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ARTICLE

Estimating the genetic diversity and potential influence of habitat segregation in Channel Catfish

Francesco H. Janzen | **Gabriel Blouin-Demers**

Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

Correspondence
Francesco H. Janzen
Email: fjanz086@uottawa.ca

Abstract

Objective: Individual habitat preference can reduce intraspecific competition for resources and may differ between age groups, sexes, and adult phenotypes. The Channel Catfish *Ictalurus punctatus* is a widespread species occurring in diverse freshwater habitats. This species displays breeding philopatry, returning to nesting sites occupied in previous years. Larger Channel Catfish tend to nest in the main channels of large rivers, whereas smaller fish tend to prefer smaller tributaries. The purpose of our study was to determine whether this habitat segregation potentially associated with habitat preference affects the genetic structure of a population. We hypothesized that spatial segregation of breeding sites in the Ottawa River and its smaller tributaries at Lac des Chats reduced gene flow within the population, resulting in genetically differentiated demes associated with lacustrine-like and fluvial habitats.

Methods: Microsatellite allelic data was collected from 162 Channel Catfish.

Result: We found little genetic variation between the Ottawa, Mississippi, and Madawaska rivers. Furthermore, our analyses suggested that the sampled specimens comprised one panmictic population. Fish from one site in the Ottawa River, however, were significantly differentiated from fish from a nearby site also in the Ottawa River as well as from fish from the Mississippi River tributary.

Conclusion: Given that fish from sites further up the Ottawa River were not differentiated from fish from these sites, it is unlikely that geography can account for the differences observed; rather, assortative mating may explain the differentiation. We propose that panmixia within the population is caused by ontogenetic changes in habitat selection, straying individuals, or sex-biased dispersal and philopatry.

KEYWORDS

gene flow, habitat preference, homing, microsatellites, migration, philopatry, straying

INTRODUCTION

Intraspecific variation in habitat preference can occur within populations, where individuals differ in the habitats they select (Robinson et al. 1996; Violle et al. 2012; Dehnhard et al. 2020). Individual habitat preference and specialization is a strategy that reduces intraspecific competition for resources (Svanbäck et al. 2008; Violle et al. 2012; Dehnhard et al. 2020). This habitat variation can occur between age groups, sexes, and polymorphic adult phenotypes (Robinson et al. 1996; Marra and Holmes 2001; Ward et al. 2006; Violle et al. 2012; Mills

et al. 2021). For example, Antarctic fur seals *Arctocephalus gazella* display sexual segregation of foraging sites (Kernaléguen et al. 2016; Jones et al. 2020). Females forage closer to pupping sites because they are constrained by parental care, whereas males travel further from pupping sites, potentially seeking areas of high food density to support their larger body sizes (Kernaléguen et al. 2016; Jones et al. 2020). Another example is the link between habitat specialization and polymorphic adult morphology of Arctic Char *Salvelinus alpinus* (Snorrason et al. 1994; Kapralova et al. 2015). Arctic Char display four adult morphs partially determined by genetics and environmental conditions (Snorrason et al. 1994; Kapralova et al. 2015). Benthic and limnetic morphs differ in cranial, fin, and gill raker morphology, as well as coloration linked with differences in diet and habitat use (Snorrason et al. 1994; Kapralova et al. 2015).

Differences in intraspecific habitat preference can lead to habitat segregation and subsequently influence the genetic structure of a population. If reproduction is restricted to individuals occupying the same preferred habitats, gene flow will be constrained between different habitats (Rausher 1984; Hellberg 1994; Stepien et al. 2009). These subpopulations may genetically diverge over time, thus increasing genetic diversity within the population, further reinforced by selection for different traits between habitats (Rausher 1984; Jaenike and Holt 1991; Hellberg 1994; Berner and Thibert-Plante 2015). Smaller subpopulations, however, are more prone to genetic drift, potentially reducing genetic diversity within the population (Lande 1976; Allendorf 1986; Lynch et al. 2016). Genetically distinct subpopulations have been observed in many species that demonstrate intraspecific habitat preference variation, such as American bullfrogs *Lithobates catesbeianus* (Cloyed and Eason 2017), flour beetles *Tribolium castaneum* (Agashe and Bolnick 2010), Arctic Char (Adams et al. 2006), and White Sharks *Carcharodon carcharias* (Jorgensen et al. 2010). As subpopulations accrue genetic differences over time due to assortative mating, reproductive isolation and speciation may occur within a metapopulation (Markert et al. 1999; Via 2001; Berner and Thibert-Plante 2015; Igarashi et al. 2018).

Another example of a widespread species that occurs in a diversity of habitats is the Channel Catfish *Ictalurus punctatus* (Ictaluridae, Siluriformes). Channel Catfish are distributed throughout North America, occupying streams, rivers, and lakes (Wellborn 1988; Dames and Coon 1989; Pellett et al. 1998; Hubert 1999; Sotola et al. 2017). Channel Catfish migrate between protective overwintering deepwater habitats and shallow-water spawning sites with abundant food in the summer (Dames and Coon 1989; Pellett et al. 1998; Hubert 1999). These migrations are prompted by water temperature; autumnal migrations coincide with water temperatures dropping between 10 and 13°C (Pellett et al. 1998). Temperatures associated with spring migrations are still unknown. On average, Channel Catfish migrate ~8–16 km but can migrate up to 100–500 km (Pellett et al. 1998; Sotola et al. 2017). Channel Catfish display breeding philopatry, an annual return to previously occupied nesting sites (Greenwood 1980; Pellett et al. 1998; Pearce 2007; Hastings et al. 2017; Sotola et al. 2017; Winger et al. 2019). During the summer, Channel Catfish return to previously occupied territories and rarely travel further than 5.7 km from this location (Pellett et al. 1998; Sotola et al. 2017). About 30–40% of the population, however, strays throughout the river and its tributaries (Pellett et al. 1998).

Impact statement

Habitat segregation of breeding Channel Catfish populations does not translate into genetic isolation of lacustrine-like and fluvial subpopulations, improving our understanding of gene flow. Ottawa River catfish are as genetically diverse as wild American populations and more diverse than domestic stocks.

Site fidelity is related to Channel Catfish size; fish of intermediate size (~280–380 mm) tend to roam throughout tributaries of large rivers (Dames and Coon 1989; Pellett et al. 1998). Both smaller (<250 mm) and larger (>380 mm) fish tend to remain within 2–5.7 km of their nesting sites throughout the summer, preferring large river channels (Dames and Coon 1989; Pellett et al. 1998; Sotola et al. 2017). Larger fish are better able to defend high-quality territories and thus could have more incentive to return to those sites in following years (Pellett et al. 1998). Furthermore, smaller fish unable to establish territories due to competition could be forced into less desirable habitats, resulting in little incentive to return to those sites (Pellett et al. 1998). Therefore, a smaller roaming fish that reaches a large size should eventually establish a territory and return to that site annually. This hypothesis, however, has not yet been formally tested. Conversely, breeding site fidelity and habitat preference may be influenced by intraspecific variation in habitat preference and genetics, reinforced by lower migration and the separation of breeding populations between different spawning habitats (fluvial and lacustrine) (Bolnick et al. 2009). Channel Catfish as short as 170 mm and weighing 0.34 kg can spawn (Wellborn 1988; Hubert 1999), indicating the possibility of a smaller adult subpopulation that may prefer smaller tributaries to large lakes and rivers. These smaller fish can reproduce within the tributaries, separated and protected

from the larger fish in lakes and the main channels of rivers. Genetic substructuring of populations has been observed between fluvial and lacustrine habitats in freshwater fishes, such as Threespine Stickleback *Gasterosteus aculeatus* (Bolnick et al. 2009). Furthermore, the migratory Neotropical Dorado *Brachyplatystoma rousseauxii* exhibits differences between habitat-associated subpopulations within ~300 km (Carvajal-Vallejos et al. 2014). Genetically distinct subpopulations potentially linked with philopatry occur within the western Amazon River and the upper Madeira River, a tributary of the Amazon River (Carvajal-Vallejos et al. 2014).

To date, few studies have investigated how the physical environment has potentially affected the genetic structure of Channel Catfish populations. The environment can influence the genetic diversity of a species at several spatial scales. Previous studies have focused on large geographical areas and have provided evidence that isolation by distance and population fragmentation via dam construction have influenced the genetic structure of the species (Sotola et al. 2017). Less is understood, however, about how local environmental heterogeneity and habitat segregation of breeding populations at smaller spatial scales (~50 km) may also influence the genetic diversity of Channel Catfish. The purpose of our study was to investigate whether breeding habitat preferences associated with fluvial and lacustrine-like breeding habitats in Channel Catfish translated into genetic differentiation within a population of the Ottawa River and its tributaries. We hypothesized that habitat segregation potentially linked with breeding site preferences has reduced gene flow and promoted genetic differentiation between shallow river subpopulations and deep lake-like subpopulations in Lac des Chats. We predicted that Channel Catfish from the Ottawa River would be genetically distinct from individuals within its tributaries. Conversely, if segregation of breeding populations is not caused by habitat preference, the population should not demonstrate genetic substructuring associated with habitat type or river. To test this hypothesis, we collected Channel Catfish from Lac des Chats of the Ottawa River and from the Mississippi, Madawaska, and Bonnechere rivers. Using microsatellite allelic data, we estimated the relative genetic differentiation of each subpopulation sampled.

METHODS

We collected 162 Channel Catfish from Lac des Chats, a ~40-km reach of the Ottawa River between Portage-du-Fort, Québec, and Chats Falls Generating Station, during summer 2018 (Figure 1). Two hydroelectric dams delineate this portion of the river and prevent upriver fish movements. This reach of the Ottawa River has become a reservoir due to the presence of both dams. Three major tributaries meet the Ottawa River between the dams: the Mississippi River, the Madawaska River, and the Bonnechere River. These smaller rivers, and the shallow banks of the Ottawa River, offer ideal summer nesting sites for Channel Catfish that provide cover, such as wood debris, large rocks, undercut river banks, etc. (Hubert 1999; Haxton and Chubbuck 2002). Throughout their distribution, Channel Catfish spawn as early as March and as late as August, exhibiting latitudinal differences in exact spawning months

FIGURE 1 Aerial view of the ~40-km Ottawa River reach known as Lac des Chats, between Portage-du-Fort and Chats Falls Generating Station at the border between Québec and Ontario, Canada. The inset depicts the study location in Canada with a white star. Collecting sites are indicated by white markers. Ottawa River collection sites are labeled Ot1–Ot5, the Mississippi River collection site is labeled Mis, and the Madawaska River collection site is labeled as Mad. Map data: Google Earth Pro, Maxar, CNES/Airbus.

(Hubert 1999). Northern American populations from South Dakota and Wyoming typically spawn from mid-June to July (June 1977; Hubert and O'Shea 1991; Hubert 1999). Given the more northern latitude of Ottawa, we collected fish between June and August from five sites along the Ottawa River and from one site in each tributary using a combination of angling and hoop nets. We selected these sites based on two criteria: (1) even distribution throughout Lac des Chats and its tributary rivers and (2) empirically determined sites of high Channel Catfish abundance. We measured total body length with a measuring board and weight with a spring scale. We collected muscle tissue samples from each individual and stored them in 95% ethanol.

We extracted DNA from the muscle tissue samples with a homemade animal extraction kit and a modified protocol from Ivanova et al. (2006). We used the resulting extractions to amplify 16 microsatellite loci (Table S1 available in the Supplement in the online version of this article) chosen from a pool of 30 available loci for Channel Catfish (Vieira et al. 2016). We chose our loci based on successful amplification and allelic length variation (Waldbieser and Bosworth 1997, 2013; Waldbieser and Wolters 1999; Tatarenkov et al. 2006). We used the following PCR recipe to amplify all microsatellite loci: 1X Dream buffer containing 2 mM $MgCl_2$ (ThermoFisher Scientific), 0.2 mM of deoxynucleotides, 0.05 μM of forward primer labeled with 5′-M13 or 5′-CAG tag (Table S1), 0.2 μM of reverse primer, 0.2 μM 5′-labeled tag primers with fluorescent dye (FAM, VIC, NED, or PET; Table S1), 0.75 U of Dream Taq, about 20–30 ng of template DNA, and nuclease-free water to adjust the final reaction volume to 15 μL. Using a Mastercycler pro S (Eppendorf Canada), we amplified our PCR products with the following heat cycling conditions: initial heating to 95°C for 3 min, 35 cycles of denaturation (95°C for 30 s), primer annealing (55°C for 30 s), and extension (72°C for 1 min and 30 s) phases, and a final extension phase at 72°C for 10 min. Samples that could not be amplified on the first attempt were reamplified using an annealing temperature of 59°C.

Once we amplified all 16 microsatellite loci, we combined the PCR products into two pools per individual for genotyping. Each pool contained eight loci: two loci of nonoverlapping allelic size ranges for each of the four fluorescent tags listed above. The first pool for each individual comprised *BM1-37*, *IpCG18*, *IpCG11*, *IpCG14*, *IpCG01*, *IpCG54*, *IpCG08*, and *IpCG195*. The second pool for each individual comprised *IpCG12*, *POMC*, *71–59*, *IpCG71*, *GY047K03*, *IpCG07*, *IpCG273*, and *BM1-33*. Each genotyping reaction contained 8 μL of PCR product (1 μL per locus), 0.4 μL of fluorescent size standard ladder (LIZ), and 9.6 μL of HIDI formamide. We genotyped each individual using a 3500 xL Genetic Analyzer (ThermoFisher Scientific). Finally, we visualized and scored alleles using GeneMarker version 2.6.4 (Hulce et al. 2011).

Using Micro-Checker version 2.2.3 (Van Oosterhout et al. 2004), we corrected allelic scoring errors in our microsatellite dataset and assessed each locus for the presence of null alleles and large allele dropout. Then, we used Arlequin version 3.5.2.2 (Excoffier and Lischer 2010) to estimate basic indices of genetic diversity within the sampled subpopulations (the number of alleles per locus [A], expected heterozygosity [H_E], and observed heterozygosity [H_O]), to test for Hardy–Weinberg equilibrium (using a Bonferroni correction), and to test for linkage disequilibrium between loci (Holm 1979; Benjamini and Yekutieli 2001; Excoffier and Lischer 2010). We also estimated allelic richness (A_R) and the inbreeding coefficient (F_{IS}) per locus for each collection site using HP-Rare version 1.1 (Kalinowski 2005) and FSTAT (Goudet 1995, 2002), respectively. To test our hypothesis, we used Arlequin to calculate pairwise subpopulation differentiation (F_{ST}) using the sum of squared differences for 16,000 permutations and a hierarchical analysis of molecular variance (AMOVA) using the sum of squared differences for 16,000 permutations. We performed the pairwise subpopulation differentiation and AMOVA analyses after excluding loci with evidence of null alleles and linkage. For these analyses, we used nine loci: *IpCG01*, *IpCG54*, *IpCG195*, *IpCG11*, *IpCG14*, *GY047K03*, *IpCG07*, *71–59*, and *IpCG71*. We assessed the statistical power of our differentiation analyses with NeEstimator (Do et al. 2014) and POWSIM (Ryman and Palm 2006) using the effective population size (Ne), number of proposed subpopulations (two [fluvial versus lacustrine], three [Ottawa, Mississippi, and Madawaska rivers], and seven [collection sites]), subpopulation size, number of microsatellite loci, and allele frequencies per locus. Finally, we inferred the number of distinct genetic populations (K) free of a priori assumptions using STRUCTURE (Pritchard et al. 2000; Falush et al. 2003). We ran seven independent runs for each value of $K = 1–8$, each run for 100,000 replicates (10,000 burn-in replicates) using an admixture ancestry model and a correlated allele frequencies model (Pritchard et al. 2000; Falush et al. 2003). Using STRUCTURE HARVESTER (Earl and VonHoldt 2012), we compared the probability of $K = 1–8$, identifying the most supported value with the highest natural logarithm of the probability of K [$\ln \Pr(x|K)$] as the number of genetic populations. We then plotted results for $K = 2$ and $K = 3$ using STRUCTURE PLOT (Ramasamy et al. 2014).

RESULTS

We collected 162 Channel Catfish: 100 individuals from five sites on the Ottawa River (~20 individuals per site), 40 individuals from the Mississippi River, and 22 individuals

from the Madawaska River (Table 1). We were unable to collect any Channel Catfish from the Bonnechere River, possibly because it is too narrow and shallow between its mouth and the Bonnechere Falls. Total body length ranged from 232 to 594 mm; sampled individuals comprised small (<280 mm, $n=12$), intermediate (~280–380 mm, $n=96$), and large (>380 mm, $n=54$) Channel Catfish as defined in previous migratory studies of the species (Dames and Coon 1989; Pellett et al. 1998; Table S2).

Within the corrected allele dataset, the total number of alleles per locus ranged from 5 to 29 (Table S3), averaging between 7.4 and 9.0 per sampling site over all loci (Table 1). Mean allelic richness of all loci per sampling site ranged from 5.7 to 6.1, mean expected heterozygosity ranged from 0.76 to 0.79, mean observed heterozygosity ranged from 0.72 to 0.77, and mean inbreeding coefficient ranged from 0.001 to 0.058 (Table 1). We detected null alleles at two loci (*IpCG08* and *BM1-33*), but we did not detect large allele dropout. Our sampled population was at Hardy–Weinberg equilibrium: only 4 of 112 tests (per locus per sampling site) significantly deviated from Hardy–Weinberg equilibrium after Bonferroni correction. In each of the four cases, observed heterozygosity was significantly lower than expected heterozygosity for locus *IpCG08* at the Mississippi River, Madawaska River, and two Ottawa River sites. We also found evidence of linkage disequilibrium between some loci (Table S4).

Pairwise differentiation tests revealed that Channel Catfish from most sites were not significantly differentiated (Table 2). We detected minor, however statistically significant, differentiation between Channel Catfish from (1) Ottawa River site 1 and Ottawa River site 5 ($F_{ST}=0.042$, $p=0.03$) and (2) Ottawa River site 1 and Mississippi River ($F_{ST}=0.033$, $p=0.02$; Table 2). When we grouped Channel Catfish from our five Ottawa River sites and repeated the analysis, the fish from the Ottawa and Madawaska rivers showed no significant differentiation ($F_{ST}=0.000$, $p=0.50$) nor did the fish from the Ottawa and Mississippi rivers display significant differentiation ($F_{ST}=0.012$, $p=0.06$). When comparing the tributaries, we did not detect any significant differentiation between the subpopulations ($F_{ST}=0.004$, $p=0.22$). Finally, when we grouped all Ottawa River sites as the lacustrine-like subpopulation and the Madawaska and Mississippi sites as the fluvial subpopulation, we did not detect significant differentiation ($F_{ST}=0.006$, $p=0.10$). The statistical power calculated for each of these comparisons is as follows: (1) lacustrine-like versus fluvial, $\chi^2=0.802$, Fisher = 0.795; (2) three rivers, $\chi^2=0.678$, Fisher = 0.642; and (3) each sample site, $\chi^2=0.610$, Fisher = 0.585, indicating that we had adequate statistical power to detect possible genetic differences between the proposed subpopulations. The hierarchical AMOVA revealed that 99.3% of the variance was attributed to differences within individuals, whereas only 0.7% of the variance was due to differences between subpopulations collected from different rivers (Table 3). Finally, our a priori STRUCTURE analysis identified $K=1$ as the best-supported K-value, indicating the 162 sampled Channel Catfish form one panmictic population (Figure S1 available in the Supplement in the online version of this article). Bar plots for $K=2$ and $K=3$ provide visual depiction of population clustering (Figure S2).

TABLE 1 Collection site information and basic genetic diversity indices for 162 Channel Catfish captured from Lac des Chats. Site information includes river, site code, GPS coordinates, and the number of individuals collected. Genetic diversity indices presented for each collection site are averaged over 16 microsatellite loci. Diversity indices include number of alleles (A), allelic richness (A_R), expected heterozygosity (H_E), observed heterozygosity (H_O), and inbreeding coefficient (F_{IS}).

River	Site code	GPS coordinates	Number of individuals	A	A_R	H_E	H_O	F_{IS}
Ottawa	Ot1	N45°27′46.4″ W076°23′13.0″	21	7.44	5.65	0.768	0.736	0.043
Ottawa	Ot2	N45°30′47.6″ W076°30′17.2″	19	7.44	5.71	0.764	0.760	0.006
Ottawa	Ot3	N45°29′48.0″ W076°26′47.0″	20	7.88	5.95	0.763	0.720	0.058
Ottawa	Ot4	N45°31′08.0″ W076°32′22.0″	20	7.50	5.65	0.766	0.750	0.022
Ottawa	Ot5	N45°26′51.0″ W076°19′04.2″	20	7.69	5.80	0.761	0.760	0.001
Mississippi	Mis	N45°25′47.0″ W076°15′40.0″	40	9.00	5.87	0.773	0.763	0.013
Madawaska	Mad	N45°26′32.92″ W076°20′54.9″	22	8.63	6.12	0.791	0.770	0.027

TABLE 2 Pairwise differentiation tests (sum of squared differences) between Channel Catfish collection sites along the Ottawa, Mississippi, and Madawaska rivers using data from nine microsatellites after excluding linked loci and loci with null alleles. The F_{ST} values calculated between each collection site are presented above the diagonal and *p*-values presented below. Significant differences are indicated with an asterisk. Collection sites are labeled as follows: Ottawa River = Ot1–Ot5, Mississippi River = Mis, and Madawaska River = Mad.

Collection site	Ot1	Ot2	Ot3	Ot4	Ot5	Mis	Mad
Ot1		0.0000	0.0000	0.0000	0.0418*	0.0330*	0.0000
Ot2	0.6985		0.0000	0.0000	0.0151	0.0191	0.0000
Ot3	0.3248	0.6091		0.0000	0.0069	0.0066	0.0000
Ot4	0.4167	0.5661	0.6578		0.0331	0.0303	0.0026
Ot5	0.0316*	0.2007	0.1882	0.1180		0.0000	0.0077
Mis	0.0154*	0.0984	0.1371	0.0547	0.8446		0.0040
Mad	0.4425	0.5765	0.4293	0.3446	0.2254	0.2165	

TABLE 3 Analysis of molecular variance (AMOVA) results using sum of squared differences in Arlequin version 3.5.2.2 between three subpopulations of Channel Catfish ($n = 162$) collected from the Ottawa, Mississippi, and Madawaska rivers.

Source of variation	Sum of squares	Variance components	Percentage variation (%)
Among rivers	3363.17	7.31	0.68
Among individuals within rivers	165,844.53	0.00	0.00
Within individuals	179,058.00	1105.30	99.32
Total	348,265.70	1112.61	100.00

DISCUSSION

Genetic structure of Channel Catfish subpopulations

Using Channel Catfish collected from the Ottawa River and its major tributaries at Lac des Chats, our goal was to determine whether habitat segregation potentially facilitated by breeding philopatry was linked with genetic differentiation within a population. We show that habitat type (large river and tributaries) is not associated with distinct demes within the sampled population. Therefore, we reject our hypothesis that spatial segregation of main river channel (lacustrine-like) and smaller tributary (fluvial) breeding subpopulations has contributed to genetic differentiation within the population. Our pairwise differentiation tests with microsatellite data revealed that Channel Catfish from the Ottawa River subpopulation were not significantly different from Channel Catfish from either the Madawaska River or the Mississippi River subpopulations. Fish from the Ottawa River subpopulation, however, showed minor yet significant differentiation from fish from the Mississippi River subpopulation. When observing differences between sampling sites, it appears that significant differentiation occurred between Channel Catfish from both the Ottawa River site 1 and Ottawa River site 5 and Channel Catfish from the Ottawa River site 1 and the Mississippi River. Channel Catfish from the Mississippi River subpopulation, however, were not significantly differentiated from Channel Catfish from other Ottawa River collection sites further upriver, indicating that differentiation is not strictly associated with each river subpopulation. Furthermore, our hierarchical AMOVA indicated that almost all genetic variation within the sampled population occurred within individuals, whereas little variation occurred between river subpopulations. Finally, our STRUCTURE analysis indicated that panmictic population was the most supported scenario within the Ottawa, Mississippi, and Madawaska rivers.

Our study is one of few to investigate how habitat preference affects the genetic structure of a population of Channel Catfish. Sotola et al. (2017) determined whether isolation by distance facilitated by long-distance migration and breeding site preference and philopatry was associated with genetic differentiation within a population of Channel Catfish from the Ohio and Wabash rivers. They sampled Channel Catfish from five sites across ~380 km of uninterrupted river, as well as from two sites separated by dams, and found evidence for isolation by distance. We did not find evidence of differentiation between Channel Catfish from our easternmost and westernmost collection sites, separated by ~25 km. The minimum distance between collection sites in Sotola et al. (2017) was 53 km, more than double the distance in our study. The relatively short distance encompassing all our sampling sites may account for the lack of differentiation between Channel

Catfish from our furthest collection sites. Our results also differ from those of Carvajal-Vallejos et al. (2014) on the genetic structure of the Dorado, a migratory catfish from the Amazon River basin. Within catfish collected from the western Amazon River and upper Madeira River, ~300 km in distance, Carvajal-Vallejos et al. (2014) found three genetic clusters. They proposed that the co-occurrence of these distinct demes may be due to spatial segregation of breeding populations associated with breeding site fidelity or temporal segregation of breeding populations.

One possible explanation for the observed panmixia within our sampled population is that habitat selection changes over a Channel Catfish's lifespan. As a Channel Catfish becomes larger with age, it may be better able to establish and defend a high-quality summer territory (Pellett et al. 1998). This suggests that fish of intermediate and larger sizes have similar habitat preferences for summer breeding sites; differences in the competitive capability for these sites may explain why each size category of Channel Catfish appears to select different habitats. We could test this hypothesis by conducting a multiyear telemetry study, tagging individuals of various sizes to characterize their seasonal movements, and determine whether these movements and habitat preferences change as the Channel Catfish grow. Ontogenetic shifts in habitat preference have been observed in several animals, such as Bluegill *Lepomis macrochirus* (Werner and Hall 1988), loggerhead sea turtles *Caretta caretta* (Turner Tomaszewicz et al. 2017), red and blue damsels *Xanthagrion erythroneurum* (Khan and Herberstein 2020), and common chameleons *Chamaeleo chamaeleon* (Keren-Rotem et al. 2006). Changes in habitat preference over an animal's lifespan can occur due to reduced intraspecific competition, predator avoidance, food availability, dispersal capability, etc. (Dahlgren and Eggleston 2000; Keren-Rotem et al. 2006; Nakazawa 2015).

Another possible explanation for the observed panmixia within our sampled population of Channel Catfish is that straying individuals may increase gene flow between fish from different breeding sites, effectively weakening possible genetic reinforcement of habitat preferences (Dionne et al. 2008; Chen et al. 2020). Given that a significant proportion (~30–40%) of Channel Catfish stray from previously occupied summer habitats (Pellett et al. 1998), subsequent gene flow may reduce the genetic isolation of breeding sites within the main river channel and its tributary rivers (Homola et al. 2010; Chen et al. 2020). It is also possible that philopatry might be sex biased as has been observed in Blacktip Sharks *Carcharhinus limbatus* (Keeney et al. 2005), lesser kestrels *Falco naumanni* (Alcaide et al. 2009), ringed salamanders *Ambystoma annulatum* (Williams et al. 2021), and several other animals. If one sex does not display philopatry, sufficient gene flow may be maintained between breeding habitats by the nonphilopatric sex, genetically homogenizing the population (Blundell et al. 2002; Portnoy et al. 2015). Channel Catfish may display male-biased philopatry because males build nests alone, mate monogamously, and provide uniparental care after driving off the female (Tatarenkov et al. 2006). These conditions favor dispersal in females, potentially reducing breeding site fidelity and habitat segregation (Greenwood 1980; Portnoy et al. 2015). To test for sex-biased habitat preferences, we could estimate the genetic structure of Channel Catfish populations using sex-linked gene markers or observe differences between mitochondrial DNA (uniparental inheritance) and nuclear DNA (biparental inheritance) (Lawson Handley and Perrin 2007; Portnoy et al. 2015).

Although we had strong statistical power when comparing lacustrine-like and fluvial subpopulations, increased sampling at each site could increase the statistical power when comparing each river and each individual site. Future studies should increase the number of fish collected at each site and could expand their scope to include several lakes and rivers throughout the distribution of Channel Catfish. Furthermore, we used microsatellites to assess fine-scale genetic differences within the sampled population. Although microsatellites can detect fine-scale intrapopulation genetic differences (Coates et al. 2009; Lemopoulos et al. 2019; Sunde et al. 2020), contemporary technologies assessing genomewide single nucleotide polymorphisms, such as restriction-site-associated DNA sequencing (RADseq), can provide added resolution for subtle substructuring within a population due to the increased number of loci (Andrews et al. 2016; Lemopoulos et al. 2019; Sunde et al. 2020).

Genetic diversity indices

Genetic diversity within a population may be a useful predictor of the adaptive potential and survival of a species when faced with climate change and habitat fragmentation due to anthropogenic activities, such as dam construction (Reed and Frankham 2003; Parmesan 2006; Exposito-Alonso et al. 2022). As genetic diversity decreases within a species, the likelihood of extinction increases in response to changing environmental conditions due to the species' reduced adaptive potential (Parmesan 2006; Exposito-Alonso et al. 2022). By assessing the genetic diversity across the distribution of Channel Catfish, biologists can identify areas of lower diversity that may indicate a need for conservation efforts (Reed and Frankham 2003; DeWoody et al. 2021). We quantified the genetic diversity of Channel Catfish at Lac des Chats and its tributaries, the northernmost population assessed to date. Allelic richness of Channel Catfish from the Ottawa,

Mississippi, and Madawaska rivers (5.7–6.1) was higher than that from Alabama hatchery populations (2.8–4.1; Lamkom et al. 2008) and within the range of American Midwestern wild populations (5.4–6.5; Sotola et al. 2017). Hatchery populations (10.6–10.9) and wild populations (8.2–16.3) from Tamaulipas, Mexico, however, were considerably more diverse than our study population (Parra-Bracamonte et al. 2011; Lara-Rivera et al. 2019). This is unsurprising given that population differentiation and speciation rates generally increase towards the equator (Mittelbach et al. 2007; Freeman and Pennell 2021).

The Hardy–Weinberg equilibrium is a useful metric when examining population genetics. When a population has departed from this equilibrium, it may indicate nonrandom mating, inbreeding, or genotyping error (Wittke-Thompson et al. 2005; Mayo 2008; Chen et al. 2017). In our study, expected and observed heterozygosity were similar at each sampling site. All four failed tests of Hardy–Weinberg equilibrium occurred at locus *IpCG08*. Thus, it is possible that these deviations are related to the presence of null alleles detected at this locus, indicating genotyping error rather than assortative mating (Van Oosterhout et al. 2006; De Meeûs 2018). The mean observed heterozygosity at each sampling site was also within the range of those observed in both American and Mexican populations (De La Rosa-Reyna et al. 2014; Sotola et al. 2017). Our study population, however, had higher observed heterozygosity than some Mexican farm populations (Perales-Flores et al. 2007; Parra-Bracamonte et al. 2011) and both wild and domestic Alabama populations (Mickett et al. 2003; Simmons et al. 2006).

Channel Catfish sampled from Lac des Chats and its tributaries displayed low levels of inbreeding as evidenced by low F_{IS} values between 0.001 and 0.058, comparable to wild Channel Catfish from the Ohio and Wabash rivers (0.008–0.115; Sotola et al. 2017) and rivers throughout Mexico (0.006–0.065; Lara-Rivera et al. 2019). These low inbreeding levels indicate that the installation of both dams bordering Lac des Chats have not yet negatively impacted the genetic diversity of this population, even though they clearly prevent upriver movement. In contrast, higher F_{IS} values have been documented for Alabama hatchery populations (−0.012 to 0.370; Lamkom et al. 2008) and Tamaulipas hatchery populations (0.140–0.320; De La Rosa-Reyna et al. 2014). Inbreeding tends to increase in domesticated populations due to the few available mates constrained over generations by hatchery space limitations (Waters et al. 2020). This inbreeding leads to an increase in homozygosity within the population, consequently reducing allelic diversity (Busack and Currens 1995; Frost et al. 2006). Furthermore, selection for specific traits that improve fitness in captivity may also homogenize farmed populations (Christie et al. 2014).

CONCLUSIONS

The purpose of our study was to investigate whether habitat segregation previously observed in Channel Catfish was associated with genetic differentiation within a population. We hypothesized that habitat preferences linked to breeding philopatry for the lacustrine-like Lac des Chats and its fluvial tributary rivers would result in spatial isolation of breeding populations and genetic differentiation of each habitat type subpopulation. Microsatellite genotyping of 162 Channel Catfish from the Ottawa, Mississippi, and Madawaska rivers revealed a panmictic population, with little differentiation between river subpopulations. Further study is required to determine whether habitat preference changes over a fish's lifespan resulting from improved ability to establish and defend high-quality nesting sites or if sex-biased philopatry could explain the observed gene flow. The logical next steps include estimating population structure with sex-specific genetic markers and telemetry to observe potential differences between the sexes or changes in movements over time, respectively.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they do not have competing interests that could have influenced the research carried out in this study.

DATA AVAILABILITY STATEMENT

Microsatellite allelic data are available for all collected Channel Catfish in the supplementary data found in the online version of this article at https://doi.org/10.1002/tafs.10433.

ETHICS STATEMENT

The research methods conducted in this study meet the ethical standards of the Canadian Council on Animal Care, Ontario Animals for Research Act, and Animal Welfare Assurance by the U.S. Public Health Service reviewed by the Animal Care Committee at the University of Ottawa (approved protocol #BL-3015).

ORCID

Francesco H. Janzen https://orcid.org/0000-0002-5285-3932

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