Minnesota Department of Natural Resources
Investigational Report 579, May 2024

Genetic structure and diversity of Channel Catfish in large river systems of Minnesota and North Dakota

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Abstract – Channel Catfish (*Ictalurus punctatus*) are widely distributed across the central United States, yet few studies have examined the genetic diversity and structure of wild populations, and none have included samples from the upper Midwest. Assessing genetic structure can reveal population relationships, connectivity, and possible stocking impacts. Using 10 microsatellite DNA markers, this study assessed genetic diversity among and within Channel Catfish populations from different drainages in Minnesota and North Dakota and among samplings sites within the Red River. Significant, but somewhat low genetic divergence, was found among populations from different drainages including the Mississippi, Missouri, James and Red Rivers. Although stocking may have affected genetic structure, the low divergence plausibly results from relatively recent post-glacial isolation and maintenance of large populations that reduced divergence. Sample sites in the Red River exhibited a weak isolation-by-distance pattern in which allele frequencies had a gradient of change with river distance, which suggested some reproductive connectivity throughout the river. The genetic data and principles support maintaining conserving genetic diversity at least at the level of the large drainages and maintaining or enhancing population connectivity in the Red River

INTRODUCTION

Channel Catfish (*Ictalurus punctatus*) are widely distributed across the central United States and support a major aquaculture industry, yet few studies have examined the genetic diversity and structure of wild populations. Existing studies have focused on moderate (Simmons et al. 2006, Lara-Rivera et al. 2019, Sotola et al. 2017) to small geographic scales (Janzen et al. 2023) and none have included samples from the upper Midwest. Assessing genetic structure can reveal population relationships, connectivity and possible stocking impacts (e.g. Walter et al. 2012, Turnquist et al. 2017).

Channel Catfish are found in the large river systems of Minnesota and North Dakota including the Missouri River, James River, Red River and Mississippi River. Broad-scale population relationships in the region could be affected by current isolation of drainages, past post-glacial connectivity, and stocking. Within drainages, dams could restrict connectivity and affect fine-scale genetic patterns. Telemetry studies have examined Catfish movements in the Mississippi River and tributaries (Joel Stiras, MNDNR, personal communication) and the Red River (Wendel 1999, Siddons 2015. Enders et al. 2019). Catfish in the Red River often moved over 500 km but dams were at least partial barriers to movements. Genetic data complements movement studies but with different resolution. On one hand, genetic data may reveal genetic structure resulting from reproduction isolation if fish home to spawning grounds with high fidelity despite large annual movements. On the other hand, genetic structure can be negligible with only moderate migration per generation (Mills and Allendorf 1996). Populations may be largely composed of resident spawners, but a few migrants may reduce or dissipate genetic divergence.

To assess genetic relationships and diversity of Channel Catfish in Minnesota and North Dakota, this study had two main objectives: 1) to assess genetic diversity among Channel Catfish populations from different drainages in both states and among samplings sites with the Red River and 2) to assess genetic diversity within populations, including heterozygosity, allelic richness and effective population size.

METHODS

Agency biologist provided small fin clips for genetic analysis in 95% ethanol or air dried in scale envelopes. MNDNR provided samples from the Red River near Wahpeton, Fargo, Grand Forks and Drayton sampled in 2022 as well as prior samples from the Mississippi River Pool 2 and the St. Croix River. NDGF provided tissues from lakes Oahe and Sakakawea sampled in 2020 and from the James River in 2020-2022. Manitoba biologists provided samples from the Red River near St. Andrews sampled in 2022 (Table 1).

DNA was extracted from tissues by boiling in a chelating resin and amplified via polymerase chain reaction (PCR) at 10 microsatellite loci previously isolated from Channel Catfish [Au1081and Au1097 (Lamkom et al. 2008); IpCG32, IpCG35, IpCG38, IpCG43, IpCG70, IpCG189, IpCG195, IpCG273 (Waldbiesser et al. 2001, 2007)]. Fluorescently labelled PCR products were then submitted to a core facility for fragment analysis (University of Minnesota Genomics Center, St. Paul) and genotypes were scored using Geneious software (Biomatters, Boston, MA).

Various measures of within-population genetic diversity were estimated from the genotypic data, including expected heterozygosity (H_e), observed heterozygosity (H_o), allelic richness (A_r), and effective population size (N_e). Allelic richness, the number of alleles in each sample standardized to a common size, here 10 individuals, was estimated using the software HP Rare (Kalinowski 2005). Allelic

richness is more sensitive than heterozygosity as a measure of genetic diversity lost due to bottlenecks (Allendorf 1986). Effective population size, one measure of the genetic health of a population, was estimated using NeEstimator (Do et al. 2014). Effective population size is related to the number of adults contributing to a population, but adjusted for varying reproductive success, and is inversely related to the loss of genetic diversity over generations.

Spatial genetic structure among populations was then examined using multiple approaches. A Bayesian clustering approach in the program STRUCTURE (Pritchard et al. 2000) was used to identify distinct populations. STRUCTURE was run with 50,000 iterations of burn-in followed by 200,000 iterations to evaluate 1-5 possible populations. Local priors, which assumed that distinct populations tend to associate with sample sites, were used to improve resolution of subtle population structure (Hubisz et al. 2009). A neighbor-joining tree of genetic relationships was constructed based on genetic distances in the program Populations (Langella 1999) and visualized using FigTree (http://tree.bio.ed.ac.uk/software/figtree/). The program Genalex (Peakall and Smouse 2012) was used to perform a Principal Coordinates Analysis, which locates populations in multi-dimensional space based on similarity of allele frequencies. Genalex was also used to estimate F_{ST}, a measure of genetic divergence, between all population pairs. The F_{ST} values were then used to test for isolation-by-distance (IBD) among the Red River samples. An IBD pattern may develop in a population that is connected but with spatially limited gene flow so that genetic divergence correlates with geographic distance.

Table 1. Sample information and genetic diversity measures for 10 samples of Channel Catfish from Minnesota and North Dakota. Diversity measures include the following: expected heterozygosity (H_e), observed heterozygosity (H_o), allelic richness standardized to a sample of 10 (A_r), and effective population size (Ne) with 95% confidence limits. Negative estimates and infinite confidence intervals indicate that sampling noise exceeds genetic signal. Red River samples from stations 1-4 were combined for effective population size (N_e) estimation.

Sample	Code	N	H_e	H_o	A_r	N_e	CI low	CI up
Mississippi P2, MN	Miss	49	0.85	0.82	8.8	1494	91	Inf
St. Croix, MN	StC	48	0.86	0.82	8.9	364	115	Inf
Oahe, ND	Oahe	41	0.82	0.81	7.9	506	97	Inf
Sakakawea, ND	Sak	41	0.82	0.81	7.7	1584	132	Inf
James, ND	James	24	0.79	0.77	8.0	133	40	Inf
Red-Wahpeton	Red 1	10	0.81	0.78	6.8	-532	279	Inf
Red-Fargo	Red 2	30	0.84	0.79	7.8	-		
Red-Grand Forks	Red 3	13	0.80	0.82	7.6	-		
Red-Drayton	Red 4	12	0.79	0.67	7.0	-		
Red-St.Andrews	StA	57	0.78	0.75	7.1	138	72	651

RESULTS

Multiple approaches indicated genetic divergence among populations at the drainage level. STRUCTURE provided support for 3-4 distinct genetic clusters among all samples. At 3 clusters, Mississippi and Missouri drainage populations each had their own predominant ancestry (i.e., mostly one color; Figures 1 and 2) whereas Red River samples had a mix of 1-3 ancestral groups. One group (green) was rare outside of Red River samples, but conversely, Red River samples commonly shared ancestry with populations in the Missouri drainage and in small amounts in the Mississippi drainage. At 4 clusters, another ancestral group became apparent that associated mostly with the James River sample (yellow). This grouping was shared at low levels with other Missouri River populations but was rare in Mississippi and Red River populations. A tree diagram based on genetic distances illustrates the watershed-based relationships among populations with Mississippi and Missouri drainage population-pairs grouped together and all Red River samples forming their own branch (Figure 3). The Principal Coordinates Analysis also generally supports this broad structure with all Red River samples positive along coordinate 2 and all other samples negative (Figure 4). The F_{ST} values indicated significant divergence among almost all population-pairs from different drainages while divergence was not significant for pairs within the Mississippi and Missouri drainages.

In contrast to the structure among major drainages, Red River sample sites showed less differentiation. The weak genetic structure is best illustrated in STRUCTURE and F_{ST} analyses. Red River sites 1-4 all had a similar mix of multiple ancestries (Figures 1 and 2). St. Andrews was somewhat distinctive with one predominant ancestry group (green), but also low levels of a second ancestry (blue) shared with other Red River sites. Pair-wise F_{ST} comparisons only indicated significant divergence between samples from opposite ends of the river, St. Andrews and Red River sites 1 and 2 (Table 2). Meanwhile, neither St. Andrews nor Red River sites 1 and 2 were significantly diverged from Red River sites 3 and 4. These patterns suggest that Red River samples exhibited a gradient of genetic differentiation, known as isolation-by-distance. The F_{ST} values did increase linearly with geographic distance, as expected with isolation-by-distance, but a Mantel test did not indicate a statistically significant relationship ($P = 0.22$) (Figure 5).

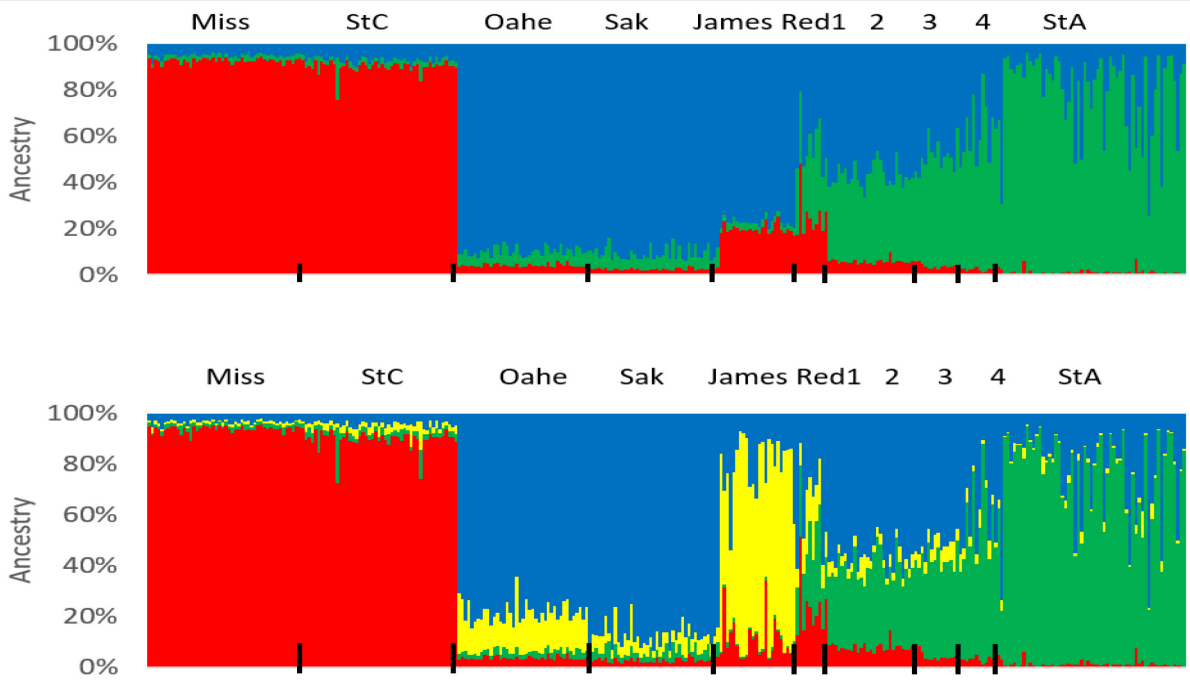

Figure 1. STRUCTURE estimation of ancestry assigned to K=3 (above) or K=4 (below) genetic clusters for 10 samples of Channel Catfish from Minnesota and North Dakota. Each thin vertical line represents one individual and the colors depict the percentage of ancestry assigned to each cluster. Short, black vertical lines separate sample sites.

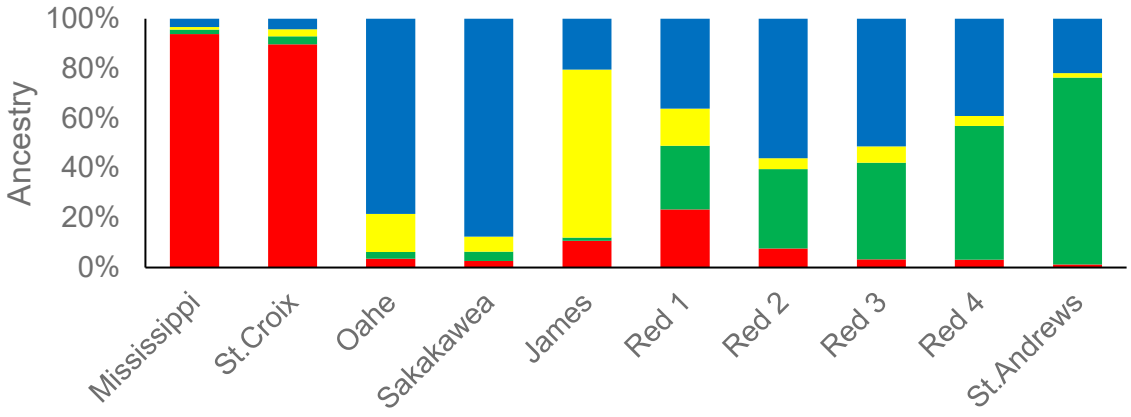

Figure 2. STRUCTURE estimation of ancestry assigned K=4 genetic clusters for 10 samples of Channel Catfish from Minnesota and North Dakota. These are the same results depicted in the lower graph of Figure 1 presented as sample site averages.

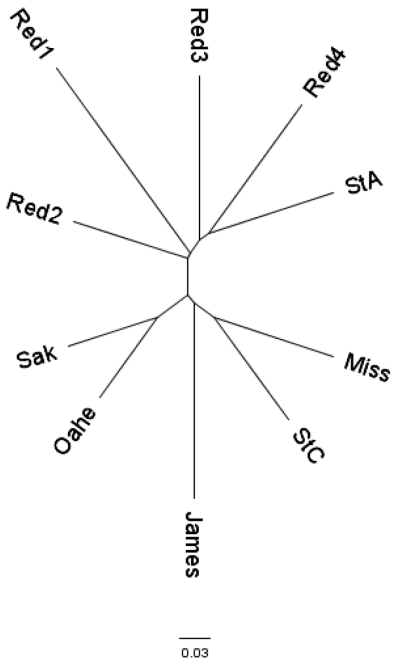

Figure 3. Tree diagram based on genetic distances showing genetic relationships among 10 samples of Channel Catfish from Minnesota and North Dakota. Sample sites on the same branch are more closely related. Sample code names are described in Table 1.

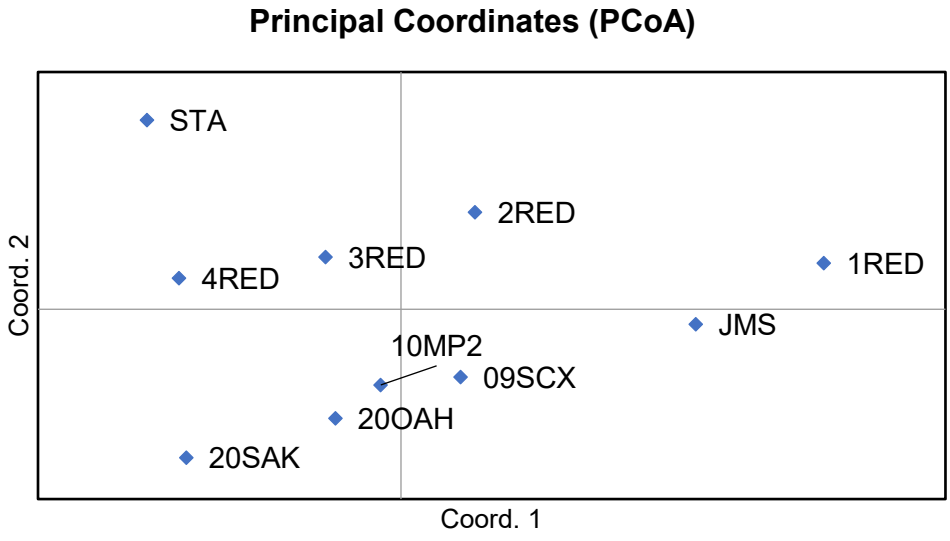

Figure 4. Principal Coordinates Analysis showing genetic relationships among 10 samples of Channel Catfish from Minnesota and North Dakota. The graphic shows the first two principals coordinates that explain the highest amount of variance in allele frequencies among samples. Sample code names are described in Table 1.

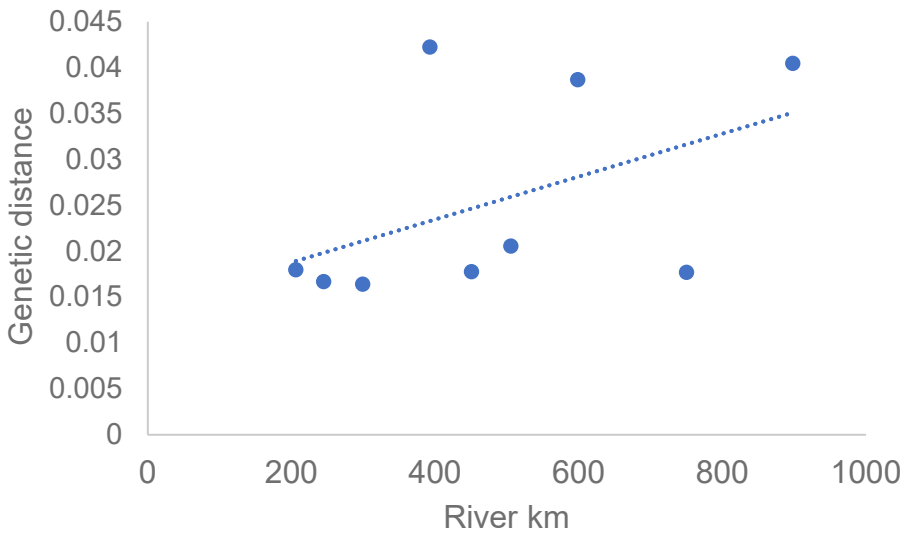

Figure 5. Relationship between genetic (Fst) and geographic (river km) distances to test for isolation-by-distance (IBD) between five sample sites along the Red River. The increasing regression line suggests IBD but a Mantel test did not provide statistical support for a positive relationship (P = 0.22).

Table 2. Pairwise Fst values (below diagonal) and p-values from permutation tests (above diagonal) for 10 samples of Channel Catfish from Minnesota and North Dakota. P-values that were not significant (i.e., P> 0.05) are in bold; values not significant after correction for multiple testing are in bold italics. Row and column headings are sample codes described in Table 1.

	Miss	**StC**	**Oahe**	**Sak**	**1Red**	**2Red**	**3Red**	**4Red**	**StA**	**James**
Miss	-	***0.028***	0.001	0.002	0.001	0.001	**0.062**	***0.032***	0.001	0.001
StC	0.008	-	0.001	0.001	0.001	0.001	0.001	***0.006***	0.001	0.001
Oahe	0.009	0.010	-	**0.730**	0.001	***0.041***	**0.070**	**0.071**	0.001	0.001
Sak	0.011	0.012	0.006	-	0.001	***0.012***	**0.136**	**0.116**	0.001	0.001
1Red	0.034	0.031	0.033	0.034	-	**0.147**	***0.009***	**0.091**	0.001	***0.005***
2Red	0.014	0.015	0.011	0.012	0.026	-	**0.497**	**0.547**	0.001	0.001
3Red	0.017	0.023	0.018	0.017	0.040	0.017	-	**0.937**	***0.019***	0.001
4Red	0.019	0.023	0.020	0.019	0.037	0.018	0.017	-	**0.254**	0.003
StA	0.026	0.025	0.026	0.025	0.039	0.018	0.021	0.016	-	0.001
James	0.020	0.023	0.017	0.021	0.040	0.027	0.031	0.032	0.037	-

Genetic diversity was relatively high within all populations and similarly high across populations (He = 0.78-0.86; Ar = 6.8-8.9) (Table 1). Although diversity levels were similar, a pattern among drainages was generally consistent with Mississippi > Missouri > Red River populations. Red River sites 1-4 were combined for estimating effective population size because of small sample sizes and structure results suggesting that they are generally one large population. Estimates of N_e ranged from 133 to 1,584 with a negative estimate for the combined Red River sample. Negative estimates indicate that sampling noise exceeds genetic signal so that the population is indistinguishable from an "infinitely large" one. Similarly, confidence intervals were large, and the upper confidence of most estimates was infinity.

DISCUSSION

Channel Catfish populations showed genetic structure among large drainages: Red River, Missouri River, James River, and the Mississippi River. This structure is unsurprising because the null condition is a single panmictic, reproductively interacting population, which is physically impossible across major drainages. However, the amount of divergence among the study populations was only moderate given the large distances and isolation among drainages. This low divergence is seen in the incompletely resolved ancestry (i.e., shared colors) in STRUCTURE results and low F_{ST} values. Additionally, population structure was poorly resolved without the use of location information, a Bayesian prior used to help resolve weak structure due to small numbers of markers, small sample sizes or close relationships between populations (Hubisz et al. 2009). The rate and amount of divergence among populations is determined by degree of isolation, population size and time. The relatively low divergence observed here suggests that catfish populations have remained abundant for long periods of time in most of these river systems. Furthermore, the Missouri, James, and Mississippi River populations may have connectivity if migrants and their descendent are able to mix genes over long periods of time. The Red River population is now obviously isolated but shared connectivity with populations in the other drainages following the most recent glaciation. The Red River and Minnesota River drainages were periodically connected during high water events even as recently as the late 1800s, prior to the building of water control structures. Few studies of population structure among wild populations of Channel Catfish are available for comparison; most genetic studies have focused on Catfish broodstocks. Simmons et al. (2006) found that genetic structure reflected isolation by watersheds across Alabama and that possible hatchery escapees had no genetic impact on wild populations. Lara-Rivera et al. (2019) found two ancestral groups among Catfish populations in Mexico.

A common anthropogenic activity that can disrupt natural patterns of genetic structure in fish is stocking. Channel Catfish were occasionally stocked between 1933 and 1989 into the Red River or its tributary, the Sheyenne River (S. Gangl, ND Game and Fish, personal communication). At least some of these came from the Missouri River system and could have reduced genetic divergence between drainages. However, natural geographic patterns of genetic structure have persisted elsewhere for fish species despite more extensive stocking than what has occurred in the Red River (e.g., Walter et al. 2012, Turnquist et al 2017, Bootsma et al. 2021). Further, an infusion of genetic diversity from another

drainage would be expected to enhance within-population diversity in the admixed population, but most Red River samples had among the lowest values of observed heterozygosity and allelic richness. The moderate divergence between populations in the Red River and other drainages seems likely to result from relatively recent post-glacial isolation and maintenance of large populations that reduced divergence.

In contrast to the structure seen across drainages, the Red River samples provided little evidence for genetically divergent, reproductively isolated spawning groups along the distance of the river. Instead, the general gradients in allele frequencies were more consistent with isolation-by-distance. With isolation-by-distance, samples from large geographic distances may differ significantly, suggesting reproductive isolation, but when intermediate samples are taken the divergence dissipates. This pattern suggests that widespread movement and reproductive mixing in the short-term is uncommon but that there is population connectivity over multiple generations. Fish may not move overly far and mix reproductively in any given year or lifetime, but their kids may stray a little and then their grandkids a little further, and so on. This is consistent with telemetry studies showing relatively small home ranges but occasional long movements by Channel Catfish in the Red River (Enders et al. 2019). Sotola et al. (2017) found genetic evidence for isolation by distance among Channel Catfish across 450 km in the Ohio and Wabash River systems, but they also found more clearly distinct genetic subpopulations across this range than were found in this Red River study. Their study system included a major river and distinct tributary and the presence of two locks and dams, which may have increased isolation and divergence among sampling locations. Janzen et al. (2023) found no genetic structure among sample sites within the Ottawa River system but sampled across only 25 km. They specifically rejected the hypothesis that tributary versus mainstem samples would differ due to microhabitat spawning preferences causing population reproductive isolation. In this study, samples over 200 km apart and separated by a dam in the Missouri River were undifferentiated as were samples from the Mississippi River and its St. Croix River tributary in Minnesota. The lack of differentiation in the Missouri River may reflect downstream movement of fish over the dam or the presence of large populations above and below the dam, resulting in minimal divergence despite possibly strong isolation. More powerful genomic markers may detect emerging divergence, but physical or acoustic tagging studies would provide more definitive estimates of contemporary population connectivity.

Genetic diversity values within population suggest that these population are robust. No population stood out with substantially lower diversity, indicating that none of these populations is isolated and at low numbers. Similarly, estimates of effective population size did not indicate concerns for the genetic health of the populations, although confidence intervals were very broad. Narrow confidence intervals are difficult to achieve with limited numbers of genetic markers, and intervals expand rapidly as Ne increases. Conservation genetic guidelines suggest a minimum N_e of 50-100 to avoid detrimental effects of inbreeding depression on population fitness (Willi et al. 2021, Frankham et al. 2014, Jamieson and Allendorf 2014). All estimates were above 100 and usually much higher; further, the linkage disequilibrium method used by NeEstimator is known to underestimate N_e when a species has overlapping generations, as do Channel Catfish. Effective population size is related to the number of adults but can be an order or two

lower due to demographic factors (Hoban et al. 2020). The relatively high diversity and N_e estimates for these Catfish populations is consistent with large riverine populations.

The genetic data and principles support maintaining conserving genetic diversity at least at the level of the large drainages (Red, Missouri, Mississippi). “Genetic Management Units,” often associated with watersheds, are commonly recommended (Jennings et al. 2010, Porak et al. 2015, Hammen and Sloss 2019) to “preserve a portfolio of genetic diversity” across the landscape. If stocking is deemed necessary, source populations within the same drainage would be preferred if there is connectivity to wild populations. The genetic divergence among drainages was significant but relatively low; however, the divergence measured by these genetic markers is slow to develop if populations remain robust. Without ongoing connectivity, populations have the chance to develop selected differences, which are not directly measured with these markers.

The data also support maintaining or enhancing population connectivity in the Red River. The Channel Catfish appear to form one large population with subtle differentiation at large distances. There may be somewhat of a shift in ancestry at Red River site 4 and St. Andrews, with increasing green and reduced blue (Figures 1 and 2), but limited sample sizes and markers prevent drawing strong conclusions about limits to dispersal. Notably, though, this pattern corresponded spatially to the last low-head dam on the Red River, which was seasonally inundated and thus provided stage-dependent fish passage. The incomplete nature of this barrier may partially explain the weak ancestry spatial patterning. Sample sizes at several Red River sites were reduced by DNA quality issues of unknown cause for many samples.

From a management perspective, populations at geographic extremes may be mostly-isolated stocks that could have differing demographics. From an evolutionary perspective, there is likely enough gene flow to reduce selective genetic divergence. Combining insights from movement and genetic data will help to understand population structure and dynamics along the river. High-resolution single-nucleotide polymorphisms (SNPs) have been identified for Channel Catfish, but they have been applied to culture settings and gene mapping (Sun et al. 2014, Lui et al. 2016), not studies of wild populations. The microsatellite markers used in this study provided useful coarse resolution of genetic diversity and structure among Minnesota and North Dakota Catfish populations, but finer-scale insights and the ability to test for adaptive divergence would best be pursued with SNPs (Wenne 2023).

ACKNOWLEDGEMENTS

I thank Scott Gangl and North Dakota Game and Fish biologists, MNDNR Detroit Lakes and East Metro Area offices, and the Manitoba Department of Natural Resources for providing samples. Gangl and Nick Kludt, MNDNR, provided helpful reviews of the manuscript.

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