Title: Population structure and genomic evidence for local adaptation to freshwater and marine environments in anadromous Arctic Char (*Salvelinus alpinus*) throughout Nunavik, Canada

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Abstract

Distinguishing neutral and adaptive genetic variation is one of the main challenges in investigating processes shaping population structure in the wild. Despite marine environments being key habitats for the growth of anadromous fishes, landscape genomics studies on salmonids have generally focused on identifying signatures of adaptation to freshwater habitats. Unlike most other anadromous salmonids, Arctic Char (Salvelinus alpinus) occupy coastal habitats near their overwintering rivers during their marine phase, thus making adaptation to marine habitats possible. The aim of this study was to document the neutral and adaptive variation of populations among anadromous Arctic Char in Nunavik and bordering regions. We used GBS to genotype 20,327 filtered single nucleotide polymorphisms (SNPs) for 650 individuals sampled in 23 locations along >2,000 km of coastline. Our results reveal a hierarchical genetic structure, whereby neighboring hydrographic systems harbour distinct populations grouping within major oceanographic basins, namely the Hudson Bay, Hudson Strait, Ungava Bay and Labrador Sea. We found genetic diversity and differentiation to be influenced by both post-glacial recolonization history and by patterns of isolation-by-distance reflecting contemporary gene flow. Furthermore, using three gene-environment association (GEA) methods we found genomic evidence for local adaptation to both freshwater and marine habitats, especially in relation to sea-surface and air temperatures during summer, precipitation, and salinity. This study is among the first to explicitly explore the genetic basis of marine adaptations in salmonids and highlights the complex interactions in selective pressures over the lifespan of anadromous fishes.

Keywords: population genomics, local adaptation, anadromous salmonid, marine ecosystems, Arctic

1. Introduction

Species experience different environmental conditions over their geographic ranges which may lead to local adaptation (Kawecki & Ebert, 2004; Williams, 1966). Local adaptation has been studied extensively via reciprocal transplant and common-garden field experiments, but these approaches do not provide information on the molecular basis of adaptation (Tiffin & Ross-Ibarra, 2014). New genomic methods are now commonly used to advance our understanding of local adaptation (Grummer et al., 2019; Luikart et al., 2018). Such adaptive genomic variation, as well as contemporary population genetic structure, are of great interest for both conservation and management to ensure actions target biologically significant units (Bernatchez et al., 2017; Funk, McKay, Hohenlohe & Allendorf, 2012).

Salmonids are a diverse family of fishes with high economic and cultural importance. Many populations have an anadromous life cycle, whereby individuals are born and reproduce in freshwater and migrate to the sea to feed and grow. Anadromous salmonids exhibit a homing behaviour, i.e. returning to their natal habitat for spawning (Quinn, 1993) and this behaviour reduces gene flow between populations, promoting genetic differentiation and local adaptation at fine spatial scales (Fraser, Weir, Bernatchez, Hansen & Taylor, 2011). Recent studies have identified genomic regions associated with many environmental parameters, including air temperature (Bourret, Dionne, Kent, Lien & Bernatchez, 2013; Hand et al., 2016; Perrier, Ferchaud, Sirois, Thibault & Bernatchez, 2017; Sylvester et al., 2018), precipitation (Hecht, Matala, Hess & Narum, 2015; Micheletti, Matala, Matala & Narum, 2018), geology (Bourret et al. 2013), upstream catchment area (Pritchard et al., 2018) and migration distances (Hecht et al., 2015; Micheletti et al., 2018) in many species of salmon and trout.

On the other hand, little is known about the genomic basis of marine adaptations for these species despite the fact that they spend a significant proportion of their lives at sea. The capacity to identify divergent selective pressures on salmonid populations at sea is limited by their use of geographically extensive and shared offshore feeding grounds (Hecht et al., 2015; Quinn, 2005). However, other studies have shown populations of salmonids consistently occupying different marine distribution ranges that could be genetically determined (Fraser et al., 2011; Kallio-Nyberg et al., 2000). Moreover, sea surface temperature (SST) and salinity have been argued to be associated to adaptive genetic diversity in cold-water marine fishes (Atlantic Cod *Gadus morhua*: Barth et al., 2017; Atlantic Herring *Clupea harengus*: Guo, Li & Merilä, 2016; Three-spined stickleback *Gasterosteus aculeatus*: Guo, DeFaveri, Sotelo, Nair & Merilä, 2015), reinforcing the possible importance of marine habitats to local adaptation.

The Arctic Char (*Salvelinus alpinus*) is a salmonid fish with a circumpolar distribution and is known for its great diversity in life-history characteristics (Klemetsen, 2010). Anadromous individuals spend 3 to 9 years in cold oligotrophic freshwater at birth (Johnson, 1980), then complete annual migrations between marine habitats for summer foraging and lakes for overwintering. Although straying (i.e., an upstream migration in a non-natal river system) can occur, several studies have shown that Arctic Char maintained philopatric behaviour during reproductive years, limiting effective dispersal (Gyselman, 1994; Moore, Harris, Tallman & Taylor, 2013; Moore et al. 2017). Moore et al. (2013) also argued that gene flow could be sufficiently low to allow for local adaptation among populations of eastern Baffin Island in the Canadian Arctic, while Moore et al. (2017) provided some genomic evidence for local adaptation to natal rivers at a fine spatial scale.

In marine environments, Arctic Char tend to stay near the surface (< 3m), with occasional dives up to 50m (Harris et al. 2020; Spares, Stokesbury, O'Dor & Dick, 2012) and preferably use nearshore habitats within 100 km from their natal river's mouth (Dempson & Kristofferson, 1987; Layton et al., 2020; Moore et al. 2016). Thus, one could expect this behaviour to lead to Arctic Char populations experiencing more diverse marine conditions than other anadromous species. Madsen et al. (2019), for example, found that variation at a phenology-related locus among anadromous Greenlandic populations of Arctic Char was associated with the duration of the period spent foraging at sea, suggesting local adaptation to temperature regimes.

During the last glacial maximum (LGM), around 21,000 years ago, most of modern-day Canada was covered by glaciers (Dyke, 2004), contracting species' ranges to ice-free glacial refugia. For most extant species in North America, contemporary intraspecific diversity was heavily impacted by post-glacial recolonization (Hewitt, 2000). Potentially strong demographic bottlenecks during glaciations has greatly reduced intraspecific genetic diversity and lead to divergent glacial lineages that survived in different refugia (Hewitt, 2000). For example, it is documented that glaciations have had an important impact on fish lineages and their genetic diversity (April et al. 2013; Bernatchez & Wilson, 1998). In addition, secondary contact between intraspecific glacial lineages have been shown to have commonly occurred among temperate freshwater fishes (e.g. Atlantic Salmon *Salmo salar*: Bradbury et al., 2015; Lake Cisco *Coregonus artedi*: Turgeon & Bernatchez, 2001; Lake Whitefish *Coregonus clupeaformis*: Bernatchez & Dodson 1990)

The contemporary distribution of Arctic Char closely matches the Weichsel-Winsconsin glaciation extent (Klemetsen et al., 2003). In North America, Arctic Char comprises four known

105 mitochondrial DNA (mtDNA) lineages associated with distinct glacial refugia (Brunner, Douglas,
106 Osinov, Wilson & Bernatchez, 2001; Moore, Bajno, Reist & Taylor, 2015). Nunavik, situated in
107 northern Québec (Canada), is one of the last regions in North America to have deglaciated
108 following LGM (Dyke, 2004). It is bordered by the Hudson Bay, Hudson Strait, and Ungava Bay.
109 These three marine regions are contrasted in their surface temperature, salinity, productivity and
110 tidal regimes (Prisenberg, 1984; Savard et al., 2014). The Arctic and Atlantic mitochondrial
111 lineages are predominant in Nunavik and bordering regions (Brunner et al., 2001, Moore et al.,
112 2015). The exact extent of secondary contact between those two lineages is still poorly
113 understood, but Salisbury, McCrakcen, Keefe, Perry and Ruzzante (2019) recently reported fully
114 admixed populations across northern Labrador.

115 The current study applies population genomic methods in order to investigate the relative
116 role of neutral (demographical and historical) vs. adaptative processes in shaping contemporary
117 population structure of anadromous Arctic Char over 3,000 km of coastline in Nunavik, Québec,
118 Canada. Specifically, we first document its neutral genetic structure in relation to post-glacial
119 history by i) delimiting putative populations via a clustering analysis, ii) comparing levels of
120 genetic diversity between geographic regions, and iii) investigating patterns of isolation-by-
121 distance and the importance of potential barriers to migration. Second, since we expected broad-
122 scale variation in both freshwater and marine environments to be the source of divergent
123 selective pressures, we attempt to detect evidence of local adaptation in Arctic Char around
124 Nunavik and bordering regions. We extracted various environmental variables representing the
125 different habitats occupied by Arctic Char to determine i) if marine and freshwater conditions

126 both explained significant proportions of the observed genetic variation, and ii) whether
127 candidate SNPs associated with environmental factors in both habitats could be identified.

128 ## 2. Methods

129 ### 2.1 Sampling

130 Arctic Chars were sampled in 23 water bodies across Nunavik, Southern Baffin Island, and
131 Labrador (Figure 1). In Nunavik and Baffin Island, adult fish were harvested during their upstream
132 migration using gillnets or counting weirs. In most localities throughout Nunavik, sampling
133 locations were selected in concert with local and regional Inuit wildlife managers, and sampling
134 was done with the assistance of local Inuit guides, in order to prioritize fish populations with an
135 importance for traditional fishing. In two locations (Deception Bay and Hopes Advance Bay),
136 samples were taken in the estuary as well as in two tributary rivers. Juvenile fish were captured
137 by electrofishing in two rivers near Nain, Labrador. Adipose fin clips were collected from each
138 fish and preserved in ethanol 95%.

139 ### 2.2 Library preparation, sequencing and SNP calling

140 DNA was extracted from fin clips using a modified version of Aljanabi & Martinez (1997).
141 Agarose gel electrophoresis was used to assess DNA quality and the quantity and quality of DNA
142 was evaluated by NanoDrop spectrophotometer (Thermo Scientific). Ten (10) µl of DNA samples
143 were normalized to a concentration of 10 ng/µl using Quant-iT Picogreen dsDNA Assay Kit
144 (Invitrogen) for precision quantification. Genotyping-by-sequencing (GBS) libraries were
145 prepared with a modified version of the Abed et al. (2019) two-enzyme GBS protocol, using *Pst*I
146 and *Msp*I restriction enzymes. Samples were randomly assigned to libraries to limit batch effects.

147 Sequencing was done on Ion Torrent p1v3 chips with a median target of 80 million single-end
148 reads per chip. Each library was sequenced on 3 separate chips, and the volume of DNA from
149 each sample was adjusted after the first chip to reduce the unbalanced representation of
150 individuals in sequences.

151 We processed the data and filtered the SNP dataset using a RADseq workflow
152 (https://github.com/enormandeau/stacks_workflow) built around STACKS2 (Rochette, Rivera-
153 Colón & Catchen, 2019). In short, the sequences were trimmed at 80 base pairs and aligned on
154 the Arctic Char reference genome (ASM291031v2; NCBI RefSeq: GCF_002910315.2; Christensen
155 et al., 2018) using Burrows-Wheeler Aligner (BWA; Li & Durbin, 2009). SNPs were called on
156 polymorphic genotypes with at least 4X coverage, present in at least 60% of samples of all
157 sampling sites and with the minor allele present in a minimum of 3 samples. Samples with more
158 than 20% of missing data or with heterozygosity (F_{IS}) under -0.2 were removed.

159 Salmonid fishes have a common ancestor that experienced a whole-genome duplication
160 approximately 60 MYA (Crête-Lafrenière, Weir & Bernatchez, 2012), and many genetic markers
161 identified in our analyses are expected to be situated on paralogous loci of similar sequences.
162 While these loci may be important for adaptation (Kondrashov, 2012), they were removed due
163 to the fact that these markers do not behave like bi-allelic SNPs and because genotyping is
164 difficult without very high coverage (>100 reads; Dufresne, Stift, Vergilino & Mable, 2014). SNPs
165 on duplicated loci were categorized and filtered using an adapted *HDplot* procedure (McKinney,
166 Waples, Seeb & Seeb, 2017), which identifies paralogs by visually comparing the allelic ratio, the
167 proportion of heterozygotes and homozygotes of the rare allele, and the F_{IS} value for each SNP.
168 We also filtered the markers to avoid linked SNPs while keeping a maximum of information: for

169 each pair of SNPs on the same locus, we assessed linkage considering samples without missing
170 data where at least one of the two genotypes contains the rare variant. If the two markers have
171 identical genotypes in more than 50% of these samples, the pair were considered linked and only
172 the first SNP was kept.

173 ## 2.3 Identification of putative neutral markers

174 Markers potentially under selection were identified using two methods: pcadapt (Luu,
175 Bazin & Blum, 2017) and Baypass (Gautier, 2015). SNPs identified as outliers by at least one
176 method were removed to produce a putatively neutral dataset. The R package pcadapt identifies
177 outlier SNPs in relation to population structure using principal components analyses (PCA). The
178 first 11 PCs were used, based on visual evaluation of PCA scores and scree plots, and SNPs with
179 minor allele frequencies under 0.05 were ignored, as recommended by pcadapt authors. The
180 core model implemented in Baypass v 2.1 computes a differentiation measure called XtX, which
181 is an analog to an SNP-specific FST corrected for the allele frequency covariance between
182 populations (Günther & Coop, 2013). The threshold to distinguish neutral from potentially
183 selected markers was set as the 5th (balancing selection) and 95th (divergent selection)
184 percentile of the XtX distribution obtained by running the core model on a pseudo-observed SNP
185 dataset produced following the Baypass manual. Briefly, this 100,000-SNPs dataset was
186 simulated with the function simulate.baypass, which allows for the inclusion of the allele
187 frequency covariance matrix of our original dataset in order to emulate its demographic history.

188 ## 2.4 Basic statistics and population structure

189 Population genetic statistics were computed from the putatively neutral dataset.
190 Observed and expected heterozygosity were calculated by population using GenoDive v3.0
191 (Meirmans & Van Tienderen, 2004). We used vcftools v0.1.13 (Danecek et al., 2011) to measure
192 the proportion of heterozygous SNPs for each individual, and we calculated the number of
193 polymorphic SNPs in each population. Effective population sizes (N_e) and 95% confidence
194 intervals were estimated with Neestimator v2.01 (Do et al., 2014) using the linkage disequilibrium
195 method on markers with minor allele frequencies over 0.05.

196 Spatial patterns of genetic diversity were compared between putative regions, using the
197 individual proportion of heterozygous SNPs. A nested ANOVA was performed with the regions as
198 groups and the non-estuarine sampling sites as subgroups. To account for our unbalanced
199 sampling design, we did a comparison of estimated marginal means (or least-square means) with
200 the Satterthwaite approximation of degrees of freedom (Satterthwaite, 1946) on a linear mixed-
201 effect model with a random effect of the sampling site, in the R packages *lme4* (Bates, Mächler,
202 Bolker & Walker, 2015) and *emmeans* (Lenth, 2019).

203 We used a principal coordinate analysis (PCoA) in the R package *dartR* (Gruber, Unmack,
204 Berry & Georges, 2018) to document population structure using the neutral data set. We also
205 estimated ancestry with the maximum likelihood approach implemented in ADMIXTURE
206 (Alexander, Novembre & Lange, 2009) with the number of genetic clusters (K) ranging from 1 to
207 20. To mitigate the effects of imbalance in sample size among geographical regions, only non-
208 estuarine sampling sites were included in the global ADMIXTURE analysis. We considered the
209 value of K yielding the lowest cross-validation error to be the number of genetic groups best

210 supported by ADMIXTURE. Based on this K value, we identified contiguous sampling sites where
211 most individuals shared a common cluster membership and repeated the ADMIXTURE analysis
212 within those sites with K ranging from 1 to 6. Estuarine sampling sites were included in this
213 second round of analyses.

214 ## 2.5 Landscape genetics

215 Pairwise population F_{ST} were calculated with the R package *StAMPP* (Pembleton et al.,
216 2013), and a 1000-permutations bootstrap estimated their significance value. F_{ST} calculations
217 were performed on both the complete and neutral datasets. The geographic marine distance
218 separating populations was measured between the coordinates at the mouth of sampled rivers
219 by a least-cost path in the R package *marmap* (Simon-Bouhet, 2013), using NOAA bathymetric
220 data at a 4-minutes resolution to discriminate land and sea.

221 We tested for the presence of isolation-by-distance (IBD) with a linear mixed-effect
222 model. Linearized F_{ST} ($F_{ST}/(1-F_{ST})$), based on the neutral dataset, was used as the dependent
223 variable and marine distance as a fixed effect. Patterns of IBD between pairs of populations on
224 the same coast versus pairs on either side of Hudson Strait were compared by the inclusion of a
225 categorical fixed effect. To characterize the impact of Hudson Strait as a barrier to gene flow both
226 locally and globally, analyses were performed on all non-estuarine sites, then only on non-
227 estuarine sites within 250 km of the Hudson Strait. To account for the non-independence of
228 pairwise distances, the model was run with a maximum likelihood population effect
229 parameterization (MLPE) (Clarke, Rothery & Raybould, 2002) with and without restricted
230 maximum likelihood (REML), using the MLPE.lmm function in the R package *ResistanceGA*
231 (Peterman, 2018). Models without REML were compared with conditional Akaike Information

232 Criterion (cAIC; Vaida & Blanchard, 2005) in the R package *cAIC4* (Säefken, Ruegamer, Baumann
233 & Kruse, 2019), and with marginal R^2 (Nakagawa & Schielzeth, 2013) in the R package *MuMIn*
234 (Barton, 2019) for models with REML.

235 ## 2.6 Gene-environment association

236 We used the ArcGIS software v10.4 (ESRI, 2011) to extract environmental data from BIO-
237 Oracle v2.0 (Assis et al., 2018), Marspec (Sbrocco & Barber, 2013), and WorldClim v2.0 (Fick &
238 Hijmans, 2017) (Table 1). Tide data were obtained from FES2014, produced by Noveltis, Legos
239 and CLS and distributed by Aviso+, with support from Cnes (https://www.aviso.altimetry.fr/).
240 Marine variables represent sea-surface values for factors of potential biological importance for
241 Arctic Char and were aggregated in a 20 km radius around each river mouth and within 5 km from
242 the coast, as to best represent the local coastal environment based on existing knowledge of
243 Arctic Char marine habitat use from other geographical regions (Spares, Stokesbury, Dadswell,
244 O'Dor & Dick, 2015; Moore et al., 2016). Freshwater variables comprise the area of the watershed
245 upstream of the sampling site, as well as air temperature and precipitation statistics on these
246 areas. Air temperature is commonly used as a proxy for freshwater temperature in remote areas
247 where, as supported by studies linking the growth rate of Lake Trout to air temperature (Black,
248 von Biela, Zimmerman & Brown, 2013; Torvinen, 2017).

249 To deal with co-linearity, a PCA was performed on each set of environmental factors, and
250 the PCs explaining more than 10% of the total variance were used as explanatory variables in
251 gene-environment association (GEA) analyses. Candidate SNPs associated with environmental
252 variables were identified with a combination of three methods: RDA, LFMM, and Baypass. Genes
253 within 10,000 base pairs were recorded using bedtools (Quinlan, 2014) for candidate SNPs

254 identified by at least 2 methods. We consulted the UniProt database (The Uniprot Consortium,
255 2019) for information on biological gene function in Atlantic Salmon, Zebrafish (*Danio rerio*), or
256 other organisms.

257 *2.6.1 RDA*

258 We used a redundancy analysis (RDA, Legendre & Gallagher, 2001), a form of constrained
259 ordination, implemented in R package *vegan* (Oksanen et al., 2012) to investigate multivariate
260 correlations of genotypes (in the form of allele frequencies by population) with environmental
261 variables. We took into account structure in the data which derives from spatial patterns with a
262 distance-based Moran's eigenvector map (dbMEM; Borcard & Legendre, 2002; Peres-Neot &
263 Legendre, 2010). In order to build this map, we transformed pairwise marine distances measured
264 in the section above in Euclidian distances by creating a Delaunay graph with the function
265 chooseCN in the R package *adegenet* (Jombart, 2008). We then used the R package *adespatial*
266 (Dray et al., 2016) to make the dbMEM. Eigenvector reflecting positive spatial autocorrelation
267 and not correlated with environmental dimensions were used as covariables in a partial RDA.
268 Significant spatial eigenvectors uncorrelated with environmental factors were included for these
269 analyses, as suggested by Forester, Lasky, Wagner and Urban (2018).

270 Spatial and environmental factors were separately submitted to a backward model
271 selection with the function ordistep in the R package *vegan*, and only significant ($p < 0.05$)
272 covariables were included in the final RDA. Proportions of genetic variance explained solely or
273 jointly by each set of covariables were estimated by comparing adjusted R^2 in a series of partial
274 RDAs (Peres-Neto & Legendre, 2010), of which we assessed significance using an ANOVA-like

275 permutation test with 1000 steps. Z-scores were obtained for the distribution of individual SNP
276 loadings on RDA axes explaining a significant portion of genetic variation ($p < 0.05$), and SNPs
277 were defined as outliers if their absolute maximal Z-score was over 2.5 ($p < 0.012$).

278 *2.6.2 LFMM*

279 Latent factor mixed models (LFMM; Frichot, Schoville, Bouchard & François, 2013)
280 determine loci-environment associations using a Bayesian mixed-model with environmental
281 variables as fixed effects. Latent factors are derived from a principal components analysis and
282 used as random effects to control for population structure. Missing data in the genetic dataset
283 were imputed based on the most frequent genotype in the sampling site and we used the
284 lfmm_ridge function of the R package *lfmm* (Caye, Jumentier, Lepeule & François, 2019). The
285 optimal number of latent factors (K-value) and regularization parameters (lambda) were chosen
286 to minimize predictor error by using a cross-validation method as advised in the *lfmm* manual. P-
287 values were calibrated using the genomic control method and false discovery rate (q-value) was
288 calculated following the Benjamini-Hochberg procedure in the *qvalue* R package. Associations
289 between a SNP and environmental factor with q-value < 0.05 were considered significant.

290 *2.6.3 Baypass*

291 The standard covariate (STD) model implemented in Baypass assesses associations
292 between allele counts and population-specific covariates using Bayesian Factors (BFs) (Gauthier
293 2015). We estimated BFs by calculating the median of 5 runs of the STD model with the
294 importance sampling algorithm (Coop et al., 2010). We controlled for the neutral population
295 structure by providing the omega matrix computed by the core model implemented in Baypass.

296 Pairs of markers and covariates with a BF > 10 decibans (dB) had strong evidence for their
297 association (Jeffreys, 1961, revised by Lee & Wagenmakers, 2013).

298 # 3. Results

299 We sequenced a total of 864 samples, of which 95 did not pass our filtering criteria. We
300 discarded 3 sampling sites (119 individuals) that either had too few samples, had no access to
301 sea, or targeted a population reintroduced from a hatchery brood. Retained individuals (n = 650)
302 had 2.217 million reads on average. A total of 31,535 SNPs was called and passed basic filtering
303 in STACK2. Among these, 7,244 SNPs were categorized as duplicates and removed (Figure S1) and
304 3,130 SNPs were pruned during linkage disequilibrium assessment. The final dataset used in
305 subsequent analyses comprised 20,327 SNPs (see Table S1 for exact criteria and number of
306 filtered SNPs), with a global 7.02% missing genotypes. The core model in Baypass identified 857
307 SNPs under balancing selection (XtX < 17.95), 643 SNPs under divergent selection (XtX > 28.02),
308 and pcadapt marked 198 SNPs as outliers (q-value < 0.05), for a total of 1,698 markers identified
309 as putatively adaptive by at least one method. The remaining 18,703 SNP markers were
310 considered as putatively neutral.

311 ## 3.1 Population structure

312 Population statistics are presented in Table 2. N_e ranged from 61.9 to 734.5 and was
313 correlated with catchment area (30 – 43,496 km^2, log-transformed, r = 0.43, p = 0.0499), but the
314 Payne River (PAY) had among the lowest N_e value (96.0) despite having the largest catchment
315 area. The first axis of the PCoA reflected the longitude of the sampling sites, while the second
316 axis differentiated populations in Western Ungava Bay from all other sampling sites (Figure 2).

317 Genetic diversity (H_e) and mean proportion of heterozygous markers in individuals were highly
318 correlated (r = 0.90) and varied regionally (Figure 3). Notably, southern Hudson Bay displayed the
319 lowest observed proportion of heterozygous markers, and both southern and northern Hudson
320 Bay had lower values than Hudson Strait (a = 0.05). In Ungava Bay, eastern sampling sites had a
321 diversity similar to Labrador, and higher diversity than western sampling sites. Mean individual
322 proportion of heterozygous markers was also correlated with number of polymorphic SNPs (r =
323 0.78) at sampling site, but not to N_e (r = 0.16, p = 0.46).

324 The number of genetic clusters best supported by an ADMIXTURE analysis with all non-
325 estuarine sampling sites was 13 (Figure S2 for comparison of cross-validation errors). At this level,
326 individuals within a sampling site were generally homogenous in their membership to clusters
327 (Figure 4). Sampling sites sharing a similar membership to clusters included sites in Labrador, two
328 groups of 3 sampling sites in Northern and Southern Hudson Bay, and all pairs of rivers with a
329 common estuary except the Leaf (FEU) and Bérard (BER) rivers. ADMIXTURE best supported K =
330 1 within those groups, but cross-validation errors for K = 2 were in some cases only slightly higher
331 (Table S2), which hints at weak population structure at a local scale. Individual cluster
332 membership for K = 2 and K = 3 was then only loosely linked to the sampling site, except in
333 Labrador sites, where samples were collected as juveniles.

334 ## 3.2 Landscape genetics

335 F_{ST} calculated by pairs of sampling sites ranged between -0.002 and 0.329 (Table S3). All
336 p-values for comparisons with neutral loci were < 0.001, except for a pair of sampling sites on
337 rivers sharing an estuary ($p_{CHR\text{-}VOL}$ = 0.568) and some pairs of sampling sites on a river and its

338 estuary ($p_{BDE-FRM}$ = 0.015; $p_{BDE-DUQ}$ = 0.003). These results suggest that all unlinked systems likely
339 harbour genetically distinct populations, although the extent of differentiation is highly variable.

340 When examining IBD over all populations, a positive correlation was found between
341 linearized F_{ST} and marine distances (Table 3), but the inclusion of the effect of crossing the
342 Hudson Bay (CROSSHS) did not improve the model, based on marginal R^2. However, similar
343 analyses focusing on sampling sites within 250 km of the Hudson Strait showed higher linearized
344 F_{ST} in pairs of populations on either side of the Hudson Strait than in pairs on the same coast
345 (Figure 5).

346 ## 3.3 Gene-Environment association

347 Freshwater and marine environmental factors were each summarized with 3 PC axes
348 (Table 2), and correlation coefficients between components of either environment ranged
349 between 0.05 and 0.62 (Figure S4). The distance-based Moran's eigenvector map produced 12
350 eigenvectors reflecting negative autocorrelation and 4 eigenvectors for positive autocorrelation
351 (MEM1 – 4, see Figure S5). Model selection for the RDA excluded MEM3 (p = 0.12), MEM4 (p =
352 0.32), as well as the third freshwater component (F3, p = 0.07). All three sets of covariables
353 (spatial, marine and freshwater) explained a significant component ($p < 0.05$) of the genetic
354 variation, with 17.0% explained exclusively by one set, 14.9% jointly by two sets, and 6.7% by all
355 three sets (Figure 6A).

356 MEM1 was highly correlated with the first marine components (M1, r = -0.94) and MEM2
357 was linked to the first freshwater component (F1, r = 0.81). Thus, no spatial covariable was
358 included in the RDA for the identification of candidate SNPs associated with the environment.

359 The three first axes of the RDA comprised a total of 41.5% of the explained variance (adj R^2 =
360 0.36, Figure 6B-E). No outliers (Z > 2.5) were identified on RDA1, but genetic markers detected
361 on RDA2 were most correlated with either M1 (n = 53) or F1 (n = 4), while markers on RDA3 were
362 most correlated with F2 (n = 79) or M2 (n = 17).

363 LFMM identified a total of 228 outlier SNPs (q < 0.05), 122 of which were associated with
364 at least one marine component and 119 with a freshwater component. A total of 22 SNPs was
365 significantly associated with more than one environmental component. The IS model under
366 Baypass identified 185 SNPs (BF > 10 dB). Of these, 113 being associated with a marine variable,
367 77 with a freshwater variable, and only 5 linked to both M2 and F2 (Figure S6).

368 Of the markers considered, 52 were identified as associated with an environmental factor
369 by at least two GEA methods (Figure 7). Of those markers, 23 were related to M1 (summer SST,
370 tides, turbidity), 18 were related to F2 (summer air temperature), and 3 were associated with
371 different environmental components depending on the method. We identified a total of 51
372 named genes within 10,000 base pairs of candidate SNPs, covering a wide range of biological
373 functions. Among those were genes related to immune response (3.5% of genes), development
374 of the nervous system (7.1%), heart (5.3%) and skeletal muscle (3.5%), as well as processes
375 affecting gene expression (Table S5).

376 4. Discussion

377 Anadromous salmonids have recently been the subject of many studies in landscape
378 genomics, as these provide key information for their conservation and management. We
379 document patterns of neutral and adaptive genetic variation in anadromous Arctic Char

380 populations in the Nunavik region using genomic data. This is the broadest assessment of
381 genomic variation in this important species to date. By combining fine- and broad-scale sampling,
382 we clearly reveal a hierarchical genetic structure. Neighboring hydrographic systems generally
383 harbor distinct populations that can be regrouped within oceanographic basins, while
384 differentiation was also influenced by isolation-by-distance. To assess the potential for local
385 adaptation to the contrasted environments in our study area, we combined three gene-
386 environment association (GEA) methods. We found genomic evidence for local adaptation to
387 both freshwater and marine habitats, a novel finding given that studies of local adaptation in
388 salmonids usually focus solely on freshwater habitat characteristics

389 ## 4.1 Neutral structure in a post-glacial context

390 The entire area surveyed in this study was covered by ice from the last glacial maximum
391 up to approximately 9,000-11,000 years ago (Dyke, 2004). Arctic Char are thought to have rapidly
392 recolonized habitats following the retreat of the glaciers (Power, Pope & Goad, 1973; Hammar,
393 1987) and have relatively long generation time (Gulseth & Nilssen, 2001). We thus expected the
394 contemporary neutral genetic structure of Arctic Char populations in Nunavik to be heavily
395 influenced by their recent post-glacial recolonization history.

396 Here, fish from the western Arctic glacial refugium would have crossed the Canadian
397 Arctic Archipelago from west to east through the Lancaster Sound, which broke free of ice around
398 9,000 years ago (Dyke, 2004), then by following the eastern coast of Baffin Island (Brunner et al.,
399 2001; Moore et al., 2015). Access to Nunavik via Foxe Basin would have been impossible until
400 less than 6,500 years ago. Fish from the Atlantic lineage, which we expect to have crossed the
401 Atlantic Ocean from the Palearctic during the last deglaciation (Brunner et al., 2001; Wilson,

402 Hebert, Reist & Dempson, 1996), could have been present in southern Labrador and
403 Newfoundland over 10,000 YBP (Dyke, 2004). Salisbury et al. (2019), through analysis of
404 mitochondrial DNA, showed an overlap of the Arctic and Atlantic lineages in Northern Labrador
405 (55 – 59° latitude), and an absence of correlation between latitude and lineage prevalence
406 suggests a complete introgression of fish from the Arctic and Atlantic lineage origins in the region.
407 While our results do not inform on the extent of the secondary contact between lineages,
408 admixture in the eastern part of our study area could explain the higher genetic diversity, as
409 expected during secondary contact of marine fishes (Bay & Caley, 2011; Grant & Bowen, 1998)

410 By 8,000 YBP, most of Hudson Strait and most of the coast of Labrador were free of ice
411 while most of the Hudson Bay and the Ungava Bay remained glaciated. Finally, by 6,500 – 7,200
412 YBP, the coasts of Hudson Bay and Ungava Bay deglaciated, meaning those regions would be the
413 last to have been colonized by Arctic Char. The loss of genetic diversity we observed along the
414 coast from Hudson Strait to southern Hudson Bay, as well as low F_{ST} values between populations
415 within the Hudson Bay region, are consistent with expectations of a recent range expansion,
416 perhaps associated with successive founder effects and loss of heterozygosity (Eckert, Samis &
417 Lougheed, 2008; Goodsman, Cooke, Coltman & Lewis, 2014). Similar patterns were found in
418 European lamprey species (*Lampetra* spp.), with diversity and differentiation decreasing in
419 populations far from the Iberic glacial refugia (Mateus et al., 2018), and in Scottish populations
420 of Atlantic Salmon, where genetic diversity was lower in more recently deglaciated regions
421 (Cauwelier et al., 2018).

422 4.2 Contemporary gene flow

423 Our results revealed a hierarchical genetic structure with most geographic regions
424 containing distinct populations of Arctic Char in every sampled river not sharing an estuary.
425 However, population structure in Hudson Bay appeared weaker, as there were signs of admixture
426 between rivers within 100 km. As discussed earlier, other studies on Arctic Char have attributed
427 low genetic differentiation over long distances to recent post-glaciation colonization events
428 (Moore et al., 2013; O'Malley et al., 2019). However, lower salinity and a longer summer period
429 in Hudson Bay could also lead to higher connectivity between estuaries.

430 As migration in Arctic Char has been found to be predominantly coastal (Moore, 1975;
431 Moore et al., 2013, 2015; Spares et al., 2012), we expected the Hudson Strait, a 120-km wide
432 open water area, to restrict gene flow between populations on opposite shores. However, those
433 pairs of populations only deviated from IBD patterns when we restricted analyses to sampling
434 sites around the Hudson Strait area. In other words, the effect of Hudson Strait as a barrier to
435 gene flow could only be observed at a regional scale. Differentiation between populations
436 separated by the Hudson Strait was lower than, for example, pairwise F_{ST} between populations
437 in western and eastern Ungava Bay, despite those populations being connected by a near-shore
438 migration route. We cannot exclude the possibility of other barriers to gene flow in our study
439 area, as inhospitable coastal habitats have been found to act as barriers to migration along the
440 shore in anadromous Brown Trout (*Salmo trutta;* Quéméré et al., 2015). Alternatively,
441 differentiation in the Ungava Bay could be also be driven by the admixture of the Arctic and
442 Atlantic lineages in the eastern sampling sites (Moore et al., 2015; Salisbury et al. 2019), while
443 populations on either side of Hudson Strait could share ancestral polymorphism rather than

444 exhibit contemporary gene flow. In this way, our results hint again at the relative importance of
445 glacial lineages over contemporary restrictions to gene flow in this recently recolonized area.

446 Arctic Char is known for its higher straying rates than other salmonids, but many studies
447 argue that this dispersal does not necessarily lead to gene flow, as individuals are more prone to
448 straying when overwintering than when breeding (Moore et al., 2013; Moore et al. 2017; Sévigny,
449 Harris, Normandeau, Cayuela, Gilbert & Moore, in prep). This case of reproductive isolation with
450 migration could explain our clustering results for some pairs of sites sharing an estuary. In
451 sampling sites around Deception Bay (BDE) and Hopes Advance Bay (HAB), individuals with a high
452 probability of membership to two subgroups were independently distributed in tributary rivers.
453 As expected, this was not the case with the pair of sampling sites in Labrador, where individuals
454 were sampled at a juvenile stage and did not have the chance to stray yet. In another more
455 surprising case, there was no signs of adult dispersers between the Leaf River (FEU) and the
456 Bérard River (BER), which also share an estuary. Interestingly, those two rivers are on either side
457 of the limit of two major geological provinces (Thériaut & Beauséjour, 2012). The Leaf River, in
458 the Superior Province, sits on plutonic rocks of the Neoarchean era (2,800 to 2,500 million years
459 BP), while the Bérard River, in the Churchill Province, sits on the sedimentary, volcanic, and more
460 ferrous rocks of the Labrador Trough, dated to the Paleoproterozoic (2,500 to 1,600 millions
461 years BP). As salmonids are thought to use their olfaction to recognize their natal rivers (Keefer
462 & Caudill, 2014), the distinct geologies of the Leaf and Bérard systems could limit straying.
463 Outside this specific case, our results highlight the limitations for assessing fine-scale Arctic Char
464 population structure when sampling non-breeding adults.

465 ## 4.3 Genomic evidence for local adaptation

466 We explored how genetic variation in Arctic Char was linked to a range of climatic and
467 physical environmental predictors in both marine and freshwater habitats, something that has
468 rarely been done in salmonids. Through a constrained ordination, we found that environmental
469 variables in both habitats independently explained significant proportions of the genetic
470 variation, even when correcting for spatial patterns expected to be linked to neutral variation.
471 While different GEA methods identified candidate SNPs with every environmental component
472 considered, we found that the best-supported candidates were mainly associated with the
473 components reflecting summer SST, tides, and turbidity (M1), as well as air temperature during
474 summer (F2).

475 Several studies have found temperature to be a driver of genetic structure and local
476 adaptation in salmonids, with most studies focusing on freshwater temperatures (Dionne et al.,
477 2008; Bourret et al., 2013; Perrier et al. 2017; Silvester et al. 2018). However, SST near the mouth
478 of spawning river was found to be correlated with migration time in species of Pacific salmon
479 (Kovach, Ellison, Pyare & Tallmon, 2015) and to phenology-related genes in Arctic Char (Madsen
480 et al., 2019). In our study, the air temperature gradient was latitudinal, while SST varied with
481 longitude, and different candidate SNPs were identified on marine and freshwater axes of
482 variation related to temperature. This is expected given that temperature in freshwater and
483 marine habitats causes selective pressures on different life stages. For example, survival rates of
484 fertilized eggs were lower when exposed to non-natal temperature conditions in Atlantic Salmon
485 (Hendry et al., 1998) and Chum Salmon (*Oncorhynchus keta*; Beacham & Murray, 1986). In
486 contrast, selective pressures in marine habitats have been argued to be weaker since observed

487 mortality rates are lower at sea (Garcia de Leaniz et al., 2007; Quinn, 2005). Furthermore, Spares
488 et al. (2012) maintained that Arctic Char's diving behavior in Frobisher Bay (Nunavut) could be
489 linked to optimal digestion temperature, suggesting behavioral thermoregulation, a plastic
490 response that could limit local adaptation to temperature (Buckley, Ehrenberger & Angilletta,
491 2015). Nevertheless, Harris et al. (2020) showed seasonality in Arctic Char diving behavior that
492 followed the warming of surface waters in Cambridge Bay (Nunavut), but little year-to-year
493 variation in thermal habitat use despite annual differences in climatic conditions, which could
494 suggest limited plasticity. Sampling sites across our study area displayed considerably different
495 SST conditions: while coastal waters surrounding sampling sites in Hudson Bay reached mean
496 summer SSTs ranging from 5.5 – 7.5°C, Hudson Strait stayed closer to the freezing point (0.5 –
497 2°C). Such contrasts in surface temperature, coupled with a discrepancy in tidal regimes, likely
498 produce widely different coastal habitats, which we argue could result in local adaptation of
499 Arctic Char populations.

500 Our GEA results also identified candidate SNPs linked to the environmental component
501 related to salinity, a factor that has a major impact on the capacity of Arctic Char to use marine
502 habitats (Spares et al., 2012). In our study area, mean annual salinity was highest at Hudson Strait
503 sampling sites (30-32 PSU) and lowest in Ungava Bay (21-26 PSU). It is debated whether low
504 marine temperatures or high salinity is the main reason why Arctic Char must migrate annually
505 to spend winter in fresh water (Bystriansky, Frick, Richards, Schulte & Ballantyne, 2007). Jensen
506 and Rickardsen (2008) noted, however, that some Arctic Chars in northern Norway are able to go
507 back to estuarine waters during winter, surviving salinities over 30 PSU. Accordingly, Larsen et al.
508 (2008) found differential expression of candidate genes for salinity tolerance among populations

509 of winter migrating anadromous Brown Trout, which suggests that adaptation to salinity is
510 associated with gene regulation. Moreover, many studies showed that landlocked Arctic Char
511 populations, which lost access to the sea since their recolonization of freshwater habitat, have
512 lost the ability to tolerate seawater (e.g: Eliassen et al., 1998; Bystriansky et al., 2007). Salinity
513 can thus act as a strong selective pressure by restraining foraging to coastal environments.

514 Some recent studies of local adaptation in salmonids have focused on tributary-specific
515 variation in freshwater conditions within a single catchment, (e.g. the Columbia River; Hand et
516 al., 2016; Hecht et al., 2015, Micheletti et al., 2018). However, the freshwater environmental
517 factors used in our study are catchment-based and could limit our interpretations. This is due to
518 sampling having been carried out during the upstream migration, which prevents us from
519 knowing the precise spawning site or overwintering lake used by the sampled individuals. In
520 marine systems, genomic evidence for local adaptation and isolation-by-environment has been
521 found both at local scales in heterogeneous habitats (e.g. Lenhert et al., 2019; Miller et al., 2019)
522 and over large geographic distances (e.g. Clucas, Lou, Therkildsen & Kovach, 2019). Arctic Char is
523 expected to use preferred habitats based on temperature, salinity, and prey availability (Spares
524 et al., 2012, 2015; Harris et al. 2020). As we averaged near-shore marine conditions around river
525 mouths, this study is limited to broad-scale environmental heterogeneity, which is in line with
526 Fraser et al. (2011), who suggest that local adaptation of anadromous salmonids to the marine
527 environment should occur at a larger spatial scale that in fresh water.

528 No matter the geographic scale being studied, an ideal sampling design for detecting local
529 adaptation should maximize the environmental variation while minimizing its collinearity with
530 neutral genetic patterns. For example, Lotterhos and Whitlock (2015) suggest sampling pairs of

531 populations with similar ancestry and contrasting environments. Such a design is suitable when
532 studying variables that may change drastically over short distances, (e.g. catchment area and
533 upstream migration distances). However, climatic and physicochemical conditions experienced
534 by geographically close populations of Arctic Char are more likely to be similar than in distant
535 ones. Similar considerations were discussed in Nadeau, Meirmans, Aitken, Ritland and Isabel
536 (2016), where patterns of isolation-by-distance, isolation-by-environment, and isolation-by-
537 colonization were hard to disentangle for two pine species in a recently recolonized range. In our
538 study, inspection of genotypes for GEA candidates (Figure S7) reveals that at least some have
539 varying allele frequencies that follow spatial patterns reminiscent of the neutral structure we
540 described earlier, especially when environmental variation followed a longitudinal gradient. In
541 some of those cases, it is possible that a GEA was detected even though neutral processes could
542 better explain the distribution of the observed allele frequencies. For example, the introgression
543 of the Arctic glacial lineage in the eastern part of the study area (Moore et al. 2015, Salisbury et
544 al. 2019) could also have led to divergence due to drift during the LGM to be falsely identified as
545 linked to environmental variation (e.g. Figure 8A). Alternatively, if colonization of Hudson Bay did
546 occur by rapid demographic expansion as we discussed earlier, allele-surfing events, where a
547 mutation can reach high frequency by chance alone (Edmonds, Lile & Cavalli, 2004), could explain
548 differential allele frequencies, regardless of whether they are adaptive or not (e.g. Figure 8C).
549 Nonetheless, local adaptation can also contribute to genetic structure across contrasting
550 environments, e.g. by selecting against maladapted migrants (Wang & Barburd, 2014), and we
551 found a significant part of genetic variation to be explained jointly by environmental variation

552 and spatial patterns, as well as by environment alone. In that sense, local adaptation in the
553 system studied here could reinforce the neutral structure discussed earlier.

554 Evidence for local adaptation was detected using three GEA methods, but the overlap of
555 candidates across methods was relatively low (respectively 14.4%, 14.9% and 26.5% of RDA,
556 LFMM and Baypass candidates were detected by at least one other method). While the
557 combination of methods is often used to mitigate false-positive rate, Forester et al. (2018) argued
558 that this approach is biased toward detection of strong selective sweeps. Accordingly, the
559 univariate GEA methods (LFMM, Baypass) used here individually identified genomic regions
560 dense in SNPs associated with environmental component (Figure S9, S10). However, candidate
561 markers, especially those identified by a multivariate RDA (Figure S11), were also distributed
562 across most linkage groups and many genomic regions, which fits with the expectation of
563 adaptation being mainly shaped by polygenic traits (Wellenreuther & Hansson, 2016).This
564 expectation would apply particularly in the case of rapid adaptation (Barton & Keightley, 2002),
565 which would be expected given the recent establishment of the Arctic Char populations studied
566 here (Moore et al., 2015). In our study, different approaches to gene-environment association
567 seem to highlight distinct signal of adaptation. We therefore suggest that the use of multiple GEA
568 methods could not only serve to augment confidence in candidates, but also paint a more
569 complete picture of different evolutionary mechanisms.

570 1.6.4 Implications for conservation and management

571 With the increasing availability of genomic data, it has become common practice to define
572 management and conservation units based on neutral genetic structure while also accounting
573 for local adaptation (Funk et al., 2012). Since Arctic Char populations in Nunavik support mainly

574 small-scale subsistence fisheries, stocks are managed on a river-by-river basis, on the premise
575 that each river contains a single and distinct population (Johnson, 1980). However, our results
576 add to the evidence for the prevalence of mixed stocks of Arctic Char in adjacent rivers (Boguski,
577 Gallagher, Howland & Harris, 2016; Moore, Lewis & Tallman, 2014; Moore et al., 2017). While
578 most pairs of sampled rivers sharing an estuary had very low genetic differentiation, we found
579 evidence of substructure within those systems, suggesting that genomic tools could be used for
580 stock assignment of adult fish (e.g. Meek et al., 2016; Moore et al. 2017). The evidence we found
581 for local adaptation to marine environments is in concordance with the neutral genetic structure
582 at a broader scale, as major oceanographic basins around Nunavik are contrasted both in their
583 environments and ancestry of their Arctic Char populations. We therefore suggest that this
584 species could be managed on a regional basis in Hudson Bay, Hudson Strait, and Ungava Bay, as
585 it may already be the case, with distinction of the eastern and western coasts in Ungava Bay.

586 There is growing interest in Arctic Char hatchery projects in Nunavik, both for
587 supplementation and reintroduction of Arctic Char in traditional fishing locations (George, 2007;
588 Rogers, 2015). The genetic information gathered here could be of great use for those initiatives,
589 and the adaptative variation explored in this study highlight the need for careful choices of source
590 populations for broodstocks, as maladapted domesticated individuals can waste efforts and
591 resources, in addition of likely being detrimental to wild populations (Fraser, Minto, Calvert,
592 Eddington & Hutchings, 2010; Tymchuk, Biagi, Withler & Devlin, 2005).

593 As the Arctic warms at a greater pace than any other regions on earth (Cohen et al., 2014),
594 there might be concern about the response of Arctic Char populations to their changing
595 environment. Traits that are currently optimally adaptive in the present environment could

596 eventually become maladaptive. Species will thus likely need to shift their distributions poleward
597 and/or will depend on the presence of appropriate genetic diversity/phenotypic plasticity to
598 adapt and persist in their current distribution. A temporal study recently showed that Arctic Char
599 populations in Greenland have exhibited stable genetic structure over the last 60 years in face of
600 rapid climate change, and argued that gene flow, although low, could allow for a modest level of
601 evolutionary rescue in the short term (Christensen, Jacobsen, Nygaard & Hansen, 2018). Our
602 study shows potential for local adaptation of Arctic Char populations to both their marine and
603 freshwater habitats. As changes in climate might operate at a different pace, scale, and stability
604 in marine and terrestrial ecosystems (Burrows et al., 2011), there is a need for continued research
605 about the interaction of selective pressures over the lifespan of anadromous organisms.

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Data accessibility

Raw sequences that support the findings of this study will be openly available on NCBI SRA. Due to the current measures of social distancing surrounding COVID-19, the data were unreachable and couldn't be uploaded to SRA in time for manuscript submission (end of April 2020). This will be done upon acceptance of the article.

Author's contribution

J.-S.M., L.B., J.M., J.-É.T. and X.D. conceived and planned the research. X.D. and J.M. performed the sampling, and X.D. and É.N. produced the dataset. X.D., É.N., J.-S.M., L.B. and J.M. contributed to the interpretation of the results. X.D. performed most of the analyses and led the writing of the manuscript, under the supervision of J.-S.M. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Table 1. Value range and source of environmental factors considered in gene-environment associations. PCA axis most associated to marine (M1-M3) and freshwater (F1-F3) factors are indicated.

Variable	Description	Value range	Unit	Temporal range	Database	Source	PCA axis
SST_summer	Mean sea-surface temperature (July to September)	0.5 – 6.8	°C	2002 – 2010	Marspec	WOA09	M1
Tide_M2	Amplitude of M2 tidal constituant	17.5 – 372.6	---	---	FES2014	AVISO+	M1
Turbidity	Annual mean diffuse attenuation	0.8 – 4.8	m^{-1}	2002 – 2009	Bio-ORACLE	Aqua-MODIS	M1
Salinity	Annual mean sea-surface salinity	21.0 – 31.8	PSS	2000 – 2014	Bio-ORACLE	ARMOR	M2
O2	Annual mean dissolved molecular oxygen	327 – 364	$mmol.m^{-3}$	2000 – 2014	Bio-ORACLE	PISCES	M2
Productivity	Annual mean primary productivity (carbon)	1.2 – 12.0	$g.m^{-3}.day^{-1}$	2000 – 2014	Bio-ORACLE	PISCES	M3
T_winter	Mean air temperature of the coldest quarter	-25.0 – -19.7	°C	1970 – 2000	WorldClim	MODIS	F1
T_summer	Mean air temperature of the warmest quarter	4.9 – 10.7	°C	1970 – 2000	WorldClim	MODIS	F1
P_winter	Mean precipitation of the coldest quarter	40.2 – 171.5	mm	1970 – 2000	WorldClim	GHCN	F1
P_summer	Mean precipitation of the warmest quarter	114.7 – 250.1	mm	1970 – 2000	WorldClim	GHCN	F2
WS_AREA	Upstream catchment area (watershed, log-transformed)	30 – 43,496	km^2	---	NHN	---	F3

ARMOR = Global Observed Ocean Physics Reprocessing; AVISO+ = Archiving, Validation and Interpretation of Satellite Oceanographic data; GHCN = Global Historic Climate Network; MODIS = Moderate Resolution Imaging Spectroradiometer; NHN = National Hydrographic Network; ORAP = Global Ocean Physics Reanalysis ECMWF; PISCES = Global Ocean Biogeochemistry Non-assimilative Hindcast; WOA09 = World Oceanographic Atlas 2009

Table 2. Summary of sampling and basic statistics. Samples were collected on adult in rivers and lakes, with exceptions († in estuaries, ‡ on juveniles).

Region	Code	Name	LON	LAT	n	H_o	H_e	Polymorphic SNPs	N_e (IC 95%)
Nunavik									
Hudson Bay									
Southern									
	IPI	Ipikituk River	-78.38	58.73	24	0.178	0.167	11,408	187.6 (3.2)
	SAP	Saputaliuk River	-78.36	58.7	17	0.19	0.171	11,139	61.9 (0.6)
	FMI	Five Mile Inlet	-78.21	58.56	24	0.163	0.168	11,739	105.0 (1.0)
Northern									
	KOA	Korak River	-77.63	60.75	28	0.181	0.183	13,015	320.9 (6.8)
	CHU	Chukotat River	-78.02	60.79	15	0.185	0.189	12,286	394.4 (21.2)
	KOV	Kovik River	-77.7	61.36	21	0.174	0.184	12,446	81.2 (0.7)
Hudson Strait									
	BDE†	Déception Bay	-74.62	62.13	30	0.205	0.207	14,283	327.3 (6.0)
	DUQ	Duquet Lake	-74.53	62.06	44	0.202	0.206	14,665	446.7 (6.9)
	FRM	François-Malherbe Lake	-74.25	62.04	38	0.205	0.207	14,611	589.0 (14.0)
	DOU	Douglas Harbour	-72.65	62.06	29	0.2	0.205	13,736	170.6 (1.8)
Ungava Bay									
Western									
	PAY	Payne River	-70.7	60.01	30	0.194	0.201	13,614	96.0 (0.5)
	CHR	Red Dog River	-69.79	59.3	39	0.19	0.191	13,324	167.2 (1.3)
	VOL	Voltz River	-69.66	59.25	25	0.196	0.19	12,448	207.4 (3.3)
	HAB†	Hopes Advance Bay	-69.63	59.32	24	0.191	0.192	12,638	205.3 (3.5)
	FEU	Leaf River	-70.11	58.77	40	0.173	0.17	11,303	616.5 (17.9)
	BER	Bérard River	-69.97	58.65	36	0.202	0.208	14,279	92.0 (0.4)
Eastern									
	GEO	George River	-65.95	58.69	37	0.207	0.208	13,858	734.5 (22.4)
	AKI	Akilasaaluk River	-65.4	59.06	17	0.211	0.21	13,241	188.1 (3.9)
Baffin Island									
	AVA	Ava's Inlet	-72.64	64.01	23	0.187	0.189	12,871	233.3 (4.8)
	LHO	Lake Harbour	-69.82	62.82	38	0.206	0.192	13,114	297.0 (4.1)
	PRZ	Pritzler Harbour	-67.32	62.12	27	0.199	0.202	13,669	134.1 (1.3)
Labrador									
	KAM‡	Kamanatsuk River	-62.54	56.74	19	0.211	0.209	13,996	269.7 (6.9)
	ANA‡	Anaktalik River	-62.15	56.49	26	0.206	0.204	13,732	74.7 (0.4)

Table 3. Parameters of isolation-by-distance mixed effect models, displaying degrees of freedom (df), conditional Akaike information criteria (cAIC) and marginal R-Squared (R^2m) compared to the null model.

	All sites			Sites within 250 km of Hudson Strait		
	df	cAIC	R^2m	df	cAIC	R^2m
FST ~ 0	20.25	-501.20	--	8.38	-133.68	--
FST ~ DIST	21.91	-761.68	0.661	9.25	-142.54	0.298
FST ~ DIST + CROSSHS	22.74	-761.35	0.660	10.57	-163.65	0.447
FST ~ DIST * CROSSHS	23.75	-761.59	0.659	11.68	-171.01	0.464

Figure 1: Sampling locations in Nunavik (Québec) and bordering regions. Red extents numbered 1 to 6 are magnified to show neighboring sampling locations. Catchment area for each site is displayed in green.

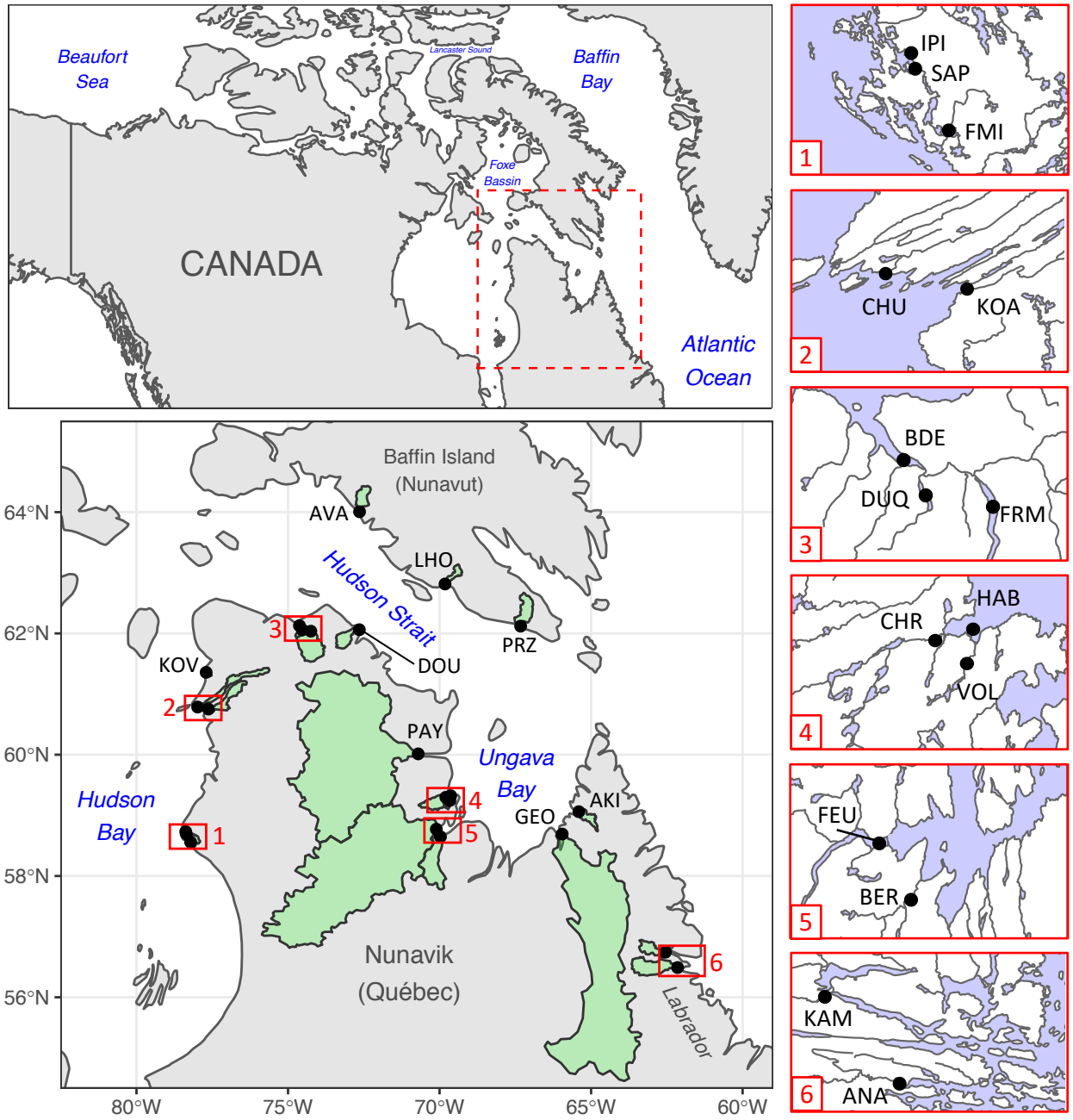

Figure 2: (A) Population structure assessed by a principal coordinate analysis (PCoA). Individual scores on PCoA axes 1 and 2 are presented as points and colored by geographical region. An ellipse representing a 95% confidence interval was drawn around each sampling site. The percentage of genetic variance explained by each axis is in parentheses. (B) Pairwise F_{ST} between neighboring sampling sites are shown, with line thickness proportional to values. Red extent is magnified to contrast F_{ST} between Leaf (FEU) and Bérard (BER) rivers (pairwise F_{ST} = 0.135). Other pairs of grouped sampling sites had their F_{ST} values averaged for better visualization.

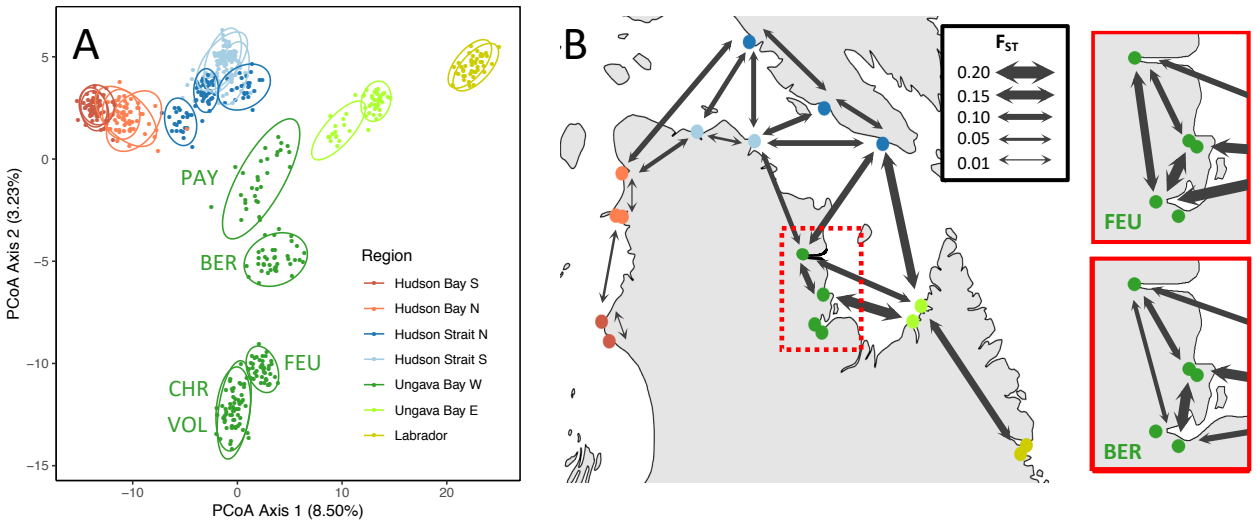

Figure 3: (A) Results of the hierarchical Bayesian clustering analysis implemented in ADMIXTURE for a number of genetic clusters (K) of 4, 6 and 13 (see Figure S3 for K = 2 to 16). Lower rows display the results for separate analyses on sampling sites sharing similar membership to clusters at K = 13, which yielded the lowest cross-validation error (CV). (B) Results of ADMIXTURE for K = 4 clusters, with individual ancestry averaged by sampling site and represented by pie charts. Approximative extent of glaciers, adapted from Dyke (2004), are represented by blue dashed lines for 6,000 - 11,000 years before present (BP).

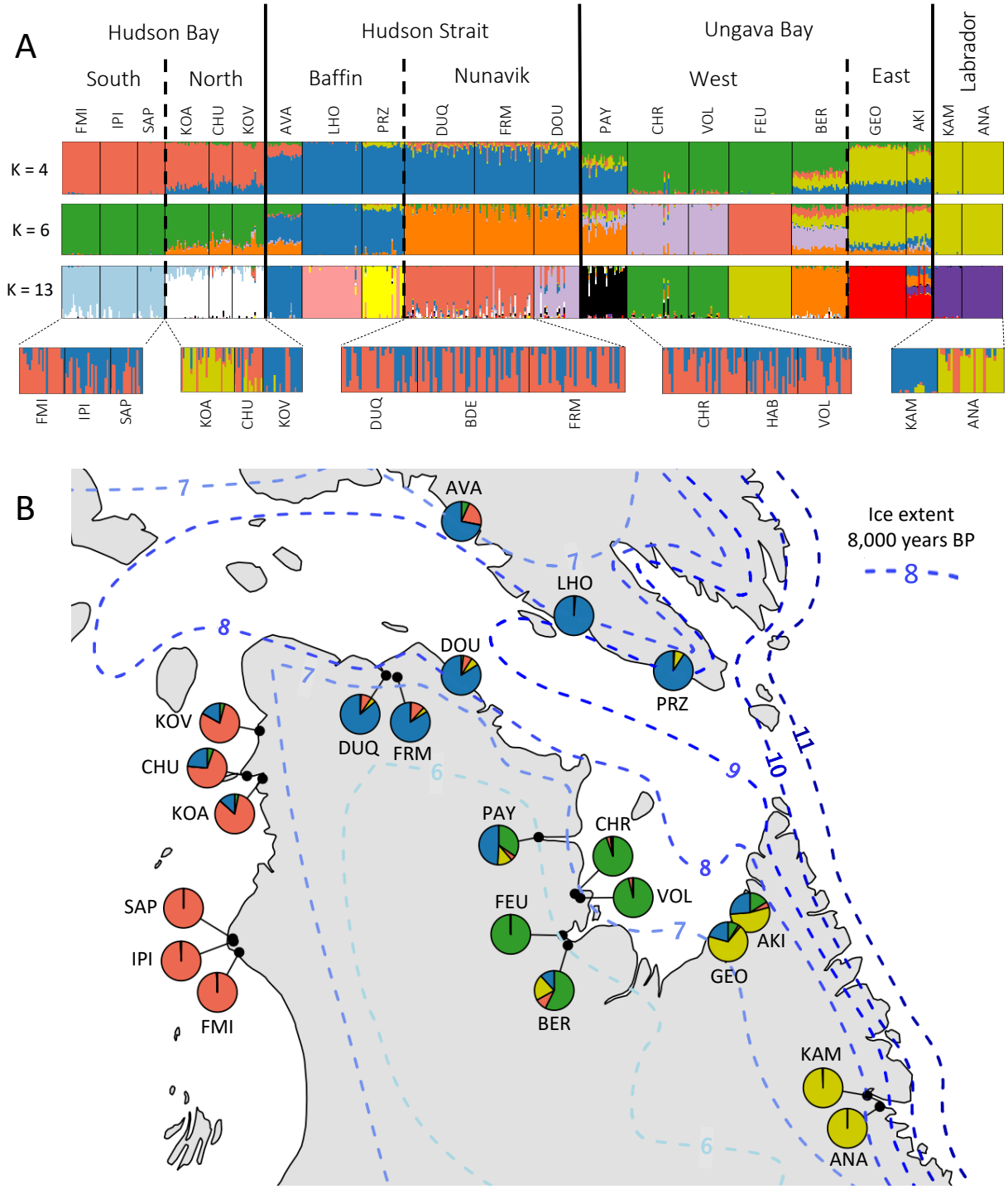

Figure 4: Individual proportion of heterozygous SNP markers in sampling sites, ordered following the coast from west to east, and colored by region. For each boxplot, bold line indicates mean, the box limits 25th and 75th percentile, and whiskers represent 10th and 90th percentile. Letters indicate group membership based on a comparison of least square means in a mixed-effect model (alpha = 0.05).

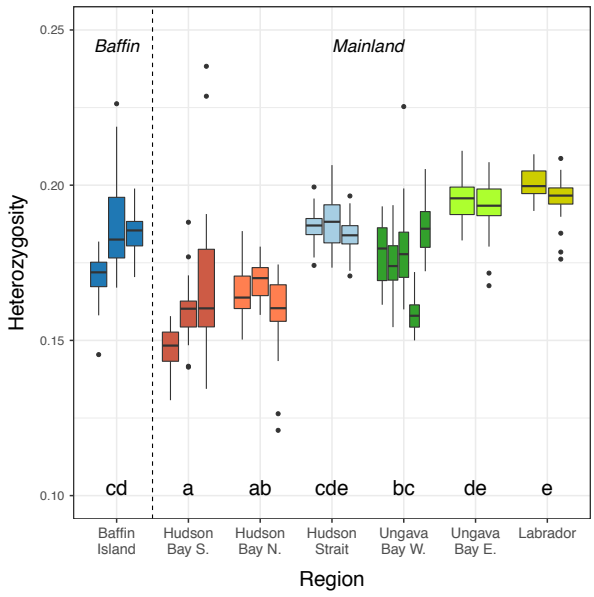

Figure 5: Isolation-by-distance represented by relation between marine distances and linearized pairwise F_{ST}, estimated between pairs of populations separated by Hudson Strait (red points) and on the same coast (blue triangles). Regression lines and 95% confidence intervals are plotted for mixed-effect models with fixed effects including marine distance and crossing of Hudson Strait. Models were fitted using (A) all sampling sites and (B) only sampling sites within 250 km of Hudson Strait.

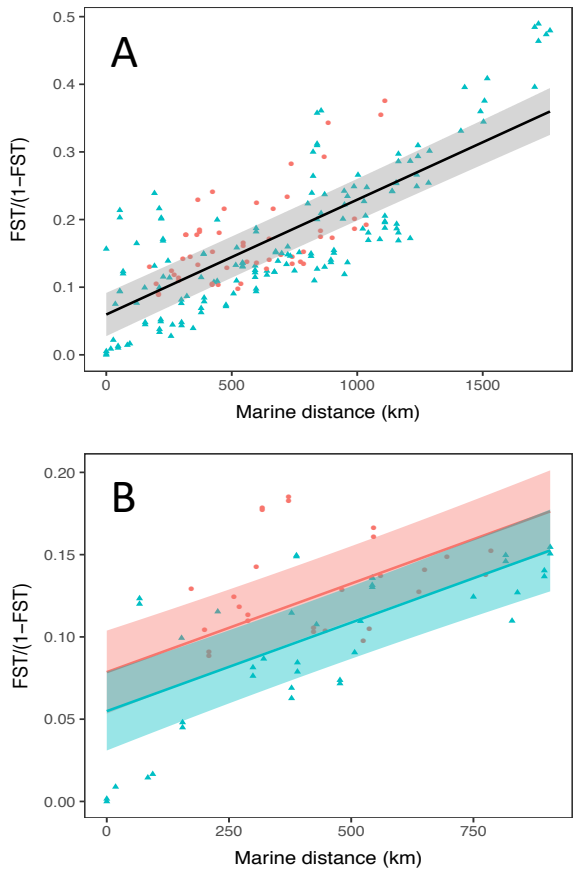

Figure 6: (A) Percentage of genetic variation explained by spatial (orange), marine (blue) and freshwater (green) factors in a redundancy analysis (RDA). Triplots for (B) axes 1 and 2, and (C) axes 2 and 3 in a RDA excluding spatial components. The dark grey cloud of points at the center of each plot represents the SNPs, and coloured points represent sampling sites with color coding by region. Triplots are magnified to highlight SNP loadings on (D) RDA axes 1 and 2, and (E) axes 2 and 3. Candidate SNPs are shown as colored points with coding by most highly correlated environmental predictor (see text for description). Vectors represent environmental predictors, according to the scales on top and right axes.

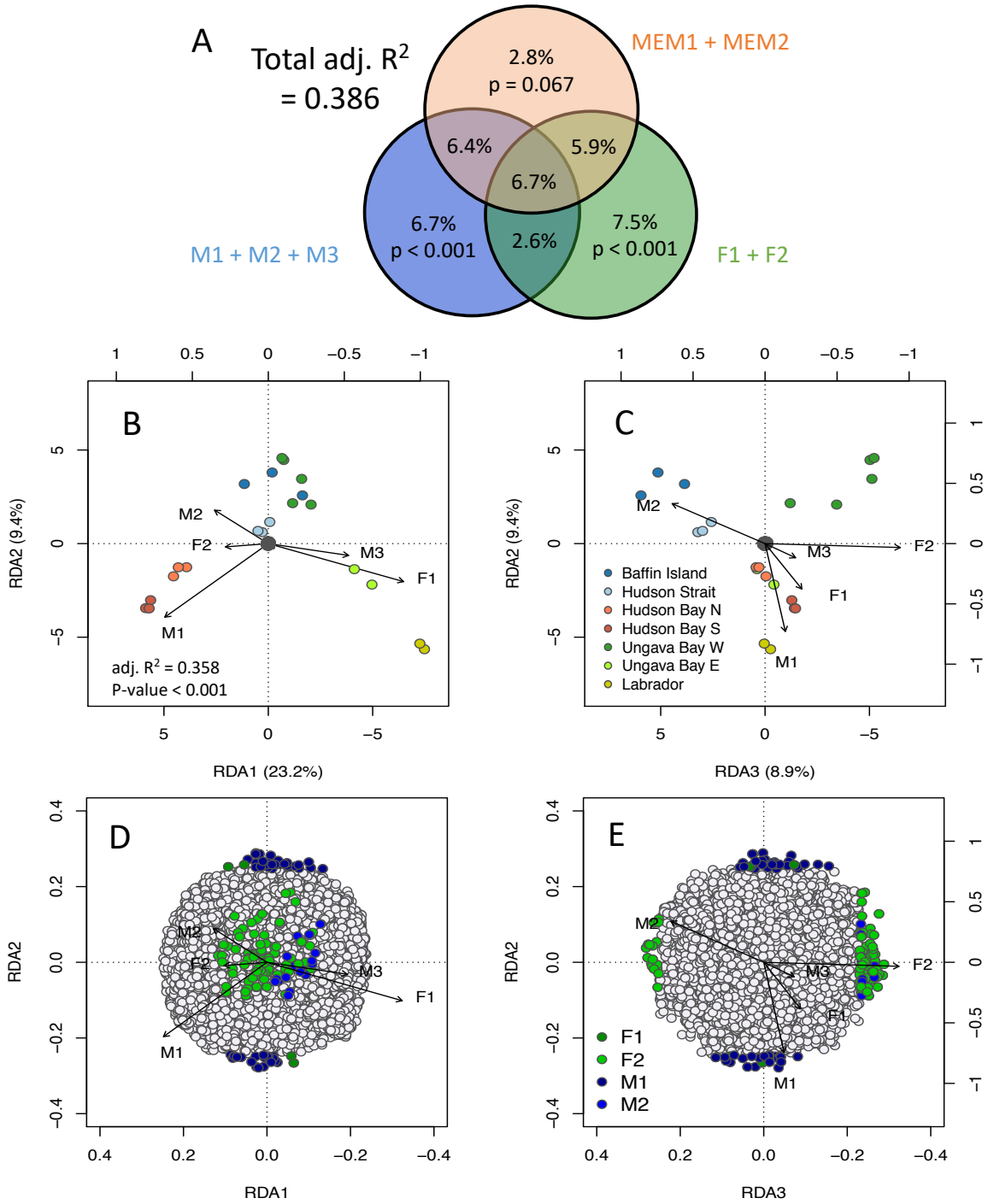

Figure 7: Intersection of candidate SNPs detected by three GEA methods. For each intersection, the box indicates the distribution of environmental components associated to candidate SNPs.

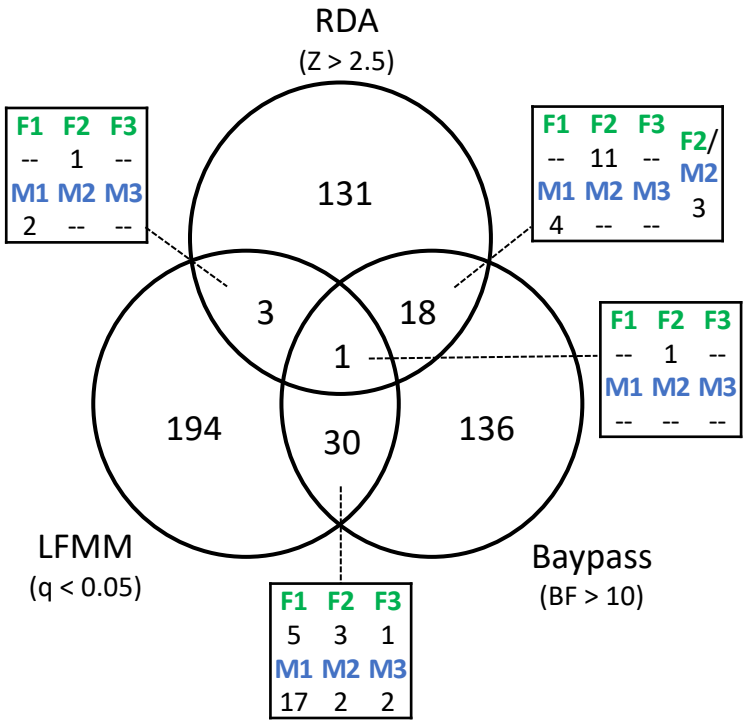
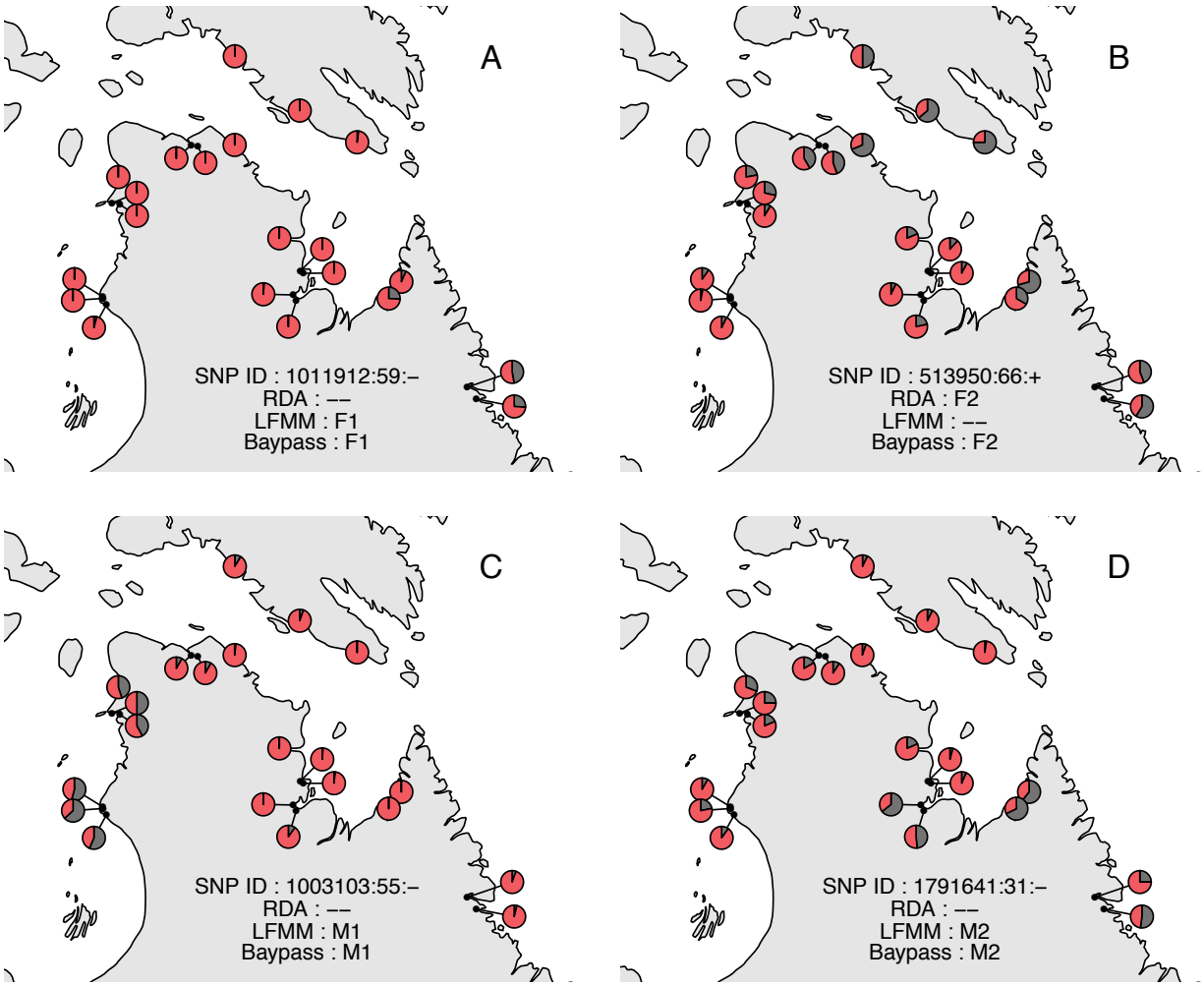
Figure 8: Allele frequency distribution of four candidate SNPs detected in GEA. Environmental components significantly associated to candidate SNPs are listed for each GEA method.