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Lack of genetic population structure of slimy sculpin in a large, fragmented lake

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Abstract

Most of what is known about sculpin population structure comes from research in streams; however, slimy sculpins are also a common benthic species in deep lakes. In streams, sculpins are considered to be a relatively inactive species, moving only small distances, and characteristically have high levels of genetic structure. We examined population genetic structure of slimy sculpin (*Cottus cognatus*) across multiple barriers and over distances up to 227 km in Lake Champlain (USA, Canada) and Lake Ontario (USA, Canada) to determine whether lake populations of sculpin are also highly structured. We predicted that slimy sculpin populations in Lake Champlain would be structured by six causeways as well as by distance, Lake Ontario populations would be structured only by distance, and differences between the lakes would be large relative to within-lake differences. We examined microsatellite variation among 200 slimy sculpins from Lake Champlain and 48 slimy sculpins from Lake Ontario to evaluate patterns of population connectivity and structure. There was no indication of population substructuring within either lake but sculpin were genetically distinct between lakes. We conclude that there is a single, panmictic population of sculpin present in Lake Champlain and another potentially panmictic population in Lake Ontario, with no indication of genetic isolation by distance. Our results contrast with data from sculpin in streams, suggesting distance and habitat fragmentation exert little influence on population connectivity of benthic fish in lakes.

KEYWORDS
barriers, gene flow, genetics, habitat fragmentation, microsatellites

1 | INTRODUCTION

Patterns of genetic variation across a species' range generally result from historic, extrinsic factors such as physical isolation due to glaciation or changes in climate (Hewitt, 1996; Petit et al., 2003), whereas genetic structure of populations across smaller spatial scales are often the result of contemporary environmental conditions like habitat availability or fragmentation. Among freshwater aquatic habitats, lotic waters are particularly susceptible to anthropogenic change (e.g., channelising, siltation, dewatering) and fragmentation (e.g., construction of dams, weirs and roads with poorly placed culverts; Dynesius & Nilsson, 1994; Ligon, Dietrich, & Trush, 1995; Graf, 1999; Templeton, Shaw, Routman, & Davis, 1990). The combination of the naturally complex structure of lotic systems with high amounts of anthropogenic disturbance often leads to high levels of population isolation and genetic structure of species living in streams and rivers (e.g., Bessert & Orti, 2008; Gouskov & Vorburger, 2016). In contrast, large lentic systems often have less habitat complexity, especially offshore lake regions, and little habitat fragmentation. Understanding how environmental heterogeneity in lakes may influence population genetic structure is nonetheless central to understanding recent evolutionary change and species' vulnerability to anthropogenic alterations.

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Determining relationships between environmental and genetic variation is particularly important for fish species that inhabit both lentic and lotic habitats, despite differences in flow, habitat complexity, connectivity and habitat predictability (Ryder & Pesendorfer, 1989). Lentic and lotic populations of the same fish species can differ in dispersal and genetic structure and are often genetically distinct from one another. For example, home ranges of 21 fish species in lakes were found to be 19–23 times larger than 25 fish species in rivers by Minns (1995), indicating movement patterns differ between lotic and lentic habitats. Additionally, patterns of genetic differentiation have been found between lentic and lotic populations of sticklebacks and cyprinids (Collin & Fumagalli, 2011; McKinnon & Rundle, 2002).

Sculpins (Cottidae) are widely distributed in lakes and streams, but little is known about their genetic structure in lentic systems. Based primarily on lotic research, sculpin are generally considered to be sedentary and disperse only short distances. For example, mottled sculpins (*Cottus bairdi*) in a small tributary in North Carolina showed patterns of genetic isolation by distance across 5.6 km, and the estimated migration rates between sites separated by <300 m were small (Lamphere & Blum, 2012). Mottled sculpin sampled in tributaries of eastern Lake Michigan also showed strong patterns of genetic structure even across short distances (Homola, Ruetz, Kohler, & Thum, 2016). Assessment of sculpin behaviour and ecology also suggests that sculpin do not move long distances. Mottled sculpin implanted with PIT tags had a maximum displacement distance from the tagging location of about 511 m over 1 year, and more than 74% of individuals moved <100 m from where they were tagged during a 1-year study (Breen, Ruetz, Thompson, & Kohler, 2009). Similarly, slimy sculpins (*Cottus cognatus*) in Little River, New Brunswick, had detectable differences in stable isotope composition among sites separated by <10 km, suggesting slimy sculpin have small home ranges (Gray, Cunjak, & Munkittrick, 2004). Otolith microchemistry of slimy sculpin also indicated that individuals generally move <10 km from their natal location throughout their lifetime (Clarke, Telmer, & Shrimpton, 2015). Few studies, however, have examined sculpin movement or genetic structure in lentic systems. Behavioural studies of slimy sculpin in lakes are challenging because they prefer depths >25 m and cold water (<15°C; Otto & Rice, 1977; Brandt, 1986). Lakes generally have lower habitat complexity and have few or no barriers akin to dams to limit dispersal, and thus, we predict that population connectivity and genetic structure of sculpin may be different in lakes than in streams.

To better understand sculpin ecology and population connectivity in lentic systems, we examined the genetic structure of slimy sculpins in two large lakes. Lake Champlain served as our focal system. Lake Champlain is a partially fragmented lake divided into three basins by causeways that may restrict slimy sculpin dispersal, providing a lentic equivalent to a fragmented lotic system (Marsden & Langdon, 2012). We also examined two slimy sculpin populations from Lake Ontario as an out-group to assess consistency of trends in population structure among lakes, and between lake and stream populations. The two lakes have a similar fish community and trophic status, but Lake Ontario is much larger than Lake Champlain (longest axis is 311 km relative to 193 km in Lake Champlain), lacks habitat fragmentation, and due to its size is more likely to have higher isolation by distance among fish populations. The two lakes have been isolated for approximately 10,000 years, providing a context for genetic differences resulting from isolation. Examining sculpin in Lake Champlain and Lake Ontario allowed us to assess potential genetic differences resulting from isolation between lakes, isolation by distance within lakes and isolation by fragmentation in two systems with similar environments.

2 | METHODS

2.1 | Study sites

Lake Champlain is a long (193 km) and narrow (20 km at the widest point) lake spanning the border of New York and Vermont, USA, and Quebec, Canada. The portion of the lake with deep water suitable for slimy sculpin is approximately 110 km long. The lake has a maximum depth of 122 m and an average depth of 19.5 m. Three large islands naturally divide the northern portion of Lake Champlain into eastern and western arms (Figure 1). The construction of six causeways built between 1850 and 1900 has linked the islands to the mainland and have isolated the lake further into three major basins: the Main Lake, Malletts Bay and the Inland Sea (Figure 1; Marsden & Langdon, 2012). All the causeways have at least one shallow (1–7 m

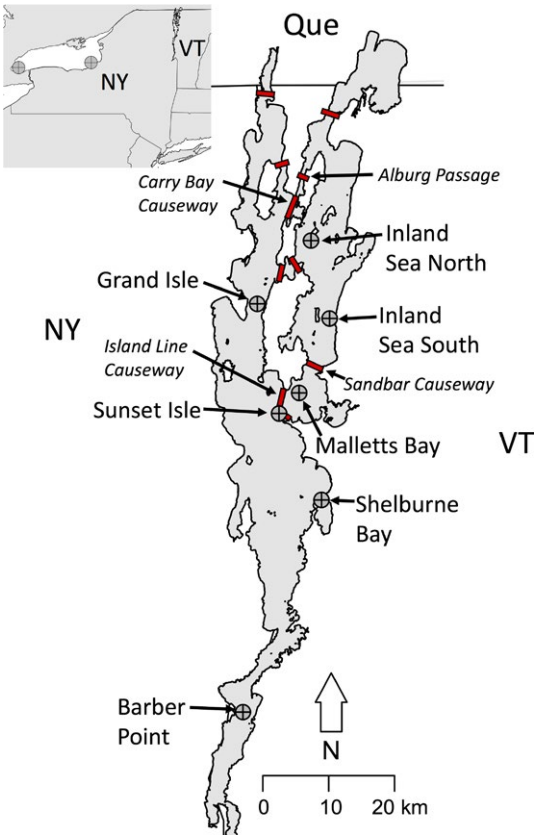

FIGURE 1 Sample sites indicated by open crossed dots for slimy sculpin in Lake Champlain and Lake Ontario (inset map), and location of nine causeways (red bars) hypothesised to pose barriers to fish movement

deep) opening that allows some flow of water and passage of boats and fish; Carry Bay and the Island Line causeways each have an additional non-navigable opening. Lake Ontario is 311 km long, with a maximum depth of 244 m; apart from a series of islands in the north-eastern portion (Bay of Quinte), the lake lacks physical isolating structures.

Slimy sculpin prefer water temperatures <10°C and rarely inhabit temperatures >15°C; to assess whether causeways would be expected to act as a substantial barrier to sculpin, we measured seasonal changes in water temperature in causeway openings. HOBO® temperature probes were placed on the bottom of all causeways openings except the North Western opening to Carry Bay (Figure 1). Temperature was recorded at openings once per hour for 12 months. Slimy sculpin are generally only found in water >25 m deep; therefore, depth profiles of all but the Island Line causeway (Figure 1) openings were measured using a weighted line from a small boat and depth of the remaining two Island Line causeway openings was estimated using chart data.

2.2 | Fish sampling and genetic analysis

Two hundred slimy sculpin were sampled during August and September 2014 and May, June and July 2015 using benthic trawls at seven sites throughout Lake Champlain (Figure 1). Forty-eight slimy sculpin were sampled in October 2016 from two locations approximately 230 km apart in Lake Ontario, NY, one near Fairhaven, New York (43°29.231′N, −76°38.053′W), and one near Hamilton, Ontario (43°20.462′N, 79°27.736′W). Individuals were euthanised by cooling directly on ice, measured to the nearest millimetre (total length), and caudal fins were collected following protocols outlined in LaHood, Miller, Apland & Ford (2008) or frozen.

DNA was extracted from fin clips using standard procedures from a DNeasy Blood and Tissue Kit (Qiagen). The concentration of DNA template was verified on a NanoDrop and ranged from 6–100 ng/μl of DNA, though most samples contained between 30 and 50 ng/μl. Following extraction, polymerase chain reaction (PCR) amplification was conducted for 10 microsatellite loci previously identified for sculpin (Table 1). Markers were multiplexed when possible in 25 μl reactions using 2X Q5 High Fidelity DNA Polymerase Master Mix (New England BioLabs Inc.), and 20 pmol of a fluorescently labelled forward primer and unlabelled reverse primer, and 6–100 ng of the DNA template. The general PCR program used was 98°C for 2 min, 30 cycles at 98°C for 30 s at marker-specific annealing temperature (Table 1), 72°C for 45 s, followed by a final extension of 72°C for 10 min. Fragment analysis of PCR products was conducted in the University of Vermont Advanced Genome Technologies Core using an Applied Biosystems 3130 Genetic Analyzer and a ROX 500 size standard and scored using GENEMAPPER software (Applied Biosystems).

TABLE 1 Characteristics of 10 microsatellites amplified in slimy sculpin. Shown are the GenBank marker name, repeat motif, forward and reverse primer sequence, fluorophore tail, amplified size range, annealing temperature (T_a) and citation for the source of the marker

Marker	Repeat	Primer (5′–3′)	Dye	Size range	T_a	Source
Cco02	Tri	F: TTCTTGTTCTCCGTCTTGAGC R: CCCATCTTCTCCTCCTGTCC	HEX	227—254	59	Fujishin, Barker, Huff, and Miller (2009)
Cco08	Tri	F: TTGCAAACTTCAGACAGTAAAGC R: GCTGAGAATCCAGGAAGGAG	FAM	87–111	55	Fujishin et al. (2009)
Cco13	Tri	F: CCTGGAATTTCACCAAGGTC R: TCACAACAAAGCCAGAGGAC	NED	221–248	55	Fujishin et al. (2009)
Cco17	Tri	F: TCGTCTTGGAAATGGAAAGC R: CATGTCAGCAGGATATCACGTC	HEX	69–142	55	Fujishin et al. (2009)
Cco11	Di	F: GCAGGAGGAACACGAAGATG R: CTCAAGGAACTACACACACATGC	NED	198–230	60	Fujishin et al. (2009)
Cco14	Tetra	F: CATAAAACCTGTGGCTTTGG R: GACGCTCTGCTGGAGAGATG	HEX	NA	60	Fujishin et al. (2009)
Cott105	Di	F: TCCTACAGGGTGCGATCGTG R: TGCAGGAGTCAGGACTCTGC	FAM	322–346	60	Nolte, Stemshorn, and Tautz (2005)
Cott128	Di	F: TCTGTGGGTGTTTGGTCGTG R: TGAACTCTGCACATGACTGC	HEX	314–350	60	Nolte et al. (2005)
Cott113	Di	F: AGCGCCAGAATGCAGCATCC R: AGTGTGGCGAGCCCAAGATC	FAM	132–142	60	Nolte et al. (2005)
Cott213	Di	F: TTGCCATGGATTTGAGGCAG R: AGCATTGCTATTATCAGGCTGC	NED	331–333	60	Nolte et al. (2005)

2.3 | Statistical analysis

Conformance to Hardy–Weinberg equilibrium (HWE) expectations at each locus was estimated using Markov chain Monte Carlo methods in ARLEQUIN (Excoffier & Lischer, 2010) with 100,000 step burn-in and 900,000 step determination. Any deviations from HWE were assessed for heterozygote excess or deficiency and significance levels were adjusted using a Bonferroni correction. All loci were assessed for the presence of null alleles with MICRO-CHECKER version 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). To quantify the genetic diversity for each locus, the number of alleles per locus was determined and observed (H_O) and expected (H_E) heterozygosity calculated using GENALEX (Peakall & Smouse, 2006, 2012). Allelic richness was calculated using rarefaction in FSTAT version 2.9.3.2 (Goudet, 1995). To test whether diversity varied between sites and lakes, mean observed heterozygosity and allelic richness were evaluated for differences between Lake Ontario and Lake Champlain and among Main Lake sites and sites in Malletts Bay and the Inland Sea in Lake Champlain by comparing observed data to 10,000 permutations in FSTAT. As an additional estimate of diversity, effective population size of each sampled location was calculated using a linkage disequilibrium method in N_eESTIMATOR (Do et al., 2014) with minimum acceptable allele frequencies of 0.05, 0.02 and 0.01. Following estimation, a minimum allele frequency of 0.02 was chosen because large changes in effective population size were found between a 0.05 and 0.02 minimum allele frequency, suggesting 0.05 may have been too stringent for our data set.

Possible genetic structure between lakes and among sites was evaluated using pairwise comparisons of F_{ST}, and their associated levels of significance were calculated in ARLEQUIN. First, population structure was evaluated by calculating F_{ST} values between Lake Champlain and Lake Ontario. Next, F_{ST} values were calculated within each lake to determine whether sculpin populations were structured within lakes. To test for a possible Wahlund effect resulting from early stage isolation, differences in H_O versus H_E of the total Lake Champlain sculpin population were measured using a Bartlett test executed in R version 3.3.0 using the bartlett.test() function available in the stats package (R Core Team, 2015). To identify statistically significant differences in allelic variance among sites, analysis of molecular variance (AMOVA) was calculated using ARLEQUIN. AMOVAs were run hierarchically, as indicated in Table 2 groupings. Sample sites were first grouped by lake, and Lake Champlain slimy sculpin were compared to Lake Ontario slimy sculpin. Next, slimy sculpin from Lake Champlain were analysed separately, comparing all sampled sites in the Main Lake to sites sampled in the Inland Sea to determine whether causeways could explain differences in allele frequencies. The site in Malletts Bay was excluded because it was the only site sampled in the basin.

To assess whether populations are isolated by distance, Lake Champlain and Lake Ontario were analysed separately. In Lake Champlain, a pairwise F_{ST} matrix was compared against a pairwise matrix of geographic distance using a Mantel's test to determine whether differences in genetic variation among slimy sculpin sample locations correspond to geographic distance measured as the shortest possible route by water between two sites. Mantel tests were conducted in IBDWeb using 10,000 permutations (Jensen, Bohonak, & Kelley, 2005). Pairwise genetic distance was estimated between the two Lake Ontario sites to evaluate whether similar levels of isolation by distance occur in Lake Ontario and Lake Champlain. Because only two sites were sampled in Lake Ontario, we were unable to run a Mantel test; however, we expected the F_{ST} between sites in Lake Ontario to be similar to F_{ST} between the two furthest sites in Lake Champlain if the effect of isolation by distance is similar in both lakes.

To further examine how slimy sculpin populations were structured among and within lakes, discriminate analysis of principle components (DAPCs) and Bayesian STRUCTURE analysis were used to

TABLE 2 Site-specific summary statistics of slimy sculpin genotypes taken from nine microsatellite loci grouped by lake, basin and site

Site	*N*	N_a	H_O	H_E	N_e	nPA	AR
Lake Champlain							
Main Lake							
Grand Isle	30	6.9	0.651	0.601	223.1	1	5.79
Sunset Isle	30	6.7	0.628	0.600	∞	3	5.59
Shelburne Bay	30	7.2	0.618	0.593	∞	2	5.94
Barber Pt.	30	7.2	0.609	0.612	∞	4	5.86
Inland Sea							
Inland Sea N.	31	7.4	0.640	0.631	139.4	5	6.17
Inland Sea S.	31	7.1	0.562	0.595	433.1	4	5.81
Malletts Bay							
Malletts Bay	18	6.1	0.617	0.586	226.3	1	5.92
Lake Ontario							
Fairhaven	24	6.1	0.534	0.509	101.5	3	5.40
Hamilton	24	5.8	0.486	0.480	140.1	4	5.09

N, number of individuals genotyped; N_a, mean number of alleles per locus; H_O, observed heterozygosity; H_E, expected heterozygosity; N_e, effective population size; nPA, number of private alleles; AR, mean allelic richness across all loci.

TABLE 3 Pairwise F_{ST} (below the diagonal) and corresponding *p*-values ± standard deviation (above the diagonal) calculated in ARLEQUIN for slimy sculpin sampled from two sites in Lake Ontario (Fairhaven and Hamilton) and three major basins in Lake Champlain isolated from one another by causeways. The three basins were the Main Lake (Grand Isle, Sunset Isle, Shelburne Bay, Barber Point), the Inland Sea (north and south sites) and Malletts Bay

	Grand Is.	Sunset Is.	Shelburne Bay	Barber Pt	Inland Sea N.	Inland Sea S.	Malletts Bay	Fairhaven	Hamilton
Grand Is.	*	0.045 ± 0.024	0.973 ± 0.018	0.874 ± 0.024	0.847 ± 0.034	0.333 ± 0.054	0.910 ± 0.017	0.00 ± 0.00	0.00 ± 0.00
Sunset Is.	0.009	*	0.604 ± 0.053	0.676 ± 0.041	0.198 ± 0.030	0.009 ± 0.009	0.189 ± 0.057	0.00 ± 0.00	0.00 ± 0.00
Shelburne Bay	−0.008	−0.003	*	0.829 ± 0.038	0.532 ± 0.042	0.153 ± 0.031	0.910 ± 0.029	0.00 ± 0.00	0.00 ± 0.00
Barber Pt	−0.007	−0.004	−0.005	*	0.964 ± 0.014	0.288 ± 0.057	0.955 ± 0.020	0.00 ± 0.00	0.00 ± 0.00
Inland Sea N.	−0.006	0.003	0.000	−0.007	*	0.802 ± 0.032	0.847 ± 0.024	0.00 ± 0.00	0.00 ± 0.00
Inland Sea S.	0.001	0.016	0.005	0.002	−0.004	*	0.423 ± 0.047	0.00 ± 0.00	0.00 ± 0.00
Malletts Bay	−0.009	0.005	−0.009	−0.011	−0.006	0.001	*	0.00 ± 0.00	0.00 ± 0.00
Fairhaven	0.091	0.098	0.083	0.096	0.106	0.115	0.065	*	0.694 ± 0.039
Hamilton	0.111	0.118	0.108	0.119	0.130	0.141	0.091	−0.004	*

identify clusters of individuals representing populations (Jombart, 2008; Jombart, Devillard, & Balloux, 2010; Pritchard, Stephens, & Donnelly, 2000). DAPC is a multivariate analysis that maximises genetic differentiation between groups while minimising within-group variation. The relationship between sample sites was evaluated hierarchically; DAPC was first run using the complete data set to visualise the relationship between all samples sites in Lake Ontario and Lake Champlain, then using only individuals from Lake Champlain. All DAPCs were conducted in R version 3.3.0 using the ADEGENET version 2.0.1 (Jombart, 2008; R Core Team, 2015). Bayesian STRUCTURE analysis was also run hierarchically, first on the total data set and subsequently on only Lake Champlain individuals. STRUCTURE was run 10 times for each value of k = 1–10 with settings of 500,000 replicates and an initial burn-in of 100,000 replicates. The most likely number of clusters (k) was then assessed using ΔK estimated in STRUCTURE HARVESTER (Earl & vonHoldt, 2012; Evanno, Regnaut, & Goudet, 2005) and the most likely estimates of k were consolidated into a single best estimate using CLUMPP (Jakobsson & Rosenberg, 2007).

3 | RESULTS

3.1 | Habitat suitability

Average depth of each causeway opening at mean lake level (29.1 m above sea level) varied among causeways, ranging from <1.0 m at the Sandbar causeway to just over 7.0 m at the Alburg Passage causeway. However, even when adjusted to the maximum reported lake level of 31.6 m, the depth of all openings was <10.0 m. Temperature in causeway openings ranged from near 0.0°C January and February when sensors became frozen in ice to 22–25°C during July and August. For causeway openings with at least 365 days of available temperature data (N = 4), temperature was above the adult sculpin avoidance temperature of 15°C for 37 ± 2% of the year and above the preferred temperature of 9°C for 53 ± 3% of the year (Otto & Rice, 1977).

3.2 | Genetic data

Genetic diversity differed slightly between lakes but was consistent within lakes. Locus Cco14 exhibited inconsistencies in allele scoring and was therefore removed from analysis. No loci showed signs of null alleles. All loci except locus Cott213 were polymorphic at all sites with 5 to 25 alleles per locus. All loci at all sites were in HWE following a sequential Bonferroni correction. Observed (H_O) and expected (H_E) heterozygosity was moderate for all sites (average = 0.59 and 0.58 respectively; Table 2). Observed heterozygosity was significantly higher (p = .03) in Lake Champlain (0.62) than in Lake Ontario (0.51) but consistent among sites within each lake. Mean allelic richness of loci was higher (p = .01) in Lake Champlain (5.9) than in Lake Ontario (5.2). Allelic richness was similar among all sites within Lake Champlain, ranging from 5.6 at Sunset Isle to 6.2 at Inland Sea North. No significant differences in allelic richness were found among Main Lake (5.8), Malletts Bay and Inland Sea populations (6.0; p = .53). Effective population size was moderate to high for all populations and the upper

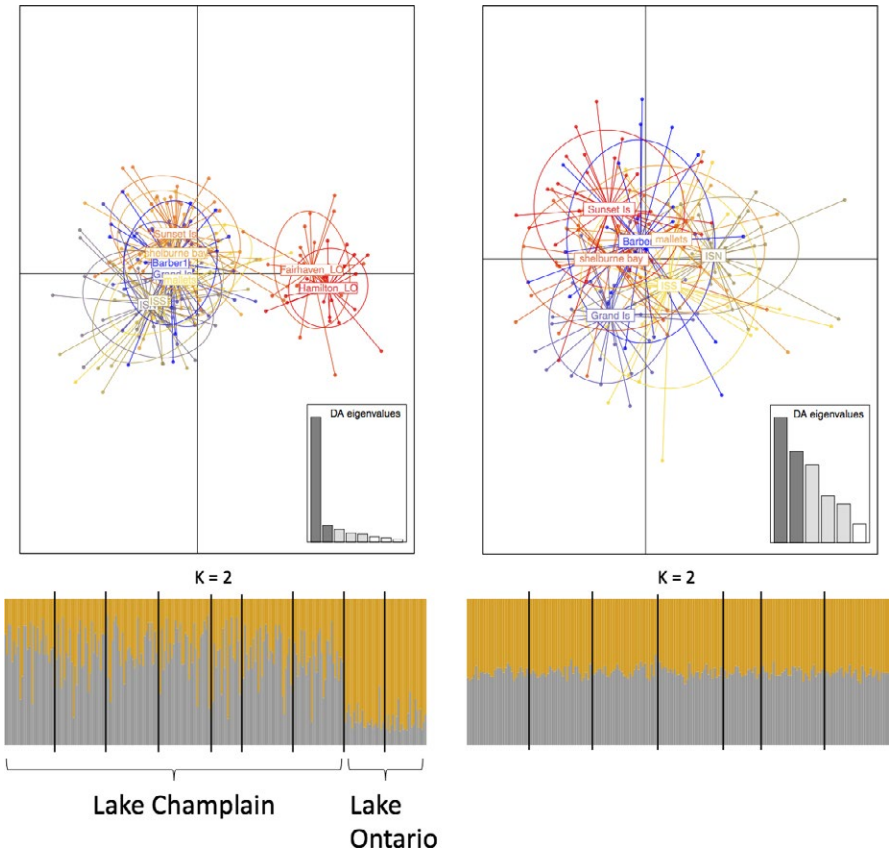

FIGURE 2 Clustering of two Lake Ontario and seven Lake Champlain slimy sculpin populations (left) based on DAPC (top) and STRUCTURE (bottom). In the scatterplot of DAPC results, individuals are represented by dots and sampled populations are coded by colour and encircled with inertia ellipses. The STRUCTURE barplot is a graphical representation of individual membership coefficient to each cluster (vertical bars). Colours represent different estimated clusters of a single admixed individual. Based on results from Δ*K* analysis, only *K* = 2 are shown

limit of the confidence interval always included infinity. Effective population sizes of Hamilton and Fairhaven sites in Lake Ontario were estimated to be 140.1 and 101.5. Within Lake Champlain, effective population sizes tended to be higher at Main Lake sites than Malletts Bay or the Inland Sea. Barber Point, Shelburne Bay and Sunset Isle exhibited the highest effective population sizes in the Main Lake ($N_e = \infty$), followed by Grand Isle ($N_e = 223.1$). Malletts Bay and the Inland Sea North and South sites had more moderate estimated effective population sizes ($N_e = 226.3$, 139.4 and 433.1 respectively).

3.3 | Between-lake genetic structure

Sculpin in Lake Ontario were genetically distinct from sculpin in Lake Champlain. Pairwise F_{ST} values between Lake Ontario and Lake Champlain populations were large (0.065–0.118) relative to within-lake pairwise comparisons (Table 3). When populations in Lake Champlain were compared to populations in Lake Ontario, 10.4% of allele frequency variation occurred between lakes (AMOVA $p < .001$) while 89.7% of the variation occurred within individual populations. Both DAPC and a delta *k* analysis of STRUCTURE indicated the presence of two clusters, offering further evidence of between-lake population structure (Figure 2).

3.4 | Within-lake genetic structure

Evidence of weak to no genetic differentiation was found among sampled populations within Lake Champlain and Lake Ontario. Pairwise

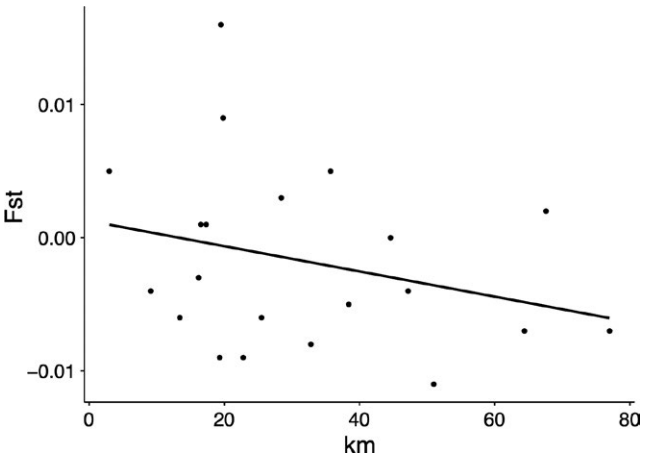

FIGURE 3 Correlations between waterway distance and all pairwise F_{ST} genetic distance estimates for slimy sculpins from seven locations in Lake Champlain

estimates of F_{ST} were small (0.00–0.016; Table 3). Only two comparisons had F_{ST} values significantly >0 and both had F_{ST} values <0.02. Additionally, there was no indication of a reduction of heterozygosity across loci characteristic of a Wahlund effect (Bartlett test $p = .91$). When populations in the Main Lake were compared to populations in the Inland Sea, <1% (AMOVA $p = .53$) of allele frequency variation occurred between basins while 99.8% of the variation occurred within individual populations. Subsequent runs of STRUCTURE and DAPC examining substructure within Lake Champlain did not reveal

TABLE 4 Diversity and basic environmental metrics from 12 microsatellite studies of sculpin compared to the slimy sculpin in Lake Champlain and Lake Ontario. Distance estimates are based approximately from site maps or Mantel plots when no exact numbers are reported as indicated by a "~". Data not reported in the cited study are indicated by "NR"

Species	Number of loci	Region/river	H_O	Allelic richness	Mean/range of pairwise F_{ST}	Distance range (km)	Source
Cottus asper	10	American, Tuolumne, Kings rivers, California	0.311	1.38	0.238	~3–200	Baumsteiger and Aguilar (2014)
Cottus asper	14	Lower Fraser River, British Columbia, Canada	0.577	6.31	0.128	~10–500	Dennenmoser et al. (2014)
Cottus asper	11	Northern California streams and rivers	0.366	3.02	0.010–0.501	2–1,250	Baumsteiger, Kinziger, and Aguilar (2016)
Cottus asperrimus	9	Hat Creek Fault, California	0.385[b]	5.25	0.320	8–25	Kinziger, Hellmair, Fong, Goodman, and Kelsey (2016)
Cottus bairdi	12	Nantahala River, North Carolina	0.598	NR	0.026	0.3–5.6	Lamphere & Blum, 2012;
Cottus bairdi	6	Lake Michigan tributaries, Michigan	0.320	2.7	0.235	~3–400	Homola et al. (2016)
Cottus beldingi	8	Truckee River, Nevada	0.665	NR	−0.002–0.046	~2–78	Peacock et al. (2016)
Cottus cognatus	8	Northern Mississippi River and tributaries	0.620	5.85	0.450[a]	~5–120	Huff et al. (2010)
Cottus gobio	10	Sense River, Switzerland	0.520	4.19	0.058	0.5–40	Junker et al. (2012)
Cottus gobio	7	River Rye, England	0.528[b]	5.04	0.268	0.2–80	Hänfling & Weetman (2006)
Cottus gulosus	10	American, Tuolumne, Kings rivers, California	0.141	1.16	0.634	~3–200	Baumsteiger and Aguilar (2014)
Cottus gulosus	6	Northern California streams and rivers	0.180	2.12	0.596	40–602	Baumsteiger, Kinziger, Reid, and Aguilar (2014)
Cottus pitensis	6	Northern California streams and rivers	0.114	1.35	0.267	7–285	Baumsteiger et al. (2014)
Trachidermus fasciatus Heckel	16	Coast of Qinhuangdao and Ariake Sea, China	0.831	9.64	0.054	70 –1200	Li, Xue, Gao, and Liu (2016)
Cottus cognatus	9	Lake Champlain, Vermont	0.617	5.87	0.000	3–77	Present study
Cottus cognatus	9	Lake Ontario, New York, USA/Ontario, CA	0.510	5.25	0.000[c]	227	Present Study

[a]Data from a recent reintroduction from three source populations.
[b]Expected, not observed heterozygosity presented.
[c]Data from single, pairwise comparison.

any further clustering, suggesting the presence of a single panmictic population (Figure 2).

No correlation was observed between waterway distance (the shortest distance by water between two sites) and pairwise F_{ST} in Lake Champlain (r^2 = .08; p = .82; Figure 3), indicating that populations of slimy sculpin were not isolated by distance. Additionally, pairwise F_{ST} was zero between Fairhaven and Hamilton in Lake Ontario, similar to pairwise F_{ST} among sites in Lake Champlain. However, Fairhaven and Hamilton are separated by more than 220 km, about four times the maximum distance between sites in Lake Champlain, indicating a lack of isolation by distance in Lake Ontario.

4 | DISCUSSION

Our findings indicate that although slimy sculpin in Lake Champlain and Lake Ontario have comparable genetic diversity to slimy and mottled sculpin in streams and rivers (Huff, Miller, & Vondracek, 2010; Lamphere & Blum, 2012), they exhibit little to no within-lake genetic structure even across numerous barriers and distances up to 227 km (Breen et al., 2009; Lamphere & Blum, 2012). The lack of any observed genetic structure indicates that sculpins in Lake Champlain and Lake Ontario represent single panmictic populations. The relatively large genetic differences observed between lakes Ontario and Champlain were expected, considering that the lakes have been isolated since the last glacial retreat approximately 10,000 years ago (Rayburn, Franzi, & Knuepfer, 2007). Although Lake Ontario and Lake Champlain remain connected by the St. Lawrence River, it is unlikely this route provides enough connectivity to maintain a genetically homogeneous population; transit between the lakes would entail a 360 km downstream trip in the St. Lawrence River, followed by 130 km of upstream dispersal through the Richelieu River, or vice versa.

Low genetic structure is usually a feature of highly connected populations with high mobility and capacity for dispersal (Muths, Le Couls, Evano, Grewe, & Bourjea, 2013; Thompson, Patel, Baker, Constantine, & Millar, 2015). However, adult slimy sculpin are not considered highly mobile. Adult sculpin in streams have patchy distributions and tend to maintain home ranges of 1–5 river km (Galloway et al., 2003; Gray et al., 2004). However, there is little information about movement of slimy sculpin in lakes. Nonetheless, the lack of any genetic structure among sculpin populations in Lake Champlain is particularly surprising given the fragmentation of the lake by causeways. Several of our sample sites were separated by large areas of shallow habitat not usually inhabited by slimy sculpins. For example, Malletts Bay and Sunset Island are only 3 km apart, but separated by a 5-km causeway built on top of a shallow (1–3 m deep) 1-km-wide sandbar. To maintain the level of population connectivity we observed, sculpin would need to disperse across at least 1 km of unsuitable habitat. To migrate from the Inland Sea to the Main Lake, slimy sculpin must pass through at least two causeways via 2–5 km of shallow (1–10 m) water. For these deep-water fish, the depth and temperature of the causeway openings should be a substantial barrier to movement (Otto & Rice, 1977; Scott & Crossman, 1973). Causeway openings were, however, within an acceptable temperature range for slimy sculpin (<10°C) during the early spring, late fall and winter (50%–70% of the year). Thus, adult slimy sculpins might disperse through the openings during these times. Given the moderate level of differentiation between Lake Champlain and Lake Ontario populations, it is possible that insufficient time has passed to detect the effects of isolation by causeways. Although we cannot conclusively refute the hypothesis that not enough time has passed to see the effects of isolation, there was little evidence of genetic structure or a Wahlund effect indicative of early stage isolation found in our study (Wahlund, 1928). Therefore, we suggest time since isolation is not the most important factor limiting population differentiation.

Genetic panmixia in the absence of adult movement could be the result of larval dispersal. In marine systems, larval fish commonly disperse substantial distances by advection (Pineda, Hare, & Sponaugle, 2007). In the Great Lakes, models of yellow perch larval drift suggest individuals could drift from southern to northern Lake Michigan, a distance of 200–300 km, before settling to the bottom (Beletsky et al., 2007). Deep-water sculpin *Myoxocephalus thompsonii* larvae are known to be pelagic (Geffen & Nash, 1992), but slimy sculpin larvae are generally assumed to be benthic, which would limit their likelihood of dispersal (e.g., Lantry et al., 2007). Nevertheless, slimy sculpin larvae have been found in the water column during spring ichthyoplankton tows in Lake Huron (Martin, Czesny, & Wahl, 2011; Roseman & O'Brien, 2013) and throughout the summer in Lake Michigan, suggesting that larvae may remain pelagic long enough to disperse long distances by advection before settling to the bottom (Geffen & Nash, 1992). Summer surface current velocities in Lake Champlain and Lake Ontario are comparable to Lake Michigan (McCormick, Manley, Beletsky, Foley, & Fahnenstiel, 2008; Rao & Murthy, 2001), so larval sculpins could disperse long distances through advection.

Larval advection could also explain why lake causeways have little to no effect on slimy sculpin populations. The flow of water through causeway openings can be substantial (34,000–325,000 m^3/hr) and thus may facilitate larval drift among basins (Myer & Gruendling, 1979). However, flow direction varies among openings and can be almost entirely unidirectional; for example, water through the Carry Bay and Grand Isle–North Hero causeways flows predominately west into the Main Lake, flowing in the opposite direction from the Main Lake into the Inland Sea only 15% of the time (Myer & Gruendling, 1979). Therefore, currents in causeway openings could facilitate asymmetric movement among basins.

Alternatively, lack of genetic structure in slimy sculpin in lakes could be explained by extremely large populations. The effective population size of sculpin in three of the seven sites sampled in Lake Champlain was estimated to be infinity, and the upper confidence interval from all sites included infinity. However, the lower confidence interval for effective population size for all sites was <450, similar to effective population sizes observed in stream populations of sculpin that showed significant levels of structure (Dennenmoser, Rogers, & Vamosi, 2014). Given that population structure has been identified in species with very large population sizes (e.g., Foley et al., 2013), we suggest that it is unlikely that large population size alone explains the lack of genetic structure observed in Lake Champlain and Lake Ontario.

The lack of genetic structure and isolation by distance of slimy sculpin in our study contrasts with the high genetic structure observed in stream populations collected only a few kilometres apart (Junker et al., 2012; Dennenmoser et al., 2014; Table 4). In 12 other microsatellite-based studies of sculpins, we identified similar observed heterozygosity and allelic richness but substantially lower F_{ST} than any other study (Table 4). All but one of the 12 other microsatellite studies of sculpin focused on rivers or river systems and the remaining study focused on coastal populations. Therefore, the higher population structure seen these studies could be partially explained by the higher degree of physical fragmentation in rivers than in our lake systems. However, even when compared to pairwise estimates in relatively unfragmented systems, our pairwise F_{ST} estimates were often an order of magnitude smaller than the minimum pairwise F_{ST} in other studies.

Our findings highlight how little is known about the life history and dispersal of sculpin in lakes and suggest that there may be significant differences in behaviour and life history between lotic and lentic populations. Other studies have also indicated that the ecology and evolution of lentic and lotic fish populations can differ substantially (Istead, Yavno, & Fox, 2015; Minns, 1995; Swain & Holtby, 1989). We recommend that future research should focus on determining whether low genetic structure in lakes is a general trait for the Cottidae family by expanding research to other common lentic and lotic species such as mottled sculpin. Additionally, we propose that direct assessment of adult and larval movement of sculpin in streams and in lakes would be an important next step in determining how sculpin populations remain connected. Finally, our results emphasise the importance of examining ecology and population structure in a variety of habitats to accurately characterise family- and species-wide trends.

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