

Genetic Divergence across a Low-head Dam: A Preliminary Analysis using Logperch and Greenside Darters

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ABSTRACT. Dams have been built on waterways for centuries, acting as barriers to fish migration and possible impediments to gene flow. We tested whether the Munroe Falls low-head dam, constructed in 1817 on the middle Cuyahoga River in the northeast Ohio portion of the Lake Erie watershed, formed a barrier for fish migration. Subsequent to our sampling, the dam was removed in fall 2005. The present study characterized the population genetic composition of two species of darters (Family Percidae), *Etheostoma blennioides* (greenside darter) and *Percina caprodes* (logperch darter), upstream and downstream from the dam in comparison with an outlying population from the Grand River, Ohio using mitochondrial DNA control region and cytochrome b gene sequences. Results found a single genotype in the greenside darter samples that was shared upstream and downstream from the dam, and thus no evidence for effect of the dam could be discerned. In contrast, samples of logperch darter differed in genotypic frequencies above and below the dam, with unique alleles occurring below the dam. It thus is possible that the Munroe Falls low-head dam acted as a one-way barrier to gene flow for logperch. Further genetic studies should test for possible after-effects of the dam removal on these darter populations, and relate these data to variation along and among river systems, including other potential barriers to gene flow.

INDEX WORDS: *Etheostoma blennioides*, greenside darter, logperch, low-head dam, *Percina caprodes*, population genetics.

INTRODUCTION

Dams form one of the oldest and most widespread anthropogenic impacts on rivers and streams (Jansson *et al.* 2000) and may lead to the elimination or decrease of invertebrate and fish species (Dynesius and Nilsson 1994). Not only do they negatively affect species, but dams also negatively impact habitats through flooding, erosion, and sediment build-up (McCully 1996). Highly migratory fishes, such as salmonids, often are impeded by dams (Raymond 1979, Helfrich *et al.* 1999, Jager *et al.* 2001). Low-head dams (< 4 m in height) appear to have as many negative impacts on water quality,

fish migration, habitat quality, and species composition as do larger dams (Santucci *et al.* 2005, Gillette *et al.* 2005). These impacts disrupt colonization dynamics, increase genetic isolation, and reduce adaptive potential of resident populations (Ward and Stanford 1995, Pringle 2001). Thus dams may act as barriers that inhibit migration of individuals, resulting in significant population genetic divergence and eventual reproductive isolation of gene pools (Hedrick 2000).

In 1817 a low-head dam was built on the middle Cuyahoga River (part of the Lake Erie watershed) in Munroe Falls, Summit County, Ohio to power a saw and grist mill. The dam was reinforced in 1913 to form the Munroe Falls low-head dam (Summit

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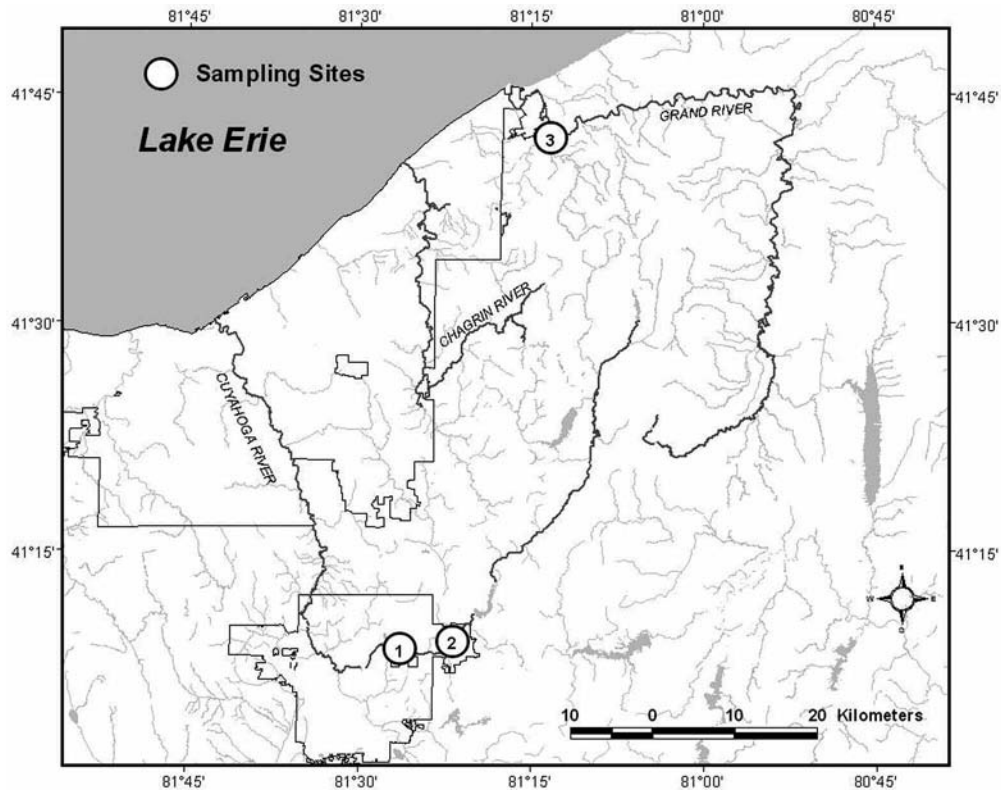


FIG. 1. Map showing sampling locations on the Cuyahoga River, above (2) and below (1) the dam and Grand River outlying population (3).

County 2006; Figs. 1 and 2). The Ohio Environmental Protection Agency (OEPA 1999) reported that the dam's pool had low dissolved oxygen levels, heavy metal contamination, moderate nutrient enrichment, and anoxic sediments. In order to increase biodiversity, as well as water quality of the river, the OEPA (1999) concluded that the dam pool needed to be removed in accordance with the U.S. Federal Water Pollution Control Act Amendments of 1972 and 1978 (Clean Water Act) Total Maximum Daily Load (TMDL) requirements. The OEPA thus recommended that the dam be lowered from a height of 4 m to 2 m and a fish passage be installed (OEPA 2000). During modifications to the dam in the summer of 2005, a natural bedrock break was uncovered that created a natural series of riffles, and so the dam was completely removed (pers. comm., William Zawiski, OEPA, 2006).

Few studies have examined the potential isolating impacts of a dam on the gene flow of fish populations (Neraas and Spruell 2001) and most have focused on highly migratory species (e.g., Hatanaka *et al.* 2006). It is likely that gene flow in non-mi-

gratory resident fish populations, such as darters, may also be significantly impacted by dams. The objective of our study was to compare the population genetic structure of two low-migration species, the greenside darter, *Etheostoma blennioides* Rafinesque (1819), and the logperch darter, *Percina caprodes* Rafinesque (1818), above and below the Munroe Falls low-head dam, constituting a potentially valuable "before" study prior to the dam's removal in fall 2005. Sequence data from two mtDNA regions (control region and cytochrome *b*) were analyzed, both having been commonly used to study fish population genetics (reviewed by Stepien and Kocher 1997).

Greenside and logperch darters are fairly common throughout the Great Lakes region and central North America, and have somewhat different ecologies (Trautman 1981). The greenside darter commonly lives in riffles with large cobble substrate, whereas the logperch darter inhabits a broader range of substrates ranging from sand bars to riffles with large cobble (Trautman 1981). Welsh and Perry (1998) found a significant difference in the



FIG. 2. Photograph of the Munroe Falls low-head dam before its removal (courtesy of William Zawiski, Ohio EPA).

manner in which these two darter species partition the habitat, with the greenside darter found on top of rocks in riffles and the logperch located above the substrate in deeper pools. The logperch darter has a swimbladder and thus occupies both pelagic and benthic habitats, whereas the greenside darter lacks a swimbladder and is confined to the benthos (Page and Burr 1991). Thus, the logperch appears to have greater potential for migration and gene flow, which was investigated in our study.

MATERIALS AND METHODS

Samples of logperch and greenside darters were collected in June 2003 above (41.150°N, 81.363°W) and below (41.143°N, 81.439°W) the Munroe Falls low-head dam in the Cuyahoga River, Ohio, using a combination of kick seining and electroshocking. Whole individuals were immediately preserved in 95% EtOH and then stored at room temperature in our Great Lakes Genetics Laboratory. We sampled 11 logperch and 9 greenside darters above the dam and 11 logperch and 8 greenside darters below. Outlying population samples of the two darters were similarly collected from the

Grand River, Ohio (logperch $N = 2$, greenside darter $N = 24$; at 41.701°N, 81.222°W).

DNA was extracted from right pectoral fin clip tissue using a QIAGEN extraction kit (Qiagen Inc., Valencia, CA), following manufacturer's directions. The mtDNA control region and cytochrome *b* gene were amplified using the polymerase chain reaction (PCR) and protocols adapted from Stepien and Faber (1998), with the primers LW-1 (Gatt *et al.* 2000) and 12Sar-H (Martin *et al.* 1992) for the control region (totaling 1218bp for logperch and 704bp for the greenside darter), and L14724 (Schmidt and Gold 1993) and H15915 (Schmidt and Gold 1993) for the cytochrome *b* gene (totaling 1078bp for logperch and 1080bp for the greenside darter). The amplification protocol was 42 cycles of 40 sec at 94°C, 40 sec at 52°C, and 90 sec at 72°C, with a final extension for 5 min at 72°C. Aliquots of the PCR products were visualized on 1% agarose minigels stained with ethidium bromide, and the remaining portions were purified using a QIAGEN PCR Purification Kit. DNA sequencing reactions were outsourced to the BioTechnology Resource Center at Cornell University, which used Applied Biosystems (ABI) Automated 3730 DNA Analyzers (Fullerton, CA).

TABLE 1. Haplotypes recovered, with GenBank Accession numbers, and their respective polymorphic sites for A) *Percina caprodes* and B) *Etheostoma blennioides*. Dashes indicate no changes from Haplotype 1.

| | | Polymorphic Site | | | | | | | | | | | | | |
|---------------|--------------------------|---------------------|-----|------|---------------------|-----|-----|-----|-----|-----|-----|-----|------|------|------|
| | | Control Region | | | Cytochrome <i>b</i> | | | | | | | | | | |
| Haplotype | GenBank accession number | 111 | 475 | 1048 | 346 | 425 | 736 | 838 | 934 | 979 | | | | | |
| <i>Pca1cr</i> | EF587842 | T | T | C | G | C | C | T | A | T | | | | | |
| <i>Pca2cr</i> | EF587843 | C | C | — | A | — | T | C | G | C | | | | | |
| <i>Pca3cr</i> | EF587844 | C | — | — | — | T | — | — | G | C | | | | | |
| <i>Pca4cr</i> | EF587845 | — | — | T | — | — | — | — | G | C | | | | | |
| | | Polymorphic site | | | | | | | | | | | | | |
| | | Control Region | | | Cytochrome <i>b</i> | | | | | | | | | | |
| Haplotype | GenBank accession number | 87 | 95 | 126 | 316 | 399 | 469 | 473 | 512 | 518 | 612 | 664 | 665 | 667 | |
| <i>Ebl1cr</i> | EF587849 | A | C | A | A | C | C | C | G | A | T | G | T | G | |
| <i>Ebl2cr</i> | EF587850 | — | — | — | — | — | — | — | — | — | C | — | — | — | |
| <i>Ebl3cr</i> | EF587851 | T | T | T | G | T | A | T | A | G | — | A | C | A | |
| | | Cytochrome <i>b</i> | | | | | | | | | | | | | |
| | | 62 | 92 | 113 | 116 | 164 | 245 | 266 | 317 | 338 | 389 | 404 | 419 | 437 | 449 |
| <i>Ebl1cb</i> | EF587846 | C | A | G | C | G | C | T | C | C | G | A | T | T | T |
| <i>Ebl2cb</i> | EF587847 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Ebl3cb</i> | EF587848 | T | G | A | T | A | A | C | A | A | A | G | C | C | G |
| | | 452 | 494 | 515 | 548 | 575 | 593 | 632 | 668 | 671 | 680 | 683 | 702 | 722 | 737 |
| <i>Ebl1cb</i> | | C | T | C | C | C | T | G | T | G | C | A | G | T | T |
| <i>Ebl2cb</i> | | — | — | — | — | — | — | — | — | — | — | G | A | — | — |
| <i>Ebl3cb</i> | | T | C | T | T | T | C | A | C | A | T | — | — | C | C |
| | | 740 | 752 | 773 | 779 | 797 | 842 | 860 | 890 | 897 | 908 | 920 | 1001 | 1004 | 1028 |
| <i>Ebl1cb</i> | | T | C | A | A | A | A | C | A | A | A | G | A | G | C |
| <i>Ebl2cb</i> | | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Ebl3cb</i> | | C | T | G | C | G | G | T | G | G | C | A | G | A | T |

We then determined the DNA sequence haplotypes with the program BioEdit 7.05 (Hall 1999). Population genetic data statistics were calculated using Arlequin 3.01 (Excoffier *et al.* 2005), including measures of haplotype diversity and F_{ST} estimates. Differences in haplotype frequencies above

versus below the dam were tested for using 2×4 contingency table tests (Zar 1999). Tests were run for each mtDNA region separately and together (as a single locus).

Haplotype diversity is based on the number and frequencies of alleles at a given locus, regardless of

TABLE 2. Distribution of haplotypes among sampling locations and genetic variation measures \pm standard error for A) *Percina caprodes* and B) *Etheostoma blennioides* based on two mtDNA regions. Haplotype frequencies for the sampled location are in parentheses.

| A) Logperch Darter | | | | |
|---------------------|----------------------|-------------|---|---------------------|
| mtDNA Region | Location | Sample size | Haplotypes present | Haplotype diversity |
| Control Region | Above dam | 11 | <i>Pca1cr</i> (54.5%), <i>Pca2cr</i> (36.4%), <i>Pca4cr</i> (9.1%) | 0.620 \pm 0.104 |
| | Below dam | 11 | <i>Pca1cr</i> (36.4%), <i>Pca2cr</i> (45.4%), <i>Pca3cr</i> (9.1%), <i>Pca4cr</i> (9.1%) | 0.710 \pm 0.100 |
| | Cuyahoga River Total | 22 | <i>Pca1cr</i> (45.5%), <i>Pca2cr</i> (40.9%), <i>Pca3cr</i> (4.5%), <i>Pca4cr</i> (9.1%) | 0.650 \pm 0.061 |
| | Grand River | 2 | <i>Pca1cr</i> (100%) | 0.000 |
| <i>Cyt b</i> | Above dam | 11 | <i>Pca1cb</i> (64%), <i>Pca2cb</i> (36%) | 0.510 \pm 0.100 |
| | Below dam | 11 | <i>Pca1cb</i> (36.4%), <i>Pca2cb</i> (45.4%), <i>Pca3cb</i> (9.1%), <i>Pca4cb</i> (9.1%) | 0.710 \pm 0.100 |
| | Cuyahoga River Total | 22 | <i>Pca1cb</i> (50%), <i>Pca2cb</i> (41%), <i>Pca3cb</i> (4.5%), <i>Pca4cb</i> (4.5%) | 0.606 \pm 0.062 |
| | Grand River | 2 | <i>Pca1cb</i> (100%) | 0.000 |
| B) Greenside Darter | | | | |
| mtDNA Region | Location | Sample size | Haplotypes present | Haplotype diversity |
| Control region | Above dam | 18 | <i>Ebl3cr</i> (100%) | 0.000 |
| | Below dam | 13 | <i>Ebl3cr</i> (100%) | 0.000 |
| | Grand River | 24 | <i>Ebl1cr</i> (88%), <i>Ebl2cr</i> (12%) | 0.237 \pm 0.105 |
| <i>Cyt b</i> | Above dam | 8 | <i>Ebl3cb</i> (100%) | 0.000 |
| | Below dam | 7 | <i>Ebl3cb</i> (100%) | 0.000 |
| | Grand River | 20 | <i>Ebl1cb</i> (85%), <i>Ebl2cb</i> (15%) | 0.281 \pm 0.116 |

their sequence relationships and the number of nucleotide differences (Nei 1987). This measure thus is defined as the probability that two randomly chosen haplotypes in the sample are different. Haplotype diversity was calculated from the sum of squares of allele frequencies, and is close in value to heterozygosity in randomly mating populations (Weir 1996). Sampling variance was calculated according to Nei (1987). Relationships among collection sites were evaluated in Arlequin using Wright's (1978) F_{ST} estimates and corresponding probability values.

RESULTS

The logperch darter had four haplotypes for the mitochondrial DNA control region (NIH GenBank

Accession # EF587842-EF587845, <http://www.ncbi.nlm.nih.gov>); and four for the cytochrome *b* gene (# EF587838-EF587841) (Table 1A). The control region haplotype here designated as *Pca1cr* (# EF587842) was the most common in both the Cuyahoga River (totaling 54.5% above the Munroe Falls low-head dam and 36.4% below) and the Grand River (100%, Table 2A, Fig. 3). A single unique control region haplotype, designated *Pca3cr* (# EF587844) was discerned below the dam in a single individual (Table 2A). These control region haplotypes differed at three nucleotide sites (Table 1A). Based on the control region, haplotype diversity of the samples above and below the dam was moderate (0.620 \pm 0.104 versus 0.710 \pm 0.100; Table 2A), with somewhat greater diversity found in samples below. Tests for genetic divergence

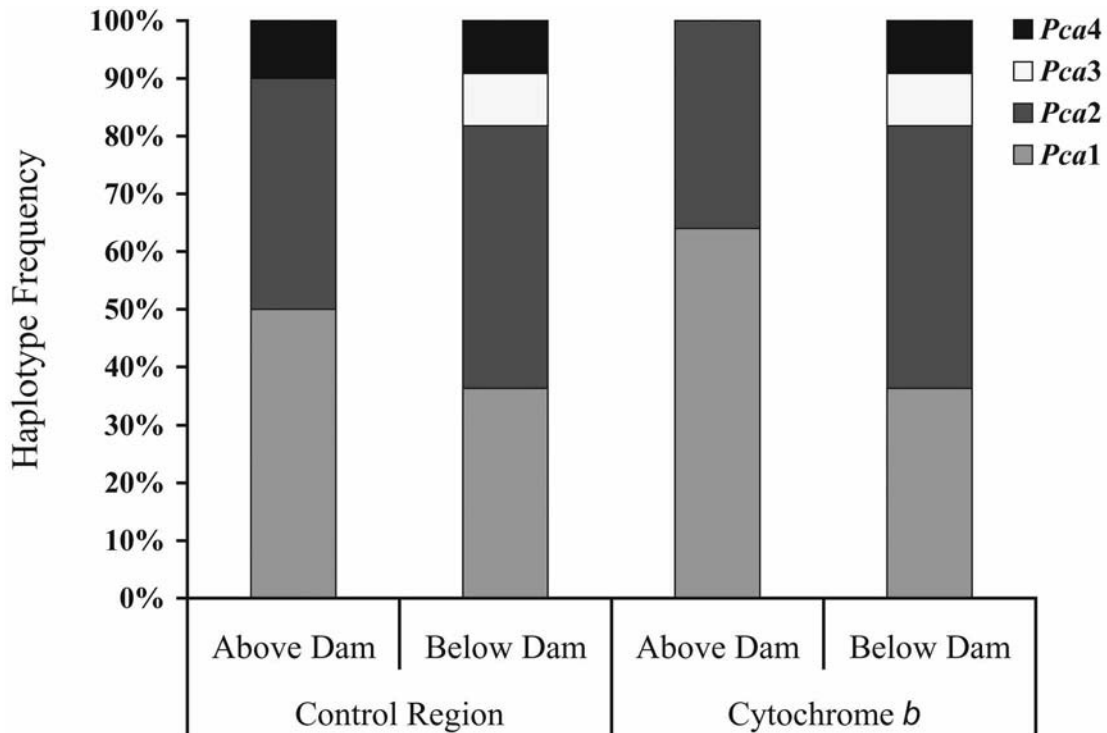


FIG. 3. Bar chart showing relative haplotype frequencies above and below the dam for logperch, *Percina caprodes*, based on sequences from control region and cytochrome *b*.

found no significant difference across the dam, based on the control region sequences and either F_{ST} (0.000; Table 3A) or a contingency test (Table 4). A slight difference was discerned when the Cuyahoga River samples overall were compared with those from the Grand River ($F_{ST} = 0.164$; Table 3A).

Cytochrome (*cyt b*) gene sequence alignments for the logperch samples revealed a similar pattern, but a greater number of polymorphic sites (Table 1A). However, two unique *cyt b* haplotypes were found below the dam, designated as *Pca3cb* and *Pca4cb* (Table 2A; #s EF587840 and EF587841). The most common *cyt b* haplotype was *Pca1cb* (# EF587838), which characterized 100% of the Grand River logperch, as well as 64% of the Cuyahoga River sample above and 36.4% below the Munroe Falls dam (Table 2A, Fig. 3.). Haplotype diversity for *cyt b* sequences was moderate, with greater diversity found below than above the dam (Table 2A), congruent with the pattern discerned using the control region. Again, tests for genetic divergence were not significant (Tables 3A and 4). Genotypic composition of the Grand River sample was similar to

that above the Munroe Falls dam ($F_{ST} = 0.001$), but differed from the sample below the dam ($F_{ST} = 0.208$; Table 3A). Since the control region and cytochrome *b* are part of the mitochondrial genome, they form a single locus (Stepien and Kocher 1997). Haplotypes from the two regions thus were combined into a single sequence, which yielded similar results and no increased significance.

Three control region haplotypes of greenside darters were discerned (Table 1B; #EF587849-EF587851). Haplotype *Ebl3cr* was the sole sequence recovered from the Cuyahoga River above and below the dam, and thus divergence across the dam could not be tested in the present study. Haplotypes *Ebl1cr* and *Ebl2cr* were recovered from the Grand River (Table 2B). Comparison of the Grand (*Ebl1cr* and *Ebl2cr*) and Cuyahoga River (*Ebl3cr*) sequences revealed 13 polymorphic sites between them (Table 1B), which appear to correspond to the subspecies hypothesized by Miller (1968) of *E. blennioides blennioides* versus *E. blennioides pholidotum*. In contrast, only a single nucleotide polymorphism separated the two Grand River haplotypes (Table 1B). Cuyahoga River greenside

TABLE 3. Genetic divergences (F_{ST}) among sampling sites for A) *Percina caprodes* and B) *Etheostoma blennioides* (control region below the diagonal, cytochrome b above). N. S. = not significant at $\alpha = 0.015$, * = Significant following Bonferroni correction (Sokal and Rohlf 1995)

| A) Logperch Darter | | | | |
|---------------------|-------------------------|-------------------------|-------------------------|----------------|
| | Above dam | Below dam | Grand River | Cuyahoga River |
| Above dam | — | 0.000 (N.S.) | 0.000 (N.S.) | — |
| Below dam | 0.000 (N.S.) | — | 0.208 (N.S.) | — |
| Grand River | 0.055 (N.S.) | 0.128 (N.S.) | — | 0.084 (N.S.) |
| Cuyahoga River | — | — | 0.164 (N.S.) | — |
| B) Greenside Darter | | | | |
| | Above dam | Below dam | Grand River | |
| Above dam | — | 0.000 (N.S.) | 0.990* ($p < 0.0001$) | |
| Below dam | 0.000 (N.S.) | — | 0.990* ($p < 0.0001$) | |
| Grand River | 0.990* ($p < 0.0001$) | 0.990* ($p < 0.0001$) | — | |

darter samples thus diverged very significantly from the Grand River population ($F_{ST} = 0.990$; Table 3B), which may indicate a species-level rather than subspecies-level separation.

Cytochrome (cyt) *b* sequence data revealed the same pattern as found for the control region sequences. Three cyt *b* haplotypes were recovered for the greenside darter, including two from the Grand River (*Ebl1cb* #EF587846 and *Ebl2cb* #EF587847) and a single haplotype from the Cuyahoga River (*Ebl3cb* #EF587848) that was found both above and below the dam (Table 1B). Analogous to the pattern discerned with the control region, 40 polymorphic sites were discerned between the Cuyahoga River and Grand River haplotypes using cyt *b* sequences (Table 1B), corresponding to $F_{ST} = 0.990$ (Table 3B) and a great genetic divergence level (see calibration of Wright 1978). Haplotypic diversity (0.281 ± 0.116) in the Grand River sample was much greater than those values characterizing the Cuyahoga River.

DISCUSSION

It has been hypothesized that low-head dams may act as barriers to gene flow in non-migratory stream fishes, such as the two darter species examined here. The present study weakly supports this hypothesis for logperch, and merits further investigation with larger sample sizes, a wider variety of species, and additional low-head dam river systems. Due to the nature of stream and riverine systems, gene flow is more likely to move regularly downstream rather than upstream. However, periodic flooding and other stochastic events sometimes reverse unidirectional gene flow in natural systems.

Our results suggest that due to the extremely low genetic variation (a single haplotype) of the greenside darter in the Middle Cuyahoga River, we cannot at the present time test this hypothesis using either mtDNA control region or cytochrome *b* sequences. This low genetic diversity may have resulted from the severe anthropogenic habitat disturbance and pollution history of the Cuyahoga

TABLE 4. A 2×4 contingency table test comparing haplotype composition above and below the Munroe Falls dam for the logperch darter. N.S. denotes a non-significant *p*-value at $\alpha = 0.05$ and *df* denotes degrees of freedom.

| mtDNA Region | Sampling location | Haplotype | | | | χ^2 value |
|---------------------|-------------------|-------------|-------------|-------------|-------------|-------------------|
| | | <i>Pca1</i> | <i>Pca2</i> | <i>Pca3</i> | <i>Pca4</i> | |
| Control Region | Above the dam | 5 | 4 | 0 | 1 | 1.19 (3 df, N.S.) |
| | Below the dam | 4 | 5 | 1 | 1 | |
| Cytochrome <i>b</i> | Above the dam | 7 | 4 | 0 | 0 | 2.93 (3 df, N.S.) |
| | Below the dam | 4 | 5 | 1 | 1 | |

River (Olive 1976), which has been ecologically recovering since its infamous “demise” in the 1960s (Brown and Olive 1995). However, a comparison between greenside darter samples from the Cuyahoga River with the Grand River (outlying population) reveals a very high degree of genetic divergence (40 polymorphic sites; Table 1B). This high genetic divergence confirms the presence of two putative subspecies (*E. b. blennioides* and *E. b. pholidotum*) within the Great Lakes region. According to Miller (1968), *E. b. pholidotum* should be the sole subspecies of greenside darter found in the Great Lakes region. Our study, however, shows that *E. b. blennioides* inhabits the Cuyahoga River and, in fact, dominates and/or is the sole greenside darter taxon in at least the middle region of the River.

Two of us (AH and CAS, in progress) have found that the greenside darter populations sampled from the Cuyahoga River are more closely related to those from the Ohio River system than to samples from other Lake Erie basin tributaries. This marked genetic separation is more characteristic of a species-level divergence than a subspecies-level separation. Stepien *et al.* (2007) also discerned a significant divergence between population samples of smallmouth bass, *Micropterus dolomieu* from the Grand and Cuyahoga Rivers using microsatellite data. Smallmouth bass from the Cuyahoga River share a closer population genetic history with samples from the Ohio River, diverging from the adjacent Grand River, similar to the population relationships found for the greenside darter in the present study. Thus, these findings of similar biogeographic relationships suggest that the fish fauna of the Cuyahoga River differ significantly from those of adjacent rivers and share a common glacial refugium history descendent from the Ohio River, which may be due to ancient stream linkages or recent anthropogenic connections through the Ohio-Erie Canal (Ohio Department of Natural Resources 1992). This merits further study to distinguish between the aforementioned causes. Also similar to smallmouth bass (Stepien *et al.* 2007), the present study finds that the greenside darter population from the Grand River is more closely related to Lake Erie samples.

Logperch darters did not significantly diverge above and below the Munroe Falls low-head dam region in the Cuyahoga River, according to F_{ST} estimates. However, some unique haplotypes were discerned exclusively below the dam, meriting further testing using larger sample sizes. This result implies that the Munroe Falls low-head dam may

have acted as a one-way barrier to gene flow in the logperch darter. Turner (2001) found that logperch larvae stay in the water column after hatching and are thus subject to downstream transport. Our results suggest a similar pattern, with logperch haplotypes *Pca1cr*, *Pca2cr*, *Pca1cb*, and *Pca2cb* occurring at a higher frequency (Fig. 3) above the dam. These logperch then reproduce and their larvae are washed downstream, thus supplying sites below the dam with additional haplotypes. Using the haplotypes recovered for control region and *cyt b* from the Grand River, we hypothesize that *Pca1cr* and *Pca1cb* are likely the most common haplotypes for the logperch darter in the northeast Ohio region, where there is only a single subspecies (unlike the marked subspecies/species-level divergence found in the greenside darter). This should be further tested with additional sampling.

The present study focused on non-migratory fishes, contrasting with studies of dams that have concentrated exclusively on highly migratory fishes (Raymond 1979, Helfrich *et al.* 1999, Jager *et al.* 2001). Other studies have found that low-head dams influenced the composition of the fish fauna by altering species distribution (i.e., darters, suckers, and minnows), as well as degrading available habitats (Santucci *et al.* 2005, Gillette *et al.* 2005). Our results suggest that for low-migration species, such as the logperch darter, low-head dams may not significantly isolate populations as found for migratory fishes. However, since the present sample sizes were small, further studies should use larger sample sizes and perhaps more rapidly evolving genetic markers, such as microsatellites.

A follow up study should be conducted to investigate the possible impact of the removal of the Munroe Falls low-head dam on darter populations, and should further sample additional sites along the Cuyahoga River. The Ohio EPA has recommended that other dams in the Cuyahoga should be removed or significantly altered to restore the river in accordance with the Clean Water Act (OEPA 2000, 2003). Additional studies thus are needed to investigate the impact of dam removal on fish communities in this and other watersheds; examining fish diversity, relative abundance, and their component genetic diversity. Moreover, further studies should investigate genetic structure of these darters along the Cuyahoga River as well as other river systems, in order to evaluate possible population isolation due to natural and anthropogenic barriers to gene flow.

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