

1 **Landscape, colonization and life history: Their effects on genetic diversity in four**
2 **sympatric species inhabiting a dendritic system**

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21 **ABSTRACT**

22 To what degree are patterns of observed genetic diversity and differentiation in spatially
23 fragmented systems the result of contemporary landscape features vs. historical processes? We
24 addressed this question by examining the spatial distribution of genetic diversity as a function of
25 colonization history and contemporary landscape in four fish species inhabiting a hierarchically
26 structured and spatially fragmented system that is largely free of anthropogenic influence, the
27 Kogaluk river drainage in Labrador: lake trout (*Salvelinus namaycush*), longnose sucker
28 (*Catostomus catostomus*), round whitefish (*Prosopium cylindraceum*), and lake chub (*Couesius*
29 *plumbeus*). The footprint of colonization history was still observable in the three species where
30 this issue could be examined regardless of the number of generations that elapsed since their
31 estimated arrival to the area. ABC analyses for all three species suggest colonization took place
32 from the southwest. All species exhibit similar diversity patterns despite their different \hat{N}_e s and
33 generation intervals. Contemporary gene flow was largely negligible across all four species with
34 the exception of gene flow up- and downstream from a centrally located lake. These results
35 suggest landscape has driven colonization history, which still has a major influence on the
36 genetic structuring across all four species. The four species examined are widespread throughout
37 Canada. Understanding how they behave in the Kogaluk drainage, which is free of direct
38 anthropogenic interference provides a baseline against which to evaluate how other systems
39 undergoing anthropogenic perturbations are performing. We conclude that an improved
40 understanding of historical and contemporary processes is required to fully explain observed
41 patterns of structure and gene flow in spatially complex metapopulation systems.

42

43 INTRODUCTION

44 To what degree are patterns of observed genetic diversity in complex metapopulation
45 systems the result of contemporary vs. historical processes? This is a fundamental question in
46 current conservation and landscape genetic studies: An understanding of their relative roles can
47 assist in the assessment of future population responses to climate and/or habitat changes (Manel
48 *et al.* 2003; Storfer *et al.* 2010; Manel & Holderegger 2013). The question is, however, not easily
49 answered since it requires the examination of processes operating over different time scales.
50 While the genetic structure of any taxon may in principle be dictated by the interaction of
51 historical and contemporary processes this is particularly likely in those metapopulations which
52 have failed to reach migration/drift equilibrium (e.g. those exposed to the Quaternary glacial
53 cycles) (Hewitt 2000; Ruzzante *et al.* 2008; Fraser *et al.* 2012).

54 In a contemporary setting, habitat fragmentation is generally thought to lead to the loss of genetic
55 diversity. Yet this is not always true, spatial configuration of the habitat fragments also matters.
56 For instance, systems that are spatially fragmented in a hierarchical, dendritic fashion have been
57 shown, at least in theory, to exhibit higher genetic diversity than panmictic systems of equal total
58 size (Morrissey and deKerchove 2009). Asymmetric gene flow occurring in these types of
59 systems can significantly influence the distribution of genetic variation, with headwater
60 populations typically exhibiting lower genetic diversity (i.e., lower heterozygosity, allelic
61 richness) and higher genetic differentiation than downstream populations (Caldera and Bolnick,
62 2008; Morrissey and De Kerckhove, 2009; Junker *et al.*, 2012). Downstream populations are
63 thus expected to exhibit higher effective population sizes than headwater populations (Morrissey
64 and De Kerckhove, 2009; Gomez-Uchida *et al.*, 2009; 2013).

65 Extrapolating from modeling studies to the natural world is however, not straightforward.
66 Theoretical studies examining spatially fragmented systems generally focus on standardized
67 ideal systems where migration follows either an island, a one- or two-dimension stepping stone,
68 a circular, or as above, a perfectly dendritic model (but see, Tufto and Hindar 2003, Hössjer *et al.*
69 2014, 2015). Most importantly though, modeling studies generally assume migration-drift
70 equilibrium. Such efforts are undoubtedly useful for holistic understanding and serve as
71 predictive tools under some circumstances, but the majority of natural systems are not easily
72 classifiable into any of these discrete categories, they are vastly more complex making
73 predictions of their behavior under most situations more difficult. Regardless, model validation
74 with empirical data are likely to be useful for an improved understanding of the natural world
75 (see, e.g., Grant *et al.*, 2007; Perkin and Gido, 2012).

76 Natural systems are unlikely to be in migration-drift equilibrium, a factor that is expected to
77 bring the footprint of colonization history to the forefront at the expense of the influence of
78 contemporary landscape features and the spatial arrangement of populations. Such a footprint of
79 colonization history is in fact expected to be particularly strong in recently colonized systems
80 with genetic diversity potentially being a function of successive founding events (e.g., Vera *et*
81 *al.* 2015, 2018; Salisbury *et al.* 2016) and the number of generations elapsed since first arrival
82 regardless of the spatial arrangement of populations.

83 In the present study we tested the hypotheses that colonization history could explain observed
84 patterns of structure and connectivity and that this relationship would be a function of the
85 number of generations elapsed since deglaciation (i.e., an inverse function of generation
86 interval). We examined the relative influence of colonization history and landscape structure

87 among species differing in life history traits and coexisting sympatrically in a spatially
88 fragmented and hierarchically structured freshwater system in northern Labrador, the Kogaluk
89 River system. Although hierarchical in nature, this system departs from the standard dendritic
90 scenario addressed by most previous theoretical studies. First, local populations are restricted to
91 the lakes (nodes in typical dendritic models) as opposed to dendritic systems where they are also
92 present in the rivers (branches) connecting the lakes (Grant *et al.*, 2007; Morrissey and De
93 Kerckhove, 2009; Perkin and Gido, 2012). Second, although gene flow is asymmetric, in some
94 cases differences in elevation among lakes and the presence of ice during large part of the year
95 reduce the probability of sustained gene flow, which can lead to a much slower progression
96 towards migration-drift equilibrium.

97 Genetic diversity was examined in four species: lake trout (*Salvelinus namaycush*), longnose
98 sucker (*Catostomus catostomus*), round whitefish (*Prosopium cylindraceum*), and lake chub
99 (*Couesius plumbeus*). These species are widespread and inhabit similar landscapes throughout
100 Canada and other regions of the world. Gaining an understanding of how this particular system
101 behaves under pristine conditions without anthropogenic interference can provide a baseline
102 against which it is possible to evaluate how other systems undergoing anthropogenic
103 perturbations are performing. In addition, the species differ in some key life history traits chiefly
104 among them, generation time (T) with $T_{\text{lake trout}} > T_{\text{longnose sucker}} > T_{\text{round whitefish}} > T_{\text{lake chub}}$ suggesting
105 they may be at different stages of a progression to migration-drift equilibrium. Colonization
106 history was examined in the first three species. We thus tested for the interactive effects of
107 landscape structure and colonization history in species that differ in life history traits. We sought
108 to identify the relative roles of colonization history and current environmental barriers, on the
109 metapopulation genetic structure of four coexisting fish species potentially differing in the
110 progression to equilibrium conditions. Explicitly, we expect species with shorter generation
111 times to achieve migration-drift equilibrium in a shorter time period. Observed patterns of
112 population structure in such species would be more influenced by current landscape features than
113 by colonization history when compared to species with longer generation times.

114 **METHODS**

115 *Study site and Sample collection*

116 The Kogaluk River drainage comprises a number of relatively shallow lakes on the barren
117 grounds of northern Labrador. The lakes are hierarchically connected through shallow streams
118 that drain from the north, west and south into Cabot Lake, a deep fjord lake. Cabot Lake, in turn,
119 empties into the Atlantic Ocean through the Kogaluk River (Figure 1). The lakes range in
120 elevation from 525 meters asl for the highest elevation to 60 m asl for Cabot lake (Table 1, Fig.
121 1). There are five waterfalls in the system, all of which prevent upstream migration. The furthest
122 downstream waterfall is located just 9 km upstream from the river's mouth (Fig. 1, WF5;
123 Anderson, 1985), effectively rendering the fish populations in the entire system landlocked
124 (Anderson, 1985). Due to the drainage's northern geographical location and distance from settled
125 areas, the system is largely free of anthropogenic influence.

126 Fish collection [lake trout, longnose suckers, round whitefish, lake chub] took place from the
127 entire system between 2002 and 2015 using gillnets and electrofishing. Gillnets were generally
128 set at 3 independent sites per lake. We used standardized nylon monofilament gillnets with mesh
129 sizes increasing from 1.27cm to 13.97cm by 1.27 cm increments. We also sampled two locations
130 per lake by electrofishing. Sampled fish were measured for fork length and weight, and were

131 assessed for sex and maturity. Their otoliths (lake trout and round whitefish) and opercula
 132 (longnose suckers) were taken *in situ* for ageing. Finclips (all 4 species) taken for DNA
 133 extraction were stored dry or in 95% ethanol. Number of individuals per species and lake are
 134 listed on Table 1. In total, considering all lakes, we collected and processed for DNA extraction
 135 867 lake trout, 869 longnose suckers, 456 round whitefish, and 734 lake chub, (Table 1). While
 136 lake trout were abundant in all sampled lakes, longnose sucker, round whitefish and lake chub
 137 were absent or present only in small numbers in lakes Hawk and Genetics B. We did not collect
 138 lake chub from Cabot Lake, as this is a deep fjord lake with limited areas suitable for
 139 electrofishing. Details of the ageing procedure for longnose suckers based on opercula growth
 140 rings are available in Salisbury *et al.* (2016).

141 ***Life history analyses***

142 Salisbury *et al.* (2016) estimated generation time, T , for longnose sucker as $T_{LNS} \approx 12-13.5$ years.
 143 In the present paper we estimate T for lake trout where

144

$$145 \quad T = \frac{\sum x l_x m_x}{\sum l_x m_x} \quad (\text{Birch 1948})$$

146

147 This requires knowledge of l_x (the probability of survival to age x) and of m_x (age specific
 148 fecundity or the number of offspring produced by an individual of age x). To estimate l_x (for each
 149 age class), we used the Robson-Chapman annual survivorship estimate, (\hat{S}) (Chapman and
 150 Robson 1960, Robson and Chapman 1961) using the age composition of gillnet caught samples.
 151 We assumed $l_0 = 1$, $l_1 = \hat{S}^1 \times l_0$, ... $l_\omega = \hat{S}^\omega \times l_0$, where ω is the maximum age observed from the
 152 sampled lake (Waples *et al.* 2014). To estimate m_x , we require knowledge of the age at 50%
 153 maturity (α), and of the adult lifespan (AL). Age at 50% maturity was estimated using a binomial
 154 logistic regression (Harry *et al.* 2013) with age as the independent variable and maturity (0 as
 155 immature, 1 as mature) as the dependent variable in R (R Core Team, 2013). Adult lifespan (AL)
 156 was estimated as $AL = \omega - \alpha + 1$. Details of the analyses for longnose suckers are outlined in
 157 Salisbury *et al.* (2016). Fecundity for lake trout was estimated for each age class from α
 158 (rounded down to the nearest age) to ω and divided by 2 to approximate m_x (the number of
 159 offspring produced by an individual of age x) to account for the fact that only half of the
 160 population is female. For round whitefish age at 50% maturity from similar high latitude
 161 locations in Ungava Bay is $\alpha \approx 4+$ years (Armstrong *et al.* 1977; Morin *et al.* 1982). Generation
 162 time for round whitefish is therefore estimated at $T \approx 6.5 - 7$ years assuming age specific
 163 survival rate among whitefish is similar to that of lake trout. For lake chub, age at 50% maturity
 164 was assumed to be $\alpha \approx 2$ based on information in Bruce and Parsons (1976). Generation time for
 165 this small cyprinid species is therefore likely $3 < T < 4$.

166 ***DNA Extraction, Amplification and Genotyping***

167 The final number of microsatellite loci genotyped for each species were 12 (lake trout), 17
 168 (longnose sucker), 12 (round whitefish), and 19 (lake chub) (Data to be made available in
 169 DRYAD). Below we describe the general procedures and note when these differ among the four
 170 species. Fin tissue samples (adipose fin for lake trout and round whitefish, pectoral or caudal for
 171 longnose sucker and lake chub) were digested with Proteinase K (Bio Basic Inc., Markham,
 172 Ontario, Canada) at 55°C for approximately 8 hours. DNA was then extracted from the resulting

173 digest using a Glassmilk protocol modified from Elphinstone *et al.* (2003) with a Perkin Elmer
174 Multiprobe II plus liquid handling system (Perkin Elmer, Waltham, Massachusetts). Random
175 selections of DNA samples were electrophoresed on 1-2% agarose gel and compared against a
176 size standard to ensure sufficient quantity and quality of DNA for subsequent polymerase chain
177 reactions. Further details regarding the choice of microsatellite markers and related procedures
178 for lake trout are available in McCracken *et al.* (2013) while details for longnose sucker are
179 available in McCracken *et al.* (2014a) and Salisbury *et al.* (2016). Species specific
180 microsatellites for lake chub and round whitefish were chosen from McCracken *et al.* (2014b and
181 2014c, respectively) based on scoring ease and consistency.

182 ***Genetic Quality Control Analyses***

183 Individual genotypes were collected using SAGA Automated Microsatellite Software 3.3 (LI-
184 COR Biosciences, Lincoln, Nebraska) followed by rigorous manual checking to ensure scoring
185 accuracy. MICROCHECKER 2.2.3 (van Oosterhout *et al.*, 2004) was used to test for the
186 presence of null alleles, or scoring inconsistencies.

187 ***Genetic Analyses***

188 Genotypic linkage and conformity to Hardy-Weinberg proportions as well as observed (H_O) and
189 expected (H_E) heterozygosities were tested with Arlequin 3.5.1.2 (Excoffier and Lischer 2010).
190 Linkage between pairs of loci were estimated using 10,000 permutations, while conformity to
191 Hardy-Weinberg proportions was tested for each locus, population and species using 1,000,000
192 steps in Markov chain and 100,000 dememorization steps. Results were then subject to False
193 Discovery Rate correction (Benjamini and Hochberg 1995) to maintain an overall type 1 error
194 probability at 0.05. Allele frequencies and allelic richness were estimated using FSTAT (Goudet,
195 2001). Genetic differentiation (F_{ST}) was estimated with MSA 4.05 (Dieringer and Schlötterer
196 2003) using 100,000 individual permutations. These values were then linearized [$F_{ST}/(1-F_{ST})$]
197 following the procedure by Rousset (1997). Principal coordinates analyses were conducted using
198 GenAlex 6.501 (Peakall and Smouse 2006).

199 ***Population Structure Analysis***

200 Population structure was examined with the program STRUCTURE 2.3.4 (Hubisz *et al.*, 2009),
201 through Principal Coordinate analyses conducted on the matrices of linearized pairwise \hat{F}_{STS}
202 using GENALEX, and through a series of hierarchical AMOVAs conducted with Arlequin
203 version 3.5 (Excoffier *et al.* 2005, Excoffier & Lischer 2010). STRUCTURE analyses were
204 conducted hierarchically for all four species, first examining the entire data set and identifying
205 clusters which were then independently subject to further STRUCTURE analyses. This process
206 was continued on individual clusters until no further evidence of population structure was
207 detected. We estimated the most likely number of clusters based on the Evanno methodology
208 (Evanno *et al.* 2005) implemented in STRUCTURE HARVESTER v0.6.92 (Dent *et al.* 2012).
209 For all species STRUCTURE runs were replicated 10 times at each level and K with each
210 replicate run for 1,500,000 iterations with an initial burn-in of 500,000. Results of the separate
211 replications for the most likely K were then combined into a single population output using the
212 program CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and visualized using the program
213 DISTRUCT 1.1 (Rosenberg 2004). STRUCTURE runs for longnose sucker (LNS) are described
214 in Salisbury *et al.* (2016).

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216

217 Identification of Migrant Individuals, Effective Population Size and Gene Flow Estimation

218 Potential migrants were identified with GeneClass2 (Piry *et al.* 2004). Effective population sizes
219 were estimated both before and after the removal of individuals identified as potential migrants.
220 Effective population size estimates were obtained with the linkage disequilibrium method
221 implemented in LDNe (Waples and Do 2008). The program implements a bias correction for
222 cases when the sample sizes are smaller than the actual effective population size (Waples 2006).
223 Estimation via LDNe was conducted using the (P_{crit}) critical value (allele frequencies greater
224 than) 0.02, as described by Waples and Do (2010) as the vast majority of our sample sizes were
225 >25, with 95% confidence intervals generated via jackknifing between pairs of loci. Estimates of
226 effective population size for longnose sucker are those published in Salisbury *et al.* (2106); they
227 were obtained by first estimating the effective number of breeders (\hat{N}_b) from a single or 2-3
228 pooled cohorts when single cohort sample sizes were low. These estimates were then
229 extrapolated to \hat{N}_e using the empirical relationships described in Waples *et al.* (2013, 2014) (See
230 Salisbury *et al.* 2016). We were unable to follow the same procedure for the other species either
231 because fish were not aged (lake chub) or because of uncertainty in the value of adult life span
232 (required for estimating N_e from N_b) and because the large number of age classes present along
233 with the fact that not all genotyped individuals were aged (lake trout, round whitefish) resulted in
234 small cohort sizes.

235 Gene flow was estimated using BayesAss+ (Wilson and Rannala 2003), which uses a Bayesian
236 framework to infer recent migration rate. BayesAss+ was run for 50,000,000 iterations with an
237 initial burn in of 5,000,000, mixing parameters varied by species so as to achieve acceptance
238 rates between 0.2 and 0.6.

239 Historical Colonization Assessment

240 We used DIYABC v2.0 (Cornuet *et al.* 2014) to assess the likelihood of colonization from the
241 west-southwest vs. colonization from the east-southeast for lake trout and round whitefish as
242 well as longnose sucker, the colonization route for which was originally described by Salisbury
243 *et al.* (2016). As no lake chub samples were available for Cabot Lake, a key location for the
244 testing of colonization from the west vs. east, no analysis of potential colonization route using
245 DIYABC was performed for this species.

246 Our first scenario depicted colonization from the west-southwest via the paleolake Naskaupi
247 (Jansson and Kleman 2004). Under this scenario T-Bone is the ancestral lake or the first lake to
248 be colonized and from which fish expanded into the remaining lakes. The second scenario
249 assumed colonization from the east-southeast implying colonization via the coast (Black *et al.*
250 1986). For freshwater species a scenario of colonization via the coast would in principle be
251 possible through the lens of freshwater that would have been formed along the coast during
252 periods of intense deglaciation. Under such a scenario, the first lake to be colonized would have
253 been Cabot Lake (Fig 5b). Thus, the major difference between the two scenarios is whether
254 colonization took place from the west-southwest (scenario 1) or the east-southeast (scenario 2).
255 The lakes were immediately adjacent to Lake Nauskapi between 8400 and 7000 years BP
256 (Jansson and Kleman 2004). Colonization was assumed to occur ca. 9000 years BP after the
257 Laurentide Ice Sheet is thought to have retreated from the Kogaluk (Bryson *et al.* 1969, Short
258 and Nichols 1977). Further colonization model details are described in Results.

259 Generation times, T , were estimated to be 24, 12-13.5, 6.5-7, and 3-4 years for lake trout,
 260 longnose sucker, round whitefish and lake chub, respectively (See Results and Salisbury *et al.*
 261 2016 for longnose suckers). The prior distributions of time points differed across species, with
 262 maximum number of generations that elapsed since colonization set at 1000 for lake trout except
 263 for t_5 and t_7 (both time points involving Cabot Lake, which likely was in existence beforehand),
 264 which were set at 3000 for longnose sucker and 4000 for round whitefish.

265 In total, 6 000 000 simulations were run for each species. A Generalized Stepwise Mutation
 266 Model was assumed and the prior for the mean mutation rate across loci was a uniform
 267 distribution between 1×10^{-4} and 1×10^{-3} , while individual locus mutation rates were allowed to
 268 range between 1×10^{-5} and 1×10^{-2} . The default value of the parameter P for the geometric
 269 distribution was used. N_e s were allowed to be variable among lakes, to range uniformly between
 270 10 and 10 000, and were assumed to be constant through time. The one-sample summary
 271 statistics employed for generation of simulated datasets included: mean number of alleles, and
 272 mean size variance. Two-sample summary statistics included mean genic diversity,
 273 Classification Index and Shared Allele Distance.

274 A Principal Components Analysis was used to pre-evaluate the similarity between scenario-
 275 generated datasets and the observed dataset. The posterior probabilities of both scenarios were
 276 assessed with the logistic regression method. Linear regression was used to determine the logit-
 277 transformed posterior parameters' distributions, using 1% of the closest simulated datasets. Bias
 278 and precision were estimated for each scenario using 500 pseudo-observed test datasets
 279 simulated using the original parameters from the 1% subset of the closest simulated datasets.
 280 Type I and type II error rates were generated for each scenario using confidence estimates
 281 derived from 500 pseudo-observed test datasets simulated using the original parameters. Model
 282 checking was completed for each scenario using five summary statistics not used in the initial
 283 dataset generation as suggested by Cornuet *et al.* (2010): mean genic diversity (one-sample), the
 284 two-sample mean number of alleles, mean size variance, \hat{F}_{ST} and $\delta\mu^2$ distance.

285

286 RESULTS

287 *Life history: Generation time*

288 For lake trout, age at 50% maturity (α) and generation time (T) were estimated as $\alpha \approx 15$ years
 289 and $T \approx 24$ years, respectively (Electronic Supplement 1). Estimates for longnose suckers ($\alpha \approx 10$
 290 and $T \approx 12 - 13.5$ years) were taken from Salisbury *et al.* (2016) and those for round whitefish (T
 291 $\approx 6.5-7$ years) and lake chub ($T \approx 3-4$ years) were inferred from knowledge of $\alpha = 4+$ for round
 292 whitefish (Armstrong *et al.* 1977; Morin *et al.* 1982) and $\alpha = 2+$ for lake chub (Bruce and Parsons
 293 1976). The four fish species therefore cover the range of plausible scenarios with $T \approx 4$ to $T \approx 24$
 294 suggesting that since deglaciation in northern Labrador around 9000 years BP (Bryson *et al.*
 295 1969, Short and Nichols 1977) the number of generations elapsed may range from 3000
 296 generations for lake chub to approximately 1500 for round whitefish, 900 for longnose sucker
 297 (Salisbury *et al.* 2016), and 500 for lake trout.

298 *General Statistics*

299 Two previous studies on this system, one on lake trout (McCracken *et al.* 2013) and the other on
 300 longnose suckers (Salisbury *et al.* 2016), reported results based on $n \approx 560$ and $n = 869$
 301 individuals, respectively. Here, we report results based on $n = 867$ lake trout genotyped at 12

302 microsatellite markers, $n = 869$ longnose suckers genotyped at 17 microsatellite markers, $n = 456$
303 round whitefish genotyped at 12 microsatellite loci, and $n = 734$ lake chub genotyped at 19
304 microsatellites. Basic statistic data for longnose sucker were reported by Salisbury *et al.* (2016)
305 and are presented here again for completeness (Table 1). The median value of missing data per
306 locus and population were, 4.5% and 5.4% for lake trout, 2.1% and 2.2% for round whitefish,
307 and 2.0% and 1.8% for lake chub. There was no consistent evidence across populations for
308 departures from Hardy-Weinberg proportions for any locus and species, or for linkage
309 disequilibrium between pairs of loci for any of the species. All loci were therefore retained for
310 subsequent analyses for all species. Observed and expected heterozygosities (H_o , H_e) as well as
311 allelic richness (A_r) averaged over loci are reported in Table 1 (Further details available in
312 Electronic supplement 1).

313 ***Population Structure, Genetic Diversity, and Gene Flow***

314 Figure 2 depicts the STRUCTURE results for all four species. Lake trout was the only species
315 collected from all 9 lakes, while no longnose sucker, round whitefish or lake chub were
316 successfully collected from lakes Genetics B and Hawk and no lake chub were collected from
317 Cabot Lake either). All four species required at least a two-level hierarchical STRUCTURE
318 analysis with lake trout and lake chub also requiring a third level (Fig. 2). At the highest
319 hierarchical level lake trout clustered into two groups, a northern group comprising lake trout
320 populations in Lake 1, Genetics H, Slushy, Strange, and Esker-WP152, and a southern group
321 comprising Cabot Lake, T-Bone Lake, Genetics B and Hawk (Fig 2 A-i). A level-2 hierarchical
322 analysis, where the northern group was examined separately, revealed individual lake-level
323 population structure with the exception of lakes Esker and WP152. A level-3 hierarchical
324 analysis revealed no difference between Esker and WP152 fish. Lake trout from Esker and
325 WP152 were thus considered as belonging to a single population in all subsequent analyses.

326 For Longnose sucker, population structure was largely revealed at the highest hierarchical level
327 with the exceptions of individuals from lakes Esker, WP152 and T-Bone (Fig 2B-i). The level-2
328 analysis revealed no differences among these three populations (Fig 2B-ii) unless the analysis
329 was conducted with location priors which distinguished suckers from T-Bone lake from those of
330 Esker and WP152, which could not be distinguished from each other (Fig 2B-iii). Like lake trout,
331 longnose suckers from these two lakes were thus also considered as belonging to a single
332 population in all subsequent analyses.

333 As was the case for longnose sucker above, round whitefish populations could also largely be
334 distinguished at the highest hierarchical level with the exception of individuals from lakes Esker
335 and WP152. This may be a consequence of the very few individuals collected from these two
336 lakes. Similarly for individuals from T-Bone and Cabot Lakes (Fig. 2C): though they were
337 somewhat distinguishable at the highest level, they could not be differentiated clearly in the
338 level-2 analysis (Fig. 2C-ii). As for lake trout, location priors for whitefish did not affect the
339 results.

340 Lastly, for lake chub, the highest hierarchical level involving all populations distinguishes
341 individuals from Lake 1 from all other populations sampled. The second level analysis
342 distinguishes the remaining populations with the exception, once again, of the individuals
343 inhabiting Lakes Esker and WP152, as well as those from Lake Strange where very few
344 individuals were collected (Fig 2D). Esker and WP152 lake chub were also considered as
345 belonging to a single population in all subsequent analyses.

346 The AMOVA analyses conducted following the STRUCTURE results revealed very similar
 347 levels of population structure across all four species with 6-8% of the total variance explained by
 348 variation among groups in all four (LT, K=7: 6.05%; LNS, K=7: 6.72%; RWF, K=7: 7.45%;
 349 LCHB, K=5: 6.26%, Table 2) (Notice that in these comparisons collections from Genetics B and
 350 HAWK were removed since they are only available for lake trout). For lake trout the AMOVA
 351 involving all 9 populations reveals the relatively large genetic differentiation that exists between
 352 the groups north and south of the Kogaluk River with 7.62% of the total variation explained by
 353 differences between groups (Table 2). This percentage increases to 8.30% when most
 354 populations (except ESKER and WP152) are considered individually (Table 2). For round
 355 whitefish (RWF), we conducted an extra AMOVA with K=5 to mimic the STRUCTURE results
 356 where T-Bone (TBN) and Cabot (CAB) are pooled with ESK and WP152 largely because of the
 357 small size of the ESK and WP152 samples (see Fig 2C). The percentage of the total variation
 358 explained by differences among groups is slightly lower than that when K=7 (7.31% vs. 7.45%,
 359 Table 2).

360 Principal Coordinate Analysis (PCoA) based on pairwise linearized \hat{F}_{ST} estimates largely reflect
 361 the species-specific STRUCTURE results (Fig. 3). For lake trout a plot of the first two axes
 362 separate the southern from the northern group of populations along axis 1 (36.6% variance
 363 explained, Fig. 3A). For longnose sucker, axis 1 (34.8% of variance) largely separates the
 364 population in Strange Lake from the rest (Fig. 3B). For round whitefish (Fig. 3C) axis 1 of the
 365 PCoA (37.6% of variance) separates populations in Lakes Slushy, Cabot and T-Bone from the
 366 rest, and finally for lake chub, axis 1 (57.1% of variance, Fig. 3D) clearly distinguishes the
 367 population inhabiting Lake 1 from the rest.

368 *Effective Population Size*

369 Effective population sizes were estimated with and without individuals identified as potential
 370 migrants for all four species (Table 1). For lake trout, only 6 potential migrants were identified
 371 over 9 lakes with no individual population exhibiting >2 potential migrants. Removal of these
 372 individuals caused no significant change in \hat{N}_e (Table 1, lake trout). Three lake trout populations
 373 exhibited $\hat{N}_e < 100$ and all three were in the southern group of populations (T-Bone, Genetics B,
 374 Hawk). Three more populations exhibited $100 < \hat{N}_e \leq 200$ (Genetics H, Slushy and Strange). The
 375 estimates of effective population size for lake trout were relatively high in Cabot lake
 376 ($400 < \hat{N}_e \leq 600$) and in particular for those in Lake 1 ($\hat{N}_e \approx 10\,000$). For lake trout, median $\hat{N}_{e(LT, 9}$
 377 $_{pops}) = 143$ over the 9 populations sampled.

378 For longnose suckers, 21 potential migrants were identified across all 7 lakes with the population
 379 from Genetics H containing the highest number of potential migrants (N=7) but also having the
 380 second largest sample size (N = 201). Regardless, as with the lake trout populations, removal of
 381 potential migrants had negligible effect on \hat{N}_e for the longnose sucker populations with the
 382 possible exception of Lake 1 where \hat{N}_e declined from $\hat{N}_e = 558$ to $\hat{N}_e = 356$ with the removal of
 383 just 2 individuals (Table 1). In contrast to lake trout, there was no longnose sucker population
 384 with an $\hat{N}_e < 100$ and only one with $\hat{N}_e < 200$ (Genetics H $\hat{N}_e \approx 162-168$, Table 1). For 3 of the 7
 385 sampled longnose sucker populations, $\hat{N}_e > 1000$. The median \hat{N}_e for longnose suckers was
 386 higher than that for lake trout (median $\hat{N}_{e(LNS, 7}$
 387 $_{pops}) = 689 > \text{median } \hat{N}_{e(LT, 7}$
 $_{pops}) = 204$; estimated over the 7 common lakes).

388 For round whitefish only 6 individuals overall were identified as potential migrants and no
 389 individual population had > 2 potential migrants removed. As for the previous two species,

390 removal of potential migrants had negligible to no effect on \hat{N}_e (Table 1). $\hat{N}_e < 100$ for two
 391 populations (Lake 1 and Esk-WP152) but sample sizes for both populations were small $N=18$
 392 and 19, respectively. Samples sizes for all other lakes were relatively high (i.e., $61 \leq N \leq 94$) and
 393 for these populations $150 < \hat{N}_e < 600$ with the exception of T-Bone where it could not be
 394 estimated. For round whitefish the median $\hat{N}_{e(RWF, 6 \text{ pops})} = 151$ considering 6 populations and this
 395 value increased to median $\hat{N}_e = 370$ when the two populations with very small sample sizes were
 396 excluded.

397 For lake chub we identified 11 potential migrants across the 6 lakes where this species was
 398 collected from, with the maximum number of potential migrants ($N=3$) collected in Esker-
 399 WP152 where the sample size was largest ($N=304$) (Table 1). As with the previous species, the
 400 removal of potential migrants had little to no effect on \hat{N}_e . No lake chub population exhibited \hat{N}_e
 401 < 100 and the smallest \hat{N}_e (i.e., $\hat{N}_e \approx 272-280$) was detected in Slushy lake; otherwise $445 \leq \hat{N}_e \leq$
 402 1040 (Table 1) and the median $\hat{N}_{e(LCHB, 5 \text{ pops})} = 471$ among the 5 lakes where it could be
 403 estimated.

404 Overall, the median effective size among populations was lowest for lake trout (median $\hat{N}_{e(LT 9$
 405 $\text{ and } 7 \text{ pops})} = 143 - 204$) followed by those for round whitefish (median $\hat{N}_{e(RWF 4 \text{ pops})} = 370$) and
 406 lake chub (median $\hat{N}_{e(LCHB, 5 \text{ pops})} = 471$) with longnose sucker exhibiting the highest median
 407 effective population size (median $\hat{N}_{e(LNS, 7 \text{ pops})} = 689$). Effective population size and lake area
 408 were not correlated in any of the four species (data not shown).

409 *Gene flow and dispersal direction*

410 For lake trout, all estimates of gene flow m between lakes were non-significant with the possible
 411 exception of migration from Esker-WP152 to Genetics B ($m [95\%CI] = 0.091 [0.009-0.173]$,
 412 Table 3A). This is inconsistent with the fact that the lakes are located on opposite sides of the
 413 Kogaluk fjord. We therefore conclude there is no evidence that lake trout migrate between lakes
 414 in the Kogaluk River drainage. Unlike lake trout, longnose suckers from Lakes Esker-WP152
 415 exhibited gene flow > 0 to four other populations: low upstream gene flow from Esker-WP152
 416 towards Genetics H, Slushy, and Strange and relatively high downstream gene flow to Cabot
 417 Lake (Table 3B). Gene flow between all other longnose sucker populations was non-significant
 418 (Table 3B). Round whitefish exhibited downstream gene flow $m > 0$ from Strange Lake to Lake
 419 Esker-WP152 ($m [95\% CI] = 0.130 [0.044 - 0.216]$, Table 3C) and was otherwise nil. Finally,
 420 lake chub exhibited upstream gene flow $m > 0$ from Esker-WP152 to Slushy and Strange, a
 421 pattern similar at least partially, to that observed for longnose sucker (Table 3D and Fig. 4).
 422 Thus, all instances in which gene flow was distinctly larger than zero involved Lake Esker-
 423 WP152 mostly as a source of gene flow.

424 *Colonization history (Fig.5)*

425 Figure 5 presents the two contrasting potential colonization scenarios and their posterior
 426 probabilities as a function of the stringency threshold used for three of the species examined in
 427 this study: (a) Lake trout, (b) Longnose sucker and (c) Round whitefish. For all three species,
 428 scenario 1 reflects colonization from the southwest via the proglacial Lake Nauskapi. Under this
 429 scenario (scenario 1) the ancestral population first colonized T-Bone Lake (TBN) from which
 430 fish expanded into the remainder of the drainage. Scenario 2, instead, reflects colonization from
 431 the east via the sea for all three species. Under this scenario (scenario 2), the ancestral population
 432 first colonized Cabot Lake from which fish expanded into the remainder of the drainage.

433 Potential colonization scenarios involve 9 lakes (populations) for lake trout but only 7 lakes for
434 each of longnose sucker and round whitefish. For all three species the relative posterior
435 probability of scenario 1 is much higher than that of scenario 2 (Fig. 5).

436 The ancestral lake trout population first colonized T-Bone Lake from which lake trout expanded
437 more or less simultaneously to Hawk and Cabot Lake followed by colonization of Genetics B,
438 and Slushy and Strange. Subsequently, lake trout from Lakes Slushy and Strange admixed to
439 expand into Esker-WP152 (EKW). Then lake trout from EKW colonized Genetics H (G-H) from
440 which lake trout colonized Lake 1 (L-1). Over all lakes, the colonization process likely started
441 approximately 700 generation ago and was complete 250 generations ago (Fig 5a). Under
442 scenario 2, ancestral lake trout first colonized Cabot Lake from which they expanded into Hawk,
443 Genetics B and T-Bone at t_7 , t_6 and t_5 , respectively. The pattern of colonization for the remaining
444 lakes is the same as under scenario 1. Scenario 1 received the highest support suggesting lake
445 trout likely colonized the Kogaluk system from the SW (Fig. 5a).

446 The same two scenarios or hypotheses were tested with longnose sucker (Fig. 5b) and round
447 whitefish (Fig. 5c): Under scenario 1, the ancestral longnose sucker population first colonized T-
448 Bone. From this lake suckers expanded into Strange followed by the more or less simultaneous
449 colonization of Cabot and Slushy and the admixture of Slushy and Strange giving rise to Esker-
450 WP152. Under scenario 1, the system's colonization by longnose sucker likely started
451 approximately 350 generations ago and was complete approximately 100 generations ago.
452 Colonization by round whitefish likely started ~1500 generations ago and was complete ~900
453 generations ago (Fig. 5c). Parameter posterior distributions and model fits are shown in
454 Electronic Supplement 2.

455

456 **DISCUSSION**

457 We have shown that historical processes are important drivers of the observed genetic structure
458 in extant fish populations inhabiting a spatially fragmented system that has been undisturbed so
459 far. This is true for all three species in our study where this issue was examined regardless of the
460 number of generations that have elapsed since their estimated arrival to the area. However, all
461 four species exhibit a hierarchical pattern of population structure with similar diversity patterns
462 despite differences in effective population size, generation interval and even contemporary
463 migration rate estimates. Combined, these results suggest that contemporary landscape is
464 important and influenced colonization history. The effects of colonization history are still
465 observable in the population structure. The four species examined, lake trout (*Salvelinus*
466 *namaycush*), longnose sucker (*Catostomus catostomus*), round whitefish (*Prosopium*
467 *cylindraceum*), and lake chub (*Couesius plumbeus*) are widespread throughout Canada and other
468 regions of the world. Understanding how they behave in this particular system that is free of
469 direct anthropogenic interference can provide a baseline against which one can evaluate how
470 other systems undergoing anthropogenic perturbations are performing. Importantly, our results
471 suggest that theoretical predictions based on equilibrium scenarios may not be a good baseline
472 for comparison in the case of species inhabiting similar lake networks. Below we discuss the
473 details of our findings and the implications for other spatially fragmented systems in northern
474 latitudes.

475 Three of the four species included in the present study most likely colonized the Kogaluk River
476 drainage from the southwest. This is the most likely colonization scenario suggested by the ABC

477 analysis for the three species with sufficient geographic sampling coverage for the testing of
478 alternate colonization hypotheses, i.e., lake trout (*Salvelinus namaycush*), longnose sucker
479 (*Catostomus catostomus*) and round whitefish (*Prosopium cylindraceum*). These analyses were
480 conducted with DIYABC (Cornuet *et al.* 2014) a software package that may not be able to
481 capture detailed demographic processes but can still capture major demographic changes
482 (Cabrera and Palsboll 2017). It is thus possible that our scenarios may not have captured the
483 precise and detailed chronological sequence of how the northern lakes were colonized. However,
484 both scenarios examined are similar in this regard: they largely only differ in the location of the
485 most ancestral population(s), whether those inhabiting the southwestern-most lake, T-Bone Lake
486 (scenario 1) or those inhabiting the easternmost lake, and the lake closest to the Kogaluk River
487 mouth, Cabot Lake. We are thus confident our models capture the essence of the two alternate
488 colonization routes for this system and species considered. In fact our results are consistent with
489 Black *et al.* (1986) who argued fish are most likely to have colonized Labrador following the last
490 glacial retreat via overland route across Quebec rather than from the sea (see Michaud *et al.*
491 2010).

492 All four species exhibit a hierarchical pattern of contemporary population structure, with
493 analyses consistently indicating, that their respective Esker and WP152 populations are
494 genetically indistinguishable from each other. Further, the percentage of the total genetic
495 variation that is explained by differences among groups is similar across species and ranges
496 between 6-8%. Thus, all species exhibit similar diversity patterns despite the fact that they differ
497 in effective population size and generation interval and at least three of them fit the same
498 colonization model. Combined, these results suggest that landscape has driven the colonization
499 history, and its effects can still be observed in the genetic structuring of all four species.

500 Gene flow among populations was largely insignificant for lake trout and round whitefish. For
501 longnose sucker though, gene flow was $m > 0$ out of the centrally located confluence Lake
502 Esker-WP152, upstream to Slushy, Strange and Genetics H and downstream to Cabot Lake.
503 Similarly for lake chub, gene flow from Esker-WP152 was significant upstream to Slushy and
504 Strange and downstream to Cabot Lake. Upstream migration for longnose sucker is consistent
505 with the spawning migration for this species (Scott and Crossman 1998). Downstream migration
506 for both longnose suckers and lake chub probably results from downstream passive transport of
507 juveniles (Ryan 1980). Upstream migration is likely to result in an increase in the genetic
508 diversity in headwater locations and in an erosion of their isolation (Salisbury *et al.* 2016).
509 Overall however, contemporary gene flow appears to play a relatively minor role in the
510 distribution of genetic diversity for at least two of the species. One possibility is that colonization
511 of downstream lakes was almost instantaneous and this was followed by little migration. For
512 these two species therefore, lower diversity in downstream lakes may be due to a strong initial
513 bottleneck and subsequent genetic drift affecting all lakes.

514 Fish collection took place over a period of 13 years from 2002 to 2015 (particularly for lake
515 trout, longnose sucker and round whitefish). Given the relatively long life spans and generation
516 intervals that characterise these species and the stable age structure composition typical of these
517 remote, inaccessible and unexploited subarctic lakes (Johnson 1976; Power 1978), it can
518 reasonably be assumed that diversity and structure have not changed over this period.

519 Estimates of effective size for longnose sucker were obtained by first estimating the effective
520 number of breeders (N_b) using single cohorts or pools of individuals of 2-3 cohorts when sample
521 sizes for individual cohorts were too small. These were then extrapolated to \hat{N}_e using the

522 empirical relationships described by Waples and coworkers (Waples *et al.* 2013, 2014; Ruzzante
 523 *et al.* 2016; see Salisbury *et al.* 2016). Our ability to follow this procedure with the other two
 524 species for which age information was available for at least some genotyped individuals, lake
 525 trout and round whitefish, was limited, because of the large number of age classes and cohorts in
 526 our samples resulting in low sample sizes per cohort and uncertainty in the value of the adult life
 527 span, a value required for the application of Waples *et al.* (2013, 2014) empirical equations. This
 528 limitation notwithstanding, effective size estimates did not change significantly with the removal
 529 of potential migrants in any of the four species. Estimates were lowest for lake trout (median \hat{N}_e
 530 _(LT 9 and 7 pops) = 143 - 204) and highest for longnose sucker (median \hat{N}_e (LNS) = 689) with those for
 531 round whitefish and lake chub being intermediate (Table 1). Species generally differed in the
 532 lakes in which their respective populations exhibited the largest effective sizes. Lake trout
 533 exhibited the highest diversity in Lake 1 while longnose sucker exhibited the greatest effective
 534 population size in T-Bone Lake. Lake chub exhibited the largest \hat{N}_e s in Esk-WP152 and T-Bone.
 535 Round whitefish, however, differed from the previous three species with its highest \hat{N}_e s observed
 536 in populations inhabiting Lakes Slushy and Genetics H. Thus, though the four species differed in
 537 the lake in which they exhibited the largest effective size, these were often found in headwater
 538 lakes.

539 Examination of the potential colonization scenarios requires knowledge of the number of
 540 generations that could have lapsed since deglaciation and hence knowledge of generation time.
 541 We estimated age at first maturity and generation time for lake trout as $\alpha = 15$ and $T = 24$ years,
 542 respectively. Our estimated generation time T therefore is longer than the value ($T=15$) used by
 543 Harris *et al.* (2015) for lake trout inhabiting Great Bear Lake located 10° of latitude further north
 544 in the Northwest Territories than the Kogaluk River. Assuming these values have remained
 545 invariant through time, lake trout would have first colonized the southern lakes in the system
 546 (i.e., Cabot, GeneticsB, Hawk) between ca. 10 500 and 16 800 BP. This is clearly unlikely or
 547 even unfeasible since the area was covered by Laurentide Ice Sheet until ca. 9000 BP (Bryson *et al.*
 548 1969, Short and Nichols 1977) and the Nauskapi Lake is thought to have first formed ca.
 549 8000 BP (Jansson and Kleman 2004). However, neither age at first maturity nor generation time
 550 are likely to have remained invariant and may indeed have been much shorter than current values
 551 during the species historical demographic expansion and colonization phase. Second, the fact
 552 that DIYABC has been shown not to be very accurate at recovering the timing of events (Cabrera
 553 and Palsboll 2017) suggests caution should be exercised when interpreting the timing of
 554 demographic events. Disregarding issues of event timing, longnose sucker ($\alpha=10$, $T\approx 12$,
 555 Salisbury *et al.* 2016) would have first expanded and colonized the system between ca. 3400-
 556 4200 BP with the expansion/colonization probably complete by 1000-1200 BP. Similarly for
 557 round whitefish, with a generation time $T = 6.5-7$ (Morin *et al.* 1982), colonization would have
 558 started a maximum of 9600-10500 BP and would have been complete by as early as 5700-6200
 559 BP. Assuming an age at first maturity $\alpha \approx 4$, the corresponding numbers would be 6000 BP and
 560 3500 BP.

561 Regardless of the uncertainties and potential biases inherent with the ABC approach
 562 implemented in the DIYABC software package (Cabrera and Palsboll 2017) the genetic variation
 563 observed still retains the footprint of the historical colonization pathways. This is true for all
 564 three species examined despite the differences in number of generations that are likely to have
 565 elapsed since their respective arrival to the region. One possibility is for the system to be in a
 566 transitional state where genetic diversity was originally seeded into the headwaters during

567 colonization, with subsequent pooling of genetic diversity in downstream lakes such as Esker-
568 WP152 and Cabot. However, the system as a whole is still out of migration-drift equilibrium
569 because of its relatively young age and may at present, only be transitioning to a dendritic
570 system. We note though that the combination of upstream migration reported for two of the
571 species along with the otherwise low migration rates observed and the long generation intervals
572 described for several of the species would tend to slow down progress towards such migration-
573 drift equilibrium (Salisbury *et al.* 2016). Landscape is also important. All species exhibit similar
574 levels of contemporary population structure despite widely diverging generation times (six-fold
575 variation from approx. 4 years for lake chub to perhaps as many as 24 years for lake trout) and
576 effective sizes (range across species median $\hat{N}_e \sim 150$ to ~ 700), both of which affect the rate of
577 approach to equilibrium (Whitlock and McCauley 1999). These results suggest an important role
578 for the landscape in influencing the observed structure (McCracken *et al.* 2013, Salisbury *et al.*
579 2016). First, it is likely that the streams connecting these lakes, which are generally frozen from
580 October to May (Wheeler 1935) and exhibit reduced flow prior to the winter freeze (Robert
581 Perry personal observation) offer little opportunity for significant connectivity. Second, the
582 various waterfalls in the system (Fig. 1) almost certainly prevent upstream migration. Thus, the
583 relatively short time since the colonization event along with the limited gene flow among lakes,
584 which delays a progression to equilibrium conditions, and the relatively long generation intervals
585 have not allowed the species in the Kogaluk river drainage to reach an equilibrium between drift
586 and gene flow. Our study clearly demonstrates that an improved understanding of historical and
587 contemporary processes is required to fully explain observed patterns of structure and gene flow
588 in metapopulation systems from regions affected by the Quaternary glaciations (see also Vera-
589 Escalona *et al.* 2015, 2018). These studies highlight the importance of a temporal perspective on
590 connectivity for the understanding of diversity in spatially complex metapopulations.

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799 **Data Accessibility Statement:** Microsatellite genotypes: MS Dryad ID: MEC-18-0629 Dryad
800 doi: data will be uploaded upon Editorial Decision on the MS

801

802 **Author Contributions:** DER, RP, DK participated in the study design; RP, DK; DER, GRM,
803 SJS participated in the fieldwork; GRM, SJS and HTB produced the genetic data for the four
804 species and together with DER and OEG were involved in the genetic analysis and
805 interpretation. DER led the writing of the MS with participation and input from all authors.

806

807 **Table 1.** Summary statistics for 9 lakes of the Kogaluk River catchment sampled between 2006 and 2015.
 808 Information is provided for N = sample size [numbers in square brackets indicate sample size after removal of
 809 potential migrants]; H_O = observed heterozygosity; H_E = expected heterozygosity; A_r = allelic richness; \hat{N}_e =
 810 estimate of effective population size. Lake trout were the only species sampled from lakes Genetics B and
 811 Hawk. No lake chub were collected from lake Cabot. Lake areas (km²) are as follows: Lake 1: 11.3, Genetics H;
 812 2.81, Slushy: 2.99, Strange: 2.09, Esker-WP152: 53.94, T-Bone: 19.76, Cabot: 25.39, Genetics B: 9.71, Hawk:
 813 57.4.

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Lake trout (*Salvelinus namaycush*)

	N	Ho	He	Ar	\hat{N}_e	\hat{N}_e (likely migrants removed)
Lake 1	119 [119]	0.495	0.494	4.41	10217 (215 - ∞)	10217 (215 - ∞)
Genetics H	111 [110]	0.510	0.508	4.14	204 (93 - 4812)	203 (91 - 544)
Slushy	86 [84]	0.508	0.489	3.71	143 (63 - 4299)	141 (60 - 4299)
Strange	159 [159]	0.471	0.479	4.02	116 (78 - 196)	116 (78 - 196)
Esker-WP152	157 [155]	0.465	0.470	5.42	350 (133 - ∞)	323 (125 - ∞)
T-Bone	40 [40]	0.530	0.531	4.74	68 (32 - 433)	68 (32 - 433)
Cabot	80 [79]	0.565	0.576	4.94	630 (120 - ∞)	436 (110 - ∞)
Genetics B	49 [49]	0.500	0.466	4.29	50 (29 - 122)	50 (29 - 122)
Hawk	66 [66]	0.438	0.409	3.44	56 (27 - 211)	56 (27 - 211)
Total	867					

Longnose sucker (*Catostomus catostomus*)

	N	Ho	He	Ar	\hat{N}_e	\hat{N}_e (likely migrants removed)
Lake 1	59 [57]	0.66	0.65	8.28	558 (202 - ∞)	356 (160 - ∞)
Genetics H	201 [194]	0.63	0.64	9.45	168 (135 - 217)	162 (130 - 210)
Slushy	103 [99]	0.65	0.64	9.92	314 (209 - 590)	314 (209 - 590)
Strange	122 [118]	0.61	0.61	8.48	821 (383 - ∞)	932 (402 - ∞)
Esker - WP152	212 [210]	0.66	0.66	14.09	2740 (1017 - ∞)	2740 (1017 - ∞)
T-Bone	115 [114]	0.63	0.64	9.62	NA (820 - ∞)	12177 (744 - ∞)
Cabot	57 [56]	0.65	0.65	10.52	1197 (302 - ∞)	1197 (336 - ∞)
Total	869					

Round whitefish (*Prosopium cylindraceum*)

	N	Ho	He	Ar	\hat{N}_e	\hat{N}_e (likely migrants removed)
Lake 1	18 [18]	0.414	0.430	2.59	86 (18 - ∞)	86 (18 - ∞)
Genetics H	87 [86]	0.487	0.473	2.73	507 (118 - ∞)	418 (108 - ∞)

<i>Slushy</i>	91 [91]	0.424	0.432	2.59	566 (98 - ∞)	566 (98 - ∞)
<i>Strange</i>	86 [84]	0.512	0.499	2.76	151 (78 - 639)	146 (76 - 590)
<i>Esker - WP152</i>	19 [19]	0.510	0.541	3.89	94 (33 - ∞)	94 (33 - ∞)
<i>T-Bone</i>	61 [59]	0.452	0.478	2.78	NA (131 - ∞)	NA (130 - ∞)
<i>Cabot</i>	94 [93]	0.441	0.434	2.65	234 (81 - ∞)	177 (75 - ∞)
Total:	456					
Lake chub (<i>Couesius plumbeus</i>)						
	N	Ho	He	Ar	\hat{N}_e	\hat{N}_e (likely migrants removed)
<i>Lake 1</i>	95 [93]	0.429	0.438	3.81	454 (161 - ∞)	459 (163 - ∞)
<i>Genetics H</i>	111 [109]	0.487	0.493	3.8	471 (188 - ∞)	445 (185 - ∞)
<i>Slushy</i>	113 [112]	0.516	0.513	4.18	280 (156 - 923)	272 (151 - 907)
<i>Strange</i>	19 [18]	NA	NA	NA	NA (212 - ∞)	NA (257 - ∞)
<i>Esker - WP152</i>	304 [301]	0.518	0.529	7.82	1040 (497 - 23560)	987 (481 - 12120)
<i>T-Bone</i>	92 [91]	0.498	0.501	3.94	815 (196 - ∞)	922 (199 - ∞)
<i>Cabot</i>	NA	NA	NA	NA	NA	NA
	734					

817 Table 2. Hierarchical AMOVAs for each of the four species (a) Lake trout (LT) under K=2 and K=6 (b)
 818 Longnose sucker (LNS) under K=7 (only ESK and WP152 pooled), (c) Round whitefish (RWF) under K=5
 819 (STRUCTURE RESULTS) and K=7 (only ESK and WP152 pooled) and (d) Lake chub (LCHUB) under K=5
 820 (STRUCTURE RESULTS). Df: Degrees of freedom. SS: Sum of Squares. L-1: Lake 1; G-H: Genetics H; SLU:
 821 Slushy; STR: Strange; ESK-WP: Esker-WP152; TBN: T-Bone; CAB: Cabot; G-B: Genetics B; HWK: Hawk.

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	SOURCE OF VARIATION	df	SS	VARIANCE COMPONENTS	% VARIATION
LT K=2	(L-1, G-H, SLU, STR, ESK-WP) (TBN, CAB, G-B, HWK)				
	Among groups	1	65.49	0.079	7.62
	Among Populations within groups	8	88.29	0.057	5.54
	Among Individuals within populations	1764	1584.28	0.898	86.84
	Total	1773	1738.05	1.034	
LT K=9	(L-1)(G-H)(SLU)(STR)(ESK-WP) (TBN) (CAB) (G-B)(HWK)				
	Among groups	8	150.95	0.082	8.30
	Among Populations within groups	1	2.83	0.012	1.19
	Among Individuals within populations	1764	1584.28	0.898	90.50
	Total	1773	1738.05	0.992	
LT K=7	(L-1) (G-H) (SLU) (STR) (ESK-WP) (TBN) (CAB)				
	Among groups	6	95.88	0.060	6.05
	Among Populations within groups	1	2.826	0.012	1.19
	Among Individuals within populations	1528	1398.75	0.915	92.76
	Total	1535	1497.46	0.987	
LNS K=7	(L-1)(G-H) (SLU) (STR) (ESK-WP) (TBN) (CAB)				
	Among groups	6	72.69	0.049	6.72
	Among populations within groups	1	-0.31	0.002	-0.27
	Within populations	1730	1190.97	0.688	93.54
	Total	1737	1263.96	0.736	
RWF K=5 STRUCTURE RESULT	(L-1) (G-H)(SLU)(STR) (ESK,WP,TBN,CAB)				

	Among groups	4	205.12	0.186	7.31
	Among Populations within groups	3	32.41	0.128	5.01
	Among Individuals within populations	904	2018.39	2.233	87.68
	Total	911	2255.93	2.547	
RWF K=7	(L-1) (G-H)(SLU)(STR) (ESK-WP) (TBN) (CAB)				
	Among groups	6	233.32	0.188	7.45
	Among populations within groups	1	4.21	0.107	4.22
	Among individuals within populations	904	2018.39	2.233	88.33
	Total	911	2255.93	2.528	
LCHUB K=5 STRUCTURE RESULT	(L-1)(G-H)(SLU)(STR,ESK,WP) (TBN)				
	Among groups	4	236.40	0.181	6.26
	Among populations within groups	2	18.48	0.037	1.28
	Among individuals within populations	1461	3912.95	2.678	92.46
	Total	1467	4167.84	2.897	

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825 Table 3. Gene flow estimates (migration rate, m , 95% CI) obtained via BayesAss+ 1.3: Columns are the source and rows are the recipient populations
 826 (A) Lake trout (*Salvelinus namaycush*) generally indicating little gene flow among lake trout populations in the Kogaluk River catchment. (B)
 827 Longnose sucker (*Catostomus catostomus*) (C) Round whitefish (*Prosopium cylindraceum*) and (D) lake chub (*Couesius plumbeus*). Significant
 828 estimates in *italics and bold*

829 (A) Lake trout (*Salvelinus namaycush*)

Into\From	Lake 1	Genetics H	Slushy	Strange	Esker-WP152	T-Bone	Cabot	Genetics B	Hawk
Lake 1	0.939 (0.902 - 0.976)	0.017 (-0.008 - 0.042)	0.011 (-0.007 - 0.029)	0.007 (-0.007 - 0.021)	0.008 (-0.006 - 0.022)	0.005 (-0.003 - 0.013)	0.004 (-0.004 - 0.012)	0.005 (-0.005 - 0.015)	0.004 (-0.004 - 0.012)
Genetics H	0.008 (-0.006 - 0.022)	0.926 (0.887 - 0.965)	0.006 (-0.006 - 0.018)	0.006 (-0.006 - 0.018)	0.030 (-0.003 - 0.063)	0.003 (-0.003 - 0.009)	0.005 (-0.005 - 0.015)	0.005 (-0.005 - 0.015)	0.011 (-0.005 - 0.027)
Slushy	0.006 (-0.006 - 0.018)	0.008 (-0.006 - 0.022)	0.912 (0.855 - 0.969)	0.008 (-0.008 - 0.024)	0.048 (-0.003 - 0.099)	0.004 (-0.004 - 0.012)	0.005 (-0.003 - 0.013)	0.005 (-0.003 - 0.013)	0.005 (-0.005 - 0.015)
Strange	0.006 (-0.004 - 0.016)	0.006 (-0.004 - 0.016)	0.004 (-0.004 - 0.012)	0.957 (0.924 - 0.990)	0.017 (-0.010 - 0.044)	0.002 (0 - 0.004)	0.002 (-0.002 - 0.006)	0.003 (-0.001 - 0.007)	0.003 (-0.003 - 0.009)
Esker-WP152	0.008 (-0.006 - 0.022)	0.011 (-0.007 - 0.029)	0.006 (-0.006 - 0.018)	0.029 (-0.004 - 0.062)	0.934 (0.891 - 0.977)	0.002 (-0.002 - 0.006)	0.003 (-0.003 - 0.009)	0.003 (-0.003 - 0.009)	0.006 (-0.002 - 0.014)
T-Bone	0.016 (-0.011 - 0.043)	0.010 (-0.010 - 0.030)	0.016 (-0.011 - 0.043)	0.012 (-0.012 - 0.036)	0.021 (-0.012 - 0.054)	0.874 (0.815 - 0.933)	0.017 (-0.012 - 0.046)	0.021 (-0.010 - 0.052)	0.012 (-0.010 - 0.034)
Cabot	0.008 (-0.006 - 0.022)	0.006 (-0.004 - 0.016)	0.006 (-0.004 - 0.016)	0.005 (-0.005 - 0.015)	0.008 (-0.006 - 0.022)	0.005 (-0.005 - 0.015)	0.948 (0.915 - 0.981)	0.007 (-0.005 - 0.019)	0.008 (-0.006 - 0.022)
Genetics B	0.054 (-0.009 - 0.117)	0.011 (-0.011 - 0.033)	0.013 (-0.012 - 0.038)	0.053 (-0.014 - 0.120)	0.091 (0.009 - 0.173)	0.007 (-0.007 - 0.021)	0.011 (-0.011 - 0.033)	0.741 (0.680 - 0.802)	0.019 (-0.018 - 0.056)
Hawk	0.005 (-0.005 - 0.015)	0.005 (-0.005 - 0.015)	0.005 (-0.005 - 0.015)	0.007 (-0.007 - 0.021)	0.007 (-0.007 - 0.021)	0.005 (-0.005 - 0.015)	0.006 (-0.006 - 0.018)	0.005 (-0.005 - 0.015)	0.954 (0.925 - 0.983)

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832 (B) Longnose sucker (*Catostomus catostomus*)

Into\From	Lake 1	Genetics H	Slushy	Strange	Esker-WP152	T-Bone	Cabot
Lake 1	0.955 (0.924 - 0.986)	0.006 (-0.006 - 0.018)	0.007 (-0.007 - 0.021)	0.007 (-0.007 - 0.021)	0.009 (-0.008 - 0.026)	0.010 (-0.007 - 0.027)	0.005 (-0.005 - 0.015)
Genetics H	0.005 (-0.003 - 0.013)	0.913 (0.878 - 0.948)	0.012 (-0.002 - 0.026)	0.007 (-0.003 - 0.017)	0.045 (0.016 - 0.074)	0.015 (-0.005 - 0.035)	0.002 (-0.002 - 0.006)
Slushy	0.008 (-0.006 - 0.022)	0.008 (-0.006 - 0.022)	0.876 (0.829 - 0.923)	0.008 (-0.006 - 0.022)	0.084 (0.039 - 0.129)	0.012 (-0.008 - 0.032)	0.004 (-0.004 - 0.012)
Strange	0.011 (-0.003 - 0.025)	0.003 (-0.003 - 0.009)	0.005 (-0.003 - 0.013)	0.947 (0.922 - 0.972)	0.026 (0.002 - 0.050)	0.005 (-0.005 - 0.015)	0.004 (-0.002 - 0.010)
Esker-WP152	0.013 (-0.005 - 0.031)	0.015 (-0.003 - 0.033)	0.017 (-0.005 - 0.039)	0.011 (-0.003 - 0.025)	0.935 (0.898 - 0.972)	0.006 (-0.006 - 0.018)	0.003 (-0.003 - 0.009)
T-Bone	0.006 (-0.004 - 0.016)	0.006 (-0.006 - 0.018)	0.005 (-0.005 - 0.015)	0.003 (-0.003 - 0.009)	0.009 (-0.007 - 0.025)	0.967 (0.943 - 0.991)	0.003 (-0.003 - 0.009)
Cabot	0.007 (-0.007 - 0.021)	0.008 (-0.006 - 0.022)	0.007 (-0.007 - 0.021)	0.009 (-0.007 - 0.025)	0.241 (0.174 - 0.308)	0.044 (-0.013 - 0.101)	0.684 (0.659 - 0.709)

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835 (C) Round whitefish (*Prosopium cylindraceum*)

Into/From	Lake 1	Genetics H	Slushy	Strange	Esker-WP152	T-Bone	Cabot
Lake 1	0.728 (0.638 - 0.818)	0.015 (-0.014 - 0.044)	0.039 (-0.020 - 0.098)	0.107 (-0.007 - 0.221)	0.014 (-0.013 - 0.041)	0.030 (-0.023 - 0.083)	0.067 (-0.075 - 0.149)
Genetics H	0.004 (-0.004 - 0.012)	0.959 (0.930 - 0.988)	0.007 (-0.007 - 0.021)	0.008 (-0.008 - 0.024)	0.004 (-0.004 - 0.012)	0.009 (-0.007 - 0.025)	0.008 (-0.008 - 0.024)
Slushy	0.004 (-0.004 - 0.012)	0.005 (-0.005 - 0.015)	0.967 (0.942 - 0.992)	0.008 (-0.006 - 0.022)	0.004 (-0.004 - 0.012)	0.006 (-0.006 - 0.018)	0.007 (-0.005 - 0.019)
Strange	0.004 (-0.004 - 0.012)	0.010 (-0.008 - 0.028)	0.006 (-0.006 - 0.018)	0.951 (0.916 - 0.986)	0.005 (-0.005 - 0.015)	0.015 (-0.007 - 0.037)	0.011 (-0.007 - 0.029)
Esker-WP152	0.016 (-0.015 - 0.047)	0.015 (-0.012 - 0.042)	0.035 (-0.024 - 0.094)	0.130 (0.044 - 0.216)	0.686 (0.649 - 0.723)	0.033 (-0.028 - 0.094)	0.085 (-0.005 - 0.175)
T-Bone	0.005 (-0.005 - 0.015)	0.010 (-0.008 - 0.028)	0.019 (-0.006 - 0.044)	0.006 (-0.006 - 0.018)	0.006 (-0.006 - 0.018)	0.932 (0.885 - 0.979)	0.021 (-0.014 - 0.056)
Cabot	0.004 (-0.004 - 0.012)	0.005 (-0.005 - 0.015)	0.012 (-0.010 - 0.034)	0.013 (-0.007 - 0.033)	0.004 (-0.004 - 0.012)	0.015 (-0.010 - 0.040)	0.946 (0.907 - 0.985)

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837 (D) Lake chub (*Couesius plumbeus*)

Into/From	Lake 1	Genetics H	Slushy	Strange	Esker-WP152	T-Bone
Lake 1	0.974 (0.954 - 0.994)	0.008 (-0.004 - 0.020)	0.005 (-0.003 - 0.013)	0.003 (-0.003 - 0.009)	0.006 (-0.004 - 0.016)	0.005 (-0.005 - 0.015)
Genetics H	0.004 (-0.004 - 0.012)	0.962 (0.933 - 0.991)	0.009 (-0.007 - 0.025)	0.003 (-0.003 - 0.009)	0.017 (-0.008 - 0.042)	0.006 (-0.006 - 0.018)
Slushy	0.005 (-0.005 - 0.015)	0.012 (-0.010 - 0.034)	0.907 (0.846 - 0.968)	0.003 (-0.003 - 0.009)	0.068 (0.011 - 0.125)	0.006 (-0.006 - 0.018)
Strange	0.010 (-0.010 - 0.030)	0.096 (0.016 - 0.176)	0.037 (-0.026 - 0.100)	0.680 (0.654 - 0.705)	0.152 (0.056 - 0.248)	0.025 (-0.024 - 0.074)
Esker-WP152	0.002 (-0.002 - 0.006)	0.004 (-0.004 - 0.012)	0.010 (-0.004 - 0.024)	0.001 (-0.001 - 0.003)	0.977 (0.959 - 0.995)	0.006 (-0.002 - 0.014)

T-Bone	0.008	0.008	0.006	0.003	0.012	0.962
	(-0.004 - 0.020)	(-0.006 - 0.022)	(-0.006 - 0.018)	(-0.003 - 0.009)	(-0.008 - 0.032)	(0.933 - 0.991)

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839

840 Figure 1. Study area showing all lakes and connecting tributaries in the Kogaluk River catchment in
 841 northern Labrador (lakes were sampled for lake trout, longnose sucker, round whitefish and lake chub).
 842 The Kogaluk River drains into the Atlantic Ocean via Voisey Bay. Waterfalls (WF1 to WF5) are
 843 indicated by small bars; their approximate heights and angles as determined by ground surveys
 844 (Anderson 1985) are as follows: WF1 \approx 15 m and 90°, WF2 \approx 12 m and 90°; WF3 \approx 5.4 m and 90°;
 845 WF4 \approx 5.4 m and 90°; WF5 \approx 9 m and 60°-90° (Anderson, 1985). The arrow represents the directional
 846 flow of water in the system. Mistastin Lake was not included in the analysis. Lake trout were
 847 successfully collected from all lakes visited. No longnose suckers, round whitefish or lake chub were
 848 collected from Genetics B or Hawk. No lake chub were collected from Cabot lake. Sample sizes per
 849 species and lake are available in Table 1.

850 Figure 2. Hierarchical population STRUCTURE analysis for (A) lake trout (*Salvelinus namaycush*)
 851 based on 12 microsatellite loci (B) Longnose sucker (*Catostomus catostomus*) based on 17
 852 microsatellite loci (C) round whitefish (*Prosopium cylindraceum*) based on 12 microsatellite loci and
 853 (D) lake chub (*Couesius plumbeus*) based on 19 microsatellite markers. Vertical coloured lines represent
 854 individual admixture coefficients. No differentiation was detected among fish from Esker and lake
 855 WP152 in any of the four species. Thus, individuals from Esker and WP152 were considered as a single
 856 population for all 4 species.

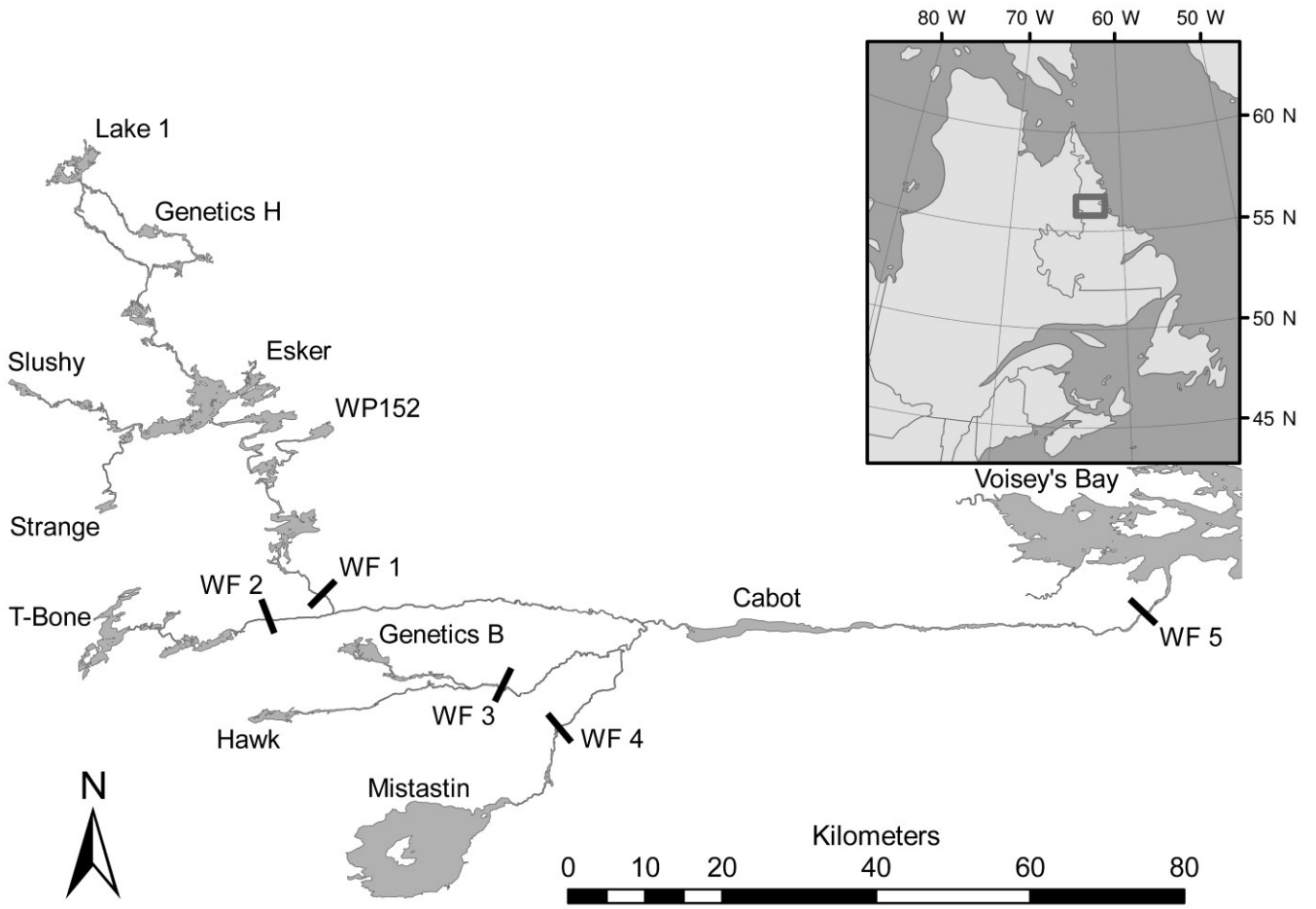
857 Figure 3. Principal Coordinate analysis based on the matrix of pairwise linearized F_{ST} estimates for (A)
 858 lake trout (*S. namaycush*) (B) Longnose sucker (*C. catostomus*) (C) round whitefish (*P. cylindraceum*)
 859 (D) lake chub (*Couesius plumbeus*). (Values in brackets indicate the % of genetic variation explained by
 860 the Principal Coordinate).

861 Fig. 4. Schematic representation of gene flow estimates \hat{m} for all species. Lake trout exhibited no gene
 862 flow among lakes. Longnose suckers exhibited upstream gene flow from Esker-WP152 into Slushy and
 863 Strange and downstream gene flow into Cabot lake. Round whitefish exhibited downstream gene flow
 864 from Strange into Esker-WP152 and lake chub exhibited upstream gene flow from Esker-WP152 into
 865 Slushy and Strange. Numbers in brackets indicate the standard deviation of the estimates.

866 Fig. 5. Kogaluk drainage potential colonization scenarios and their posterior probabilities as a function
 867 of the stringency threshold used for three of the four species examined in this study: (a) Lake trout
 868 (*Salvelinus namaycush*), (b) Longnose sucker (*Catostomus catostomus*) and (c) Round whitefish
 869 (*Prosopium cylindraceum*). For all three species, scenario 1 reflects colonization from the southwest
 870 via the glacial lake Nauskapi. Under scenario 1 the ancestral population first colonized T-Bone Lake
 871 (TBN) from which fish expanded into the remainder of the drainage. Scenario 2, instead, reflects
 872 colonization from the east via the sea for all three species. Under scenario 2 the ancestral population first
 873 colonized Cabot lake from where fish expanded into the remainder of the drainage. The system
 874 comprises nine major lakes, from north to south: Lake 1 (L-1), Genetics H (G-H), Slushy (SLU),
 875 Strange (STR), Esker-WP152 (EKW), T-Bone (TBN), Cabot (CAB), Genetic B (G-B) and Hawk
 876 (HWK) (See Fig. 1). Lake trout were successfully collected from all 9 lakes but no longnose sucker or
 877 round whitefish were found in the two lakes south of the Kogaluk river (Genetics B and Hawk).
 878 Potential colonization scenarios thus involved 9 lakes for lake trout but only 7 lakes for both longnose
 879 sucker and round whitefish. The Y axis reflects time into the past (in number of generations indicated
 880 for scenario 1) starting with the contemporary population at time $t_0 = 0$. Times are not shown at scale.
 881 For all three species the relative likelihood of scenario 1 is much higher than that of scenario 2. (a) Lake
 882 trout: The ancestral lake trout population first colonized T-Bone lake from which lake trout expanded
 883 more or less simultaneously to Hawk (HWK) and Cabot lake (median estimate: 768-731 generations

884 before present (BP), for details see ES-lake trout) followed by colonization of Genetics B (694
885 generations BP), and Slushy and Strange (684 generations BP). Subsequently lake trout from lakes
886 Slushy and Strange admixed to expand into Esker-WP152 (EKW 439 generations BP). Then lake trout
887 from EKW colonized Genetics H (G-H, 370 generations BP) from which lake trout colonized Lake 1 (L-
888 1 246 generations BP). Under scenario 2, ancestral lake trout first colonized Cabot lake from which they
889 expanded into Hawk, Genetics B and T-Bone at t_7 , t_6 and t_5 , respectively. The pattern of colonization for
890 the remaining lakes is the same as under scenario 1. (b) Longnose sucker and (c) Round whitefish: Both
891 scenarios are the same for both species. Under scenario 1, the ancestral longnose sucker population first
892 colonized T-Bone from which suckers expanded into Strange (STR; 336 generations BP), followed by
893 the more or less simultaneous colonization of Cabot and Slushy and the admixture of Slushy (SLU) and
894 Strange (STR) giving rise to Esker-WP152 (EKW; 159 generations GBP). EKW subsequently expanded
895 to colonize G-H (145 generations BP) from which fish subsequently expanded into L-1 (108 generations
896 BP). Under scenario 2, ancestral longnose suckers first colonized Cabot lake from which they expanded
897 independently into EKW and TBN at times t_6 and t_5 , respectively. STR then is colonized from TBN at
898 time t_4 and STR subsequently gives rise to SLU at time t_2 while EKW gives rise to G-H at time t_3 and L-
899 1 is formed from G-H at time t_1 . The pattern of colonization for Round whitefish is the same as that for
900 longnose sucker with the exception of the timing (in number of generations during which the various
901 populations have been created under scenario 1. Parameter posterior distributions and model fits are
902 shown in ES2. The three panels on the right show estimates of the posterior probability (Y-axis) of
903 scenarios 1 and 2 estimated with a logistic regression. The proportion of the scenario is the dependent
904 variable and the difference between the observed and simulated data set summary statistics are the
905 independent variables. Ten (10) estimates corresponding to the top 1 % (60 000) simulated data sets are
906 shown.

907 **Fig. 1**



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910

911

Fig. 2

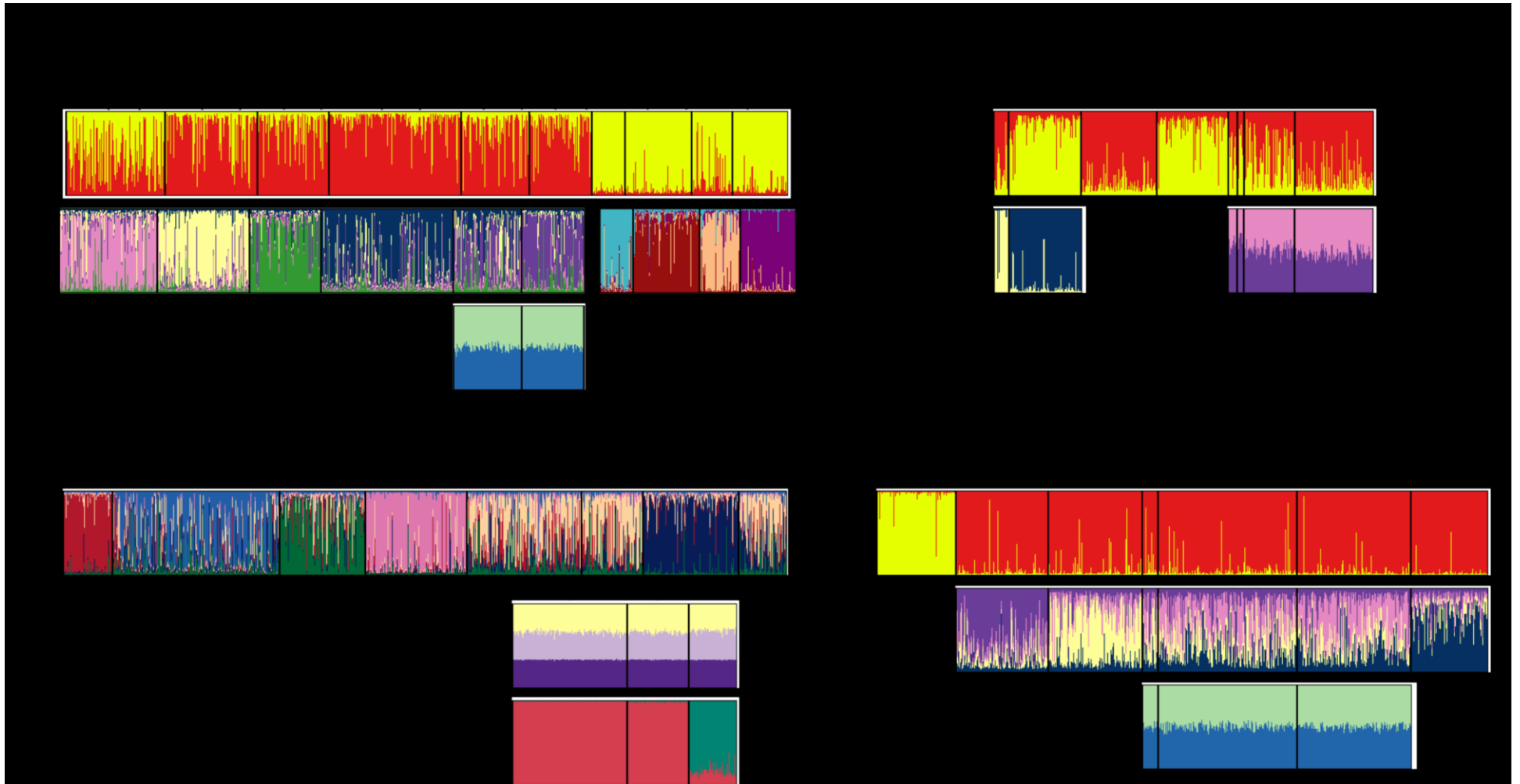
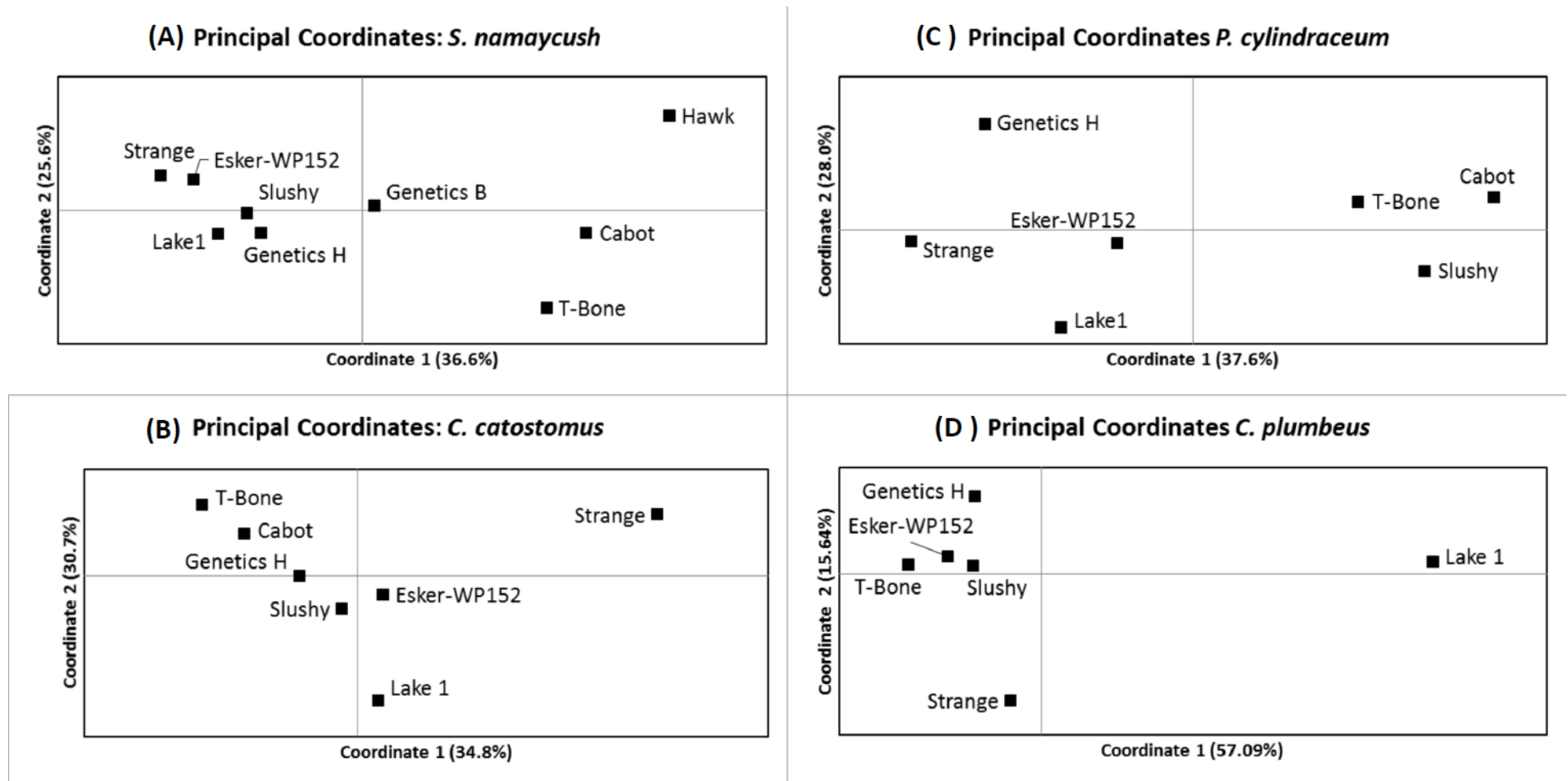


Fig. 3



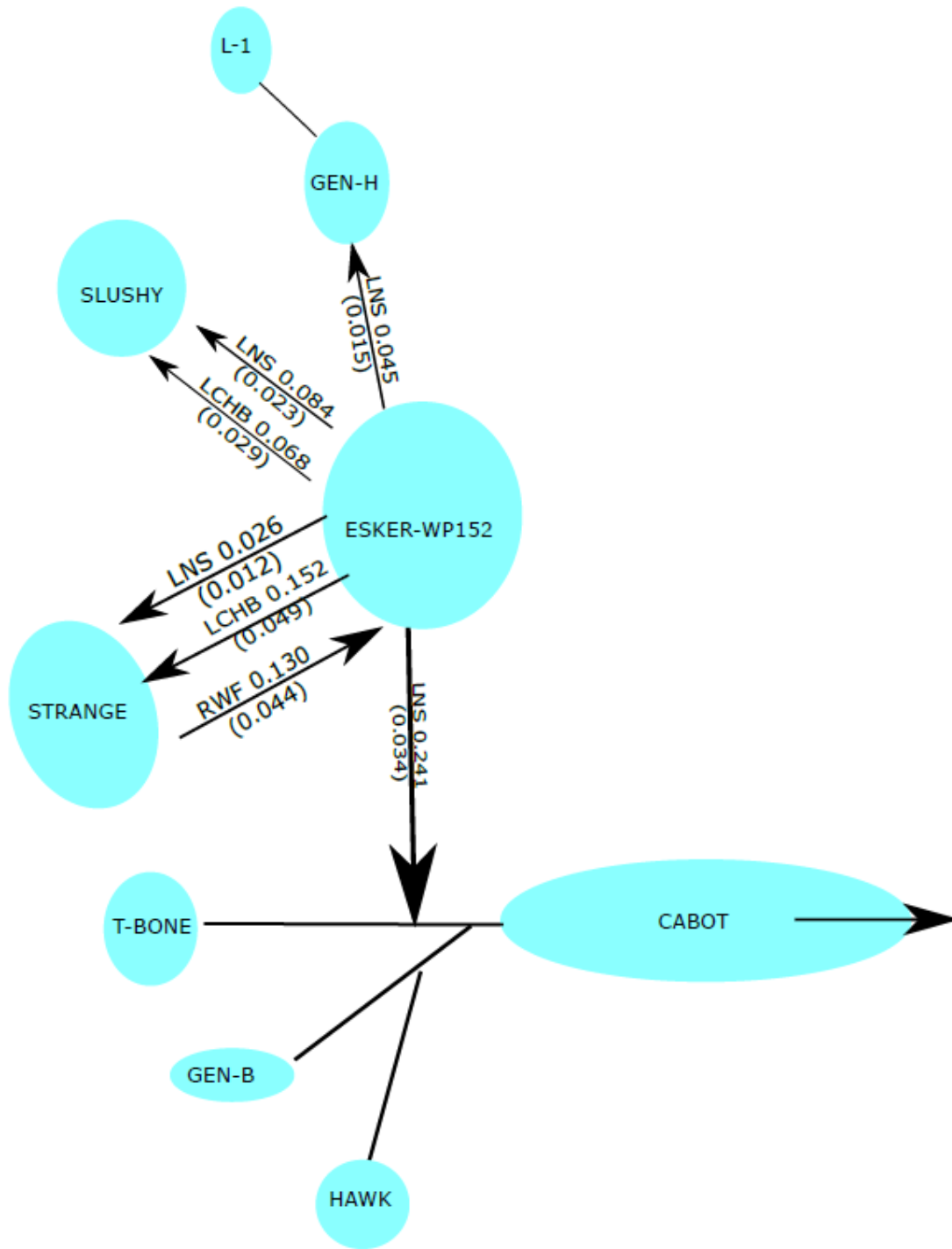
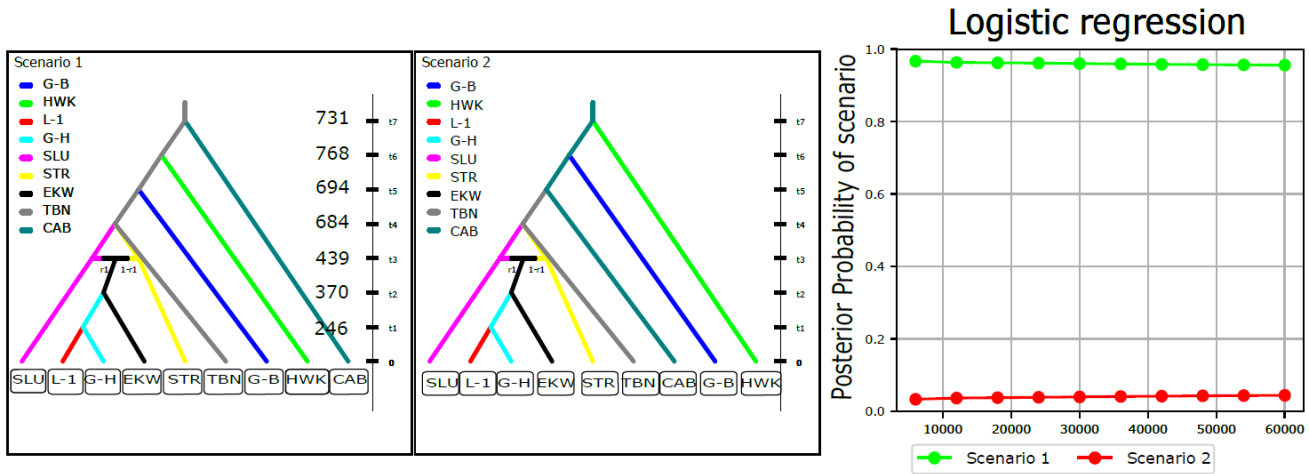


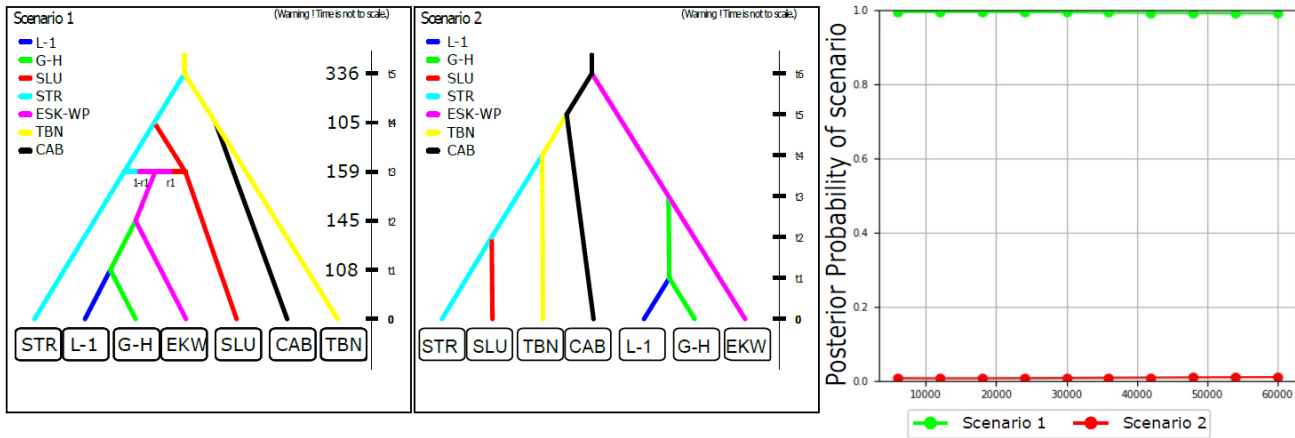
Fig. 4

Fig 5

a) Lake trout (*Salvelinus namaycush*) colonization scenarios and relative likelihoods



b) Longnose sucker (*Catostomus catostomus*) colonization scenarios and relative likelihoods



c) Round whitefish (*Prosopium cylindraceum*) colonization scenarios and relative likelihoods

