\pm$ 8.69	144.67 $\pm$ 92.68	8.17 $\pm$ 0.12	7.41 $\pm$ 0.12	26.00 $\pm$ 2.83	3.50 $\pm$ 3.54
	Down	0.11 $\pm$ 0.05	0.38 $\pm$ 0.25	18.17 $\pm$ 5.15	100.74 $\pm$ 134.44	22.12 $\pm$ 28.22	7.64 $\pm$ 6.78	4.66 $\pm$ 5.19	35.80 $\pm$ 15.93	149.00 $\pm$ 97.86	8.33 $\pm$ 0.21	6.75 $\pm$ 0.21	27.43 $\pm$ 0.12	2.95 $\pm$ 2.71



**Figure 3.** Catch per trap effort of crayfish on streams with intact, breached, and relict dams across all study reaches (a), catch per trap effort of crayfish at each study reach on streams with dams in different conditions (b), and abundance of predatory fishes (as total catch) (c), at each study reach on streams for dams in different conditions (see text). White columns represent upstream reaches, black columns are dam reaches, and gray columns are downstream reaches. Mean + SE.

For streams with intact dams, CPUE was lower at mill reaches than at upstream or downstream reaches ( $X_r^2=21.88$ ,  $p<0.0001$ ). For streams with breached dams, CPUE was significantly higher upstream than at mill or downstream sites ( $X_r^2=10.83$ ,  $p=0.005$ ). For streams with relict dams, CPUE did not differ among sites ( $X_r^2=1.90$ ,  $p=0.39$ ; Fig. 3B).

*Predatory fish.*—Individuals from 5 fish families known to consume crayfishes were collected during the study (B. Helms unpublished data). For streams with intact dams, there were significantly higher abundances of predatory fishes at mill reaches (i.e., immediately below dams) than at upstream or downstream reaches (Fig. 3C). The numerically dominant taxa of predators were centrarchids.

#### *Crayfish population genetics*

A total of 562 base pairs of COI were obtained from each of 22 *Cambarus striatus* at Sandy Creek. From these, 19 (3.38%) polymorphic sites were recovered from 12 haplotypes found at all 3 reaches (upstream, mill, and downstream).  $\pi$  was higher upstream than overall or at mill or downstream reaches, whereas  $H_d$  was higher overall than at any single reach except the mill reach, where only 2 individuals were collected, and each represented a different haplotype.  $S_{nn}$  was significant and approached 1 ( $S_{nn}=0.705$ ,  $p=0.009$ ), implying genetic differentiation between upstream and downstream subpopulations. Furthermore, whereas  $F_{st}$  was not high (0.378),  $Nm$  was <1 (0.410), suggesting limited gene flow among subpopulations (Table 3). Of the 12 haplotypes, 8

(67%) were found at the downstream reach, with 2 being shared by downstream and mill reaches, and 4 haplotypes found at the upstream reach. The upstream reach shared no haplotypes with downstream and mill reaches (Fig. 4A), again suggesting limited to no longitudinal gene flow among subpopulations. The NCA of *C. striatus* found one 2-step clade to be significant (2-1:  $D_n=1.420, p<0.0001$ ; I-T:  $D_c=-1.467, p=0.013$ ), with a conclusion of contiguous range expansion based on the inference key. All other clades yielded inconclusive outcomes in the NCA.

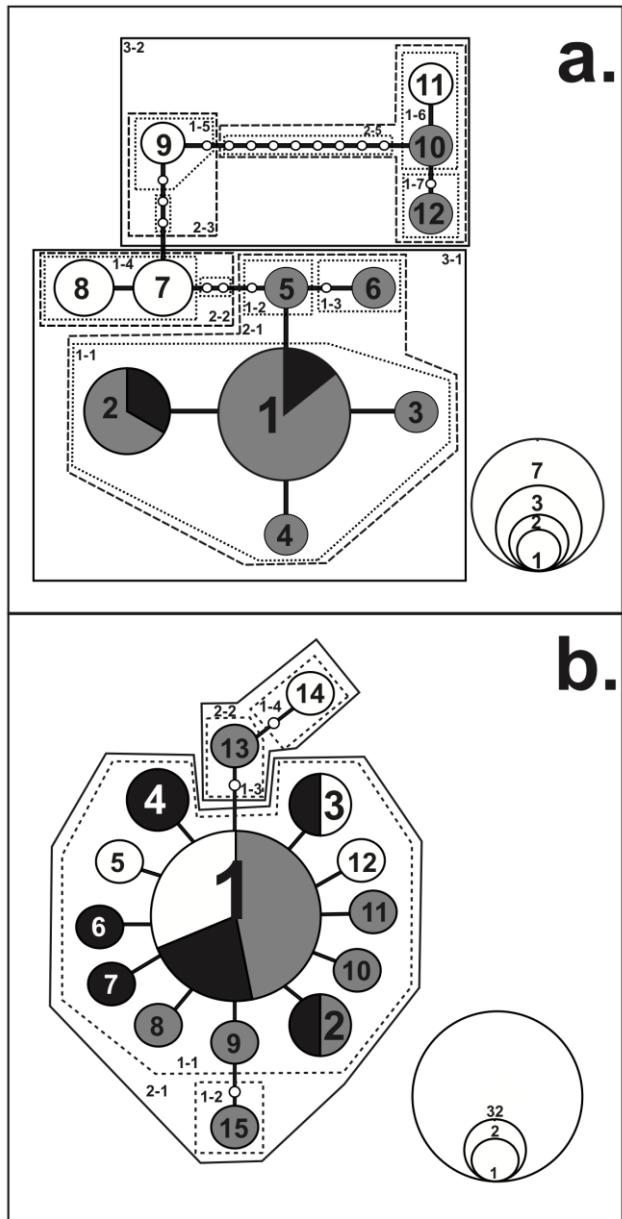
A total of 598 base pairs of COI were obtained from each of 50 *Cambarus coosae* at Hatchett Creek. Overall, 16 haplotypes were collected across the 3 study reaches, with a total of 15 (2.51%) polymorphic sites.  $\pi$  was higher upstream than overall or at mill or downstream reaches, with  $H_d$  being highest at the mill reach.  $F_{st}$  was low, whereas  $Nm$  was high, but  $S_{nn}$  was not significant (Table 3), suggesting little to no genetic differentiation among subpopulations. This pattern was visually apparent in the TCS network: of the 16 identified haplotypes, the most commonly recovered (i.e., haplotype 1) was found at the upstream, mill, and downstream sites at a similar frequency. The remaining haplotypes were singletons and/or unique to a reach (Fig. 4B). The NCA of *C. coosae* revealed no clades with significant divergence.

## Discussion

A wide range of biotic and abiotic factors influence crayfish abundance and distribution in streams. Abiotic factors involve appropriate substrate sizes and/or types (i.e., the availability of refugia), water depth, hydrologic

**Table 3.** Genetic diversity and differentiation among subpopulations of the crayfish *Cambarus striatus* and *C. coosae*.  $\pi$  = nucleotide diversity,  $H_d$  = haplotype diversity,  $F_{st}$  = genetic variation among subpopulations within the metapopulation, and  $N_m$  = effective number of migrants exchanged between subpopulations per generation,  $S_{nn}$  = estimate of genetic differentiation of the crayfish subpopulations (see text).

Species	Population	No. of indiv.	No. of haplo- types	$\pi$	$H_d$	$F_{st}$	$N_m$	$S_{nn}$
<i>C. striatus</i>	Overall	22	12	0.0107	0.887	0.3778	0.41	0.70519
	Upstream	6	4	0.0108	0.867			$p=0.009$
	Mill	2	2	0.0018	1.0000			
	Downstream	16	8	0.0084	0.824			
<i>C. coosae</i>	Overall	50	16	0.0016	0.593	0.0094	26.81	0.35432
	Upstream	15	7	0.0019	0.625			
	Mill	13	5	0.0013	0.667			
	Downstream	22	8	0.0015	0.545			



**Figure 4.** Haplotype networks showing nesting levels used to infer historical processes for *Cambarus striatus* at Sandy Creek (a) and *C. coosae* at Hatchett Creek (b). Numbered circles each represent a unique sampled haplotype whereas small open circles represent unsampled (i.e. missing) haplotypes. The size of a circle is proportional to the frequency at which that haplotype was recovered. Shading corresponds to sites where individuals were collected (white = upstream, black = mill, and gray = downstream). Note that despite variable lengths, each branch implies a single mutational difference between haplotypes. For example, haplotype 1 in 4a differs from haplotype 5 by one mutation, whereas haplotype 5 differs from haplotype 7 by 4 mutations.

permanence, and water chemistry (Bovbjerg 1970, Jordan et al. 2000, Flinders 2003, Ratcliffe and DeVries 2004, Larson et al. 2009). Biotic factors can include inter- and intraspecific competition and predation by fish, wading birds, and mammals, each of which may affect crayfish behavior, distribution, and overall assemblage structure (Bovbjerg 1970, Stein and Magnuson 1976, Garvey et al. 1994, Englund and Krupa 2000). On streams with intact mill dams crayfish I found crayfish abundance to be lower at mill reaches than at upstream or downstream reaches. In addition, abundance of predatory fish was higher at mill reaches (vs. upstream or downstream) of these same streams. Dams may serve as sources of fish aggregations downstream of the impoundment (Agostinho et al. 2007), which may, in turn, act as “predator gauntlets” (sensu Hein and Crowl 2010, see also Creed 2006), decreasing crayfish abundance in these reaches through direct consumption by fish, behavioral avoidance, or a combination of these factors. Irrespective of the source, presence of predators immediately downstream of impoundments may impose additional limits on longitudinal dispersal by crayfishes, thus exacerbating the influence of the physical barrier on crayfish movements.

Interactions between abiotic factors and biotic factors also may be driving reductions in crayfish abundance at intact mill sites. Our data did show evidence of reduced amounts of fine sediments immediately downstream of intact dams (unpublished data). Decreased current velocity in the impounded reaches can greatly increase sediment deposition upstream of the dam, often causing tailwaters to become sediment-starved and downstream sections to exhibit

increased scour, streambed lowering, and bed coarsening (Baxter 1977, Chien 1985, Graf 2005). Decreased deposition causes tailwaters to become less geomorphically complex, with fewer bars and islands and reduced shallow-water habitat (Poff et al. 1997, Graf 2006). Moreover, coarsening of the stream bed reduces habitat availability for benthic species by decreasing habitat heterogeneity (Hauer et al. 1989, Armitage and Blackburn 1990). At the watershed scale, these geomorphic changes may transform slow-flowing marshy streams into fast-flowing gravel-bottomed systems (Walter and Merritts 2008). Our habitat data revealed few significant differences among sites on streams with intact dams, but the influence of abiotic factors on aquatic populations may be transient and/or difficult to detect empirically because of high spatial and temporal variation; thus, it is possible that our sampling regime may have not adequately characterized the potentially critical habitat conditions affecting crayfishes.

It is important to note that there was high variability in structural conditions of breached dams, as well as habitat across these breached sites. In this context, dams at most (60%) of our breached sites were breached intentionally by landowners or managers for safety or conservation concerns, whereas all other breaches ostensibly occurred by natural erosion during storm events. Some breaches (both intentional and natural) were the result of removal of a small portion of the dam, whereas the spillways were opened on others allowing free-flowing conditions. Duration of time following intentional breaches was easily determined from the landowners, whereas time since natural breaches often was less clear, as these structures often were frequently unmaintained and/or occurred

in remote areas. According to landowner accounts, most dams were breached between the late 1980s and the early 1990s (E. Hartfield, personal observation), indicating a 20- to 30-y post-breach period for biotic and abiotic conditions to change within our study sites.

Surprisingly, breached dams appeared to have a greater negative impact on crayfish abundance than intact or relict dams, as many breached mill and downstream reaches supported fewer crayfishes than upstream reaches. Large deposits of fine sediments are characteristic of the reaches immediately upstream of breached (and intact) dams, often extending for >1000 m upstream of impoundments. At the dam, the breach often constricted the stream to a narrow exit point where water velocity is greatly increased during major storm events, resulting in a “pressure hose effect.” It is possible that episodic pulses of fine sediments from behind the breached dams may reduce the availability of crevices, interstitial space, and other refugia, reducing crayfish habitat quality, heterogeneity, and stability for considerable distances downstream of the breach. This effect could explain why our sampling regime did not show higher fine sediment loads in mill or downstream reaches compared with upstream reaches.

The lack of significant differences in abundance among sites on streams with relict dams suggests that after total dam removal, crayfish abundance homogenizes longitudinally and may return to pre-impoundment levels. Assessment of recovery after dam removal was beyond the scope of this paper, as exact estimates of time since dam failure at relict sites often could not be obtained. According to landowner accounts, most relict dams failed between the

1940s and 1960s; if these estimates are correct, then recovery of crayfish assemblages may take years to decades, depending on how much of the structure was removed. The time for captured sediment in formerly impounded reaches to move through the system may play a key role in recovery time, making time since breach or removal of dams an important factor when studying recovery time of these systems. Unfortunately, such historical data are not typically available.

Genetic diversity measures ( $H_d$  and  $\pi$ ) for *C. striatus* in Sandy Creek were not higher downstream than upstream, as would often be expected if upstream subpopulations were isolated for long periods and experienced subsequent reductions in diversity. However, values estimated for  $S_{nn}$ ,  $F_{st}$  and  $N_m$  all suggest genetic structure exists for *C. striatus* in Sandy Creek, with differentiation and limited gene flow among subpopulations. Abundance of *C. striatus* at the mill reach was low, but the 2 haplotypes found also occurred downstream, suggesting unrestricted gene flow between these reaches. The upstream reach shared no haplotypes with downstream or mill reaches, but 2 haplotypes found downstream (haplotypes 10 and 12 in Fig. 4A) were more similar to upstream haplotypes than to other downstream haplotypes. Presence of upstream haplotypes in downstream reaches implies the occurrence of migration/dispersal over the dam, but only in the downstream direction. Such downstream unidirectional movement across a dam has been documented in fish populations (Neraas and Spruell 2001).

In contrast, for *C. coosae* in Hatchett Creek,  $S_{nn}$ ,  $F_{st}$  and  $N_m$  values suggested no population structuring. This result also was reflected in the haplotype network, where one haplotype was numerically dominant across all 3

subpopulations. Overall genetic diversity (as  $H_d$  and  $\pi$ ) for the endemic *C. coosae* was much lower than the widespread *C. striatus*, which is consistent with the idea that restricted-range endemic species are less genetically diverse than widespread species (Frankham 1997). Differences in apparent gene flow between the 2 species also may be the result of the relatively young age of the Hatchett Creek dam (~80 y) compared to the age of Jones Mill dam on Sandy Creek (at least 160 y). This time difference would be equal to many generations of crayfishes, and may explain why the COI gene fragment used in this study revealed no population structuring. It is possible, that use of more sensitive genetic markers, such as microsatellites (Avise 2004), might detect finer-scale (i.e., shorter-term) genetic structuring within this system.

Aging and degraded low-head dams are a hazard to recreational activities and may also threaten survival of sensitive aquatic taxa. Our data suggest that streams with intact dams negatively affect crayfishes by creating predaceous fish aggregations downstream of dams that may reduce crayfish abundance. In addition, low-head dams and their resulting reservoirs have the potential to limit longitudinal movements by crayfishes, and serve as an additional source of fragmentation of these populations. As such, dams make excellent targets for restoration projects. However, partial removal (i.e., breaching) of these structures may actually increase threats to downstream biota because of decreased habitat stability due to potentially rapid and catastrophic delivery of multiple decades of sediment buildup directly behind dams. When designing instream restorations in such regulated systems that support at-risk freshwater biota, extensive case-by-

case evaluations are needed to weigh the costs and benefits of dam removal  
(Stanley and Doyle 2003).

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**Appendix A.** Crayfish species, streams where each species was collected, drainage, and study reaches (Up=upstream reach; Mill=mill reach; Down=downstream reach; X=present).

<b>Species</b>	<b>Streams</b>	<b>Drainage</b>	<b>Up</b>	<b>Mill</b>	<b>Down</b>
<b><i>Cambarus coosae</i></b>	Little Cahaba Creek	Cahaba	X	X	X
	Hatchett Creek	Coosa	X	X	X
	Big Canoe Creek	Coosa	X	X	X
	Yellow Leaf Creek	Coosa	X	X	X
<b><i>C. englishi</i></b>	Little Hillabee	Tallapoosa	X		X
<b><i>C. girardianus</i></b>	Turkey Creek	Tennessee			X
<b><i>C. halli</i></b>	Choctafaula Creek	Tallapoosa	X	X	X
	Sandy Creek	Tallapoosa	X	X	X
	Loblookee Creek	Tallapoosa	X	X	X
<b><i>C. howardi</i></b>	Halawakee Creek	Chatahoochee	X	X	X
	Osanippa Creek	Chatahoochee	X	X	X
<b><i>C. latimanus</i></b>	Halawakee Creek	Chatahoochee		X	X
	Hatchett Creek	Coosa		X	X
	Big Canoe Creek	Coosa	X	X	X
<b><i>C. striatus</i></b>	Blue Springs Creek	Black Warrior	X	X	X
	Brushy Creek	Black Warrior	X		X
	Little Cahaba River	Cahaba	X		X
	Cahaba River	Cahaba			X
	Little Uchee Creek	Chatahoochee	X	X	
	Choctafaula Creek	Tallapoosa		X	X
	Little Hillabee Creek	Tallapoosa		X	X
	Sandy Creek	Tallapoosa	X	X	X
	Turkey Creek	Tennessee	X		
	Pearce's Mill Creek	Tombigbee		X	X
<b><i>C. obstipus</i></b>	New River	Tombigbee	X		
	Brushy Creek	Black Warrior	X		X
<b><i>Falicambarus fodiens</i></b>	Pearce's Mill Creek	Tombigbee			X
	Choctafaula Creek	Tallapoosa		X	
<b><i>Orconectes erichsonianus</i></b>	Blue Springs Creek	Black Warrior	X	X	X
	Cahaba River	Cahaba		X	X
	Big Canoe Creek	Coosa	X	X	X
	Paint Rock River	Tennessee	X		X
<b><i>O. forceps</i></b>	Paint Rock River	Tennessee	X	X	X

**Appendix A.** Crayfish species, streams where each species was collected, drainage, and study reaches (Up=upstream reach; Mill=mill reach; Down=downstream reach; X=present).

<b>Species</b>	<b>Streams</b>	<b>Drainage</b>	<b>Up</b>	<b>Mill</b>	<b>Down</b>
<i>O. holti</i>	Big Flat Creek	Alabama	X	X	
<i>O. perfectus</i>	New River	Tombigbee	X	X	X
	Lost Creek	Black Warrior	X	X	X
<i>O. putnami</i>	Turkey Creek	Tennessee	X	X	X
<i>O. spinosus</i>	Turkey Creek	Tennessee	X	X	
<i>O. validus</i>	Brushy Creek	Black Warrior	X	X	X
	Paint Rock River	Tennessee	X	X	
	Turkey Creek	Tennessee	X		
	Buttahatchee River	Tombigbee	X	X	X
	Pearce's Mill Creek	Tombigbee	X	X	X
<i>O. virilis</i>	Cahaba River	Cahaba	X	X	X
	Little Cahaba River	Cahaba	X	X	X
<i>Procambarus spiculifer</i>	Big Flat Creek	Alabama	X	X	X
	Halawakee Creek	Chatahoochee	X	X	X
	Little Uchee Creek	Chatahoochee	X	X	X
	Osanippa Creek	Chatahoochee	X	X	X
	Little Hillabee	Tallapoosa	X	X	X
	Loblockee Creek	Tallapoosa		X	
<i>P. versutus</i>	Yellow Leaf Creek	Coosa	X		X
	Choctafaula Creek	Tallapoosa	X	X	X
	Loblockee Creek	Tallapoosa	X	X	
<i>P. verrucosus</i>	Choctafaula Creek	Tallapoosa	X	X	
	Sandy Creek	Tallapoosa	X		