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Geography, environment, and colonization history interact with morph type to shape genomic variation in an Arctic fish

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Abstract

Polymorphic species are useful models for investigating the evolutionary processes driving diversification. Such processes include colonization history as well as contemporary selection, gene flow, and genetic drift, which can vary between intraspecific morphs as a function of their distinct life histories. The interactive and relative influence of such evolutionary processes on morph differentiation critically informs morph-specific management decisions and our understanding of incipient speciation. We therefore investigated how geographic distance, environmental conditions, and colonization history interacted with morph migratory capacity in the highly polymorphic fish species, Arctic Charr (*Salvelinus alpinus*). Using an 87 k SNP chip we genetically characterized recently evolved anadromous, resident, and landlocked charr collected from 45 locations across a secondary contact zone of three charr glacial lineages in eastern Canada. A strong pattern of isolation by distance across all populations suggested geographic distance principally shaped genetic structure. Landlocked populations had lower genetic diversities and higher genetic differentiation than anadromous populations. However, effective population size was generally temporally stable in landlocked populations in comparison to anadromous populations. Genetic diversity positively correlated with latitude, potentially indicating southern anadromous populations' vulnerability to climate change and greater introgression between the Arctic and Atlantic glacial lineages in northern Labrador. Local adaptation was suggested by the observation of several environmental variables strongly associating with functionally relevant outlier genes including a region on chromosome AC21 potentially associated with anadromy. Our results demonstrate that gene flow, colonization history, and local adaptation uniquely interact to influence the genetic variation and evolutionary trajectory of populations.

KEYWORDS
anadromy, colonization history, gene flow, isolation by distance, local adaptation, morph

1 | INTRODUCTION

Intraspecific variation in the form of ecologically, phenotypically, and genetically distinguishable morphs offers a unique opportunity to investigate evolution on a contemporary time frame. Because intraspecific variation can be the source of subsequent speciation (West-Eberhard, 1986), its study can provide insights into the patterns and processes of diversification across the tree of life. Given that morphs may differ in their economic and cultural value as well as their ecological roles (Des Roches et al., 2018) an understanding of the underpinnings of morph differentiation is essential for their conservation. But the potential for gene flow among morphs means that they cannot be understood in isolation (Coates et al., 2018). Successful management of polymorphic species therefore relies upon knowledge of the genetic and evolutionary relationships among all morphs.

Recent advances in genomic techniques have facilitated discovery of the genetic causes and consequences of reproductive isolation and adaptive differentiation associated with morph radiation events (Seehausen et al., 2014). Ecological speciation, where divergent selection drives reproductive isolation, is a key contributor to morph differentiation (Schluter, 1996a, 1996b), particularly in environments with multiple unoccupied niche spaces (such as postglacial environments) (Smith & Skúlason, 1996).

Contemporary neutral processes can enhance or ameliorate these adaptive genetic differences between morphs. Migratory morphs exhibiting low amounts of gene flow among populations are expected to demonstrate isolation by distance (IBD) as defined by a correlation between genetic and physical distance between populations (Wright, 1943). Alternatively, nonmigratory morphs lack gene flow with other populations and therefore experience higher genetic drift leading to lower genetic diversity (Waters et al., 2020). The accumulation of random genetic differences among such isolated, nonmigratory populations uncouples genetic differentiation from geographic distance, resulting in a lack of IBD (see case III of Hutchison & Templeton, 1999).

Historical colonization can also influence morph differentiation, particularly in recently colonized post-glacial populations that have not reached an equilibrium state (Ruzzante et al., 2019; Vera-Escalona et al., 2015). During the Pleistocene, many species were separated into allopatric refugia from which subsequent recolonization of post-glacial habitats took place (Hewitt, 2000). Glacial lineages descended from different refugia can genetically differ, resulting in isolation by colonization (Orsini et al., 2013) and consequences for contemporary morph evolution. For example, wave-adapted periwinkle morphs evolved from different glacial lineages showed little genetic parallelism, suggesting the independent evolution of this morph in each lineage (Kess et al., 2018). Genetic diversity may also be locally reduced at the edges of a species' range as it recolonizes postglacial habitat (e.g., Rougemont et al., 2020; Willi et al., 2018). This can be due to founder effects in leading edge populations or reduced gene flow and limited carrying capacities in trailing edge populations (Eckert et al., 2008). Introgression of historically allopatric lineages can also increase local genetic diversity (Dlugosch & Parker, 2008) and thereby fuel subsequent phenotypic differentiation (Marques et al., 2019; Salisbury & Ruzzante, 2022). Consideration of colonization history in addition to contemporary neutral and adaptive processes is therefore essential not only to inform morph-specific conservation strategies but also to understand the relative importance of such processes in shaping evolutionary trajectories.

Here, we investigated the influence of these evolutionary factors and their interaction on the genetic structure of Arctic Charr (*Salvelinus alpinus*). This species is ideally suited to this task because of its many recently evolved polymorphisms (Jonsson & Jonsson, 2001) and its well-characterized glacial lineages (Brunner et al., 2001; Moore et al., 2015). Many of the polymorphisms found within Arctic Charr (e.g., migratory and resident morphs) are also found within and between other species. For example, migratory and nonmigratory intraspecific morphs are found in many insect and fish species and migration has also been lost from species within otherwise migratory clades of birds, fish, and insects (Waters et al., 2020). Therefore, understanding the genomic and evolutionary basis of Arctic Charr morphs may provide insights into morph differentiation and incipient speciation across the larger tree of life.

However, there has been no investigation of the neutral and adaptive processes shaping genetic structure of Arctic Charr morphs across a wide geographic range. Previous studies of Arctic Charr have tended to focus on the genetic structure of a single morph, particularly the more economically important anadromous morph (e.g., Dallaire et al., 2021; Layton et al., 2020, 2021). Studies that have investigated multiple landlocked and anadromous morph types have used neutral markers and sampled relatively small geographic ranges (e.g., a single drainage in Doenz et al., 2019 and several neighbouring fjords in Salisbury et al., 2018, but see Kapralova et al. (2011) who sampled charr populations across Iceland). Here, we examine the evolutionary processes shaping the population genetic structure of Arctic Charr morphs across Labrador, Canada,

Labrador is uniquely suited for examination as it is home to a variety of recently evolved charr morphs in close proximity. These morphs are also known to have descended from the introgression of multiple charr glacial lineages (Salisbury et al., 2019) allowing investigation of the effects of this colonization on morph differentiation. Following its deglaciation ~9000 BP (Jansson & Kleman, 2004) Labrador was colonized by likely anadromous charr (Power, 2002) from three different glacial lineages (Arctic, Atlantic, and to a lesser extent, Acadian) (Salisbury et al., 2019) that had been previously separated during the Pleistocene for up to ~1 my (Moore et al., 2015). Landlocked populations were later independently isolated due to isostatic rebound (Johnson, 1980). The genetic similarity between sympatric morphs relative to allopatric populations of the same morph type suggests sympatric morph differentiation was independent across locations (Salisbury et al., 2018, 2020, 2022). Anadromous, resident, and landlocked populations exhibit mtDNA haplotypes of all three lineages and sympatric small and big morphs do not differ by mtDNA haplotype, suggesting morphs were not founded by distinct lineages

(Salisbury et al., 2018, 2019, 2020, 2022). The lack of segregation of sympatric and allopatric morphs by mtDNA haplotype as well as the presence of mtDNA haplotypes from multiple lineages within genetically homogeneous populations (based on nDNA) supports the extensive introgression among lineages (Salisbury et al., 2018, 2019), yet the influence of this on the contemporary genetic structure of charr in Labrador is unknown.

We used a newly designed 87 k SNP array (Nugent et al., 2019) to examine five predictions regarding the interactive effects of contemporary neutral processes (e.g., genetic drift), historical colonization, and selection on the population genetic structure of anadromous, landlocked, and resident Arctic Charr morphs across Labrador, Canada. We predicted that genetic diversity estimates (including heterozygosity and effective population size [N_e]) would be (1) relatively low in nonanadromous morphs due to the absence of gene flow, (2) relatively low in southern anadromous populations due to edge effects, and (3) relatively high at the site of greatest nDNA introgression between colonizing glacial lineages. Because random genetic drift is expected to shape the genetic relationships among isolated populations (i.e., case III of Hutchison & Templeton, 1999), we expected (4) patterns of isolation by distance (IBD) in anadromous but not in nonanadromous morphs. Finally, we investigated for evidence of (5) adaptive differentiation across all populations and morph types consistent with strong environmental gradients across Labrador (Barrette et al., 2020; Davis et al., 2021). We investigated for evidence of selection associated with habitat elevation as landlocked populations tend to inhabit lakes at higher altitudes than anadromous populations. We also investigated the selective effects of precipitation and temperature, which shape terrestrial productivity in Labrador (Davis et al., 2021) and thereby dictate lake primary productivity (Finstad & Hein, 2012). Given that higher lake productivity is known to favour resident over anadromous charr (Finstad & Hein, 2012), we expected precipitation and temperature to shape the population structure of resident, landlocked, and anadromous charr populations in Labrador (see Predictions and Results in Supporting Information Appendix S1).

2 | MATERIALS AND METHODS

2.1 | Sampling

Tissue samples (gill and fin) (N = 1302, Table 1) of Arctic Charr were collected between 2010 and 2017 from 45 locations in Newfoundland, Labrador, and Ungava (Figure 1). Samples were collected using variable sized standardized nylon monofilament gillnets (1.27–8.89 cm diagonal), electrofishing, angling, or counting fences. All samples were immediately stored in 95% ethanol or RNAlater. Additional metadata including weight, fork length, sex, maturity, and mtDNA D-loop haplotype (as assigned by Salisbury et al., 2019) measured for samples collected between 2010 and 2015 are available in the Supporting Information Appendix S2 metadata file.

2.2 | Extraction, sequencing, genotyping and quality control

DNA was extracted using either a glassmilk protocol (modified from Elphinstone et al., 2003), a phenol chloroform protocol (modified from Sambrook & Russell, 2006), or a Qiagen DNeasy 96 Blood and Tissue extraction kit (Qiagen) and quantified using QuantIT PicoGreen (Life Technologies).

DNA samples were sent to the Clinical Genomic Centre of Mount Sinai Hospital (Toronto, Canada) for sequencing using an 87 k Affymetrix Axiom Array (Nugent et al., 2019). This SNP chip was designed using wild Arctic charr from Iceland as well as aquaculture strains of Arctic charr sourced from Arctic Canada (Nauyuk, Tree River, Fraser) (Nugent et al., 2019). This SNP chip is appropriate for Labrador charr given its design based on fish likely sourced from the Atlantic (i.e., Icelandic charr, Moore et al., 2015) and Arctic (i.e., Nauyuk and Tree River charr, Moore et al., 2015) lineages, the two glacial lineages whose haplotypes dominate contemporary Labrador charr populations (Salisbury et al., 2019). In addition, the Fraser River aquaculture strain used to design this SNP chip was sourced from the Fraser River in Labrador (Nugent et al., 2019), a location also sampled in this study and previously found to contain fish with Arctic and Atlantic lineage mtDNA haplotypes (Salisbury et al., 2019). The design of this SNP chip using fish sharing a recent common ancestor with the populations studied here has likely minimized ascertainment bias.

We genotyped samples using this SNP chip using the "best practices workflow" (according to the Axiom Genotyping Solution Data Analysis Guide) for a diploid organism in Axiom Analysis Suite (version 4.0.1.9) to analyse the resulting. CEL genomic data files (see Supporting Information Appendix S1, for details on quality control measures). After filtering samples, we retained a total of N = 1206 individuals (Table 1) for further analyses.

A minor allele frequency (MAF) filter of 0.01 was applied using PLINK (version 1.9; Chang et al., 2015) across all populations, a threshold previously used in a previous study on Atlantic Salmon population structure (Lehnert et al., 2020) with similar numbers of samples and populations. PGDSpider (version 2.1.1.5) (Lischer & Excoffier, 2012) was used to convert between PLINK and Genepop files and the R package (R Core Team, 2013) genepopedit (Stanley et al., 2017) was used to order and arrange Genepop files for downstream analyses.

2.3 | Population structure analyses

Earlier work had identified genetic substructuring consistent with small (s) and big (b) morphs in five locations in Labrador using the same samples used in this study (Salisbury et al., 2020, 2022). Samples from these locations were therefore designated as small (s), big (b), and (where applicable) hybrid (h) morphs as assigned by Salisbury et al. (2020) or Salisbury et al. (2022) using ADMIXTURE clustering based on genomic data. Small and big morphs occurred in

TABLE 1 Sample location information.

Sampling Location	Sampling Location Name	Latitude (°N)	Longitude (°W)	Sampling Year	Access	N	Number of genetic groups	Genetic Group Code	PCA Group	N Passing QC	Sampling Method
1	Hope Advance Bay	59.30191	-69.609050	2017	Sea-accessible	30	1	HAB	Ungava	29	Gill-netting or Counting Fence
2	Kangalaksiorvik River	59.38715	-64.2668	2017	Sea-accessible	30	1	KAN	Anadromous Northern Labrador	30	Electrofishing
3	Komaktorvik	59.22694	-64.0092	2017	Sea-accessible	30	1	KOM	Anadromous Northern Labrador	28	Electrofishing
4	Kogarsok River	59.10934	-63.911	2017	Sea-accessible	30	1	KOG	Anadromous Northern Labrador	30	Electrofishing
5	Nachvak River	58.97935	-64.2381	2017	Sea-accessible	30	1	NAC	Anadromous Northern Labrador	30	Electrofishing
6	McCormick's River	58.97814	-63.6984	2017	Sea-accessible	30	1	MCC	Anadromous Northern Labrador	30	Electrofishing
7	Palmer River	58.92509	-63.8775	2017	Sea-accessible	30	1	PAL	Anadromous Northern Labrador	30	Electrofishing
8	Stecker River	58.86846	-63.4575	2017	Sea-accessible	30	1	STC	Anadromous Northern Labrador	30	Electrofishing
9	Ramah Lake	58.84138	-63.4774	2014	Sea-accessible	61	2	sR	Resident/ Landlocked Northern Labrador	32	Gill-netting
								bR	Anadromous Northern Labrador	28	
10	North Arm River	58.57114	-63.4974	2017	Sea-accessible	30	1	NOR	Anadromous Northern Labrador	30	Electrofishing
11	Southwest Arm	58.46825	-63.6462	2017	Sea-accessible	30	1	SWA	Anadromous Northern Labrador	30	Electrofishing
12	Kiyuktok River	58.39627	-62.9823	2017	Sea-accessible	30	1	KIY	Anadromous Northern Labrador	28	Electrofishing
13	Pangertok River	58.32611	-63.2087	2017	Sea-accessible	30	1	PAN	Anadromous Northern Labrador	30	Electrofishing
14	WP132 Lake	58.28016	-63.9693	2014	Landlocked	30	3	sWP	Resident/ Landlocked Northern Labrador	28	Gill-netting
15	WP133 Lake	58.27167	-64.0314	2014	Landlocked	28		bWP	Resident/ Landlocked Northern Labrador	24	
								hWP	Resident/ Landlocked Northern Labrador	6	

TABLE 1 (Continued)

Sampling Location	Sampling Location Name	Latitude (°N)	Longitude (°W)	Sampling Year	Access	N	Number of genetic groups	Genetic Group Code	PCA Group	N Passing QC	Sampling Method
16	River 109	58.22318	-63.6706	2017	Sea-accessible	30	1	R109	Anadromous Northern Labrador	30	Electrofishing
17	Ikarut River	58.16057	-63.1614	2017	Sea-accessible	30	1	IKA	Anadromous Northern Labrador	25	Electrofishing
18	Hebron Lake	58.14611	-63.5913	2015	Landlocked	30	1	HEB	Resident/ Landlocked Northern Labrador	30	Gill-netting
19	River 105	58.06341	-63.6845	2017	Sea-accessible	30	1	R105	Anadromous Northern Labrador	30	Electrofishing
20	River 103	58.03142	-63.0371	2017	Sea-accessible	30	1	R103	Anadromous Northern Labrador	29	Electrofishing
21	River 104	57.95381	-63.56	2017	Sea-accessible	30	1	R104	Anadromous Northern Labrador	29	Electrofishing
22	Todayfivk Lake	57.74385	-63.353	2015	Sea-accessible	21	1	H16	Resident/ Landlocked Northern Labrador	18	Gill-netting
23	Brooklyn Lake	57.72648	-62.4734	2015	Sea-accessible	60	2	sB	Resident/ Landlocked Northern Labrador	42	Gill-netting
								bB	Resident/ Landlocked Northern Labrador	16	
24	Beachy Strip Lake	57.66161	-62.9544	2015	Landlocked	30	1	BS	Resident/ Landlocked Northern Labrador	29	Gill-netting
25	Lonely Lake	57.63915	-63.2329	2015	Landlocked	30	2	sLO	Resident/ Landlocked Northern Labrador	21	Gill-netting
								bLO	Resident/ Landlocked Northern Labrador	8	
26	North River	57.50159	-62.7432	2015	Sea-accessible	30	1	K05	Anadromous Northern Labrador	29	Electrofishing
27	Ikinet River	57.40427	-62.6411	2017	Sea-accessible	30	1	IKI	Anadromous Northern Labrador	27	Electrofishing
28	Puttuaalu River	57.25526	-62.2207	2017	Sea-accessible	30	1	PUT	Anadromous Northern Labrador	24	Electrofishing
29	Esker North Lake	57.14884	-62.8782	2015	Sea-accessible	60	3	sE	Resident/ Landlocked Northern Labrador	33	Gill-netting
								bE	Resident/ Landlocked Northern Labrador	21	
								hE	Resident/ Landlocked Northern Labrador	6	

(Continues)

TABLE 1 (Continued)

Sampling Location	Sampling Location Name	Latitude (°N)	Longitude (°W)	Sampling Year	Access	N	Number of genetic groups	Genetic Group Code	PCA Group	N Passing QC	Sampling Method
30	Kingurutik River	56.84256	-62.6216	2017	Sea-accessible	30	1	KIN	Anadromous Northern Labrador	24	Electrofishing
31	Kamanatsuk River	56.75377	-62.5381	2017	Sea-accessible	30	1	KAM	Anadromous Northern Labrador	29	Electrofishing
32	Fraser River	56.69082	-63.465	2017	Sea-accessible	30	1	FRA	Anadromous Northern Labrador	23	Electrofishing
33	Knumandi Lake	56.58141	-63.3234	2011	Landlocked	20	1	KNU	Resident/ Landlocked Northern Labrador	16	Gill-netting
34	Anaktalik River	56.49753	-62.9331	2017	Sea-accessible	30	1	ANA	Anadromous Northern Labrador	30	Electrofishing
35	Slushy Lake	56.41561	-64.1022	2010, 2011, 2012, 2013	Landlocked	11	1	SLU	Resident/ Landlocked Northern Labrador	10	Gill-netting
36	Ikadlavik River	56.3126	-62.1688	2017	Sea-accessible	30	1	IKL	Anadromous Northern Labrador	17	Electrofishing
37	Reid River	56.30319	-62.0852	2017	Sea-accessible	30	1	REI	Anadromous Northern Labrador	9	Electrofishing
38	Genetics B Lake	56.11067	-63.3886	2010, 2011	Landlocked	13	1	GB	Resident/ Landlocked Northern Labrador	12	Gill-netting
39	Notakwonan River Site a	55.97279	-61.7544	2015	Sea-accessible	3	1	W0	Anadromous Northern Labrador	21	Electrofishing
40	Notakwonan River Site b	55.9334	-62.0709	2015	Sea-accessible	12					
41	Notakwonan River Site c	55.90273	-62.1129	2015	Sea-accessible	8					
42	River 78	55.64627	-60.6898	2017	Sea-accessible	30	1	R78	Anadromous Northern Labrador	24	Electrofishing, Counting Fence, Angling
43	English River	54.96969	-59.7494	2017	Sea-accessible	30	1	ENG	Southern Labrador and Newfoundland	30	Electrofishing, Counting Fence, Angling
44	Muddy Bay Brook	53.62977	-57.0299	2017	Sea-accessible	30	1	MBB	Southern Labrador and Newfoundland	26	Electrofishing, Counting Fence, Angling
45	Parkers Pistolet	51.49828	-55.7327	2017	Sea-accessible	15	1	PBP	Southern Labrador and Newfoundland	15	Electrofishing

Note that some sampling locations contain multiple genetic groups and some genetic groups occurred in multiple sampling locations. Sampling location access was either sea-accessible or landlocked as characterized by Anderson (1985) for all Labrador samples. PCA Group assigned to each genetic group include: Ungava, Anadromous Northern Labrador, Resident/Landlocked Northern Labrador, Southern Labrador and Newfoundland (see results for further details).

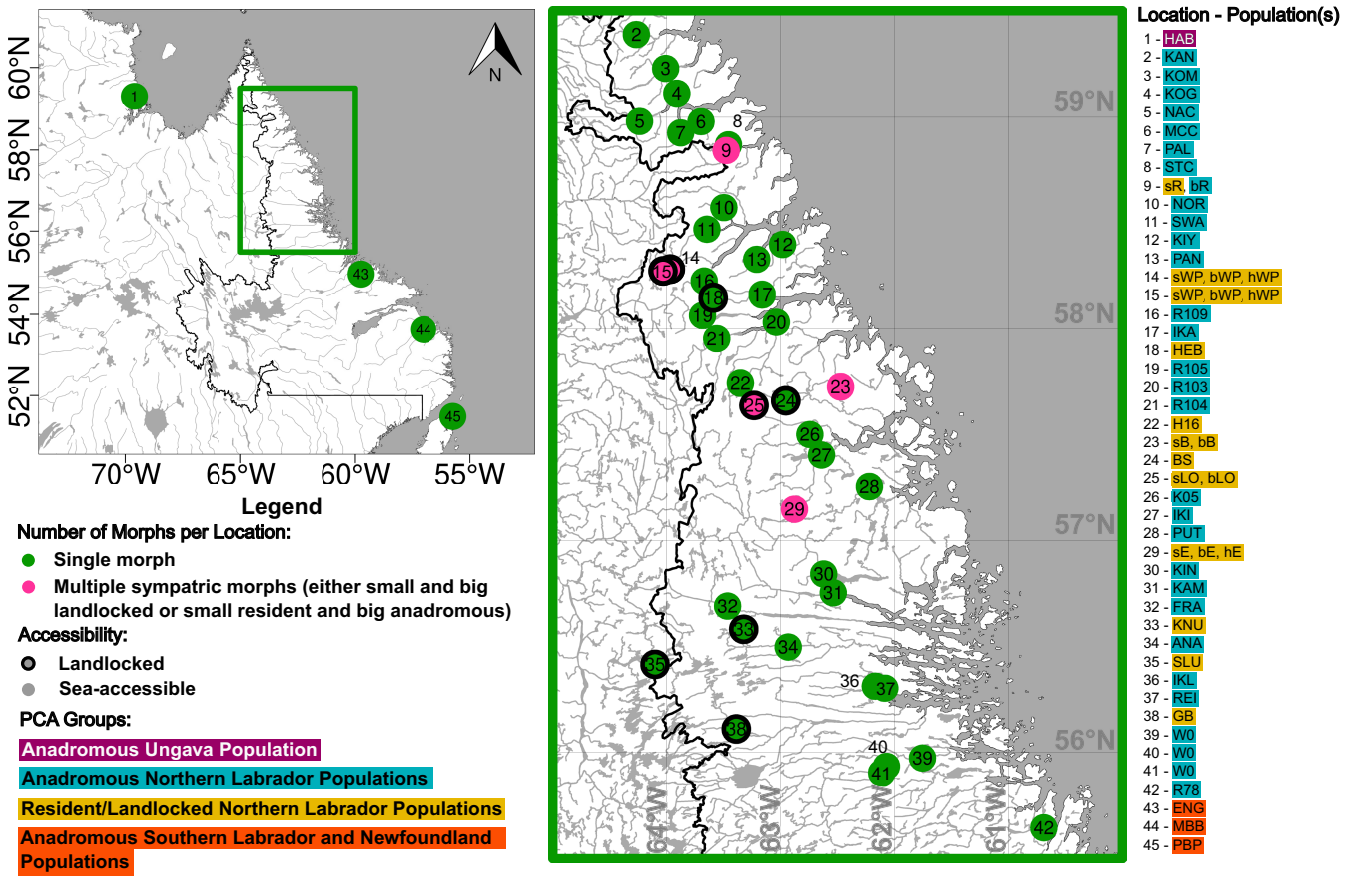

FIGURE 1 Map of 45 sampling locations. The 49 Arctic Charr populations found within each of the sampling location are labelled and coloured by their assigned PCA Group. Map generated using data from CanVec (Government of Canada).

each of the neighbouring lakes WP132 and WP133 (locations 14 and 15, respectively in Figure 1) and morphs of the same type were genetically homogeneous across lakes. Therefore, samples from both lakes were grouped together and assigned to either the small, big, or hybrid group (sWP, bWP, hWP, respectively). We found no evidence of genetic differentiation between samples collected from three locations along the Notakwonan River (W01, W02, W03) (Table S1, Figures S1 and S2, Supporting Information Appendix S1), so these samples were pooled into a single population W0. All other individuals were assigned to populations based on their sampling location. Samples from our 45 locations were therefore assigned to 49 populations prior to downstream analyses.

Using a common set of SNPs after applying a MAF of 0.01, the genetic structure of all populations was assessed using (1) the R package PCAdapt (version 4.1.0; Luu et al., 2017) testing K = 1–100 with the default Mahalanobis distance and (2) ADMIXTURE (version 1.3.0; Alexander et al., 2009) testing K = 1–67 with 10 cross-validations. Weighted pairwise F_{STs} (Weir & Cockerham, 1984) were estimated between all genetic groups using the package hierfstat (Goudet, 2005) using all SNPs and only putatively neutral SNPs (excluding outliers using PCAdapt and the RDA analyses described below). The PCAdapt analysis was then redone using an optimal K-value visually identified from the screeplot of the previous analysis and outlier SNPs were then identified based on an $\alpha = 0.05$ after *p*-values were corrected using the false discovery rate (FDR; Storey & Tibshirani, 2003) with the R package qvalue (version 2.14.1; Storey et al., 2015). Outliers identified using PCAdapt and from the RDA analyses below were removed before estimating genetic diversity estimates (i.e., $\hat{H}_O$, $\hat{H}_E$ and $\hat{N}_e$).

To assess and compare the genetic diversity of each genetic group, heterozygosities and historical and contemporary effective population sizes (N_e) were estimated. For each genetic group, observed and expected heterozygosities (H_O, H_E) were estimated for each SNP using PLINK and then averaged. To investigate historical changes in genetic diversity we used LinkNe (Hollenbeck et al., 2016) a method which uses linkage disequilibrium to estimate historical N_e as a function of recombination rate. We ran LinkNe using a common set of SNPs that passed the initial global MAF of 0.01 and had a known recombination rate (Christensen et al., 2018; NCBI assembly ASM291031v2). We used the default MAF cutoff of 0.05 (applied independently to each population) to be consistent with linkage-based N_e estimates (see below) and the default bin size of 0.05 Morgans. Any negative 95% parametric confidence interval estimates and $\hat{N}_{e(LinkNe)}$ resulting from the LinkNe analyses were designated as "infinite". The same set of SNPs used for the LinkNe analyses were also used to estimate $\hat{N}_{e(NeEstimator)}$ using the linkage disequilibrium method with NeEstimator version 2.1 (Do et al., 2014). We used a MAF cutoff of 0.05 for each population given the low sample sizes

for some populations (Waples & Do, 2010). The jackknife method was used to calculate 95% confidence intervals.

To examine the effects of geographic distance on genetic structure, and particularly to look for evidence of IBD, we performed a Mantel test. We generated a pairwise geographic distance matrix between all genetic groups using the "distm" function of the geosphere R package (Hijmans et al., 2017) based on latitude and longitude of each sampling location. Some genetic groups occurring in sympatry (i.e., those locations with small and big morphs) therefore had geographic distances of zero. The latitude and longitude of the genetic groups that included samples from multiple locations (i.e., W0, sWP, bWP, hWP) were averaged over the sampling locations. Pairwise distances calculated based on latitude and longitude likely underestimate the contemporary waterway distance experienced by a fish between locations. However, this underestimation may more faithfully approximate the likely increased historical connectivity among populations (particularly among what are now landlocked populations in close geographic distance but contemporarily in separate watersheds) during the hydrologically dynamic deglaciation of Labrador ~9000 years ago (Jansson & Kleman, 2004). For comparison, we also conducted all IBD analyses using contemporary waterway pairwise geographic distances between all locations as measured using Google Earth Pro (7.3.0.3832). A Mantel test to assess for a significant correlation between pairwise $\widehat{F}_{STs}$ and pairwise geographic distances was conducted using the R package cultevo (Stadler, 2018) using the default Spearman method and 9999 trials. We further investigated for associations between pairwise $\widehat{F}_{STs}$ and pairwise geographic distances within certain subgroups of populations (as designated by the results of our PCA), using linear regressions performed in R.

To further investigate the effects of geographic distance as well as those of environmental variables on genetic structure we conducted a redundancy analysis (RDA). We downloaded data for the 19 "bioclimatic" variables and the elevation variable from the WorldClim version 2.1 database (Fick & Hijmans, 2017). We used a resolution of 30 s for all locations except two (HAB, R78) for which we used a resolution of 2.5 min as no data was available at 30 s resolution. For those genetic groups collected in multiple locations (W0, sWP, bWP, hWP) climatic and elevation data were averaged across sampling locations. We assessed for correlation among elevation and climatic variables, removing climatic variables until no variables had a correlation (as measured using the Pearson's correlation coefficient) >0.75 with any other variable. Missing genotypes were imputed as the most common genotype for each SNP across all samples. We then conducted an RDA using the R package vegan (Oksanen et al., 2013) to assess the genetic variation explained by elevation and each of the remaining climatic variables. We also included latitude and longitude as explanatory variables to help reduce the effects of spatial structure on outlier detection (Meirmans, 2012). Given that our samples fall along the Labrador coast, corresponding to several environmental gradients, we recognize the innate difficulty of teasing apart the effects of geographic and environmental variation on our genetic data. However, our inclusion of the spatial explanatory variables latitude and longitude was done to directly visualize the potential correlation between spatial and environmental variables. A partial RDA (pRDA), conditioning out the effects of the linear distance of each population to the most northern Labrador population (KAN), again to help reduce the effects of spatial structure on outlier detection (Meirmans, 2012), was also conducted using the same environmental variables employed in the RDA. We assessed the significance of the entire RDA correlation as well as for each of the variables using the anova.cca() function of the vegan package, using 999 permutations for each analysis. Putative outlier SNPs were identified as those that loaded >3 SD from the mean distribution of each of those RDAs explaining the majority of the genetic variation (Forester et al., 2018). We associated outlier SNPs with the closest coding sequence within 5 kbp based on the *Salvelinus* genome (Christensen et al., 2018; NCBI assembly ASM291031v2) using BEDOPS (Neph et al., 2012). Allele frequencies of outlier SNPs were visualized using the R package ComplexHeatMap (Gu et al., 2016).

3 | RESULTS

The number of SNPs that passed filtering after applying a MAF of 0.01 was $N = 22{,}935$ with a total genotyping rate > 99%. The first two PCs from our PCAdapt analysis explained a combined 11% of the variation in the data and separated all populations consistent with their geographic locations (Figure 2) such that the diagonal of the PCA roughly corresponds to population latitude. The PCA further suggested the presence of four groups of populations: Ungava anadromous, anadromous northern Labrador, resident/landlocked northern Labrador, southern anadromous. The anadromous Ungava population (HAB) and three anadromous southern populations (PBP, MBB, ENG) are located at opposite corners of the PCA indicating their genetic distinctiveness. Within the northern Labrador sampling locations, individuals from anadromous populations form a conspicuous "smear" of populations ordered by latitude between the Southern and Ungava populations, suggesting the potential for gene flow among anadromous populations. Orthogonal to this group in the PCA are a series of isolated, genetically distinguishable populations many of which are known to be landlocked (based on Anderson, 1985). However, several populations with apparent sea-access based on Anderson (1985) are also included in this group including H16, the small morphs within Ramah (sR) and all morphs within Esker North (sE, bE, hE) and Brooklyn (sB, bB). The life history of these populations with respect to anadromy is uncertain, but given their genetic distinctiveness from known anadromous populations, these populations may comprise nonanadromous individuals. Brooklyn, Esker North, and H16 in particular may be landlocked, contrary to Anderson (1985). As previously noted (Salisbury et al., 2022) the genetic similarity of the big morphs from Ramah (bR) but not those from Esker North (bE) and Brooklyn (bB) with nearby anadromous populations suggests that the big morphs from the latter two populations may not be contemporarily anadromous (in contrast to what had been suggested by Salisbury et al., 2020).

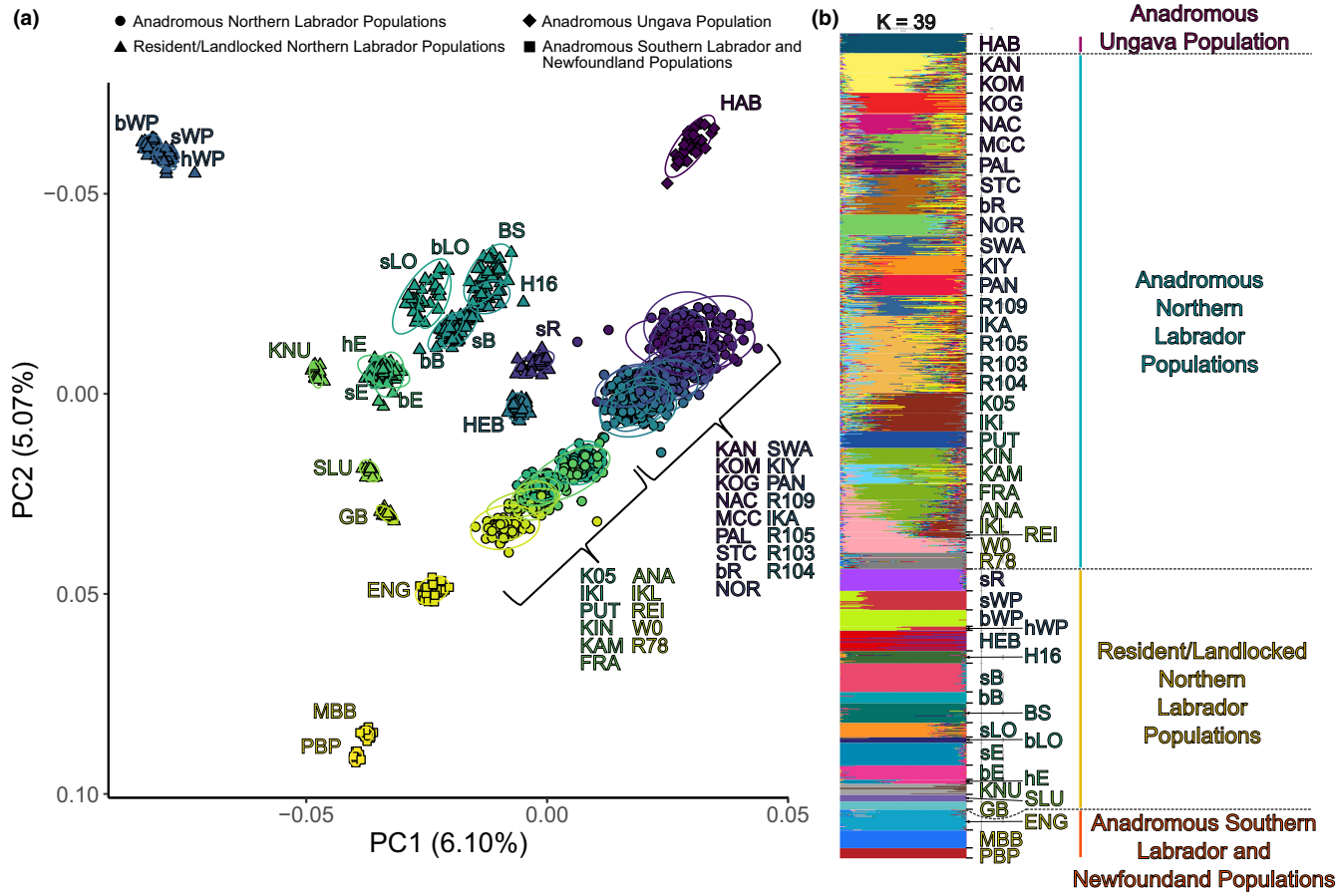

FIGURE 2 PC1 versus PC2 of genetic variation in 1206 samples within 49 Arctic Charr populations (N = 22,935 SNPs) based on PCAdapt analysis of 100 PCs. Shape of points indicate the assigned PCA genetic group: Anadromous Ungava (diamond; i.e., HAB population), Anadromous Northern Labrador (circle), Resident/Landlocked Northern Labrador (triangle), Anadromous Southern Labrador and Newfoundland (square). Circles indicate 95% normal ellipses for each population. Populations are coloured from purple to yellow starting with the Ungava population (HAB) and then from north to south.

We therefore refer to this group of populations as the "Resident/Landlocked" PCA group henceforth, with the acknowledgement that the life history of some populations is uncertain. These results are further supported by our ADMIXTURE analyses where a K-value of 39 was found to have the lowest cross-validation error. The resulting ADMIXTURE plot (Figure 2b) reveals the genetic distinctiveness of most populations with greater admixture apparent among the anadromous northern Labrador populations. Some anadromous populations were not genetically discernable from anadromous populations in neighbouring watersheds at this K-value, however, given that all such populations were sampled using electrofishing (Table 1) which target small fish that are unlikely to have undergone smoltification, the individuals in these locations were likely sampled in their natal habitat. Therefore, our consideration of such sampling locations as distinct populations for all subsequent analyses was appropriate. Weighted pairwise $\hat{F}_{STs}$ were also notably lower among populations within the northern Labrador anadromous group, consistent with connectivity among these populations (Figure S3, Supporting Information Appendix S1). Pairwise $\hat{F}_{STs}$ were nearly identical when using all SNPs (N = 22,935 SNPs) as when excluding putative outliers detected using PCAdapt and RDA (N = 22,259 SNPs), therefore only results using all SNPs are reported (see Supporting Information Appendix S1 for results using putative neutral SNPs only Figures S4–S6).

Based on the screeplot for the initial PCA using K = 100 PCs (Figure S7), a reduced K-value of 6 was chosen for outlier selection. A total of 560 outlier SNPs were detected from the PCAdapt analysis, a further 144 SNPs were identified from the RDA (see below) with 30 SNPs detected by both outlier detection methods. These 676 unique outlier SNPs detected across both methods were removed before estimating heterozygosity and N_e.

$\hat{H}_E$ and $\hat{H}_O$ ranged from a low of 0.05 for both estimates in the most southern anadromous population PBP, to a high of 0.30 for both estimates in the anadromous population MCC (Figure S8a, Supporting Information Appendix S1). $\hat{N}_{e(NeEstimator)}$ based on 1105 SNPs ranged from a low of 24.2 in the anadromous population KIY to a high of 617.8 in the putative resident sR population (Figure S8b, Supporting Information Appendix S1) (for all results see Table S2, Supporting Information Appendix S1).

Results of all LinkNe analyses based on up to 1105 polymorphic SNPs are shown in Figure S9, Table S2 (Supporting Information Appendix S1). Infinite $\hat{N}_{e(LinkNe)}$ and/or 95% confidence intervals

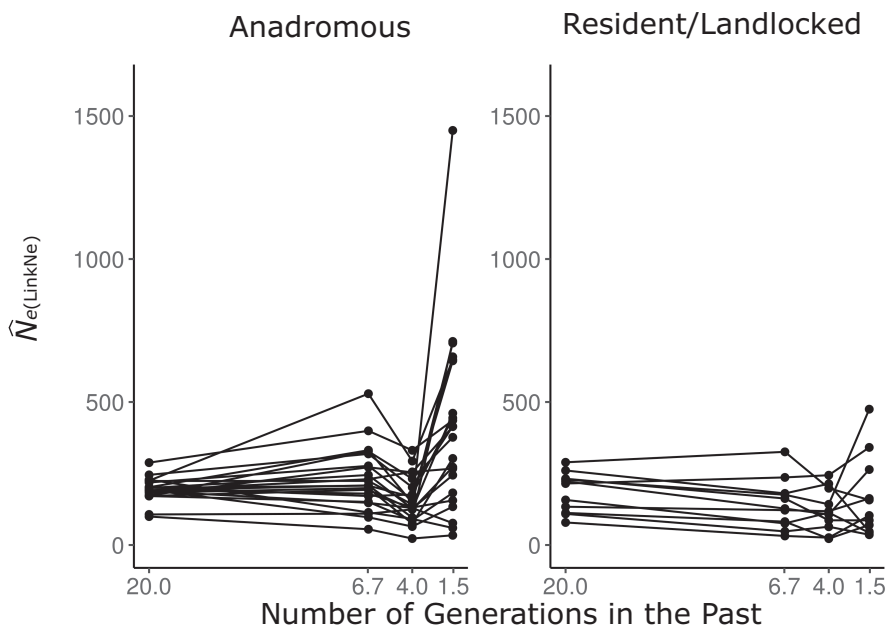

FIGURE 3 Results of LinkNe analysis for all Arctic Charr populations in northern Labrador with a non-infinite $\widehat{N}_{e(LinkNe)}$ or upper 95% parametric confidence interval estimate for all four historical time points for which N_e was estimated. More anadromous populations exhibited an increase in $\widehat{N}_e$ between 4 and 1.5 generations ago than resident/landlocked populations (20/22 vs. 6/11 populations respectively) and their increase was higher than for resident/landlocked populations (6 anadromous but no resident/landlocked populations had $\widehat{N}_e > 500$ at 1.5 generations ago.)

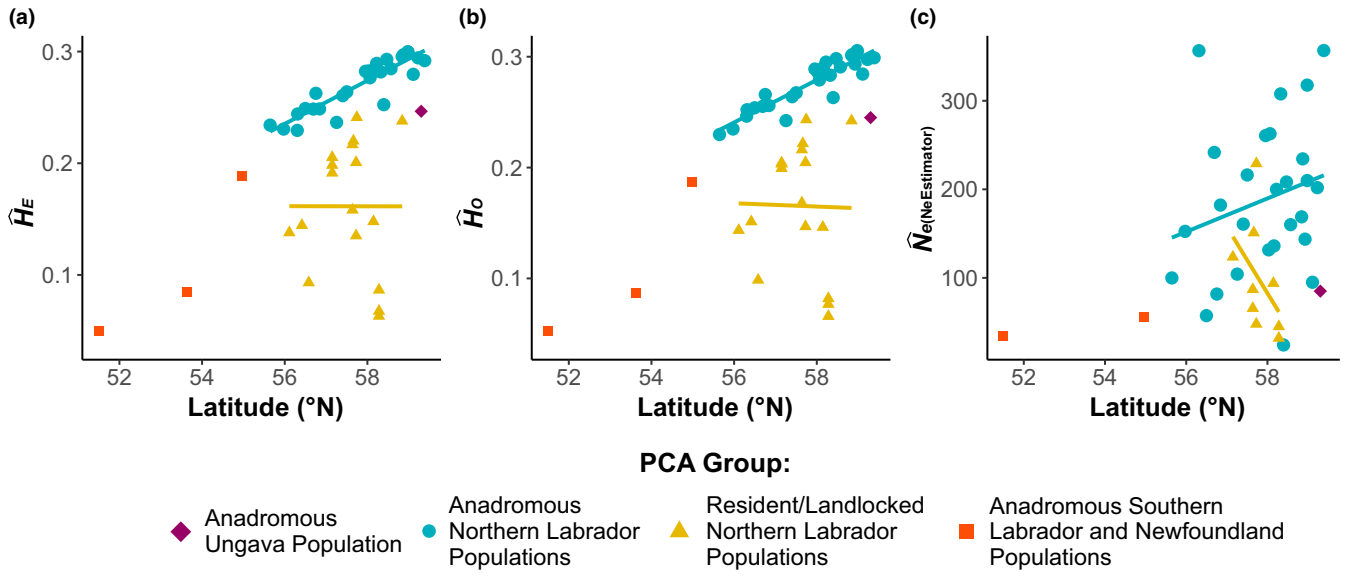

FIGURE 4 (a) Expected Heterozygosity ($\widehat{H}_E$), (b) Observed Heterozygosity ($\widehat{H}_O$), and (c) $\widehat{N}_{e(NeEstimator)}$ estimates versus latitude using $N = 22{,}259$ putative neutral SNPs for Arctic Charr populations from four PCA Groups: Anadromous Ungava, Anadromous Northern Labrador, Resident/Landlocked Northern Labrador, Anadromous Southern Labrador and Newfoundland.

for some populations may be due to relatively small sample sizes (Waples & Do, 2010) (e.g., hWP ($N = 6$), bLO ($N = 8$), hE ($N = 6$), GB ($N = 10$), SLU ($N = 12$), W0 ($N = 21$)). Alternatively, several populations (KAN, MCC, sR, PAN, R104, IKL, MBB) only demonstrated infinite $\widehat{N}_{e(LinkNe)}$ and/or infinite 95% parametric confidence intervals within the last four generations. This might reflect a rapid population growth or a recent introgression event leading to elevated $\widehat{N}_e$'s that are more difficult to estimate precisely using the LD method (Waples & Do, 2010; Waples & England, 2011). For clarity, only those populations in northern Labrador with noninfinite $\widehat{N}_{e(LinkNe)}$ and 95% parametric confidence intervals for all four time points (1.5, 4, 6.7, 20 generations in the past) are shown in Figure 3. Within this subset, more anadromous populations demonstrated an increase in $\widehat{N}_{e(LinkNe)}$ some 4 to 1.5 generations ago than resident/landlocked (20/22 vs. 6/11 respectively, $\chi^2 = 5.8055$, df = 1, $p < .05$, based on a two-sample test for equality of proportions with no continuity correction using "prop. test" in R). Furthermore, at 1.5 generations ago six anadromous populations but no resident/landlocked populations had an $\widehat{N}_{e(LinkNe)} > 500$. The $\widehat{N}_{e(LinkNe)}$ of the Ungava population (HAB) declined slightly from 20 generations ago to 1.5 generations ago. Within the southern anadromous populations between 20 to 1.5 generations ago the $\widehat{N}_{e(LinkNe)}$ of ENG declined whereas that of PBP remained relatively constant but notably lower than other anadromous populations.

Within northern Labrador, both $\hat{H}_E$ and $\hat{H}_O$ were significantly correlated with latitude in anadromous populations (t_{26} = 10.823, t_{26} = 11.698, and $p < .01$, $p < .01$, respectively), but not in resident/landlocked populations (t_{15} = −0.003, t_{15} = −0.073, and $p > .99$, $p = .94$, respectively) (Figure 4a,b). Both $\hat{H}_E$ and $\hat{H}_O$ were significantly higher in anadromous than in resident/landlocked populations, after adjusting for latitude ($F_{1,42}$ = 80.038, $F_{1,42}$ = 83.232, and $p < .01$, $p < .01$, respectively). The Ungava population (HAB) had a notably lower $\hat{H}_E$ and $\hat{H}_O$ than those anadromous populations in northern Labrador at similar latitudes. $\hat{H}_E$ and $\hat{H}_O$ increased with latitude in the three southern anadromous populations which generally had lower $\hat{H}_E$ and $\hat{H}_O$ than those anadromous populations in northern Labrador. Similar trends were also observed for $\hat{N}_{e(NeEstimator)}$ after removing populations with infinite upper 95% jackknife confidence intervals as well as a high and potential outlier $\hat{N}_{e(NeEstimator)}$ for the sR population (Figure 4c, for all populations see Figure S10, Supporting Information Appendix S1). Within northern Labrador, $\hat{N}_{e(NeEstimator)}$ were significantly higher in anadromous than resident/landlocked populations, after adjusting for latitude ($F_{1,33}$ = 8.044, $p < .05$). $\hat{N}_{e(NeEstimator)}$ positively, but not significantly, correlated with latitude in anadromous populations (t_{25} = 1.20, $p = .24$) and did not positively correlate with latitude in resident/landlocked populations (t_7 = −1.3, $p = .24$). The Ungava population (HAB) had a notably lower $\hat{N}_{e(NeEstimator)}$ than anadromous populations from northern Labrador at similar latitudes. $\hat{N}_{e(NeEstimator)}$ increased with latitude in the two southern anadromous populations which generally had lower $\hat{N}_{e(NeEstimator)}$ than those anadromous populations from northern Labrador.

Analyses of IBD using the "as the crow flies" and contemporary waterway pairwise distances yielded near identical results, and we report only the former here (see Figure S11–S14, Supporting Information Appendix S1). A significant correlation was detected between pairwise $\hat{F}_{ST}$ and pairwise geographic distances using a Mantel test for all populations (r = 0.288, $p < .01$) (Figure 5a) but not when restricting the analysis to only those populations (both anadromous and landlocked/resident) from northern Labrador (r = 0.087, p = .14). However, when comparisons were conducted exclusively between (1) pairs of anadromous populations, (2) pairs of resident/landlocked and anadromous populations, and (3) between pairs of resident/landlocked populations, all three groups demonstrated a significant linear regression between pairwise $\hat{F}_{ST}$ and pairwise geographic distance (t_{376} = 20.62, $p < .001$; t_{474} = 2.113, $p < .05$; t_{134} = 5.118, $p < .001$, respectively, Figure 5b, see Figure S15, Supporting Information Appendix S1, for comparisons between all PCA groups).

After assessing the correlation between all World Clim variables (Figure S16, Supporting Information Appendix S1), we retained the following environmental explanatory variables (all $r < 0.75$) (Figure 6): Elevation, BIO1 (annual mean temperature), BIO2 (mean diurnal range), BIO7 (temperature annual range), BIO8 (mean temperature of wettest quarter), BIO9 (mean temperature of driest quarter), BIO12 (annual precipitation) (see Supporting Information Appendix S2). We report only the RDA results here given that pRDA can prevent detection of environmentally-associated outliers if environmental variables are strongly correlated with geography. However, overall, pRDA results were generally similar to RDA results (see Figures S17–S19, Tables S3 and S4, Supporting Information Appendix S1). The RDA model significantly explained the genetic variation ($F_{9,1196}$ = 20.154, $p < .01$) and the first two RDA components explained a combined 63.46% of the genetic variation (Figure S20, Supporting Information Appendix S1). All explanatory variables significantly explained the genetic variation (all $p < .01$, Table S5, Supporting Information Appendix S1). However, the 144 outlier SNPs associated with either RDA1 or RDA2 were found to be most strongly associated with only latitude (42 SNPs), annual mean temperature (BIO1, 13 SNPs), mean diurnal range (BIO2, 2 SNPs), annual precipitation (BIO12, 26 SNPs), and elevation (61 SNPs) (Table S6, Supporting Information Appendix S1).

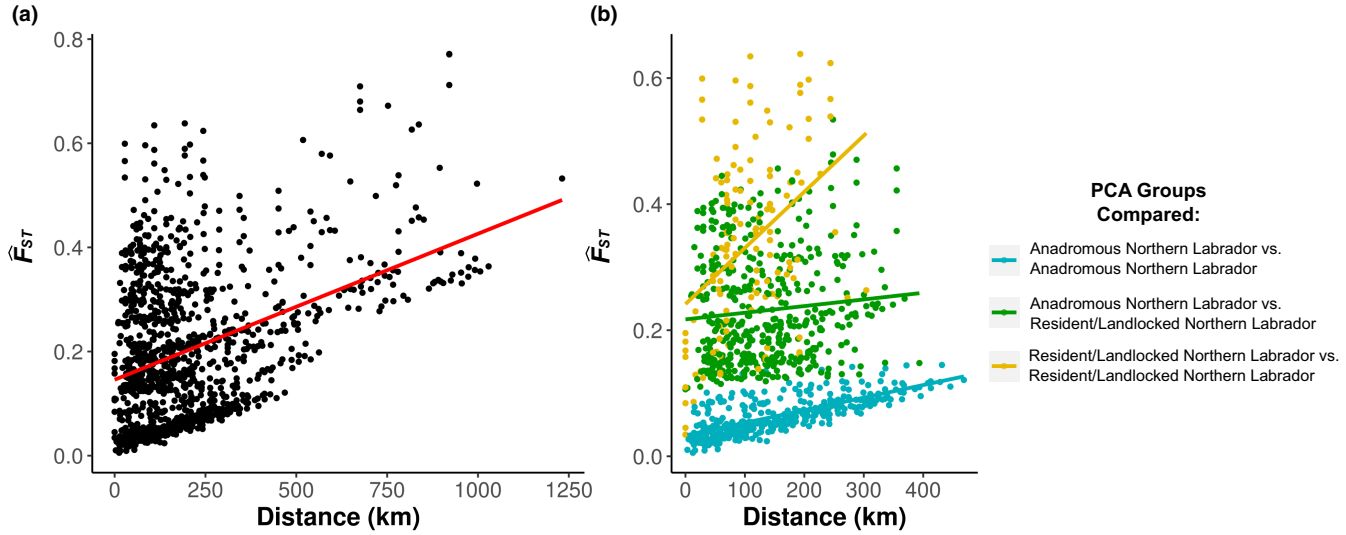

FIGURE 5 Pairwise $\hat{F}_{ST}$ (based on all SNPs, N = 22,935) versus "as the crow flies" distance (km) between (a) all 49 Arctic Charr populations, and between (b) only those Arctic Charr populations (N = 45) in the Anadromous Northern Labrador and Resident/Landlocked Northern Labrador PCA Groups.

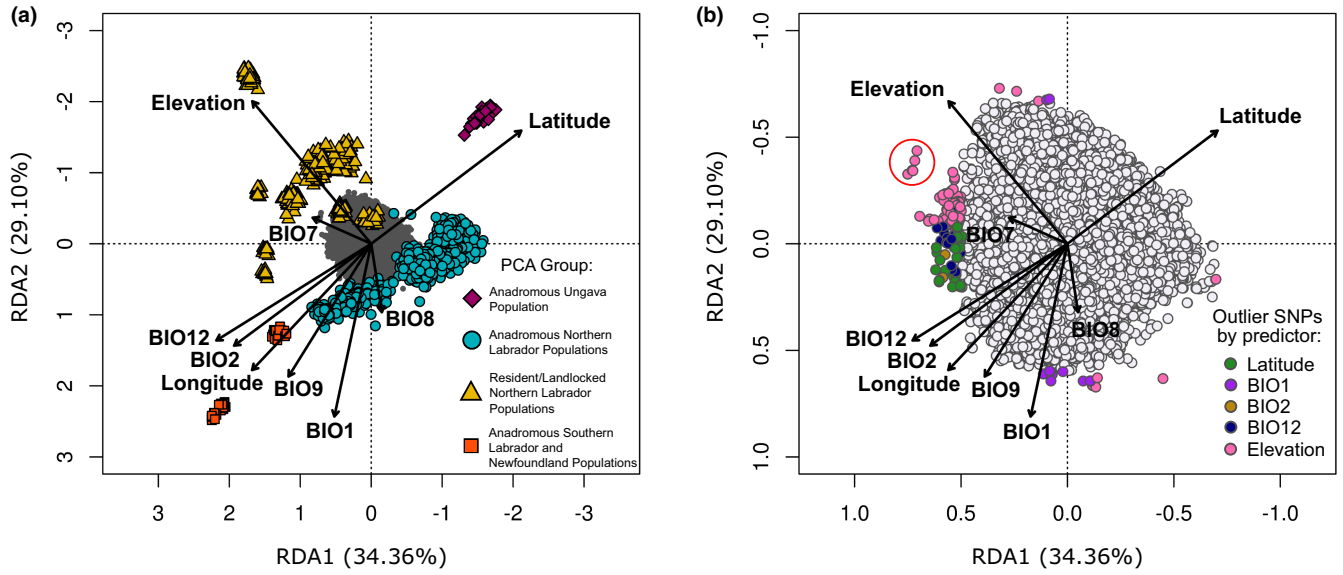

FIGURE 6 Results of RDA analysis for RDA1 versus RDA2 testing the influence of 9 predictor variables on the genetic variation ($N = 22{,}935$ SNPs) in 49 populations of Arctic Charr. The predictor variables include: Latitude, Longitude, BIO1 (Annual Mean Temperature), BIO2 (Mean Diurnal Range), BIO7 (Temperature Annual Range), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO12 (Annual Precipitation), and Elevation. (a) loadings of 9 predictor variables in relation to 1206 Arctic Charr individuals grouped by PCA Group: Anadromous Ungava, Anadromous Northern Labrador, Resident/Landlocked Northern Labrador, Anadromous Southern Labrador and Newfoundland. Data points for each sample are in shapes and colour as in Figure 2. (b) loadings of 9 predictor variables in relation to 22,935 SNPs. Outlier SNPs with loadings >3 SD from the mean distribution of RDA1 and RDA2 are coloured by the predictor variable with which they most closely associate. Five outlier SNPs on AC21 demonstrating significant loadings on RDA1 and RDA2 are circled in red (see Figure 7 for allele frequencies).

Five of these outlier SNPs which clustered together and demonstrated extreme loadings on RDA1 and RDA2 (Figure 6b) and were most strongly associated with the elevation environmental variable, were all found within 150 kb on AC21. Consistent with the fact that nonanadromous populations tend to occur at higher elevations, a heatmap of these five SNPs (Figure 7) indicates that opposite alleles are most frequent in the anadromous and resident/landlocked populations within northern Labrador. In contrast to this trend, the putative resident morphs in Ramah (sR) demonstrate an allele frequency similar to that of northern Labrador anadromous populations. Intriguingly, southern anadromous populations as well as the Ungava anadromous population demonstrate allele frequencies similar to that of resident/landlocked populations in northern Labrador.

4 | DISCUSSION

Our results demonstrate that the genetic structure of Arctic Charr populations is not dictated by a single evolutionary force but rather by the interactive effects of geography, migratory life history, colonization history, and local adaptation, resulting in unique evolutionary trajectories for each population. We found support for our hypotheses for decreased genetic diversities in nonanadromous morphs (likely due to their inherent genetic isolation, prediction 1) and in southern anadromous populations (potentially due to edge effects, prediction 2). Greater nDNA introgression between the Arctic and Atlantic glacial lineages in this region of Labrador could have resulted in the elevated diversities in more northern anadromous populations (prediction 3). IBD was detected in anadromous, but in contrast to our expectations (prediction 4), also in nonanadromous populations within Labrador, potentially driven by decreasing introgression of Arctic glacial lineage nDNA in more southern populations. Finally, we demonstrate environmentally associated, putatively adaptive differentiation both between landlocked and anadromous morphs but also across the geographic range of populations (prediction 5). In particular, we identify a genomic region on AC21, containing genes functionally associated with anadromy, that is similar between southern anadromous and nonanadromous populations. We discuss these findings in detail below.

4.1 | Genetic variation across and within sampling regions

The importance of geography is evident from the clear latitudinal cline in genetic variation in the PCA and the strong signal of IBD across all populations, as has been reported for other anadromous fishes (Hendry et al., 2004) as well as a wide range of taxa including mammals (e.g., Lucena-Perez et al., 2020), invertebrates (e.g., Straus & Avilés, 2022), and plants (e.g., Twyford et al., 2020).

Within northern Labrador, lower pairwise $\hat{F}_{STs}$ and higher $\hat{H}_E$, $\hat{H}_O$, and $\hat{N}_e$ among anadromous populations suggest greater connectivity than among resident/landlocked populations, consistent with straying (Layton et al., 2020; Salisbury et al., 2018). Additionally,

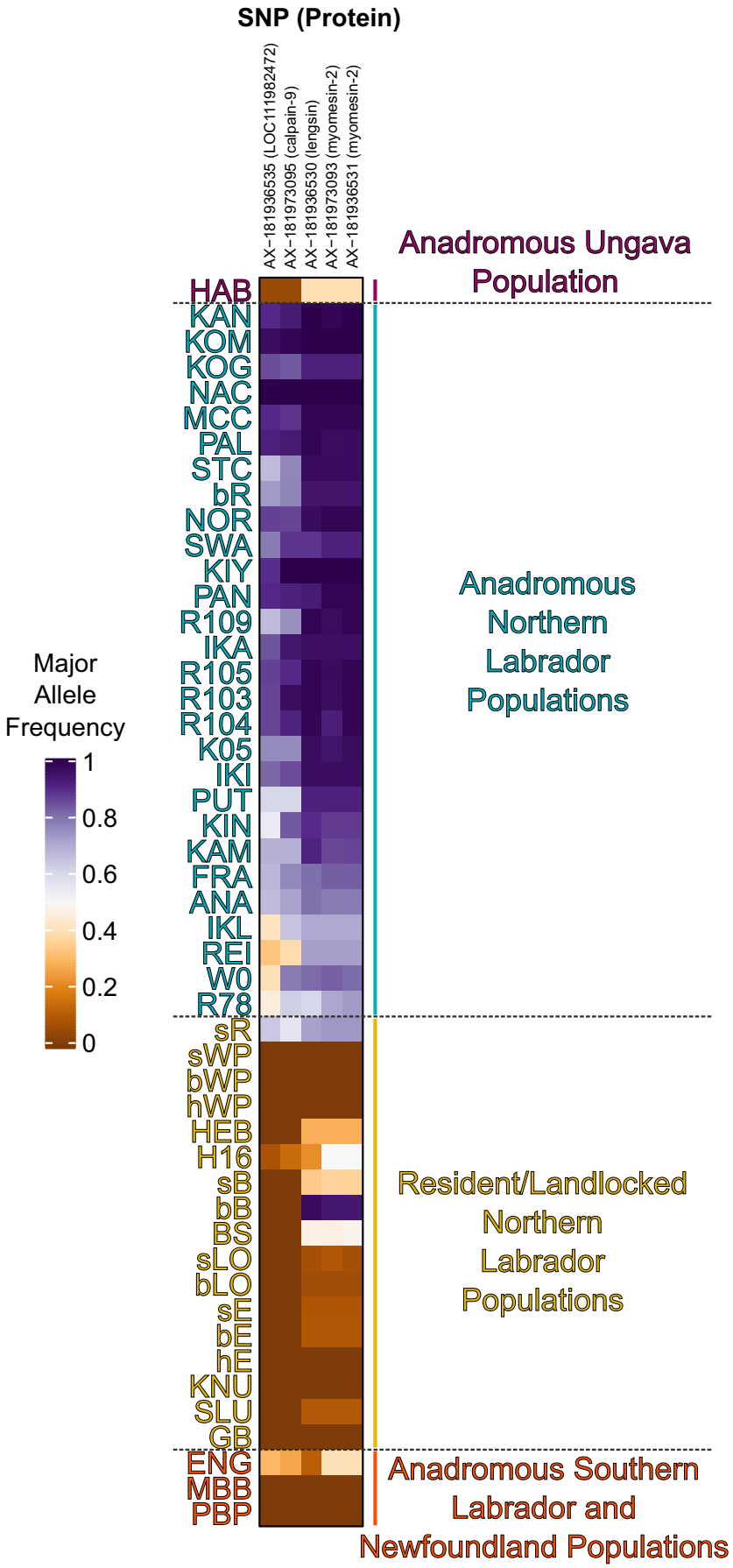

FIGURE 7 Allele frequencies for five SNPs on AC21 with extreme loadings on RDA1 and RDA2 (Figure 6). Populations are clustered by PCA groupings (Figure 2) and ordered from north to south within each cluster.

our results suggest the propensity for genetic drift in landlocked and freshwater resident populations (DeWoody & Avise, 2000; Gyllensten, 1985) as previously observed in Atlantic Salmon (*Salmo salar*, Tonteri et al., 2007), Alewife (*Alosa pseudoharengus*, Palkovacs et al., 2008) and *Galaxias maculatus* (Delgado et al., 2019, 2020, 2023). Such landlocked populations are therefore analogous to island populations (Frankham, 1997) that demonstrate similar reductions in connectivity and increased genetic distinctiveness compared to mainland populations (e.g., von Takach et al., 2022; Wiens et al., 2022).

Given this isolation and anticipated genetic drift, the strong pattern of IBD we observed among resident/landlocked populations was surprising (Hutchison & Templeton, 1999). Because these populations were recently colonized, sufficient time may not have passed for drift to erode a pattern of IBD due to historical connectivity (Bernatchez & Wilson, 1998; Slatkin, 1993). Additionally, variable nDNA introgression between the Arctic and Atlantic lineages latitudinally along Labrador could have also resulted in this pattern. Although mtDNA haplotypes of both lineages are pervasive throughout northern Labrador (Salisbury et al., 2019) this may not reflect nDNA introgression, as there are many examples of mitonuclear discordance in fish where mtDNA but little nDNA has been incorporated from a distantly related lineage (Perea et al., 2016). We suspect that the greatest introgression between these lineages might have occurred in northern Labrador, with reduced introgression of Arctic lineage nDNA southward along the Labrador coast. This would have resulted in more geographically proximate populations having more shared genetic variation, such that even with random fixation of that genetic variation due to drift, such populations would maintain greater genetic similarity than more geographically distant populations. For example, northern populations could fix Arctic alleles which were never present in southern populations, thus maintaining the pattern of IBD despite no ongoing gene flow. Therefore, the pattern of IBD between resident/landlocked populations likely reflects colonization history rather than ongoing/recent gene flow and supports the significant role colonization history can play in shaping contemporary population structure (Ruzzante et al., 2019; Salisbury et al., 2016; Vera-Escalona et al., 2015).

4.2 | Genetic variation among anadromous populations by region

$\hat{H}_E$, $\hat{H}_O$, and $\hat{N}_e$ were generally lower in the three southern anadromous populations than in the northern Labrador anadromous populations. This could reflect selection against anadromy in southern populations (Finstad & Hein, 2012) causing reduced gene flow. Reduced straying in southern populations of anadromous Brook Trout (*Salvelinus fontinalis*) similarly has resulted in lowered genetic diversities (Castric & Bernatchez, 2003).

Colonization history might also explain the correlation in heterozygosity (and to a lesser extent $\hat{N}_{e(NeEstimator)}$) with latitude in anadromous northern Labrador populations. As mentioned above, nDNA from the Arctic lineage may have introgressed more freely in the most northern populations upon secondary contact with the Atlantic lineage, contributing to elevated genetic diversities as similarly observed in several tree species (e.g., Havrdová et al., 2015; Sakaguchi et al., 2011). We cannot rule out though that this cline in diversity was driven by recent increases in N_e in more northern anadromous populations or reduced carrying capacity or reduced gene flow in more southern populations. However, the Ungava population (HAB) exhibited lower genetic diversity than anadromous northern Labrador populations at similar latitudes suggesting that latitude does not solely shape genetic diversity. In addition, unlike northern Labrador anadromous populations, the Ungava population is presumed to have been founded by only the Arctic lineage (Dallaire et al., 2021), which has notably less genetic diversity than other lineages (Moore et al., 2015). Furthermore, a similar decline in genetic diversity with distance from Labrador observed in nearby anadromous Nunavik populations was attributed to reduced introgression of Atlantic lineage nDNA west of Labrador (Dallaire et al., 2021). Our complementary results suggest that reduced introgression of Arctic lineage nDNA into the south of Labrador may have critically reduced the genetic diversity of anadromous charr populations in this region.

4.3 | Historical changes in $\hat{N}_e$

LinkNe results revealed varying patterns of change in effective size across populations over the last 20 generations. Because generation times may differ between migratory and nonmigratory charr (Tallman et al., 1996) and by latitude (Venne & Magnan, 1989) it is difficult to directly compare $\hat{N}_{e(LinkNe)}$ results across populations. In addition, we acknowledge that overlapping confidence intervals for $\hat{N}_{e(LinkNe)}$ across timepoints in some populations temper our observed trends in historical effective population size. Despite these caveats, our results suggest a recent, rapid increase in $\hat{N}_{e(LinkNe)}$ in most anadromous populations as previously observed by Layton et al. (2021) (examining only the 2017 anadromous samples used in this study but not those samples collected from 2010–2015). However, reductions in $\hat{N}_{e(LinkNe)}$ and low $\hat{N}_{e(NeEstimator)}$ for anadromous KIY, ENG, and ANA populations suggest their vulnerability to extinction. This is particularly concerning for the location ANA, Anaktalik, which is harvested as part of the Nain commercial fishery (Dempson et al., 2008). In contrast to anadromous populations, effective sizes for landlocked populations have remained relatively stable through time. This historical fluctuation in $\hat{N}_e$ for anadromous charr populations in this region has been attributed to environment-driven changes in prey abundance (particularly capelin, *Mallotus villosus*) (Côté et al., 2021). The lack of a similar fluctuation in $\hat{N}_e$ in landlocked populations could therefore reflect a more stable freshwater environment or the lack of exposure to a shifting saltwater environment (Reist et al., 2006). The putative resident morph in Ramah lake (sR) is, however, an exception. A sharp recent increase in $\hat{N}_{e(LinkNe)}$ was observed in this morph (Figure S9, Table S2, Supporting Information Appendix S1), which also had an unusually high estimate of contemporary effective

size $\hat{N}_{e(\text{NeEstimator})}$. This could be due to residents occasionally introgressing with sympatric anadromous morphs (though we detected no hybrids between morphs based on ADMIXTURE Q-values in this population, Salisbury et al., 2020) and/or it could also reflect increased carrying capacity for residents fueled by climate change. Indeed, Ramah has demonstrated a noted increase in shrub vegetation since 1985 in comparison to neighbouring watersheds, likey fuelled by local increases in temperature and precipitation (Barrette et al., 2020; Davis et al., 2021). Therefore, while at a coarse scale, effective sizes may have been influenced by colonization, they have also likely been tempered by local environmental conditions.

4.4 | Environmentally associated adaptation

Our RDA further supports the importance of the environment in driving adaptive genetic variation across charr populations. Three variables, annual temperature (BIO1), annual precipitation (BIO12), and mean diurnal range (BIO2) were associated with putative outlier loci. Increased precipitation-induced terrestrial primary productivity has been suggested as a key driver of charr residency (Finstad & Hein, 2012). Several outlier loci were associated with elevation, a factor previously shown to exert strong selective pressure on Arctic charr (Moore et al., 2017) and Coho Salmon populations (Rougemont et al., 2022). Elevation was also the environmental variable in our RDA most strongly associated with the genetic differences between anadromous and resident/landlocked populations within northern Labrador. This is consistent with the fact that populations at higher elevations are more likely to lose their anadromous life history due to greater migratory fitness costs or a greater chance of physical barriers preventing migration (Hendry et al., 2004).

Of the 144 outlier SNPs detected by the RDA, 14 were previously noted to consistently differentiate paired landlocked and anadromous populations of Arctic Charr in Labrador (Salisbury et al., 2022). This included the five SNPs located within a ~150 kbp region of AC21 demonstrating extreme loadings on RDA1 and RDA2 that also associated most strongly with the elevation environmental variable and differentiated resident/landlocked and anadromous northern Labrador populations (Figures 6 and 7). AC21 has also been found to contain many environmentally-associated SNPs in anadromous charr populations across Labrador (Layton et al., 2021). The 5 SNPs in this genomic region were associated with the genes: myomesin-2, lengsin, calpain-9, and uncharacterized protein LOC111982472. Given its association with muscle development (Schoenauer et al., 2008), myomesin-2 is particularly functionally relevant to an anadromous life history (Delgado & Ruzzante, 2020). Additionally, myomesin-1, is upregulated during Atlantic Salmon smoltification (Seear et al., 2010). The striking allele frequency differences between anadromous and independent resident/landlocked populations in northern Labrador (Figure 7) suggests that there has been consistent selection for this genomic region across nonanadromous populations. This is despite the strong genetic drift experienced by landlocked populations due to a contemporary lack of gene flow and also potentially due to historical founder effects. By reducing the effectiveness of consistent selection as well as the shared genetic variation among landlocked populations such genetic drift would have driven the fixation of different alleles in different landlocked populations. The consistent allelic differentiation observed here across all landlocked populations in contrast to this expectation therefore suggests the strong adaptive value of this genomic region. In addition, if the allele frequencies that are contemporarily observed in anadromous populations in this genomic region reflect those of the ancestral anadromous populations that founded these landlocked populations, then the independent selection for the alternative allele in all landlocked populations is strongly suggestive of the potential functional importance of this genomic region for anadromy. Given the young evolutionary age of Labrador populations, we suspect that this putative adaptive variation existed as standing variation in one or more glacial lineages which colonized Labrador (Welch & Jiggins, 2014); however, recurrent mutation in relatively young populations of freshwater sticklebacks is also known to occur (Xie et al., 2019) and could be the case here. The age and origin(s) of this putative adaptive variation are therefore unknown but may be discernable in future by comparing high-coverage sequencing of this region between populations within Labrador and across this species Holarctic distribution.

Regardless of the origin of this allelic variation, it is intriguing that the southern anadromous populations are more similar in this genomic region to resident/landlocked populations than they are to northern Labrador anadromous populations. We suspect that these genetic differences are not due to colonization history differences, as both the southern anadromous populations and the northern Labrador populations have been colonized by the Atlantic and Acadian lineages (Moore et al., 2015; Salisbury et al., 2019). We also suspect some introgression with the Arctic lineage in at least the two southern anadromous populations in Labrador (ENG, MBB) given their close proximity to anadromous populations known to demonstrate Arctic lineage haplotypes (i.e., sites W1, W2, W3). We acknowledge that differential introgression between the three glacial lineages could mean that the genomic basis of anadromy differs between the southern anadromous from the northern anadromous populations. However, the most southerly anadromous populations within northern Labrador (i.e., R78, W0, REI, IKL) (that share the same colonization history as other anadromous populations in this region) also demonstrate the same trend. That is, these populations demonstrate allele frequencies in this genomic region on AC21 more similar to resident/landlocked populations than other northern anadromous populations. We speculate this pattern may reflect a shift to a less anadromous life history with decreasing latitude with implications for local commercial, recreational, and subsistence fisheries for the anadromous morph (Dempson et al., 2008). This is consistent with the loss of anadromy anticipated to occur in this species with rising temperatures due to climate change (Finstad & Hein, 2012; Reist et al., 2006) and earlier work forecasting future genetic shifts to residency in southern anadromous populations in this region (Layton et al., 2021). Large genomic regions have also

previously been associated with anadromy in other salmonids, particularly a double inversion in *Omy05* in Rainbow Trout (Pearse et al., 2019). While the importance of this genomic region in AC21 requires confirmation in an experimental setting and across a wider geographic range of populations, our results suggest it may critically influence anadromy in Arctic Charr.

5 | CONCLUSION

Geographic distance tempered by colonization history, morph type, and local adaptation have influenced the genetic differentiation of Labrador charr populations. The elevated genetic diversities in northern anadromous populations, potentially because of greater glacial lineage introgression in this region, may facilitate a greater capacity to respond to future environmental changes. In contrast, the low genetic diversity observed in southern anadromous charr populations indicate their potential vulnerability. These populations are also most at risk of experiencing rising temperatures and primary productivity driven by climate change which are expected to select against anadromy (Finstad & Hein, 2012; Reist et al., 2006). Our observation that more southerly anadromous populations exhibit allele frequencies similar to landlocked/resident populations on chromosome AC21, a genomic region containing genes functionally related to anadromy, could reflect a genomic shift towards nonanadromy. Further research is needed, however, to investigate this genomic region's mechanistic links to anadromy and the consistency of its association with anadromy across the charr species range.

More broadly, our finding that a confluence of historical and contemporary factors shape genetic structure is unlikely to be unique to the charr populations studied here. In addition to local adaptation and neutral processes such as drift and gene flow, our results add to a growing body of evidence that colonization history can significantly influence contemporary population structure in nuanced ways that may not be immediately apparent without direct knowledge of the colonization history of a given system. This is likely to be particularly true for post-glacial species which are more likely to have been separated into allopatric refugial lineages during glacial periods (Hewitt, 2000) and less likely to have populations in equilibrium (such that historical colonization is more likely to be reflected in contemporary population structure) (Bernatchez & Wilson, 1998; Slatkin, 1993). Our results therefore strongly argue that a more holistic consideration of the interaction of neutral, adaptive, and historical processes underlying observed genetic structure is needed to improve the identification of vulnerable populations and inform management decisions.

AUTHOR CONTRIBUTIONS

Sarah J. Salisbury and Daniel E. Ruzzante designed the study. Sarah J. Salisbury, Robert Perry, Don Keefe, Gregory R. McCracken, Daniel E. Ruzzante, Ian R. Bradbury collected samples. Gregory R. McCracken and Sarah J. Salisbury performed the laboratory work. Sarah J. Salisbury primarily lead the data analysis with assistance from Kara K. Layton, Tony Kess and Ian R. Bradbury. Sarah J. Salisbury primarily wrote the manuscript in collaboration with Daniel E. Ruzzante and with assistance from all coauthors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

A .ped file and corresponding .map file for all samples has been deposited in Dryad and is available at: https://doi.org/10.5061/dryad.wdbrv15sg. Additional metadata including weight, fork length, sex, maturity, and mtDNA D-loop haplotype (as assigned by Salisbury et al., 2019) measured for samples collected between 2010 and 2015 are available in Supporting Information Appendix S2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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