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EFFECT OF SMALL DAMS ON FRESHWATER MUSSEL POPULATION GENETICS IN TWO SOUTHEASTERN USA STREAMS

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ABSTRACT

The global imperilment of freshwater mussels is strongly linked to widespread habitat destruction by dams, but more subtle mechanisms by which dams impact mussels are not well studied. For example, dams fragment populations in free-flowing reaches, potentially leading to low survival probability due to genetic effects, but few studies have addressed the genetic effects of fragmentation on mussel populations. We examined patterns of genetic variation in the mitochondrial CO1 and ND1 genes in populations of two mussel species that were fragmented by >175 y old small dams. We found that only a few rare haplotypes were restricted to reaches either upstream or downstream of the dams, and an array of genetic parameters showed little differentiation among upstream and downstream reaches. These results can be interpreted in one of two ways. First, gene flow across these dams may remain high, resulting in little genetic fragmentation. Alternatively, the apparent lack of population differentiation could be a historical artifact of high, pre-dam gene flow, and the genetic markers we used may not yet reflect relatively recent population isolation.

KEY WORDS stream; dam; conservation; biodiversity; invertebrates

INTRODUCTION

Dams are responsible for many freshwater mussel population declines and extinctions (Williams et al., 1992; Neves et al., 1997; Vaughn & Taylor, 1999). Streams are impacted by dams through alterations in habitat, modifications in river hydrology and temperature, and blocked migration routes of host fishes (Watters, 1996; Lessard & Hayes, 2003; Graf, 2006). These effects may reduce freshwater mussel distribution, egg fertilization, infection of host fishes, and juvenile settlement particularly downstream of large dams (Fisher & LaVoy, 1972; Layzer & Madison, 1995; Moles & Layzer, 2008). Small dams (<5 m) also have negative effects, but mussel density, species richness, and growth rates can be higher immediately downstream of small dams compared to other parts of some watersheds (Gangloff et al., 2011; Singer & Gangloff, 2011). Dam age and height, stream physiochemistry, and watershed land use may be key factors responsible for the observed benefits of these small dams (Gangloff et al., 2011). In contrast to the effects of dams on physical stream habitats, more subtle effects such as genetic population fragmentation are not well known for mussels.

Genetic evidence for population fragmentation by dams has been documented in highly mobile fishes such as white-spotted charr (*Salvelinus leucomaenis*) and bull trout (*Salvelinus confluentus*) (Neraas & Spruell, 2001; Yamamoto et al., 2004) and in less mobile fishes such as logperch darters (*Percina caprodes*; Haponski et al., 2007). Conversely, populations of other fishes, including greenside darters (*Etheostoma blennioides*) and black redhorse (*Moxostoma duquesnei*), as well as crayfishes, showed no genetic differentiation between populations upstream and downstream from dams (Haponski et al., 2007; Reid et al., 2008, Hartfield, 2010). The few studies of mussel genetic population structure provide similarly mixed results, but none show evidence of reduced gene flow or isolation by dams. Populations of several mussel species showed little or no detectable genetic population structure despite the presence of dams that separate these populations (Berg et al., 1998; Grobler et al., 2006; Szumowski et al., 2012), but other populations show evidence of significant structure apparently unrelated to recent dam effects (Hughes et al., 2004; Elderkin et al., 2008; Grobler et al., 2011). These studies suggest that dam-induced genetic effects on aquatic organisms are highly situation-specific and may depend on factors such as dam porosity, the number and proximity of dams within a river system, and the mobility and life history of species. In addition, because mussels are dependent on fish hosts and host fish use varies among species, genetic structure of mussel populations is highly influenced by differences in mobility and life history traits among fish species.

In this study, we examined the genetic structure of *Elliptio arca* and *Elliptio complanata* populations located upstream and downstream from two >175 y old small dams that impound short reaches of the streams (< 2 km). *Elliptio arca* is endemic to the Mobile Basin and has declined substantially, making it a species of high conservation concern (Mirarchi et al., 2004). Primary fish hosts of *E. arca* are darters (Haag & Warren, 2003). Darters are known for their low mobility that can be greatly reduced or blocked by stream barriers (Warren & Pardew, 1998; Schaefer et al., 2003). *Elliptio complanata* is widespread in Atlantic slope drainages and is considered stable (Williams et al., 1993). *Elliptio complanata* is reported to use members of the Centrarchidae, Percidae, and Fundulidae as host fishes, but recent evidence suggests that American eels (*Anguilla rostrata*) may also be an important host (Lellis, 2001; Cummings & Watters, 2004). Juvenile eels are able to climb wet dam faces directly, and adults can move short distances over-land, allowing them to circumvent stream obstructions such as dams (Sorensen & Bianchini, 1986; Tesch, 2003). We predicted that if the dams are acting as barriers for these two mussel species and their host fishes then we should find unique haplotypes restricted to reaches either upstream or downstream from the dams, low gene flow values, population structuring values that suggest no interbreeding, and statistically significant genetic differentiation values.

METHODS AND MATERIALS

We studied genetic diversity in *Elliptio arca* (Alabama Spike) in Sandy Creek, a third-order tributary of the Tallapoosa River (Mobile River Basin), in east-central Alabama, and *Elliptio complanata* (Eastern Elliptio) in the upper Tar River (Pamlico River Basin), a fourth-order stream in north-central North Carolina (Fig. 1). Both of the study streams drain largely forested catchments in rural, sparsely-populated sections of the southern Appalachian Piedmont and are fragmented by historic mill dams (height <5 m), which impound short reaches of the streams (<2 km).

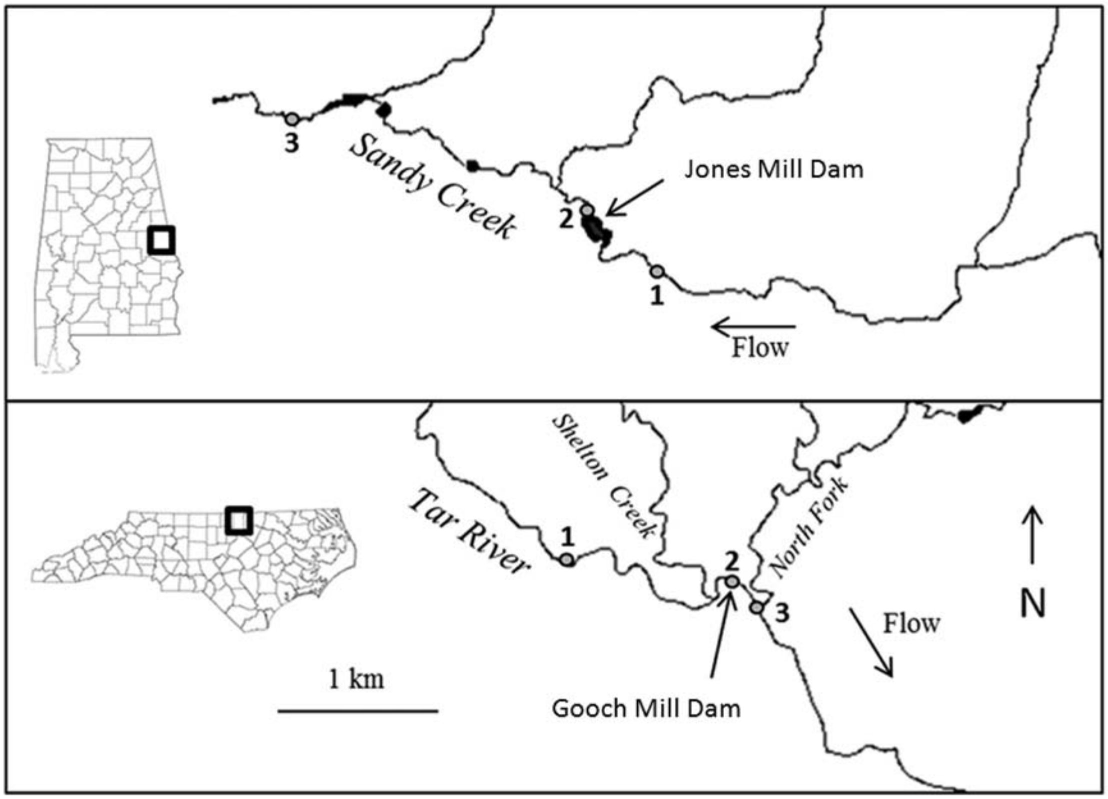

FIGURE 1

Mussel collection sites on Sandy Creek, Chambers Co., Alabama, and the Tar River, Granville Co., North Carolina. On both streams, site 1 is upstream of the mill dam impoundment, site 2 is immediately downstream of the dam, and site 3 is 0.5 km (Sandy Creek) or 5.0 km (Tar River) downstream of the dam. On Sandy Creek, the darkened area in the stream channel upstream of site 2 represents the mill dam impoundment; darkened areas downstream of site 2 are artifacts of the map and do not represent impoundments.

Sandy Creek is impounded by Jones Mill Dam (c. 1836) in Chambers County, Alabama, and the Tar River is impounded by Gooch Mill Dam (c. 1797) in Granville County, North Carolina. Both dams are structurally intact and do not have obvious routes for upstream fish passage. The sluiceways that powered the millworks of both dams are now sediment-filled and have not been operational for at least 50 y. Water moves over the top of these dams, except in periods of low flow, and seasonal high flow events create substantial flow over the dams. We collected mussels in free-flowing reaches upstream, immediately downstream, and farther downstream of the dams (Fig. 1). Large populations of the study species exist in all of these reaches (Gangloff et al., 2011; McCormick, 2012).

We excised fresh tissue (adductor muscle) in the lab and stored it in TE buffer in a -20°C freezer. We sampled adductor muscle to reduce the possibility of sampling male mitotypes, because unionid reproductive tissues can exhibit doubly uniparental mtDNA inheritance (Breton et al., 2007). Any male mitotypes that were sequenced were omitted from the data set. DNA was extracted using a Qiagen DNeasy® kit and animal tissue extraction protocol and stored in a -20°C freezer. We examined fragments of the mitochondrial NADH dehydrogenase 1 (ND1) and cytochrome c oxidase 1 (CO1) genes. These markers were chosen due to their widespread use in freshwater mussel phylogenetic and phylogeographic studies (Serb & Lydeard, 2003; Campbell et al., 2005, 2008; Elderkin et al., 2008).

Approximately 600 base pairs of the CO1 gene and 700 base pairs of the mitochondrial ND1 gene were amplified with polymerase chain reaction (PCR) using available primers (Serb et al., 2003; Campbell et al., 2008). PCR product was then sent to Retrogen, Inc. (San Diego, CA) for sequencing with an ABI 3730 DNA Analyzer (Applied Biosystems, Grand Island, NY). Forward and reverse sequences were compiled and edited in Sequencher (Gene Codes Corporation, Ann Arbor, Michigan) and aligned in MEGA5 (Tamura et al., 2011). CO1 and ND1 sequences for each specimen were concatenated in order to create a single sequence for each individual and one haplotype network for each species. TCS was used to construct haplotype networks (Clement et al., 2000). Reference individuals in these haplotype networks are concatenated *Elliptio arca* sequences from the Black Warrior Drainage (GenBank Accession Number AY655093) and the Coosa Drainage (AY654995) and *Elliptio complanata* from the Connecticut River (AY158780) and the James River (EU448173; Serb et al., 2003; Campbell et al., 2005; M. Gangloff et al., unpublished data). Individual sequences within our dataset that represented unique haplotypes (when not concatenated) were uploaded to GenBank (Accession numbers KC708454 – KC708480). DnaSP was used for population genetics analyses (Rozas et al., 2003).

We computed several standard population genetics statistics, including nucleotide diversity, haplotype diversity, population structuring, gene flow, and genetic differentiation. Nucleotide diversity (π) is defined as the mean number of nucleotide differences between any two sequences and was calculated using equation 10.5 from Nei (1987). Values of nucleotide diversity range from 0 (low) to 0.2 (high) in animals (Daniels et al., 2002; Marko, 2004). Haplotype diversity (H_d) reveals haplotype richness within a subpopulation and was calculated using equation 8.4 from Nei (1987). Values of haplotype diversity range from 0 (low) to 1 (high) in animals (Barber et al., 2002; Cross et al., 2007). The population structure statistic (Fst) calculates the genetic variation among subpopulations, with values ranging between 0 and 1, with values closer to 1 suggesting less interbreeding (Hudson et al., 1992, equation 3). Gene flow (N_m) is an estimate of the effective number of migrants exchanged between subpopulations per generation (Hudson et al., 1992, equation 4). Values between 0 and 1 are considered low and those greater than 1 high. Negative F_{st} and N_m values are a result of more diversity within subpopulations than between populations. Genetic differentiation (S_{nn}) determines the probability of haplotype recovery from the same location (Hudson, 2000). Values near 1 are indicative of highly-differentiated populations, and values near 0.5 suggest populations are panmictic.

RESULTS

The population of *E. arca* in Sandy Creek had eight haplotypes, two of which were found only upstream of the dam (haplotypes 3 and 4) and two were found only downstream (haplotypes 2 and 8; Fig. 2A). Two of the most common haplotypes were found in all three reaches (haplotypes 1 and 5), and two were shared between only two reaches (haplotypes 6 and 7). Nucleotide diversity was low for all populations, ranging from 0.00179 to 0.00196, and haplotype diversity was relatively high, ranging from 0.68 to 0.79 within reaches (Table 1). Population structuring was low (F_{st} = 0.00683), and gene flow between reaches was high (N_m = 72.69). Genetic differentiation was closer to 0.5 than to 1 (S_{nn} = 0.38), suggesting that *E. arca* populations separated by Jones Mill Dam are one panmictic population.

The population of *E. complanata* in the Tar River had nine haplotypes, one of which was found only upstream from the dam (haplotype 6) and two were found only immediately downstream of the dam (haplotypes 2 and 4; Fig. 2B). Three of the most common haplotypes were shared between all three reaches (haplotypes 1, 5, and 7), and three haplotypes were shared between the upstream reach and at least one downstream reach (haplotypes 3, 8, and 9). Nucleotide diversity was also low in this species, ranging from 0.01011 and 0.01047, and haplotype diversity was high, ranging from 0.69 to 0.83 (Table 1). Population structuring was low (F_{st} = -0.06181), and gene flow was high between the three populations (N_m = -8.59). Genetic differentiation was closer to 0.5 than to 1 (S_{nn} = 0.31), suggesting that *E. complanata* populations separated by Gooch Mill Dam are one panmictic population.

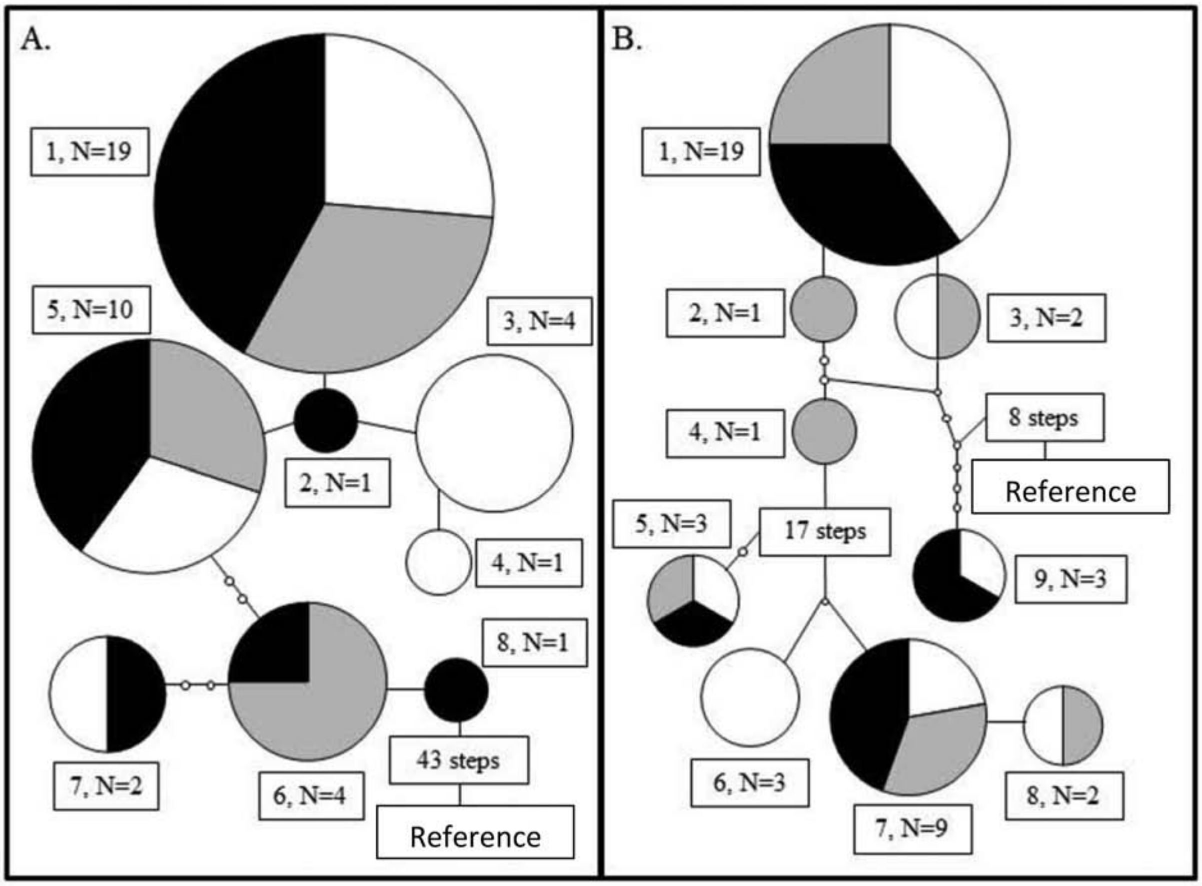

FIGURE 2

Parsimony network of mtDNA haplotypes for the concatenated CO1 and ND1 genes in (A) *Elliptio arca* and (B) *Elliptio complanata*. Each pie chart represents a unique haplotype with connecting lines representing one nucleotide difference (step) between haplotypes, except where otherwise noted. Observed haplotypes are labeled with an identifying number followed by the number of individuals having that haplotype (N). Colors represent the proportion of individuals from each reach having a particular haplotype (white, upstream of the dam; grey, immediately downstream of the dam; black, farther downstream of the dam; see Fig. 1). Pie charts with only one color are haplotypes unique to a particular reach. See Methods for information about reference individuals.

DISCUSSION

We found no strong evidence of genetic isolation in either *Elliptio arca* or *E. complanata* as a consequence of stream fragmentation by mill dams. Although we did observe unique haplotypes upstream (3 out of 17 haplotypes) and downstream (4 out of 17 haplotypes) from both dams, this small number of unique haplotypes does not conclusively suggest that isolation is occurring (Grobler et al., 2006; Perrin et al., 2008). If occurring, isolation would also be evident from low gene flow, high population structuring values, and significant genetic differentiation parameters (Hamilton, 2009).

Because evidence for isolation is weak, either unidirectional or bidirectional gene transfer may be occurring across these small dams. Downstream gene transfer for both species could happen easily by sperm drift or during high flow events when infected host fishes are washed over the top of mill dams. Upstream gene transfer is more difficult to envision, especially for *E. arca*. Darters, host fishes for *E. arca*, are known for their low mobility that can be greatly reduced or blocked by stream barriers (Schaefer et al., 2003). Darters would have a difficult time moving upstream over Jones Mill Dam during the flooding events when there is substantial flow over the dam. On the other hand, the American eel, a likely host fish for *E. complanata* in the Tar River, is well-known for its ability to circumvent stream obstructions such as dams (Sorensen & Bianchini, 1986; Tesch, 2003). This ability provides a plausible mechanism for upstream movement of glochidia and gene flow. Although eels were not found by recent surveys at Gooch Mill Dam, they have been found upstream of other small mill dams in the Tar River (J. Holcomb, unpublished data). Other potential host fishes for *E. complanata* present at Gooch Mill Dam, *Lepomis cyanellus*, *Lepomis gibbosus*, *Lepomis macrochirus*, and *Micropterus salmoides*, would likely have a difficult time getting upstream of Gooch Mill Dam (Ellis, 1974; J. Holcomb, unpublished data). In contrast to downstream gene flow, upstream dispersal is probably less frequent and highly context-specific, and we are unable to propose mechanisms of upstream gene flow for *E. arca* in Sandy Creek. Nevertheless, the distribution of unique haplotypes and other genetic measures do not support a primarily downstream mode of gene flow in either population.

Although we found no evidence of genetic isolation or unidirectional gene flow, a number of factors need to be considered when assessing the extent to which populations upstream and downstream of the dams are isolated. More rapidly evolving genetic markers such as microsatellites might detect population structure that was not evident from mtDNA, which may not show evolutionary changes over the 177-216 year existence of these dams and the relatively small number of mussel generations during this time. Similarly, because population sizes of both species remain large at all of our sites, they may retain a large percentage of historical genetic diversity such that our measures reflect signatures of former, pre-dam gene flow rather than contemporary gene flow (see Grobler et al., 2011). Our relatively small sample size may also have limited our ability to detect rare haplotypes or other patterns of genetic variability and structuring in these populations. Future work could take advantage of non-lethal DNA collection techniques such as viscera, mantle, and foot swabbing to allow increased sample size without sacrificing more individuals (Henley et al., 2006).

Our study provides a first look at the extent to which small dams might fragment freshwater mussel populations. Dams are a pervasive component of stream ecosystems with > 2.5 million small dams in the United States (National Research Council, 1992), and stream fragmentation by dams poses serious demographic risks to isolated populations in addition to potential genetic consequences (Morita & Yamamoto, 2002; Schick & Lindley, 2007). Dam removal projects are an increasingly important tool for re-establishing biological connectivity and ecosystem function and may provide benefits to numerous aquatic species, but they may also have substantial negative short-term impacts (Stanley et al., 2002; Stanley & Doyle, 2003; Sethi et al., 2004). In Sandy Creek and the Tar River, dense, species-rich mussel assemblages occur immediately downstream from these dams (Singer & Gangloff, 2011; McCormick, 2012). Although more research is needed to determine patterns and mechanisms of gene flow, the lack of strong evidence for genetic isolation in our study suggests that, at least in the short-term, removing Jones and Gooch mill dams should be considered low priority objectives relative to other habitat restoration projects in these watersheds.

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TABLE 1

Nucleotide diversity (π), haplotype diversity (H_d), population structuring (F_{st}), gene flow (N_m), and genetic differentiation (S_{nn}) for the concatenated genes (CO1 and ND1) in *Elliptio arca* and *Elliptio complanata*. Reaches represent populations in the vicinity of mill dams on Sandy Creek, AL, (*E. arca*) and the Tar River, NC, (*E. complanata*). The upstream reaches were upstream of the mill dam impoundments, the mill dam reaches were immediately downstream of the dams, and the downstream reaches were 0.5 km (Sandy Creek) or 5.0 km (Tar River) downstream of the dams (see Fig. 1).

Species	Reach	n	π	H_d	F_{st}	N_m	S_{nn}
Elliptio arca	Upstream	14	0.00186	0.79			
	Mill dam	12	0.00179	0.68			
	Downstream	16	0.00196	0.72			
	Overall	42	0.00188	0.73	0.00683	72.69	0.38
Elliptio complanata	Upstream	17	0.01047	0.76			
	Mill dam	14	0.01011	0.83			
	Downstream	13	0.01036	0.69			
	Overall	44	0.00993	0.75	-0.06181	-8.59	0.31